

## Headwaters to oceans: Ecological and biogeochemical contrasts across the aquatic continuum

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### Abstract

While the disciplines of oceanography and limnology often operate in isolate, freshwater, estuarine, and marine ecosystems are intricately linked. The emphasis of this special issue for *Limnology and Oceanography* is on the aquatic continuum and the connectivity between aquatic ecosystems from headwater streams and inland waters, to coastal and marine systems. Changes in the transport and transformation of elements as well as ecological functions occur along this aquatic continuum. Assemblages of organisms change in a way that reflects the ecological and biogeochemical conditions of the aquatic gradient. Here, we highlight research progress in limnology and oceanography across the aquatic continuum and at the interfaces of headwaters to oceans. Contributions explored nutrient and carbon dynamics which included release, transportation, transformation, and stoichiometry from freshwaters to marine. The special issue also explored food web continua, including functional changes, biodiversity gradients, and photosynthesis and respiration comparisons among ecosystems at different points in the continuum. Rapid improvements in biomolecular techniques, use of long-term datasets, applications of novel statistical methods, and improved upscaling methods can transform the way aquatic scientists are describing biological organisms and communities from freshwaters to oceans. One important conclusion is the recognition that anthropogenic activities such as invasive species and nutrient pollution trigger challenge the current concepts of aquatic continua including the river continuum concept, the land to ocean continuum, river to estuary systems, and the submarine groundwater discharge. Both limnologists and oceanographers have much to gain from exchanging information with one another, especially in light of global change.

### From trees to seas

Between the terrestrial ecosystem and the open ocean is a closely connected transitional zone consisting of a network of pore waters, streams, creeks, groundwater, springs, aquifers, lakes, rivers, wetlands, and estuaries. Through this

aquatic network, a sequence of geological, physical, chemical, and biological systems transport, transform and deliver elements during their transit from uplands to the ocean coastal zones and possibly into the deep ocean (Billen et al. 1991; Bouwman et al. 2013). Along the way, the landscape features, the hydrodynamics, the water chemistry, and the structural and functional properties of biota change to reflect the modified environmental gradients. In turn, these altered ecosystems impart their changing and unique footprints on the elements, organic matter and energy transferred.

Scientific progress has improved our understanding of the many differences between habitats of different salinity, as well as the importance of the land-to-ocean continuum especially its significant role in global biogeochemical cycles (e.g., Gattuso et al. 1998; Fowler et al. 2013). However, large uncertainties and research gaps remain ranging from the description of some of the fundamental biogeochemical

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**Special Issue:** Headwaters to Oceans: Ecological and Biogeochemical Contrasts Across the Aquatic Continuum

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processes to the mechanisms describing the rates at which transformations within elemental cycling occur. These gaps arise from limited field data but also from absence of upscaling approaches (e.g., Regnier et al. 2013). The Association for the Sciences of Limnology and Oceanography (ASLO) was founded with the idea of exchanging information across those two fields (Lauff 1963). Recent work suggests that the problems worked on by limnologists and oceanographers are converging with global change (Downing 2014), but there is still room for improvement in the frequency of collaboration across these disciplines (Kavanaugh et al. 2013). The purpose of this special issue is to highlight research progress in limnology and oceanography across the continuum and at the interfaces of headwaters to oceans.

The Earth's aquatic systems connectivity is evident from space (Fig. 1). Despite the interrelatedness of the Earth's water bodies, most aquatic research is done piece-by-piece, typically in isolation, with the majority of traditional experimental freshwater science being performed on systems of 100 m<sup>2</sup> or less (Lodge et al. 1998) and ocean work limited to seagoing expeditions within prescribed stations. Furthermore, scientific exchange and sharing of knowledge across aquatic boundaries occurs too infrequently. This is unfortunate since a large number of freshwater studies may provide valuable insights for marine systems (e.g., Hessen and Kaartvedt 2014) and vice versa (e.g., Hecky et al. 1993), particularly in light of global change (Downing 2014). For example, top predators can have an effect on freshwater primary production as captured by the top-down trophic cascade in lakes (Hodgson 2005). This concept can be applied to marine systems to address how fishing may propagate through the ocean's food web and, in turn, impact primary production, carbon storage, and ultimately the global carbon cycle (Hessen and Kaartvedt 2014; Lynam et al. 2017). Similarly, the Redfield ratio, first defined for marine plankton has been used by limnologists as a metric of nutrient limitation (Hecky et al. 1993). ASLO has recently emphasized to its membership the importance of bridging the fresh-salt divide so that future aquatic scientists no longer work in isolation. Exchanging information and increasing synergy across boundaries to solve emerging problems in aquatic systems is especially important in a political and research funding atmosphere in which scientists strive to show the relevance of their work to global environmental issues.

