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BRIDGES

BRIDGES is a recurring feature of J-NABS intended to provide a forum for the interchange of ideas and information relevant to J-NABS readers, but beyond the usual scope of a scientific paper. Articles in this series will bridge from aquatic ecology to other disciplines, e.g., political science, economics, education, chemistry, or other biological sciences. Papers may be complementary or take alternative viewpoints. Authors with ideas for topics should contact Associate Editors Ashley Moerke and Allison Roy.

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Overview: the links that bind aquatic ecosystems

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Abstract. Aquatic research historically has focused on separate aquatic ecosystems (i.e., freshwater, estuarine, and marine). We argue that this separation into subdisciplines is artificial and may even be counterproductive. Instead, scientists should consider the physical linkages between different aquatic ecosystems and the many similarities in properties and processes among those ecosystems (conceptual linkages). The 4 papers in this J-NABS *BRIDGES* cluster demonstrate the value of integrating information from different aquatic ecosystems. For example, the papers illustrate that transformation and transportation of nutrients and energy physically and conceptually link all aquatic ecosystems and are facilitated by the characteristics of the medium that defines them all—*water*. To promote the exchange of information within aquatic science, more interecosystem studies should be published in journals and books so that scientists will see parallels and linkages among freshwater, estuarine, and marine systems. Over the longer term, such studies would benefit from the funding and teaching of aquatic science as an integrated whole.

Key words: research integration, marine, freshwater, estuarine, interecosystem research.

Freshwater, estuarine, and marine ecosystems are linked by the medium that defines them all—*water*. Historically, the different subdisciplines of aquatic science have developed independently. This separation has been reinforced by obvious differences in organisms, chemical composition, and the size of the aquatic ecosystem studied (Dobson and Frid 1998). Broader integration of research from different aquatic ecosystems has been limited despite the enormous growth of knowledge over the last 50 y. Aquatic scientists are aware of the connections or linkages between aquatic ecosystems, and cross- or interecosystem studies have been published in journals (e.g., Hecky and Kilham 1988, Amon and Benner 1996, Elser et al. 2007) and books (e.g., Maser and Sedell 1994, Wotton 1994, Dobson and Frid 1998). However, the presence of such linkages is not reflected more generally in published aquatic research, which remains largely separated by subdiscipline.

The titles and contents of many aquatic journals (e.g., Freshwater Biology, Marine Ecology Progress Series, River Research and Applications) suggest lack of integration within aquatic science. For example, Lamberti et al. (2010) found that >75% of articles published in J-NABS were concerned exclusively with fresh waters. Furthermore, an evaluation of 50 of the most-cited and of the most recently published J-NABS papers indicated that ≤7%, on average, of the citations in those articles were to marine or estuarine

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TABLE 1. Summary of citations given in J-NABS publications, either in the 50 most-cited (1988–2002) or 50 most recently published (2009–2010). Citations were categorized according to the aquatic ecosystem or combination of ecosystems that were studied.

	50 most-cited papers		50 most-recent papers	
Ecosystem(s) studied	Number	%	Number	%
Freshwater	3174	79.03	2120	74.26
Estuarine	2	0.05	6	0.21
Marine	69	1.72	71	2.49
Marine–freshwater	8	0.20	11	0.39
Marine–estuarine	0	0	0	0
Freshwater–estuarine	11	0.27	1	0.04
Marine–estuarine–freshwater	153	3.81	98	3.43
Not aquatic (e.g., taxonomy)	599	14.92	548	19.19
Total citations	4016		2855	

journals or to journals more broadly aquatic in their subject matter (Table 1). The freshwater benthos is the publication niche for J-NABS, so a predominance of freshwater studies is not surprising. Furthermore, a freshwater focus is appropriate for some research topics, such as stream restoration, to which the contribution of marine and estuarine research is likely to be limited. However, the predominance of freshwater citations suggests little consideration of research from estuaries, marine coasts, and oceans or that researchers in these ecosystems do not consider J-NABS as a publication outlet for their work. The lack of integration in journals reflects the current separation and arguably reinforces the continued separation of research in freshwater and marine ecosystems.

Our central argument is that aquatic science would benefit from better integration of knowledge from all types of water bodies. Given the technological advances that facilitate the acquisition, analysis, and sharing of information, more integration of research from aquatic subdisciplines seems a reasonable expectation. Such interecosystem studies also require a more holistic view of aquatic science in which different water bodies are studied comparatively to reflect similarities in properties and processes among those ecosystems (conceptual linkages) and, as broadly as practical, to reflect physical linkages among aquatic ecosystems. Such interecosystem studies reveal important similarities and differences and allow the establishment of general frameworks from which further hypotheses are generated.

