Icefield-to-Ocean Linkages across the Northern Pacific Coastal Temperate Rainforest Ecosystem

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Rates of glacier mass loss in the northern Pacific coastal temperate rainforest (PCTR) are among the highest on Earth, and changes in glacier volume and extent will affect the flow regime and chemistry of coastal rivers, as well as the nearshore marine ecosystem of the Gulf of Alaska. Here we synthesize physical, chemical and biological linkages that characterize the northern PCTR ecosystem, with particular emphasis on the potential impacts of glacier change in the coastal mountain ranges on the surface–water hydrology, biogeochemistry, coastal oceanography and aquatic ecology. We also evaluate the relative importance and interplay between interannual variability and long-term trends in key physical drivers and ecological responses. To advance our knowledge of the northern PCTR, we advocate for cross-disciplinary research bridging the icefield-to-ocean ecosystem that can be paired with long-term scientific records and designed to inform decisionmakers.

Keywords: ecosystem response, climate change, glacier change, biogeochemistry, hydrology, marine ecology

The Pacific coastal temperate rainforest (PCTR) ecosystem extends 4000 kilometers (km) along the west coast of North America from northern California to Kodiak Island, Alaska (Kellogg 1992). The northern portion of this ecosystem is one of the least anthropogenically modified ecosystems on Earth, home to intact old-growth forests, extensive glaciers and icefields, robust wild fisheries, and many resource- and tourism-based communities. In the coming decades, the northern PCTR is projected to undergo warming and to become wetter, with less precipitation occurring as snow (McAfee et al. 2013). Moreover, there is evidence that the area's climate is becoming less influenced by regional, decadal timescale climate processes (e.g., El Niño Southern Oscillation, ENSO; Pacific Decadal Oscillation, PDO; Arctic Oscillation, AO) and more strongly affected by global-scale warming (e.g., Arendt et al. 2009). This projected warming has the potential to substantially alter the storage and release of water in the PCTR. In particular, changes in seasonal snowcover and glacier volume may induce pronounced changes in physical and chemical hydrology (e.g., Hood and Berner 2009, Moore et al. 2009). Changes to the function of the northern PCTR ecosystem also have the potential to affect the Arctic given that the PCTR serves as the primary source of freshwater input to the Bering Sea (Weingartner et al. 2005).

The ecosystem-level impacts of glacier change will be most apparent in the northern PCTR, where glaciers cover approximately 16% of the landscape (Pfeffer et al. 2014). Today, the region's glaciers are losing mass at rates among the highest on Earth (Gardner et al. 2013), continuing a trend that began in the late 1800s at the termination of the Little Ice Age (Barclay et al. 2009). Glacier mass loss increases the volume of glacier runoff, defined as annual discharge of water (via melt, rain runoff, and calving) derived from precipitation over the glacier footprint (O'Neel et al. 2014). Glacier runoff plays an important role in the northern PCTR with annual glacier-fed discharge through the region roughly equal to the discharge of the Mississippi River (approximately 450 cubic kilometers [km^3] per year; Neal et al. 2010). Regional rates of glacier mass loss are projected to increase, with a 26%–36% reduction of total glacier volume (7200–10000 km^3) by the end of the century (Radić et al. 2013). Downstream transmission of these hydrological changes through the icefield-to-ocean continuum will affect biological communities, which include species such as Pacific salmon (*Oncorhynchus* spp.) and herring (*Clupea pallasii*) with complex life histories linked in part to physical processes (e.g., Litzow and Mueter 2014).

The rapid and ongoing cryospheric changes in the northern PCTR highlight the importance of improving our

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understanding of the biophysical linkages between glacier mass loss and downstream freshwater and marine ecosystems. Although ecological responses to abrupt climate shifts are well documented (i.e., climate-biology covariation or “regime shifts”; Hare and Mantua 2000, Litzow and Mueter 2014), there is much left to learn about how climate variability and change propagate through the northern PCTR ecosystem. Important knowledge gaps include the roles of positive and negative feedbacks among physical and ecological processes and the integrated icefield-to-ocean ecosystem response to rapid, step-like changes in climate forcing. Ultimately, improving our understanding of how climate change will perturb biophysical linkages in the northern PCTR will be of great benefit to land and resource managers in the region who are currently forced to make decisions about valuable ecological and recreational resources with limited scientific knowledge. Such integrated research is particularly relevant to fisheries management, which may be improved with an understanding of how climate and ocean drivers affect productivity of economically important fish populations. For example, increases in Alaskan salmon catches were documented following a major shift in atmosphere–ocean conditions in 1976–1977, which led to widespread changes in biological productivity across the North Pacific Ocean (Hare and Mantua 2000). Developing a more integrated understanding of the effects of physical drivers, including glacier runoff, on ocean productivity patterns may allow fisheries scientists to better forecast changes in growth and survival of salmon and other economically important species.

Here, we synthesize existing knowledge of longitudinal physical, chemical and biological linkages that characterize the icefield-to-ocean ecosystem in the northern PCTR. We specifically address the affects of glacier change on surface-water hydrology, biogeochemistry, coastal oceanography and ecology. We do not, however, address lateral terrestrial–aquatic linkages (e.g., Milner et al., 2007). We also evaluate the interplay between interannual variability and long-term trends as physical and ecological drivers. Many of the changes, linkages and feedbacks that we explore are applicable to the entire PCTR as well as to other glacierized coastal margins containing CTR such as Patagonia, New Zealand, and Scandinavia. Despite the geophysical, ecological and economic importance of the northern PCTR, relatively little data collection has been undertaken in most of the subdisciplines discussed in this synthesis, therefore the linkages and feedbacks described herein are somewhat speculative rather than solidly founded on observations and models.

Regional overview

Ice-covered mountains, lush temperate rainforests, extensive estuaries, and fjords characterize the northern PCTR (figure 1), which we define as the perhumid and subpolar region extending from the Skeena River watershed in British Columbia, to Kodiak Island, Alaska (total area = 448,550 square kilometers [km^2], figure 2). Abundant precipitation, averaging 2.0 meters (m) per year and peaking at over 7 m per year, (figure 2; Daly et al. 2008), arrives primarily in autumn and winter, predominantly as snow at higher elevations (McAfee et al. 2013). As a result, the northern PCTR is densely ice covered, or glacierized (72,320 km^2, Pfeffer et al. 2014), with all but a handful of the glaciers currently losing mass (retreating or thinning; figure 3; Arendt et al. 2013, McNabb and Hock 2014). Most of the glaciers terminate on land, however 141 lake-terminating glaciers and 49 tidewater glaciers are found in the northern PCTR. Interannual variability of climate forcing results in substantial runoff variability, in both magnitude and subseasonal timing (Stabeno et al. 2004, Arendt et al. 2009, O’Neel et al. 2014). On average, freshwater discharge through the northern PCTR totals approximately 870 km^3 per year, with approximately 50% of runoff originating from the glacierized landscape (Neal et al. 2010). Only a handful of large rivers penetrate the coastal mountain ranges; approximately 80% of the runoff is delivered from the mountains via small, short and steep watersheds (Neal et al. 2010) to a complex coastline dotted with islands and deeply incised, often sill-protected fjords. In southeast Alaska alone, over 10,000 streams drain into estuaries, totaling 35,000 km^2 along the 25,000 km coastline (Edwards et al. 2013). The average glacier-to-ocean stream length is approximately 10 km, upward of two orders of magnitude shorter than the headwater-to-coast distance in the western contiguous United States. This tight coupling between coastal watersheds and the ocean ensures short delivery times of riverine material (sediment, organic matter, and nutrients) to estuaries and fjords, thereby linking the near-shore marine ecosystem to the terrestrial hydrologic cycle.