In this review, we briefly summarize the research progress published in the special issue "Headwaters to oceans: ecological and biogeochemical contrasts across the aquatic continuum." We begin our review by describing how the global carbon cycle connects the terrestrial ecosystem to the sea and highlight special issue papers that advance our knowledge on carbon dynamics in river and coastal systems. We next present four aquatic continua concepts or models that have, in the past, guided our understanding of how aquatic systems are intricately linked (Table 1). Through the

description of the past guiding models, we embed new research from the special issue that addresses some of the research holes in our aquatic connectivity knowledge. We end by looking forward and proposing tools and methods to assist in addressing remaining research gaps.

### ***Carbon connects the Earth's hydrosphere***

The flow of water drives the global carbon cycle (Ward et al. 2017). One of the many important advances made in recent years is better integration of the knowledge on the freshwater carbon cycle into the global carbon cycle as carbon moves from land to the ocean (Cole et al. 2007; Tranvik et al. 2009; Laruelle et al. 2010). For example, we now know that river systems receive and process large quantities of terrestrial dissolved organic carbon (DOC) and that internal production can stimulate (prime) transformation of terrestrial organic matter to CO<sub>2</sub> (Guenet et al. 2010; Bianchi 2011; Hotchkiss et al. 2014). The freshwater aquatic gradient not only includes a vertical exchange of significant amounts of greenhouse carbon gases with the atmosphere (e.g., Sawakuchi et al. 2017) but also a moderate loss and storage of carbon to the sediments in transit to the ocean (Regnier et al. 2013). Despite these advances in our knowledge of the global carbon cycle, there are still large gaps in current coverage of environmental observations along the aquatic continuum (Ward et al. 2017). For example, the effects of river plumes, tidal environments, and coastal wetlands on near-shore coastal regions carbon dynamics are not completely understood (Bauer et al. 2013). Among coastal ecosystems, marshy lands and mangrove forests can be important carbon sinks with sedimentation considered one of the most important pathways of carbon loss to the sediments. By studying cores collected along a tidal creek (Big Bend, Florida) stretching from mouth to coastal forest, Arriola and Cable (2017) set out to understand variability in carbon burial rates as they relate to sedimentation in a tidal salt marsh. Their results suggest a clear negative relationship between sediment accumulation and carbon burial rates which suggests that this salt marsh system is likely vulnerable to inundation and carbon loss driven by sea level rise.

Also in this issue, using intensive spatial and temporal methods, Crosswell et al. (2017) show that carbon flows and balances in a shallow estuary along the river-ocean gradient are controlled by a number of variables including river plume discharge, light availability, vertical stratification, and spatial variability in channel and shoal metabolic rates. With their detailed measurements, the authors show that the system can be net autotrophic whereas models only predict net heterotrophy. The authors conclude the importance and need of more complete datasets to be able to correctly capture all natural processes encompassing the carbon budget. Indeed, Vlahos and Whitney (2017) also report that their study system can alternate between net autotrophy and net heterotrophy based on the riverine flow conditions. Using a