Interecosystem studies that have been published provide important insights into many different aspects of aquatic ecosystems. A summary of these studies (Table 2) shows that their authors considered a variety of aquatic organisms (e.g., viruses, bacteria, algae, fish), processes (e.g., denitrification, respiration), physicochemical factors (e.g., ultraviolet light, nutrient availability), and materials (e.g., particulate organic matter, dissolved organic matter). The studies were focused generally on ecosystem structure (e.g., species composition) over function (e.g., respiration) and usually on lower (e.g., viruses, bacteria, algae) rather than higher trophic levels (e.g., invertebrates, fish). The few studies of ecosystem function addressed nutrient cycling (e.g., nutrient limitation) rather than energy flow (e.g., C sources). Most interecosystem studies were focused exclusively on the pelagic habitat (60%), and fewer considered the benthic (16%) or both the pelagic and benthic (24%) habitats. Most studies compared freshwater and marine ecosystems (64%), whereas the remainder of the studies (36%) also included estuarine ecosystems in their comparisons. Published information, either as literature surveys or, most recently, in meta-analyses was used in ~½ of the studies, whereas new data were generated from experimental manipulations or field sampling, often complemented by literature surveys, in the other ½. Not surprisingly, the explicitly cross-ecosystem journal *Limnology and Oceanography* has published the most interecosystem studies (34% of articles considered), whereas the other journals, including J-NABS, have published far fewer (<8%).

Interecosystem studies published to date highlight several important features of aquatic ecosystems. First, similarities among aquatic ecosystems (40%) are almost as evident as differences (46%); the remaining 14% found both similarities and differences in the same study. Similarities include the effects of light (Sommaruga et al. 1997, Bancroft et al. 2007) and nutrient limitation (e.g., Guildford and Hecky 2000, Elser et al. 2007) on aquatic organisms. Second, differences that exist between aquatic ecosystems appear to reflect the local environmental context,

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TABLE 2. Summary of interecosystem publications. Ecosystem (Ecosys) abbreviations: E = estuarine, F = freshwater, M = marine; habitat abbreviations: P = pelagic, B = benthic; method abbreviations: E = experimental, LS = literature survey, MA = meta-analysis, S = sampling; conclusion (Con) abbreviations: D = differences, S = similarities. DOM = dissolved organic matter, POM = particulate organic matter.

				Times cited					
Authors	Year	Journal[a]	Subject	Total	Per y	Ecosys	Habitat	Method	Con
Paerl	1974	LO	Pelagic bacterial uptake of DOM	114	3	F, M	P	E	S
Paerl	1975	ME	Microbial attachment to POM	81	2	F, M	P	E	S
Reeburgh and Heggie	1977	LO	Benthic and pelagic methane consumption	120	4	F, M	P, B	LS	D
Bird and Kalff	1984	CJFAS	Pelagic bacterial abundance and chlorophyll *a*	261	10	E, F, M	P	LS, S	S
DeMott	1988	LO	Zooplankton feeding and selectivity	78	4	F, M	P	E	D
Hecky and Kilham	1988	LO	Nutrient limitation of phytoplankton	628	29	F, M	P	LS	D
Kilham and Hecky	1988	LO	Comparative ecology of phytoplankton	60	3	F, M	P	LS	S
Baines and Pace	1991	LO	Bacterial use of phytoplankton DOM	274	14	F, M	P	LS	D
Seitzinger et al.	1991	EST	Benthic NH_4^+ sorption	50	3	E, F, M	B	E, LS	D
White et al.	1991	ME	Pelagic bacterial production and growth	230	12	E, F, M	P	LS	D
Sanders et al.	1992	MEPS	Pelagic bacteria and plankton relationships	297	17	E, F, M	P	LS	S
Hecky et al.	1993	LO	Particulate organic matter stoichiometry	242	14	F, M	P	LS, S	D
Sander and Kalff	1993	ME	Benthic bacterial production	70	4	E, F, M	B	LS	S
Schallenberg and Kalff	1993	ECO	Benthic bacteria and macrobenthos	68	4	F, M	B	LS, S	D
Baines et al.	1994	LO	Material flux and planktonic production	61	4	F, M	P	LS	D
Elser and Hassett	1994	NAT	Stoichiometry of plankton interactions	129	8	E, F, M	P	S	D
del Giorgio and Scarborough	1995	JPR	Pelagic bacteria and plankton abundance	95	6	E, F, M	P	LS, S	D

Table 2. Continued.