Links between PCTR ecosystem components and glaciers

In this section we describe links between several of the ecosystem components in the PCTR and glaciers.

Glacier impacts on surface-water hydrology. The connection between glaciers and streamflow has long been a topic of research, dating at least back to the 1960s (e.g., Fountain and Tangborn 1985). Compared with ice-free basins, glacier-fed streams exhibit modified flow patterns, even when less than 5% of a basin is ice covered (Fountain and Tangborn 1985, Jansson et al. 2003, Moore et al. 2009). In general, glacierized watersheds in the northern PCTR have higher annual specific discharge and a lengthier freshet, or spring snowmelt increase (Fleming 2005), and lower winter flows than ice-free basins (figure 4). These differences in basin hydrology reflect the fact that runoff in glacier-free basins is primarily influenced by precipitation, whereas in glacierized basins, the surface energy balance and resultant ice melt are typically first-order controls on runoff (Jansson et al. 2003).

Over interannual timescales, glacierized basins exhibit lower streamflow variability than rain- or snow-dominated basins. The energy-balance dependence of glaciers tends to reduce streamflow in cool wet weather, while augmenting it during drought (Fountain and Tangborn 1985, Jansson

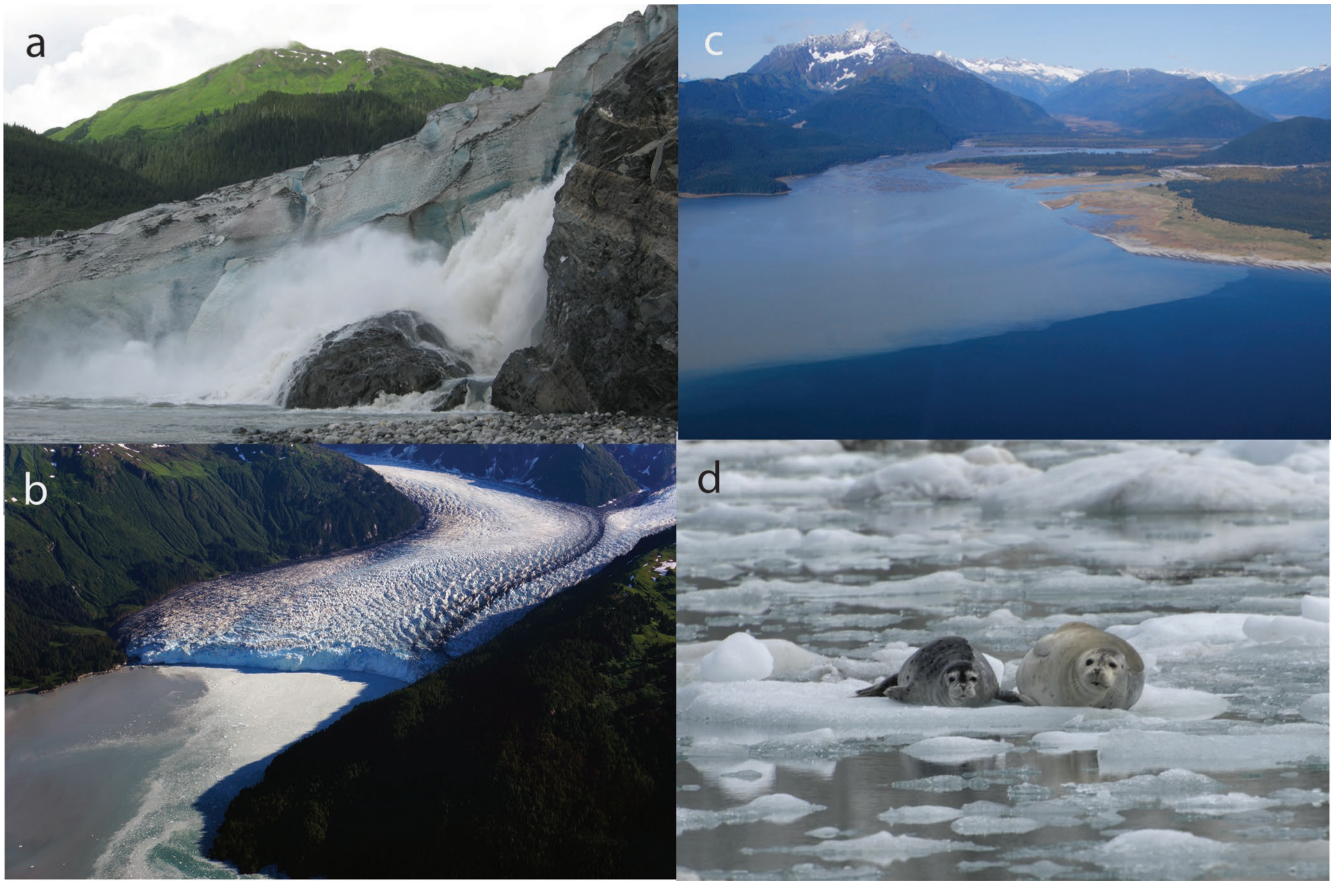

Figure 1. (a) Glacier runoff emanating from the terminus of Mendenhall Glacier, Alaska (Photograph: Rob Spencer). (b)Meares Glacier terminus and fjord, Prince William Sound, Alaska, (Photograph: USGS) showing forested hillslopes above the glacier (c) mixing of ocean and silt-laden water in Berners Bay, Alaska (Photograph: Kevin White). (d) Mother and pup harbor seals hauled out on icebergs calved from McBride Glacier, Glacier Bay National Park, Alaska (Photograph: Jamie Womble).

et al. 2003). At longer timescales, glaciers profoundly affect streamflow responses to ocean–atmospheric circulation patterns like ENSO, PDO, and the AO, most notably through timing shifts (both earlier or later) of the seasonal distribution of streamflow (Neal et al. 2002, Fleming et al. 2006). At centennial or longer timescales, the presence or absence of ice cover modulates the amplitude and direction of long-term streamflow trends. For example, a positive step change in air temperature will cause an initial reduction in glacier mass, and coincident increase in streamflow. However, years to decades later, streamflow will decrease as the ice reservoir becomes depleted (Jansson et al. 2003). Currently, it is unclear whether glacierized basins in the northern PCTR are on the ascending or descending side of this discharge curve (Bliss et al. 2014). In the future, as glacier volume is further reduced, and as increasing air temperature reduces the proportion of winter precipitation delivered as snow (McAfee et al. 2013), streamflow seasonality is likely to become more variable and less predictable, characterized by increased winter flows, attenuated peaks in snowmelt runoff, lower summer flows and flashier peak flows (Neal et al. 2002, O'Neel et al. 2014).