**Fig. 1.** Connectivity along the aquatic continuum. **(A)** Natural-color image of the Mackenzie Delta and the Beaufort Sea taken on 19 July 2017 by Landsat 8. In this image, milky-tan colored sediments mixed in with freshwater were pouring out of the Mackenzie River into the Beaufort Sea. Image source: NASA Earth Observatory, <https://earthobservatory.nasa.gov/IOTD/view.php?id=90703>. **(B)** Submarine groundwater seeping through sediments right before reaching the coastline, forming a small stream on the beach of Les Fonts (Alcossebre, Castelló, Spain). Credit: J. Garcia-Orellana. **(C)** Natural-color image of the Zambezi Delta taken by Landsat 8 on 29 August 2013. The Zambezi River is the fourth largest river in Africa and drains nearly 1.6 million square kilometers, a watershed spanning eight countries. Image source: NASA Earth Observatory, <https://earthobservatory.nasa.gov/IOTD/view.php?id=82361&src=eoa-iotd>. **(D)** Image of the Lena River Delta, captured by the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) on NASA's Terra satellite on 16 July 2005. The Lena River begins its greater than 4000 kilometers journey north from the mountains of south-central Russia, then splits into a network of streams across the tundra before emptying into the Arctic Ocean via the Laptev Sea. Image source: NASA Earth Observatory, <https://earthobservatory.nasa.gov/IOTD/view.php?id=7343>.

**Table 1.** Formalized past guiding concepts to describe aquatic continua in limnology and oceanography.

Model	General proposition	Key references
<b>River Continuum Concept (RCC)</b>	Physical, chemical, and biological gradients of rivers gradually change from headwater streams to river mouth	Vannote et al. (1980)
<ul style="list-style-type: none"> <li>• Serial Discontinuity Concept</li> <li>• Hyporheic Corridor Concept</li> <li>• Flood-Pulse Concept</li> <li>• Nutrient Spiraling Concept</li> <li>• U-shaped Concept</li> <li>• Pulse-Shunt Hypothesis</li> </ul>	Improvements to the RCC to better integrate fluvial geomorphology, inflows and shoreline influences as well as flooding, uptake and release of nutrients, and transformation of organic matter	Ward and Stanford (1983), Stanford and Ward (1993), Junk et al. (1989), Tockner et al. (2000), Ensign and Doyle (2006), Webster (2007), Raymond et al. (2016)
<b>River-Estuary Systems (RES)</b>	River/freshwater plumes have a vast influence on estuarine environments	
<b>Land-Ocean Aquatic Continuum (LOAC)</b>	Transition zone, between terrestrial ecosystems and the open ocean	Billen et al. (1991)
<b>Submarine Groundwater Discharge (SGD)</b>	The ocean is connected to the land via groundwater discharge	Moore (1996, 1999, 2010)

mass balance approach, the authors show that the Long Island Sound estuary system ranged between net organic carbon import from the continental shelf and heterotrophy during low flow and net export of organic carbon and autotrophy during high flow.

Carbon dynamics along the continuum are further explored by Tiwari et al. (2017) and Barber et al. (2017). Tiwari et al. (2017) tackle the problem of how carbon is transported from headwaters to coasts toward the Bothnian Bay in the northern most part of the Baltic Sea. Carbon transport from headwaters to intermediate sized rivers transitioned between surface water and groundwater base flow. Carbon processing is further mediated by spatial and temporal patterns within drainage networks over short and long time-scales. The authors conclude that transfer of carbon to marine systems involves brusque alterations in chemistry due to flocculation and sedimentation. Barber et al. (2017) used a comprehensive  $\delta^{13}\text{C}$ -DOC dataset along the freshwater—marine continuum from the St. Lawrence toward Newfoundland along Canada's East Coast. The authors found that  $\delta^{13}\text{C}$ -DOC changed from typical terrestrial-freshwater to marine values along the salinity gradient. Marine end-members covered a broad range of isotopic values ( $> 3\text{‰}$ ), thus highlighting the difficulty of using stable isotope mixing models to assess the fate of DOC.

The potential for rivers to alter global carbon fluxes has been highlighted in the last few decades, and of particular interest is the reactivity and fate of DOC and especially whether rivers transport or modify carbon (passive pipes or active reactors *sensu* Cole et al. 2007). The type of hydrological event (e.g., large storms, episodic events, snowmelt) appears to be an important factor driving whether or not DOC is transported conservatively down the river network (Raymond et al. 2016). Indeed, the fate and reactivity of