Authors	Year	Journal[a]	Subject	Times cited: Total	Times cited: Per y	Ecosys	Habitat	Method	Con
Elser et al.	1995	AME	Pelagic bacterial nutrient limitation	68	5	F, M	P	E	D, S
Maranger and Bird	1995	MEPS	Pelagic viral abundance	113	8	F, M	P	LS, S	D
Amon and Benner	1996	LO	Pelagic bacterial use of DOM	347	25	F, M	P	E, S	D, S
del Giorgio and France	1996	LO	Zooplankton and POM isotopic composition	89	6	E, F, M	P	LS, S	D
Malinsky-Rushansky and Legrand	1996	MEPS	Pelagic bacteria use of plankton exudates	44	3	F, M	P	E	D
West and King	1996	EST	Fish communities	39	3	E, F, M	P, B	S	S
del Giorgio et al.	1997	NAT	Pelagic respiration and production	335	26	E, F, M	P	LS	D, S
Hassett et al.	1997	LO	Plankton stoichiometric interactions	68	5	E, F, M	P	S	D
Myers et al.	1997	CJFAS	Spatial scale of fish recruitment	83	6	F, M	P, B	S	D
Sommaruga et al.	1997	AEM	Effects of solar radiation on bacterioplankton	84	6	F, M	P	E	S
Methé et al.	1998	LO	Pelagic bacterial communities	89	7	F, M	P	LS, S	D
Glöckner et al.	1999	AEM	Bacterioplankton composition	383	35	F, M	P	S	D, S
Guildford and Hecky	2000	LO	Phytoplankton nutrient limitation	152	15	F, M	P	S	S
Bell and Kalff	2001	LO	Factors influencing picophytoplankton	62	7	F, M	P	LS	D, S
Havens et al.	2001	EP	Autotrophic succession	49	5	E, F, M	P, B	LS	D
Hillebrand	2002	J-NABS	Controls of autotrophic biomass	68	9	F, M	B	MA	S
Repeta et al.	2002	GCA	Benthic and pelagic DOM composition	45	6	F, M	P, B	S	S
Shurin et al.	2002	EL	Strength of trophic cascades	245	31	F, M	P, B	MA	D
Simon et al.	2002	AME	Organic aggregate formation	188	24	E, F, M	P, B	LS	S
Mei and Danovaro	2004	LO	Benthic virus production	44	7	F, M	B	LS, S	S

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such as water movement and sediment composition (e.g., Mermillod-Blondin and Rosenberg 2006), nutrient concentrations (e.g., Guildford and Hecky 2000, Elser et al. 2007), and C sources (e.g., Baines and Pace 1991, Amon and Benner 1996), rather than just the more obvious differences among ecosystems in organisms, salinity, or size (e.g., Seitzinger et al. 1991). Third, many areas of aquatic science have not been considered from an interecosystem perspective. Examples of where an interecosystem comparison would be worthwhile include invertebrate functional groupings, allochthonous vs autochthonous inputs, and a comparison of structural and functional metrics.

The papers in this *BRIDGES* cluster demonstrate the benefits of a broader integration of research from different aquatic ecosystems. Collectively, Mermillod-Blondin (2011), Petticrew et al. (2011), and Wotton (2011) describe how diverse aquatic organisms (e.g., microorganisms, oligochaetes, polychaetes, insects, gastropods, and fish) and their products (e.g., tubes, burrows, feces, mucus, silk, chitin, carcasses, and dissolved organic matter) influence the nutrient and energy fluxes within and between aquatic ecosystems. Articles in this *BRIDGES* cluster also demonstrate that ecological similarities among disparate aquatic ecosystems are equal to and can be larger than the differences, as others have argued (e.g., Dobson and Frid 1998). For example, Mermillod-Blondin (2011) makes a compelling case for considering the role of water flow in both freshwater and marine ecosystems (cf. Legendre and Demers 1984). Wotton (2011) stresses the importance of exudates to aquatic biota and their role in the dynamics of organic matter in all water bodies. Articles in this *BRIDGES* cluster also illustrate how aquatic ecosystems, in general, are replete with physical and conceptual linkages, all underpinned by the presence of water. Highlighted physical linkages include the movement of organic matter within, and between different water bodies (Petticrew et al. 2011, Wotton 2011) and conceptual linkages include the role of environmental context (Mermillod-Blondin 2011, Petticrew et al. 2011). Water facilitates linkages among aquatic systems by virtue of its physical and chemical characteristics, such as high specific-heat capacity, the nonlinear relationship between its density and temperature, high viscosity, and capacity to dissolve more substances than any other liquid (Dobson and Frid 1998). These characteristics and the aquatic organisms that have evolved in response to them influence the capacity of aquatic ecosystems to *transport* and *transform* nutrients and energy.