Glacier impacts on physical oceanography. Freshwater runoff and wind provide first-order forcing for northern PCTR coastal ocean circulation. The Alaska Current and Alaska Stream compose the large-scale offshore circulation, but coastal circulation is dominated by the counterclockwise, alongshore Alaska Coastal Current (ACC; figure 2; Weingartner et al. 2005). As it enters the ocean, freshwater runoff produces a strong, salinity-dominated horizontal density gradient that drives the typically narrow (less than 50 km wide) and shallow (approximately 150 m deep), coastally trapped ACC (Royer 1982, Weingartner et al. 2005). This swift current provides a primary mechanism by which heat, nutrients and organisms are transported northward along the PCTR coast, and eventually through the Aleutian Islands and into the Arctic (Stabeno et al. 2004, Aagaard et al. 2006). In addition to coastal circulation, the timing and magnitude of freshwater runoff influence the annual cycle of vertical water column stratification. In winter, coastal waters become well mixed, and recharged with vital nutrients, but a stratified water column forms with the onset of freshwater runoff each spring. Because roughly half of the freshwater

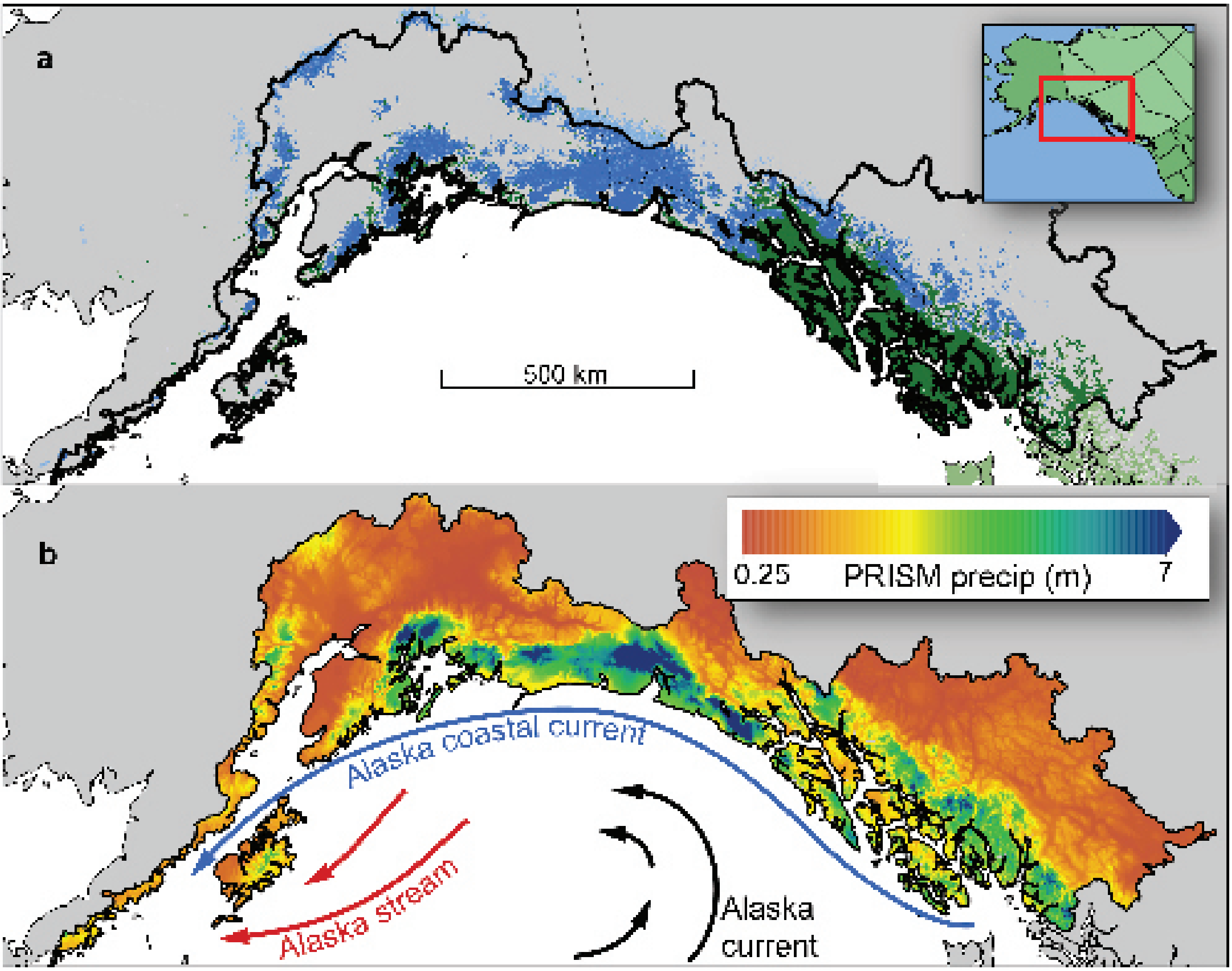

Figure 2. (a) The northern Pacific coastal temperate rainforest (PCTR) ecosystem is outlined as an aggregate watershed boundary (black), with broader geographic context given in the inset. The glacier outlines are taken from the Randolph Glacier Inventory (Pfeffer et al. 2014), with glaciers draining into the Gulf of Alaska shaded blue, and glaciers that drain to interior rivers shaded light blue. Rainforest is shaded green, darker within the northern PCTR boundary. (b) Precipitation and ocean currents in the northern PCTR. The color scale shows 30-year normal, annual total precipitation (1971–2000) from PRISM (Daly et al. 2008). Over the region the mean precipitation rate is 2 meters (m) per year, but maximum precipitation rate exceeds 12 m per year. The location of the major ocean currents, including the Alaska Coastal Current, the Alaskan Stream, and the Alaska Current are shown with arrows (Stabeno et al. 2004). Abbreviations: km, kilometers.

discharged from the northern PCTR is derived from glaciers (Neal et al., 2010), glacier-mediated changes in freshwater discharge have important implications for the strength of the ACC as well as for nearshore primary productivity.

Physical oceanographic processes exhibit variability across seasonal and interannual to decadal and longer time scales, which is mirrored in the physical, chemical, and biological structure of the nearshore and shelf ecosystems (Stabeno et al. 2004, Childers et al. 2005). For example, summertime vertical stratification and temperature conditions are sensitive to freshwater runoff anomalies during the previous winter (Janout et al. 2010). Therefore, predicted changes to the winter rain–snow fraction and associated winter runoff have the potential to perturb coastal oceanographic processes (Royer 1982, Janout et al. 2010). Glaciers will also respond to shifts in winter precipitation, with attendant changes in the magnitude of freshwater delivery to the marine system. Indeed, increased glacier mass loss provides a partial explanation for decadal-scale ocean freshening observed during an interval of regional warming (Royer and Grosch 2006).

The influence of glaciers on the physical oceanography of the northern PCTR is directly evident in glacierized fjords. The discharge of cold, but buoyant freshwater at the seafloor–glacier interface of deep-water calving glaciers strongly influences both fjord circulation (Motyka et al. 2003) and ecosystem structure (Renner et al. 2012, Lydersen

Figure 3. Repeat photography of Mendenhall Glacier, Alaska showing thinning and retreat through the 1958–2011 interval and the rapid vegetative succession that follows coastal glacier retreat.

et al. 2014). As the lower-density freshwater turbulently mixes with fjord water, it upwells to the surface (Greisman 1979), establishing convective circulation and stratification within the fjord and efficiently melting the submarine ice cliff at the ice–ocean interface (figure 5) (Motyka et al. 2003, Bartholomaus et al. 2013). Nonlinear flow dynamics related to deep-water calving fronts allow for so-called catastrophic retreats that proceed over a few decades, orders of magnitude faster than at land-terminating glaciers (Post et al. 2011), which has allowed disproportionately large contributions from calving glaciers in the PCTR glacier mass budget (Meier et al. 2007). The number of deep-water, active tidewater glaciers in Alaska is decreasing (McNabb and Hock 2014), reducing the number of fjords where glacier-driven circulation exists, as well as the overall area of crucial tidewater glacier habitat.