DOC along a river network is controlled by in-stream processing which is driven in large part by hydrology as measured using estimations of water residence time (Catalán et al. 2016 and in this issue Casas-Ruiz et al. 2017). Even so, rivers can deliver a substantial source of aged terrestrial dissolved and particulate organic carbon to the oceans (Raymond and Bauer 2001). Using carbon isotopes, Xue et al. (2017) find that with increasing river discharge the transport and export of millennial-aged DOC and particulate organic carbon in the Yellow River also increases. The authors conclude that the millennial-aged organic carbon exported into coastal seas by the Yellow River can thus have profound impacts for carbon cycling in the coastal and marginal areas of seas. Drought and flooding can play an important role in the carbon dynamics of estuarine systems as found in the study of Yao and Hu (2017). By focusing on the carbonate system response in the Mission-Aransas estuary, a subtropical estuary in the Gulf of Mexico, the authors report notable removal of dissolved inorganic carbon during the drought period and in particular higher  $\text{pCO}_2$  levels leading to higher  $\text{CO}_2$  flux to atmosphere compared to flood conditions. The authors conclude that although modest  $\text{pCO}_2$  levels are found in this estuary, it remains a source of atmospheric  $\text{CO}_2$  mainly because of strong winds and warm conditions throughout the year.

### **The river continuum concept**

Over the years, aquatic continua have been conceptualized as “models” to classify and describe contrasts along aquatic gradients (Table 1). The most famous of these classification models is the River Continuum Concept (RCC; Vannote et al. 1980) which posits that as water and materials move downstream, streams and rivers change constantly



with respect to their physical, chemical and biological characteristics. The RCC hypothesis has had an important impact on the field and is used today by scientists, water managers, stakeholders, and policy analysts. In brief, physical gradients such as light, water flow, and geomorphology of rivers gradually change from source to river mouth. This approach can be applied, for example, to habitat size (from small order streams to large rivers), biodiversity of functional groups (e.g., from shredder macroinvertebrates to gatherer-collectors), organic matter transformations (from coarse particulate to fine particulate organic matter), and metabolism (heterotrophy vs. autotrophy) in a predictable manner along the entire length of a river network. Widely accepted and used the RCC is nonetheless limited in its applicability. Some of the criticism of RCC is that it does a poor job of incorporating naturally occurring climatic events such as droughts (Pacheco et al. 2017) and floods (Junk et al. 1989). The RCC is typically described under naturally forested conditions and does not include disturbances such as dams (Humborg et al. 1997; Maavara et al. 2015) and other human influences such as urbanization (Hill et al. 2017; Larsen and Harvey 2017).

Other river ecosystem formalized concepts have since expanded the RCC to address deficiencies in the original RCC model. These include the Serial Discontinuity Concept to better integrate geomorphology and inflows (Ward and Stanford 1983), the Hyporheic Corridor Concept to better connect river depth and shoreline influences (Stanford and Ward 1993), the Flood-Pulse Concept (Junk et al. 1989; Tockner et al. 2000) which better incorporates the contributions of flooding to the nutrients and organic matter budgets, the Nutrient Spiraling Concept (Ensign and Doyle 2006) which considers uptake and release of nutrients along the river, the U-shaped Curve which better incorporates energy inputs longitudinally (Webster 2007) and more recently the Pulse-Shunt Hypothesis (Raymond et al. 2016) which predicts the evolution of organic matter transformation in stream networks based on hydrological patterns. Human disturbances continue to pose challenges to the above extended models. For example, using a large dataset of over 1800 streams, Hill et al. (2017) show that cumulative respiratory carbon losses increased from headwaters to small streams, then decreased with increasing stream size as expected based on the RCC. However, the expected U-shaped respiration curve (*sensu* Webster 2007) was not evident when streams were classified based on disturbance, suggesting that anthropogenic activities mask the expected organic matter processing signature of the river continuum.

Indeed, applying the original RCC for the management and restoration of urban streams and rivers can be challenging. Urban streams are subject to a number of anthropogenic activities but can also have disrupted carbon cycles when fine sediment accumulation is prohibited by built channel morphology or other structures that impact the natural flow of materials along a river bed. In this issue, Larsen and Harvey

(2017) find that urban rivers were limited by particulate carbon and disturbances to primary producers cascaded through the entire heterotrophic community. The authors postulated that the tight coupling between gross primary production and ecosystem respiration enhances the stream's vulnerability to storm surges. Consequently, management activities, including restoration activities should consider the channel storage zones as well as focus on in-stream scour.