Water provides an exceptional *transportation* system because it is a universal solvent and has high viscosity. As a universal solvent, water dissolves many substances and holds them in solution wherever they are carried. The high viscosity of water facilitates passive and active movement of aquatic organisms and their products (Mermillod-Blondin 2011, Petticrew et al. 2011, Wotton 2011). Thus, water is an effective delivery system of dissolved and particulate matter via currents that organisms generate and currents that already exist. One consequence is that suspension feeders are present in all aquatic ecosystems (Wotton 1994, Dobson and Frid 1998). Movements of organisms and their products, in turn, constitute important linkages within and between aquatic ecosystems. Examples include benthic–pelagic coupling (e.g., Blumenshine et al. 1997), upstream–downstream (e.g., Mulholland et al. 1995) and surface–subsurface connections (e.g., Valett et al. 1997), and movements between aquatic ecosystems (e.g., Chaloner et al. 2004). Mermillod-Blondin (2011) and Wotton (2011) provide examples of how organisms facilitate benthic–pelagic linkages, which have been neglected by some branches of aquatic research (Lamberti et al. 2010) and certainly have yet to be compared among ecosystems.

The physicochemical characteristics of water and the actions of organisms also facilitate the *transformation* of material. Examples include the generation of flocs, or 'snow', from dissolved organic matter resulting from chemical, physical, and biological processes (Wotton 2011). Consumers also transform organic material by compacting egested material into fecal pellets that sink to form biodeposits (Mermillod-Blondin 2011) or are carried away by currents (Wotton 2011). In addition, aquatic organisms create biogenic structures from organic and inorganic material and act as ecosystem engineers (e.g., Mermillod-Blondin and Rosenberg 2006). Such transformations can have profound effects on the pelagic and benthic environment (Mermillod-Blondin 2011, Petticrew et al. 2011, Wotton 2011). Producers and consumers release compounds directly into the surrounding water (Petticrew et al. 2011, Wotton 2011) where these exudates are transformed or metabolized, often rapidly, by other organisms (e.g., Baines and Pace 1991, Amon and Benner 1996, Malinsky-Rushansky and Legrand 1996). Such transformations are facilitated by interfaces that are abundant in all aquatic ecosystems (Naiman et al. 1988), especially those between sediments and overlying water (Mermillod-Blondin 2011, Petticrew et al. 2011, Wotton 2011). Organisms and resources are brought together at these interfaces for important biogeochemical transformations.

Some aquatic organisms can facilitate both the transport *and* transformation of material among

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systems. Pacific salmon (*Oncorhynchus* spp.) provide one such example (Petticrew et al. 2011). Salmon transport nutrients and energy as they migrate from the ocean via estuaries to fresh waters where they spawn and die. The marine-derived nutrients they deliver as carcasses, gametes, and excretory products are an important ecosystem resource subsidy (Polis et al. 2004) that increases growth and abundance of freshwater producers and consumers (e.g., Chaloner and Wipfli 2002, Chaloner et al. 2004). Salmon spawners also act as ecosystem engineers (Wright and Jones 2006) by constructing redds or nests, which transform sediment size and topography and alter biofilm and invertebrate abundance (e.g., Moore et al. 2004). A considerable amount research has accumulated about the ecology of Pacific salmon (see Quinn 2005), but a comprehensive interecosystem study of their ecological role has yet to be done.

Interecosystem studies suggest that information must be integrated at contrasting spatial and temporal scales. For example, microorganisms use exudates and particles aggregate and fragment at smaller scales (i.e., μm–m, s–d), whereas water currents move particles over large distances and at larger time scales (i.e., km–10^3 km, days to 10 y) (Wotton 2011). Similarly, the construction of biogenic structures by invertebrates (Mermillod-Blondin 2011) occurs over small spatial and temporal scales but may modify substratum characteristics that persist over larger scales. Last, disturbance associated with salmon spawning redds occurs at smaller spatial scales and persists for limited time (Petticrew et al. 2011), whereas salmon migrations take place over larger scales. Also, the nutrient-enrichment effects of salmon carcasses occur downstream, in adjacent riparian and hyporheic habitats, and as carryover effects beyond the salmon run and into the subsequent year. The role of organisms in the transformation and transportation of organic material should be compared among aquatic ecosystems. For example, the extent to which egestion, excretion, construction, and bioturbation influence the quality and quantity of material present should be determined by using functional groupings (Mermillod-Blondin 2011). The significance of such activities may be indicated by the abundance or diet of organisms. Last, the role of environmental context in the similarities, differences, and linkages among aquatic ecosystems should be considered (Mermillod-Blondin 2011, Petticrew et al. 2011, Wotton 2011).