Glacier impacts on biogeochemistry. Glacier ecosystems are increasingly recognized as biologically vibrant environments that support active microbial communities and affect the biogeochemistry of downstream aquatic ecosystems through the cycling and release of nutrients, organic matter (carbon), and contaminants (e.g., Anesio and Laybourn-Parry 2012). Organic matter accumulates on glaciers as a result of both atmospheric deposition and *in situ* production, primarily by viruses, bacteria, and protozoan and algal communities on the glacier surface (Anesio and Laybourn-Parry 2012, Stibal et al. 2012). In the northern PCTR, glacier organic

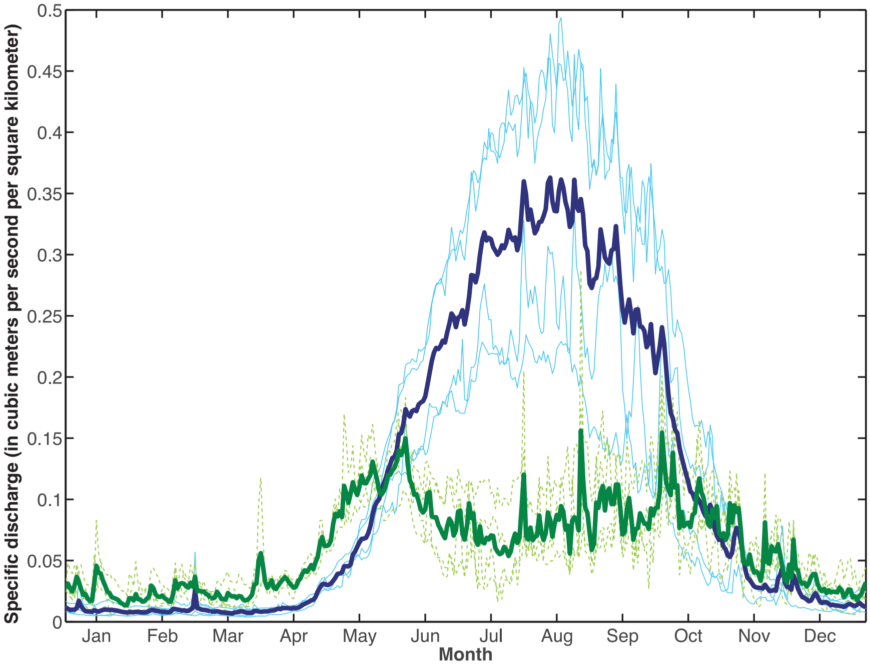

Figure 4. Average daily discharge for eight streams in the northern Pacific coastal temperate rainforest (PCTR) that have greater than 5 years of data are shown. Four (light solid blue) are glacier-fed, and four are streams in ice-free basins (the light dashed green). An average curve representing the glacier-fed streams (the heavy blue) exhibits a single peak in late summer, whereas the average for the ice-free streams (the heavy green) has two peaks, the first from spring snowmelt and a second, in autumn, from rain. Color figure can be viewed online at **http://bioscience.oxfordjournals.org.**

matter appears to be sourced primarily from microbial production and atmospheric deposition rather than plant detritus and is therefore highly bioavailable to heterotrophic organisms (Hood et al. 2009, Stubbins et al. 2012). The release of organic matter (measured as dissolved organic carbon) in glacier runoff from the northern PCTR can be substantial (more than 15 kilograms of carbon per ha per year), approaching the low end of riverine fluxes of dissolved organic carbon from watersheds in the boreal forest (Hood and Scott 2008). As a result, glacier ecosystems in this region are an important source of bioavailable carbon for heterotrophic microorganisms in rivers and nearshore marine ecosystems that receive runoff from glaciers (Hood et al. 2009, Fellman et al. 2010). The high erosion rates characteristic of glacierized watersheds in the northern PCTR (Hallet et al. 1996) can also produce greater riverine fluxes of rock-derived nutrients and micronutrients such as phosphorus and iron compared with ice-free watersheds (Hood and Scott 2008, Schroth et al. 2011). Productive fjords and estuaries with high freshwater residence times characterize much of the coastline of the northern PCTR, suggesting that uptake of riverine nutrients and organic matter could be substantial (e.g., McLeod and Wing 2009).

The chemistry of runoff from glacier ecosystems is also influenced by the storage and release of atmospherically deposited constituents over time scales ranging from decades to centuries. Recent research has shown that melting mountain glaciers act as secondary local sources for persistent organic pollutants in Europe and North America (Grannas et al. 2013). In the northern PCTR, glaciers store and release carbonaceous fossil fuel combustion by-products (Stubbins et al. 2012), as well as mercury, predominantly in a particulate inorganic form that does not readily bioaccumulate (Nagorski et al. 2014). However, ongoing glacier recession and the accompanying increase in

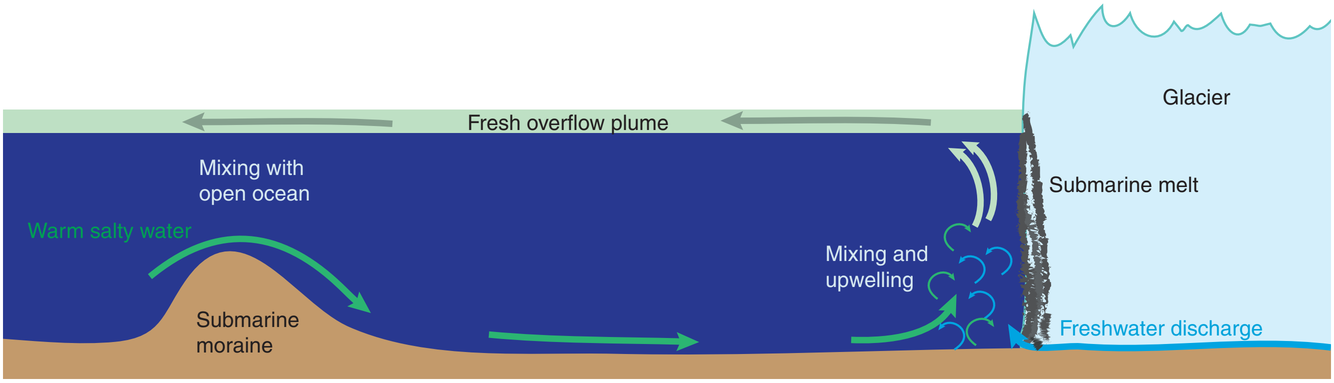

Figure 5. Schematic of circulation in sill-protected, actively glacierized fjords. Arrows depict large-scale buoyancy-driven circulation, emphasizing mixing and upwelling of freshwater at the seafloor–glacier interface. As this cold, fresh water rises to the surface, it melts the submerged portion of the ice cliff further contributing to the fresh overflow plume. Source: Adapted with permission from Motyka and colleagues (2003).

the prevalence of peatlands and forested wetlands have the potential to indirectly increase inputs of toxic methylmercury to coastal watersheds (Nagorski et al. 2014).