### ***The land-ocean aquatic continuum***

Unlike the RCC, the land-ocean aquatic continuum (LOAC) has not been formalized into a "concept" but rather is often referred to for research that links the land to the oceans. Initially coined to refer to the changing biogeochemistry of nitrogen, phosphorus, and silica from land to ocean by Billen et al. (1991), the LOAC encapsulates the transition zone between terrestrial ecosystems and the open ocean and has been used in this way to describe a series of biogeochemically and physically active systems that process carbon and nutrients as these elements move from upland soils to the open ocean (e.g., Syvitski et al. 2005; Bouwman et al. 2013; Fowler et al. 2013; Laruelle et al. 2013).

The global mass balance of dissolved substances in seawater is driven, in part, by material transport from land to oceans, which in turn is affected by river input rates, residence times of elements as well as sedimentation/removal rates in the ocean (Goldberg 1965; Li 1982). Of all the elements that move across the LOAC, nitrogen has been one of the most studied. Nitrogen supply from land to the ocean has more than doubled in the past decades mainly from growing nitrogen demand for food production and fossil fuel combustion (Galloway et al. 2008). Although a significant portion of the reactive nitrogen is actively removed along the passage way from land to the ocean, there is still a major nitrogen load delivered by rivers and groundwater to the coastal ocean where then denitrification on shelves remove roughly 40% (Seitzinger et al. 2006). The atmosphere spreads nitrogen oxides and ammonia very efficiently (Gruber and Galloway 2008) resulting in nitrogen depositions in the coastal but also open oceans where it supports carbon sequestration (Jickells et al. 2017).

Nutrient dynamics across aquatic ecosystems are shaped by complex environmental and ecological processes which can alter the quantity and ratio (stoichiometry) of elements transported across the aquatic continuum. However, patterns of stoichiometry across the LOAC and the factors that affect them remain relatively understudied (cf. Downing 1997). To better understand these patterns, Weyhenmeyer and Conley (2017) examined the relative availability of carbon (C) and nutrients (e.g. phosphorus, nitrogen, iron, and silicon), to show that the balance between these elements change from headwaters to the sea. The half-life of C along the LOAC was more than twice as long as that of iron (Fe) and silicon (DSi), resulting in rapidly increasing C:Fe and C:DSi ratios

along the LOAC. Such an increase can mean greater Fe and DSi limitation for the growth of aquatic organisms along the LOAC (Weyhenmeyer and Conley 2017). In a study that highlights the land to large lake aquatic continuum (parallel with LOAC), Prater et al. (2017) examine nutrient stoichiometry (C:N:P) of particulates in the into the Lake Erie continuum seeking to find how human activities in catchments alter the nutrient supply to the lake and processing within it. They found that nutrient supply ratios varied systematically across from tributaries to its outlet (C:P and N:P increasing) but that patterns varied seasonally. In general, as water flows from tributaries to the lake, phosphorus is removed, driving up these ratios. Interannual variations in weather also led to differences in stoichiometry, with colder weather decreasing P losses. In general, however, the authors suggest that far too little is known about the processes involved in altering C:N:P ratios as water is delivered from streams, passes through coastal zones, and is delivered to open, large water bodies.

Besides its use to describe patterns in ecological stoichiometry, LOAC may also be applied to describe changes in ecological function from land to ocean (e.g., Rabouille et al. 2001 for benthic respiration). In this issue, Vizza et al. (2017) examined physicochemical patterns and changes in ecosystem function in freshwater ponds from “mountains to sea” along a 40-km trajectory from glacial headwaters to the Alaskan Ocean (U.S.A.). Ponds higher in the landscape and, therefore, more heavily influenced by glacier flow path length were more heterotrophic with higher decomposition rates and ecosystem respiration, functions which were linked to phosphorus and iron availability. In contrast, ponds near the ocean were more autotrophic exhibiting higher gross primary production and net ecosystem production, functions which were linked to nitrogen availability and N:P ratios.

Our understanding of the supply and type of river inputs in the LOAC is typically over-simplified and does not include inputs from groundwater, coastal wetland, or other transitions across the relevant LOAC where unique biogeochemical and ecosystem processes can occur in transit (e.g., subterranean estuary; Moore 1999). Human activities can modify the LOAC which can further complicate our understanding of naturally changing ecosystem processes in many globally significant ecosystems. Human interference on LOAC are noticeable through (1) land use changes (Bhomia et al. 2016), (2) eutrophication (Woodland et al. 2015; Van et al. 2015), (3) construction of dams (Chen 2000), (4) acidification of streams and river waters (Gałuszka and Migaszewski 2013), (5) groundwater pollution (Slomp and Van Cappellen 2004), and (6) climate change that can alter coastal exchanges due to sea level rise.