Strong zonation between the nearshore and offshore regions characterizes biogeochemistry of the northern PCTR marine ecosystem. Offshore waters are nitrogen rich and depleted of iron, whereas coastal waters are iron rich and nitrogen poor (e.g., Stabeno et al. 2004). Wind-forced onshore Ekman transport causes downwelling-favorable coastal conditions throughout much of the year, resulting in a nutrient-delivery paradox for the observed high levels of nearshore primary production (Childers et al. 2005, Coyle et al. 2012). The high flux of glacier runoff in the northern PCTR is considered an essential process in structuring circulation (via salinity) and supplying iron to offshore areas (Weingartner et al. 2005, Coyle et al. 2012). Dispersal is facilitated through several mechanisms of seasonal cross-shelf exchange and renewal, including episodic upwelling and mesoscale eddy formation (Childers et al. 2005, Strom et al. 2006, Waite and Mueter 2013). Assessing the relative geochemical importance of runoff, episodic upwelling, bathymetric steering and tidal mixing in the nearshore and inner shelf environments over seasonal to decadal timescales (e.g., Waite and Mueter 2013) is crucial to improved understanding of phytoplankton production, which is essential for growth and productivity of higher trophic levels.

Glacier impacts on freshwater ecology. The cold water temperatures, high turbidity, and unstable channels of glacier-fed streams can have pronounced impacts on freshwater biota (Milner and Petts 1994, Hood and Berner 2009, Moore et al. 2009, Fellman et al. 2014). Aquatic macroinvertebrate species richness within watersheds tends to increase with decreasing ice cover (Milner et al. 2000). However, harsh habitats influenced by glacier runoff often select for specialized and endemic taxa (Muhlfeld et al. 2011). As a result, both regional (gamma) species diversity and species turnover (beta diversity) tend to increase in regions with glacier runoff. Streams with moderate basin ice cover (5%–30%) tend to have the highest macroinvertebrate taxonomic (alpha) diversity (Jacobsen et al 2012), although macroinvertebrate abundance is generally low in these watersheds.

Fluctuations in populations of Pacific salmon represent a complex and management-relevant biophysical issue in the northern PCTR. Salmon populations respond in part to the same physical drivers (e.g., PDO) as the region's glaciers, streams and ocean currents (Hare and Mantua 2000, Di Lorenzo et al. 2013, Litzow and Mueter 2014). These anadromous fish can be split into two primary groups based on species-variable lifecycle partitioning between fresh and salt water. Pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon migrate to saltwater soon after emergence from river gravel, whereas sockeye (*Oncorhynchus nerka*), coho (*Oncorhynchus kisutch*) and chinook (*Oncorhynchus tshawytscha*) salmon spend more of their juvenile lifecycles in freshwater (Bryant 2009). During the freshwater phase of life, stream discharge, water temperature, water turbidity, and channel stability are known to affect growth and survival rates (Dorava and Milner 2000). Salmonid rearing habitat is often restricted to clearwater tributaries, off-channel habitats or mainstem reaches far downstream from glacier termini (Bidlack et al. 2014). However, glacierized systems may provide access to these habitats during regional low-flow intervals when glacier-fed streams maintain higher flows (Dorava and Milner 2000).

Future changes in climate and glacier runoff are expected to substantially alter streamflow timing and distribution, as well as thermal regimes of PCTR streams. Because heavily glacierized streams are typically characterized by temperatures that are suboptimal for salmon rearing and overwintering (Fellman et al. 2014), future reductions in basin ice-coverage may result in an increase in salmon productivity. Moreover, expected increases in proglacial lake establishment as glaciers retreat may also enhance downstream habitat suitability by altering water temperature, turbidity, and flow conditions, particularly for sockeye salmon, as illustrated in the Kenai River system (Dorava and Milner 2000, Fleming 2005). Conversely, salmon productivity may be negatively affected by elevated summer stream temperatures in lower elevation, increasingly rain-dominated watersheds, particularly in the southerly reaches of the northern PCTR (Moore et al. 2009, Fellman et al. 2014). Warmer water temperatures in these streams have the potential to shift pink salmon fry migration earlier, potentially causing a mismatch with optimum environmental conditions and food supply (Taylor 2008). The response is likely to be complex; survival and growth declines are anticipated for pink and chum salmon fry in the estuarine environment (Bryant 2009), whereas newly forming proglacial lakes may increase sockeye salmon habitat.

Glacier impacts on marine ecology. The nearshore estuaries and fjords and continental shelf region of the northern PCTR supports robust upper trophic level community assemblages (Etherington et al. 2007, Renner et al. 2012), on which important fishing and tourism industries depend. Such a rich upper trophic level community is indicative of high primary production, but the linkages between freshwater runoff, physical oceanography (stratification and stability of the water column), geochemical processes, and predation are complex and remain poorly resolved (Strom et al. 2006, Arimitsu et al. 2012, Renner et al. 2012). Interactions between physical and chemical processes and primary production exhibit strong gradients across the nearshore and shelf regions, evidenced in part by the different lower tropic level communities found in each region (Strom et al. 2006). Although iron plays a limiting nutrient role on the outer shelf, nitrogen limits production closer to shore (Strom et al. 2006, Wu et al. 2009). The fjords and estuaries are more complex. Nutrients are supplied by runoff-driven upwelling near the glacier terminus, whereas tidal current mixing is important near their shallow, sill-protected entrances. In addition, early-season blooms suggest that nutrients are of secondary importance, and that light availability is often the dominant control on primary production (Etherington et al. 2007, Hill et al. 2009). Primary production exhibits unresolved variability from seasonal to multidecadal time scales, forced by complex interaction of physical drivers, predation, and space–time variability in phytoplankton species composition (Waite and Mueter 2013).

Glaciers also directly influence upper trophic level species in fjords. Fjords and estuaries are important feeding, breeding, nursery and wintering grounds for upper trophic level species (Arimitsu et al. 2012, Lydersen et al. 2014). Physical and biological gradients are established away from the glacier terminus by freshwater inputs at the glacier–seafloor interface and the resulting fjord circulation (figure 5). In Glacier Bay Alaska, marine predator and fish community assemblages are more closely aligned with turbidity, water temperature, stratification, and iceberg distribution (i.e., calving glacier processes) than with prey distribution (Renner et al. 2012). For example, estuarine circulation advects macrozooplankton (e.g., krill) close to calving glaciers, where it upwells to the surface and is capitalized on by fish (e.g., capelin, *Mallotus villosus*; walleye pollock, *Theragra chalcogramma*), seabirds (e.g., kittiwakes, *Rissa* spp.; murrelets, *Brachyramphus* spp.), and mammals (seals) (Arimitsu et al. 2012, Lydersen et al. 2014). The icebergs calved from these same glaciers provide predator protection and haul-out habitat for harbor seals (*Phoca vitulina*) during pupping season (figure 1d; Blundell et al. 2011) and offer energetic savings when used by resting seabirds (Lydersen et al. 2014).

Timescales of glacier change and impacts on ecosystem function

Positive and negative feedbacks among northern PCTR ecosystem components accumulate in the downstream direction, resulting in a complex set of physical, chemical and ecological drivers and responses. Developing an integrated understanding of glacier influence in the northern PCTR ecosystem requires not only quantifying functional relationships among ecosystem components (e.g., how glaciers influence streamflow and, subsequently, freshwater aquatic and coastal marine organisms) but also resolving relative roles of variability and trend over seasonal to centennial time scales. Long-term trends constitute a primary focus of global change research (e.g., global temperature increase, IPCC 2013; glacier mass loss, Gardner et al. 2013; species declines, Womble et al. 2010). However, biophysical components of the northern PCTR, including snow accumulation, timing of peak streamflows, and salmon returns, exhibit large subannual to interdecadal variability that challenges an integrated understanding of the ecosystem (Hare and Mantua 2000, Stabeno et al. 2004).

An example of the interplay between variability and trend is evident in the recent mass balance history of PCTR glaciers, where substantial short-term variance is superimposed on a well-accepted trend of glacier mass loss. The average annual mass loss from the 48-year measurement program at Wolverine Glacier (O'Neel et al. 2014) is represented as a water equivalent thickness change of –0.33 m per year over the entire glacier area, and provides a good representation of regional glacier change as measured by the GRACE mission (figure 6; Arendt et al. 2013). Wolverine Glacier gained mass in three years between 2002 and 2012, but the cumulative change over this period is –7.93 m, more than double the long-term average rate. Highly variable snow accumulation drives the interannual mass variability, whereas nonlocalized summer warming and resultant increased summer melting offers the best explanation for the long-term mass loss trend (Arendt et al. 2013). Consequently, the long-term runoff trends for glacier-fed rivers in the northern PCTR will likely be forced by glacier mass loss, whereas short time scale variations in streamflow are more likely to be driven by annual precipitation and seasonal snowmelt patterns unrelated to glacier volume change (Bliss et al. 2014, O'Neel et al. 2014). For example, in Wolverine Creek, the streamflow component related to Wolverine Glacier volume change averages less than 5%, making it difficult to detect streamflow trends related to reductions in glacier volume. However, even if perturbations in annual runoff are small, the glacier response to climate may induce substantial changes in the timing and quality of runoff from northern PCTR rivers.

The slow, low-amplitude glacier mass loss trend has deep hydrologic implications. First, there is a feedback between glacier mass loss and precipitation. As a result of warming temperatures and increases in freezing level heights, snow accumulation is being reduced over the upper reaches of glaciers (Arendt et al. 2009). A reduction in snow accumulation decreases glacier mass balance, which, if sustained over several years will thin the glacier, especially when surface slopes are low. This mass balance-thinning feedback reduces the mean elevation of the glacier (Böhvarsson 1955) and is therefore likely to increase the rain–snow fraction over the glacier, with the potential to accelerate glacier mass loss faster than temperature shifts alone. As such, we can expect a greater fraction of total precipitation as rain, which is released immediately as runoff rather than stored in the snowpack until spring (Royer 1982, Janout et al. 2010, McAfee et al. 2013). Earlier peak flows, flashy hydrographs, and increased interannual variability are likely results of this glacier–climate feedback. The superposition of strong variability on top of subtle trend challenges direct detection of glacier change in streamflow; however, some outcomes can be anticipated. For example, the trend of reduced glacier area will increase the available landscape for evapotranspiration, further reducing runoff. Greater variability in timing and volume of freshwater delivery to coastal waters, especially winter runoff, will likely affect the dominant circulation pattern in nearshore waters (i.e., ACC), and therefore influence

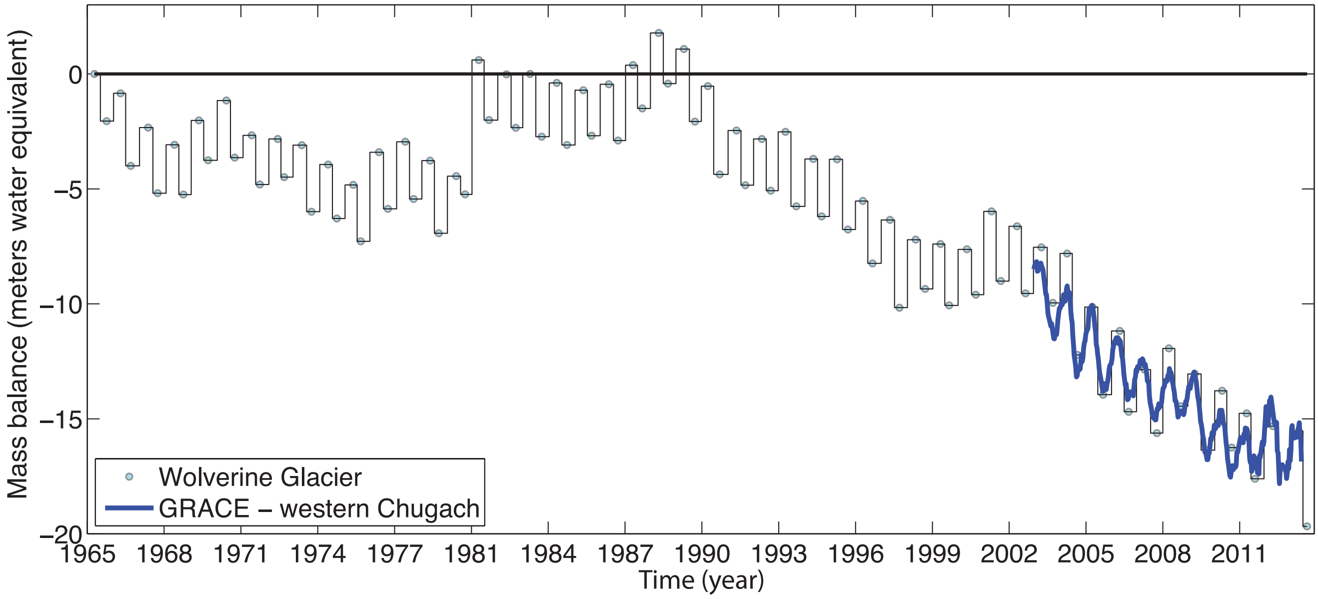

Figure 6. Cumulative mass balance time series from Wolverine Glacier, Alaska, compared with gravity measurements of ice mass change in the western Chugach Mountains as measured by satellite gravimetry (GRACE; Arendt et al. 2013). GRACE mass balance estimates are normalized by the surface area of glaciers in the solution domain, for direct comparison with area-averaged observations at Wolverine Glacier. The plot shows a cumulative thickness change since the US Geological Survey mass balance program began in 1966, with total glacier-wide average thickness changing by nearly 20 meters.

cross-shelf transport of materials such as iron to the marine ecosystem (Janout et al. 2010).

Given the multiple temporal scales of variation characterizing the icefield-to-ocean ecosystem, cross-disciplinary investigations need to be well coordinated, ensuring that observations and sampling strategies can be integrated across multiple disciplines and timescales. Highly prioritized and aligned management and science goals are necessary to develop accurate projections of the impacts of glacier change on the northern PCTR ecosystem. Achieving this goal will require the collection of long-term physical (e.g., meteorology, glacier mass balance, streamflow, and fjord circulation) and ecological (e.g., riverine nutrients and marine faunal abundance) data sets sampled at subannual intervals to allow for trend resolution while avoiding misinterpretation because of undersampled or overly short data sets. The collection of these data sets will also facilitate interpretation of how physical processes interact with and influence ecological processes along the icefield-to-ocean continuum that characterizes the northern PCTR.

Integrated science across the icefield–to–ocean continuum

Here, we highlight several biophysical linkages within the icefield-to-ocean continuum of the northern PCTR to illustrate the scientific and management complexities of this interconnected ecosystem and to provide a roadmap for future research. In table 1, we list six natural resource management issues facing the northern PCTR, where decisionmaking hinges on improved understanding of linked physical and biological processes. For each management issue, we identify key research questions as well as relevant data collection or modeling approaches that will help to address the overarching management issue with a foundation in data-validated analyses.