### **The river-estuary systems**

Beyond the river network drainage, river plumes form one of the primary connectors between river-estuary systems

(RES) and the coastal ocean. Freshwater river plumes have a major impact on oceans because of their effects on salinity, sea surface temperature, pollution, carbon, and nutrient levels. Variation in plume characteristics, in turn, affect the biota and ecology of marine ecosystems. For example, river discharge changes the salinity gradient of coasts and is important for estuarine circulation. This in turn can drive plankton abundance, distribution and even the occurrence of toxic species (e.g., Harvey and Menden-Deuer 2012). The impact of freshwater plumes goes beyond the impacts on coastal ecosystems and also plays a significant role on air-sea interaction and climate in the open ocean (D’Silva et al. 2012).

As nutrients are delivered through the RES, they can be processed in transit protecting the open water from excess nitrogen and phosphorus. Asmala et al. (2017) collected data on the losses of nitrogen via denitrification and the loss of phosphorus due to burial in five types of coastal systems: estuaries, archipelagos, open coasts, embayments, and lagoons surrounding the Baltic Sea. Denitrification losses were greatest in systems with high N and sediment organic carbon while phosphorus sedimentation was greatest in archipelagos. The upscale their results to show that these coastal systems likely remove 16% of the land-derived N and 53% of the P. They suggest that management can improve the coastal filter efficiency, especially through eradication of coastal hypoxia and coastal erosion.

Nitrogen supplied to marine systems by rivers via estuaries drives primary production, coastal eutrophication, and the health of marine environments. N from anthropogenic sources is processed during transport, especially via denitrification and this processing determines the amount, form, and timing of N supplied downstream. Further, climate determines water supply via drought and flooding, which also influence the ability of river and estuarine systems to protect marine environments. In this issue, Bruesewitz et al. (2017) analyzed how riverine fluxes of nitrogen are altered by anthropogenic forces and climate. This contribution compares N-processing responses of two river systems during a period of drought with periodic floods. One system is heavily influence by effluent from waste water treatment and the other not. This paper suggests that riverine processing of waste water N offers little permanent N removal during drought so that estuaries will be unprotected from anthropogenic influences under altered drought frequency.

Fish and fish production are also greatly affected by the greater nutrient riverine delivery in near-shore coastal zones which drives greater phytoplankton prey availability. Using long-term RES datasets, Winder and colleagues (2017) found that the magnitude of harvestable fisheries production is related to the quality of food, mainly long-chain essential fatty acids (LCEFA) with an overall positive correlation between the LCEFA fraction, nutrient input and salinity. This relationship varied by region and seasonally but overall relatively small shifts (< 10%) in food quality had enormous effects on fisheries yield.

Aquatic invasive species can also alter the dynamics within the RES. Along the estuarine gradient of San Francisco Bay (U.S.A.), a unique example of a full-scale ecosystem change is illustrated through long-term data that have documented changes in habitats, biota, and biogeochemistry (Cloern et al. 2017). In particular, the invasion of an Asian clam has significantly reduced the phytoplankton summer bloom, reducing food sources for higher trophic levels and decimating pelagic copepods and rotifers (Cloern et al. 2017).

Further, the papers by Bierschenk et al. (2017) and Soria-Píriz et al. (2017) explore the RES from a biological point of view. Bierschenk et al. (2017) studied 21 rivers around the coast of New Zealand examining how catchment land use influences biological changes along the river as it moves from upstream to the estuary and coastal system. They found that the nutrient influences of land use did not dissipate as the contribution of marine waters increased. They caution managers that management decisions depend on the entire source-to-sea continuum and that the influence of intensive agriculture reaches far downstream to the coastal zone.