Our focus is on the nearshore ecosystem because important interactions among several ecosystem components occur here and, in addition, because management boundaries often inhibit study across this terrestrial–marine convergence zone (figure 7). Interactions between physical and biological processes at a tidewater glacier fjord system are examined as a case study, considering potential ecosystem impacts if freshwater subglacial discharge ceases to occur at the ice-cliff–seafloor boundary. Such a case study not only has potential to address scientific knowledge gaps, it will also help to address concrete management issues such as how many calving glaciers will remain visible along present-day cruise ship routes 30 years from today. Providing decision support to plan for ecosystem changes requires interagency collaborations, cross-disciplinary research and technical tools that enable integration of multitemporal and spatially varying data sets.

The response of calving glaciers to climate processes is complex (Post et al. 2011). The calving terminus is an important boundary in this ecosystem, and from a geophysical perspective, its broad influence is understood only qualitatively. It is through this boundary that glacier mass

Table 1. Illustrative management issues facing the northern Pacific coastal temperate rainforest (PCTR) and involving glacier–ecosystem interactions.

Management issue *(reference to section three impacts, case study)*	**Key research questions**	**Approach**
Glacier viewshed evolution (glacier impacts, fjords)	Can image-based features be used to estimate potential for glacier change, then classify glaciers via this estimate?	Glacier inventory; produce and difference Digital Elevation Models (DEMs); predictive geometry model; develop automated classification methods
Changing hydropower potential (hydrologic impacts, snow)	What are the dominant forcings and linkages between glacier mass balance and streamflow in the PCTR? How can we constrain future changes to these forcings, including a better understanding of future changes in flow variability versus trend?	Predictive Temperature (T) and Precipitation (P) models with improved data constraints; constrained snow distribution; improved snow–rain fraction projections; coupled glacier–hydro models
Shipping infrastructure and hazards changes (oceanographic impacts, fjords)	Which tidewater glaciers still have potential for rapid retreat? What is the potential for Alaska region glacier change over decadal to centennial time scales?	Physical oceanography in fjords; ice–ocean coupled modeling to understand instability at calving front
Stream and lake contamination (biogeochemical impacts, snow)	Which contaminants have been historically trapped by glaciers, and what are typical flowpaths for release? Are there localized sites to examine in detail?	Predictive flow models; develop space–time history of deposition
Changes in salmon growth and survival (freshwater ecology, snow)	Identify potential for large-scale changes to transboundary river systems. Will newly formed proglacial lakes create sockeye habitat? Will major sport fishing streams change from snow to rain-dominated flow, and decrease spawning/rearing habitat? How may a short-term increase in population variability mask long-term trends? Will extreme event (floods, mass wasting) occurrence increase in the future, impacting spawning/rearing habitat?	Predictive T and P models with improved data constraints; widespread stream temperature observation and modeling, coupled to atmosphere changes; improved snow–rain fraction projections; monitor fish life history adaptations
Fjord-based tourism changes (marine ecology, fjords)	Which fjords are likely to lose their calving glaciers, therefore cease to sustain current levels of marine life and visual interest? Will current conditions that allow life to thrive in fjords increase or decrease in prevalence?	Quantify fjord circulation; identify physical processes that control community structure; monitor species richness and abundance

Note: These issues are drawn from the six subdisciplines discussed in section III, and are linked to the fjord or snow case studies outlined in the text. Each management issue is paired with key research questions that enhance integrated understanding of cross-disciplinary linkages in the northern PCTR ecosystem. Each research topic is subsequently paired with high-priority data collection/ model integration requirements to complete the research.

changes occur, via ice flow, calving and submarine melt, all of which are forced by freshwater discharge at the sea floor and the resulting estuarine circulation in the fjord (figure 5). This deep circulation facilitates sediment and nutrient dispersal in actively glacierized fjords (Renner et al. 2012, Bartholomaus et al. 2013). Commonly observed, vigorous upwelling at the calving front entrains nutrients and planktonic organisms from all depths, bringing them to the surface where they fall easy prey to marine predators such as plunge-diving seabirds (Lydersen et al. 2014). In addition, highly variable photic conditions occur around the transient sediment-laden plume that rises to the fjord surface (Etherington et al. 2007, Arimitsu et al. 2012). These conditions typically limit phytoplankton abundance; however, occurrences of high zooplankton abundance along tidewater termini (Arimitsu et al. 2012, Lydersen et al. 2014) indicate that zooplankton can be entrained and transported to the calving fronts. These observations from glacierized fjords challenge our understanding of classical bottom-up marine food webs (Vargas et al. 2011) but also provide motivation to better understand trophic dynamics in fjord habitats.

Most tidewater glaciers in the northern PCTR have completed large-scale retreats since the Little Ice Age and are in retracted positions near the heads of their fjords (McNabb and Hock 2014). If retracted tidewater glaciers continue to retreat onto land, the transition from freshwater discharge at the sea floor toward prevailing discharge at the surface will strongly alter fjord circulation. How these oceanographic changes will affect fjord ecology is unknown. For example, will populations of upper trophic level species be affected by changes in prey availability or, alternatively, will some species, such as harbor seals, migrate to fjords that still host tidewater glaciers? Research in Glacier Bay, Alaska, suggests that species that have adapted to cold, turbid conditions will suffer (e.g., Kittlitz's murrelet, *Brachyramphus brevirostris*), perhaps because of changing prey conditions, whereas those that prefer warmer, less turbid conditions are more likely to thrive (e.g., walleye pollock; Renner et al. 2012). Populations of some seabirds and harbor seals have been on the decline in Glacier Bay for several decades, possibly as a result of reduced iceberg refuge and increased predation (e.g., Womble et al. 2010, Piatt et al. 2011).

Understanding the links between tidewater glacier dynamics and nearshore food web dynamics in northern PCTR fjords will require a new level of cross-disciplinary collaboration. In particular, a coordinated research program should address linkages among glacier dynamics, freshwater

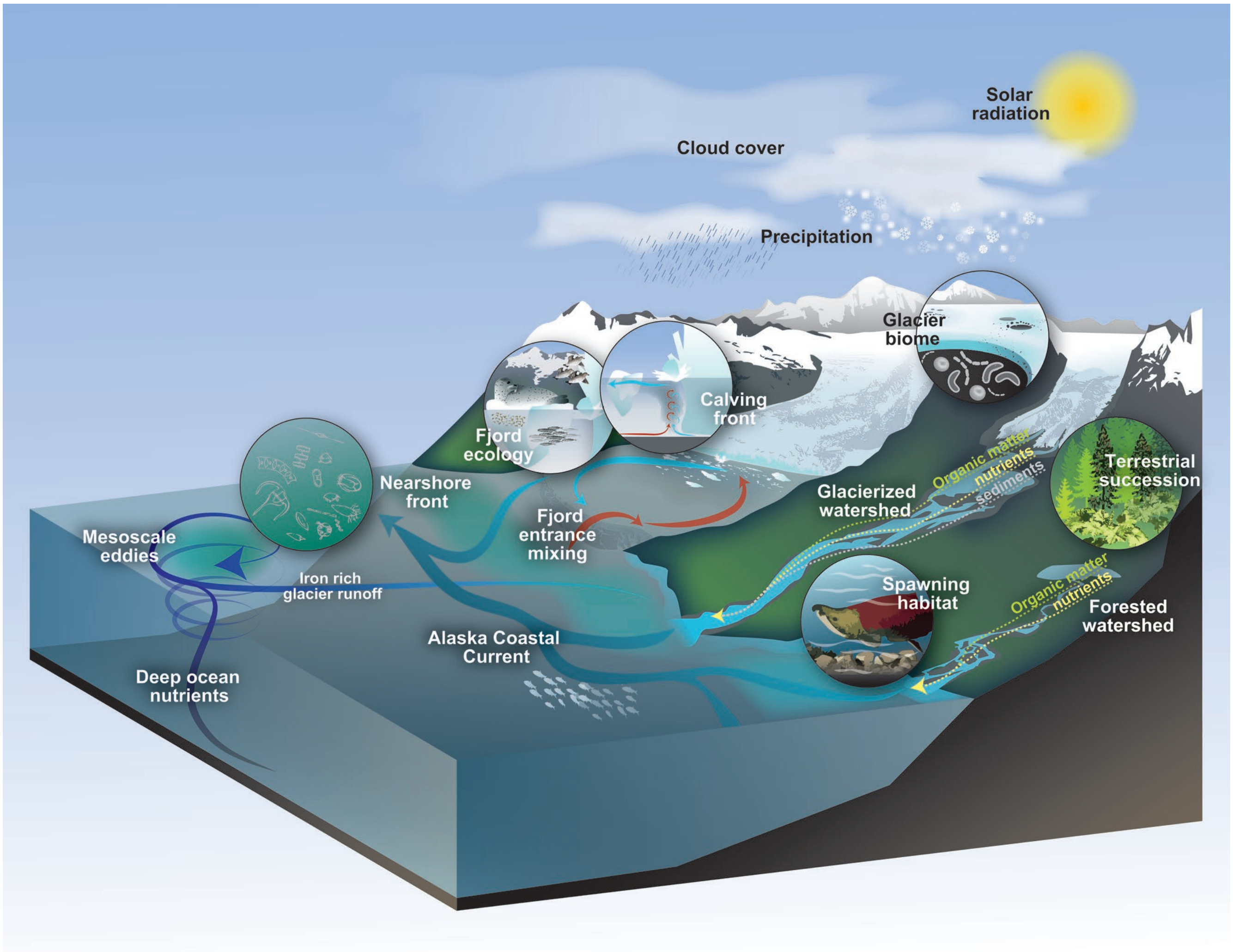

Figure 7. Ecosystem linkages in the northern Pacific coastal temperate rainforest (PCTR). The diagram illustrates how climate and ocean-forced changes to glaciers propagate throughout the icefield-to-ocean ecosystem, affecting land cover, nutrient cycling, ocean currents, and wildlife habitat. The inset pictures depict key processes such as carbon fixation and storage on the glacier surface, potential for proglacial lake formation as glaciers retreat, changing invertebrate and fish habitat, regions of vegetative succession, and the influence of runoff on ocean currents that are discussed in more detail in the text.

discharge, physical oceanography and the trophic structure in glacierized versus ice-free fjords. A crucial piece of this effort should be ensuring that data collection meets temporal and spatial resolution for cross-disciplinary analyses. In addition, new observational efforts should, whenever possible, be directly linked to long-term and historical proxy data sets (e.g., figure 6). Finally, communication barriers between disciplines working in this region need to be addressed to allow productive exchange of information between research groups not accustomed to working together.

In the fjord case study presented above, we focused on subglacial freshwater discharge, not only because it represents a large knowledge gap, but also because resolving this knowledge gap will elucidate multiple cross-disciplinary linkages, while at the same time informing tangible management issues. A second example of a knowledge gap with cascading science and management implications is winter snow accumulation (table 1). In the northern PCTR, there are few measurements of snow depth or snow water equivalence because of prohibitive access or cost issues. This data gap is crucial because snow accumulation provides the primary governance on coastal glacier mass balance and runoff, with errors estimated to be over an order of magnitude larger than for melt (Machguth et al. 2006). Release of this water during the melt season impacts every component of the ecosystem from climate-albedo feedbacks, glacier change, and water-resource planning to water-column stratification, phytoplankton blooms, survival of juvenile fish, and community structure of marine predators (Gargett 1997, Bryant 2009, Janout et al. 2010, Renner et al. 2012, McAfee et al. 2013). From an economic standpoint, changes in snow accumulation will influence hydropower potential in the PCTR (e.g., Cherry et al., 2010).

Manifold knowledge gaps within and among ecosystem components currently limit the utility of model output and warrant detailed observational studies, such as the fjord case-study above, to form a quantitative foundation of linkages and feedbacks among the physical, chemical, and biological components of the northern PCTR icefield-to-ocean ecosystem. Integrated understanding, especially in a predictive sense, requires coupled-model development, expanding, for example, on innovative coupled glacier–hydrology models (Jost et al. 2012) to include biogeochemical processes and fluxes. Spatially and temporally consistent observations across disciplines will be essential for developing coupled models to avoid aliasing seasonal or shorter variability (e.g., concluding that a sample collected at a seasonal maximum represents a mean value), while maintaining sufficient precision to reproduce subtle but potentially impactful trends.

Ultimately, developing a holistic biophysical understanding across the icefield-to-ocean ecosystem will require not only coordination across scientific disciplines but also integration with stakeholders (e.g., forest and fisheries managers, recreation managers), industry (e.g., cruise ship operators), and utility and highway managers and planners. As an example, issues associated with changing glacier viewsheds in the northern PCTR (table 1) are illustrated by the retreat of Portage Glacier and associated changes in visitation statistics at Begich, Boggs Visitor Center. Upon opening in 1986, and during the eight subsequent years when Portage Glacier was visible from the facility, the glacier viewshed served as a key interpretive attraction, and one of the most visited sites in south-central Alaska. However, as anticipated by glaciologists (Mayo et al. 1977), the lake-calving glacier quickly retreated out of view of the visitor center by around 1994. The loss of the glacier viewshed contributed to an incremental drop in visitations to the Begich, Boggs Visitor Center (Lezlie L. Murray, Visitor Services Director, Chugach National Forest, Alaska, personal communication, 14 August 2014).

Summary

Extending from icefield to ocean, the northern PCTR ecosystem is increasingly being recognized as a tightly interconnected biophysical system. Glaciers are an integral component of the landscape, because they are the source of much of the water that links the physical and biological components of the ecosystem. Given projected anthropogenic climate warming, the extensive glaciers in this region will continue to lose mass, likely at increasing rates. However, the region is also characterized by extreme year-to-year variability in precipitation that is reflected in streamflow, riverine material export, physical oceanography and population dynamics. This variability (low signal-to-noise ratio) often precludes effective trend detection, and because its historical magnitude can be larger than detected trends (e.g., O'Neel et al. 2014), it can have a profound impact on the ecosystem.

From a resource and tourism perspective, the northern PCTR is economically important to both Alaska and British Columbia. At present, management decisions lack clear understanding of the impacts of changing glaciological processes over long time scales versus response to short-term variability. Key example issues (table 1) point to the need for distinguishing shorter-term variability from longer-term change, and concomitantly understanding how trends interact with interannual-to-interdecadal variability. Expansion of continuous, consistent, long-term environmental monitoring in the remote northern PCTR will be a key aspect of this process of better partitioning variability and trend.

In the high mountains of the PCTR, changes in climate are forcing complex glaciological responses, many of which will converge in the nearshore coastal ecosystem. Issues such as climate-induced increases in winter rainfall are introducing ecosystem feedbacks with unresolved hydrological, oceanographic, geochemical, and ecological implications. A holistic scientific approach should be undertaken to begin to resolve these uncertainties in ways that maximize utility to the resource management community and allow efficient and informed decisionmaking in an era of rapid ecosystem change.

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