The majority of analyses on plankton abundance, distribution, and diversity of estuarine systems have been conducted in coastal areas of temperate and arctic regions, leaving much to be discovered about the tropics. Studying the Gulf of Nicoya, one of the most productive estuaries globally, Soria-Píriz et al. (2017) provide a thorough description of the plankton production, and through comprehensive statistical analysis deliver insights into underlying environmental, chemical, and ecological drivers. Light availability was identified as a major limiting factor of primary production. At this coastal interface, river discharge had a major influence on the availability of nutrients but that did not translate to a river driven production regime, suggesting either compensatory mechanisms or other control factors of primary production.

Anthropogenic alterations of freshwater flow to coastal areas are common, due to demands of upstream water needs. Shanguan et al. (2017) report on the effects of flow alterations on nutrient loading, hydrology, and plankton community composition through the Everglades Restoration Plan in Florida Bay. Alterations of freshwater input to bays affected salinity profiles and circulation, nutrient concentrations and their ratios, and subsequently species composition. The authors found a shift toward chemically reduced forms of N which were linked to increased abundance of smaller picoplankton, relative to larger diatoms. In comparison, P concentrations were low and unchanged in response to the restoration. The data collected are important in untangling the complex responses of coastal systems to large scale manipulations.

### ***Submarine groundwater discharge***

Submarine groundwater discharge (SGD) is another formalized concept recognized as an important component of

the hydrological cycle connecting land, groundwater and oceans (Moore 2010). SGD includes the entire water flow along confined layers to the coastal ocean and the advective pore water flow enhanced by tidal pumping and wave action (Burnett et al. 2003), with SGD considered to be synonymous to the pore waters of coastal sediments where brackish waters are mixed into the ocean, a subterranean estuary (Moore 1999). SGD can widely vary in volume and composition and over space and time. Global estimates of this discharge vary from 6% to 10% of surface water input to up to 30% (Bokuniewicz 1980) and 40% to the South Atlantic Bight alone (Moore 1996, 2010). Nevertheless, precise estimation of the SGD is difficult since it varies based on typology of coastal areas where precipitation, geology, and the water budget are important structural features (Bokuniewicz et al. 2003). Volume and age of the water entering the ocean is difficult to estimate even at single sites but several approaches can be used to estimate SGD including the classical seepage flux meters, salinity or temperature measurements, tracer techniques, and hydrologic models.

Researchers are now uncovering new or hidden sources of marine pollution along global coastlines associated, in part, with SGD (e.g., Beusen et al. 2013). SGD can add substantial quantities of nutrients to coastal ecosystems mostly with a N:P ratio above 16 because the phosphate is more easily removed from groundwater (Slomp and Van Cappellen 2004; Tait et al. 2014). Since SGD waters display high nutrient and dissolved organic matter concentrations they are likely important nutrient sources supporting coastal eutrophication (Krest et al. 2000). Other substances like trace metals have also been reported in SGD (Charette and Buesseler 2004; Bone et al. 2007). Although we may have left the “exploratory stage of this field” (Valiela and D’Elia 1990) there is still a high uncertainty about the details of the nutrient release and the consequence the solute input has on coastal biogeochemistry.

Contribution of groundwater flows to coastal biogeochemical processes is often ignored because of its strong variability in space and time. Human activities can also complicate our understanding of SGD on biogeochemical processes. In this issue, Richardson et al. (2017) examined the influence of two contrasting SGD systems on the biogeochemistry of Hawaiian reef systems. They combined a month-long autonomous sampling platform time-series observations with 24-h high resolution studies of chemical parameters in both systems but with one SGD having greater sewage associated nitrogen loading. Results showed that irrespective of differences in groundwater compositions at the discharge points waters across the salinity gradients emit CO<sub>2</sub> to atmosphere at both locations. The reef metabolism changed from net dissolution to net calcification across the salinity gradient from the source point and that the former was elevated in systems exposed to high groundwater discharges.



### **Looking forward, research gaps and importance of integration**

From viruses (e.g., Liu et al. 2017) to fish (e.g., Winder et al. 2017), this special issue has highlighted important contrasts and gradients from headwaters to oceans. Despite the fundamental differences between freshwater aquatic life and saltwater life, the main environmental problems in limnology and oceanography are converging with global change (Downing 2014). There is much to be gained by working together, integrating between the fresh and salty and thus learning from each other.

Rapid improvements to biomolecular, biomonitoring, and computational techniques are transforming the way limnologists and oceanographers are describing biological organisms and communities along the continuum. Tools in metagenomics and sensing technologies are expected to improve our mechanistic understanding of the ecological and biogeochemical functions that occur along the aquatic continuum. In this issue, Liu et al. (2017) are using high throughput pyrosequencing techniques and cross-transplantation viral reduction approaches to better understand the microbial dynamics of bacteria and viruses in two Hong Kong estuaries: (1) a nutrient rich environment influenced by Pearl River estuary, and (2) a pristine system away from freshwater influence. Survival of bacteria and its biodiversity are dependent on quantity and quality of DOM, and products of viral lysis. Viral regulation of bacterial communities is dominant in eutrophic waters whereas DOM assumes significance under nutrient depleted conditions. Interestingly, viral infection seems to be the key in sustaining bacterial diversity by suppressing the proliferation of species strains capable of faster growth in DOM rich waters.

Long-term monitoring datasets and better analytical tools are increasingly available across limnology and oceanography to better capture unique events, complete biological life cycles, time lags, and highly variable systems (Dodds et al. 2012). Advances in measurement capacity, driving observational capacity to finer scales and a larger swath of parameters including in situ measurements, allow better characterization of both freshwater and marine systems. Several studies in this special issue highlight the importance of long-term datasets. For example, in the Cloern et al. (2017) study a 30 yr long time series revealed a shift in the San Francisco Bay system due to the invasion of new clam species. Winder et al. (2017) relied on long-term data from several coastal sites to separate natural variability from fundamental ecosystem change. Long-term data records are essential to our understanding of ecosystem dynamics, given the tremendous complexity in chemical, biological, geological, and physical characteristics along the continuum.

Application of novel statistical methods such as neural networks and Bayesian statistics can go beyond traditional-based laboratory, monitoring, or analytical techniques to

better disentangle the multiple influences that occur throughout aquatic continua. In this issue, Pacheco et al. (2017) use a new approach called self-organizing maps (SOM), a type of artificial neural network, to disentangle the multiple influences of human activities (e.g., drought, urban areas, urban sewage) on river water quality, providing valuable information for water managers. Using their SOM methodology, the authors conclude that pristine forests and protected natural areas lead to improved river bed functionality thus arguing for the conservation of larger natural forest systems. Nevertheless, the authors claim that better management facilities especially during drought periods are required.

To increase our understanding of global biogeochemical cycles along the aquatic continuum, improved upscaling methods for carbon, nutrients, and water fluxes are also needed (e.g., Regnier et al. 2013; Ward et al. 2017). As an example, rivers are both passively transporting carbon from the terrestrial environment to the ocean and experiencing significant carbon turnover along stream reaches but upscaling methods from individual reaches to the global scale are missing. In this issue, a novel approach for the upscaling of net ecosystem metabolism across seasons and reaches is introduced by Rovelli et al. (2017). The authors use the ratio of base flow to stream discharge as a parameter to describe the net stream metabolism. They validate their new upscaling method using benthic and water column respiration rates, temperature and light regime and new noninvasive eddy covariance techniques to assess the oxygen exchange of a streambed.

More integration between limnology and oceanography is needed in the coming decades, especially with a focus on how global cycles of elements change and, conversely, how changes in the global environment affect marine and freshwater ecosystems. This special issue has highlighted fundamentals of the patterns and processes occurring along the aquatic continuum and how anthropogenic activities whether from urbanization, invasive species or nutrient pollution trigger changes across the aquatic continuum. Understanding the drivers and implications of these anthropogenic disturbances on the ecological and biogeochemical connectivity from headwaters to the ocean is a key concern for the conservation of aquatic biodiversity and ecosystem functions. Future research directions should link land to ocean by incorporating how climate and land use alter material transfers from inland waters to the sea. As well, the mechanistic foundations of patterns across the aquatic continuum need to be explored further. For example, what are the mechanisms involved in altering nutrient stoichiometry as water passes from tributaries to large lakes (e.g., Prater et al. 2017) and marine systems? A better understanding of the mechanistic underpinnings will also prepare us to better use and apply aquatic continuum concepts to better tackle future restoration and management projects.



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#### Conflict of Interest

None declared.

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