Several broader recommendations to encourage a more holistic, integrated approach to aquatic research are evident from this *BRIDGES* cluster. Recommendations have been made for *interdisciplinary* research (Committee on Inland Aquatic Ecosystems 1996, National Academies 2004, Lamberti et al. 2010), but we make recommendations specifically for *interecosystem studies in aquatic science*. Such recommendations extend beyond academic institutions to professional societies, publishers, and funding agencies involved in aquatic research.

Academic institutions should encourage interecosystem research in the aquatic sciences. Organizations exist to assist with such endeavors. These organizations include the National Center for Ecological Analysis and Synthesis (NCEAS; www.nceas.ucsb.edu/; Andelman et al. 2004), and the John Wesley Powell Center for Analysis and Synthesis (US Geological Survey; powellcenter.usgs.gov/). Such efforts are part of a larger interdisciplinary movement to facilitate the synthesis of data (Parr and Cummings 2005). NCEAS encourages use of existing data to address major issues in ecology and, in so doing, encourages application of science to management and policy issues. NCEAS argues that it can influence how science is conducted and facilitate understanding by fostering the collaborations and data sharing that enables the synthesis and analysis of scientific information, a view that is in line with our central argument. Specific interecosystem studies have benefited from the NCEAS (Shurin et al. 2002, Elser et al. 2007), and these studies have had a significant effect (Table 2). Still, the usefulness of such an approach depends, in part, upon the research questions being asked.

The scientific community should encourage research questions that embrace different aquatic ecosystems. Such questions should include the role of scale because many phenomena can exist over different spatial and temporal scales. For example, use of dissolved organic matter takes place at exceptionally small scales, whereas movement of nutrients and energy can occur at much larger spatial and temporal scales. Such questions also should extend beyond the identities and feeding strategies of organisms, whether consumers or predators, to consider them as transporters and transformers of nutrients and energy (i.e., organisms are important not just because of what they eat, but what they excrete, egest, and build). Arguably, studies involving functional feeding groups (Cummins 1974) and stoichiometry (Elser et al. 2000) have encouraged the perspective reflected in the content of this cluster of *BRIDGES* papers. Generation of new data, or integration of existing information, could further facilitate such comparative studies in aquatic science.

Data generation and integration needed for interecosystem studies are realistic goals given the availability and reduced cost of techniques for producing (e.g., compound separation and characterization) and

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analyzing (e.g., Geographical Information Systems) such data, especially at larger and smaller scales. Powerful database tools (e.g., Web of Science™) allow relevant literature to be found and analyzed more easily. Such analyses require new modeling and statistical approaches (Hobbs and Hilborn 2006), including meta-analysis tools that enable analysis of data from several independent studies as one data set (Gurevitch et al. 2001). Meta-analysis already has provided important insights in ecology and especially interecosystem research (Hillebrand 2002, 2009, Piña-Ochoa and Álvarez-Cobelas 2006, Bancroft et al. 2007, Elser et al. 2007). Such tools will only be used to generate new data if aquatic scientists are trained in their use and application.

Broader-based programs are needed to train aquatic scientists. The compelling argument made by Wetzel (1996) for broader training in limnology is appropriate for aquatic science in general. However, underlying philosophies differ among subdisciplines of aquatic science. Dobson and Frid (1998) remarked that scientists in different aquatic subdisciplines often use different terms for the same thing and the same terms for different things. For example, collector-gatherers (freshwater biology; Cummins 1974) and deposit feeders (marine biology; Dobson and Frid 1998) have the same feeding method. In contrast, littoral zone refers to the 'illuminated shallows' in freshwater biology and to the intertidal in marine biology (Dobson and Frid 1998). Broader training of aquatic biologists and the publication of interecosystem studies and books with a broader aquatic perspective (Maser and Sedell 1994, Wotton 1994, Dobson and Frid 1998) would help reconcile these contrasts in philosophies and terminology.

Journal editors, especially those of journals with broad scope (e.g., J-NABS) should encourage publication of interecosystem aquatic research, a call already made by others (e.g., Lamberti et al. 2010). Individuals with research experience in several ecosystems could be included on editorial boards, and special issues concerned with such research could be created. Many journals publish special issues (e.g., Danovaro et al. 2008) or have developed sections (e.g., J-NABS *BRIDGES*) in which the existence and importance of interecosystem research can be highlighted. However, peer review of such manuscripts will require recruitment of referees with broad experience and knowledge of aquatic science.

Many important physical and conceptual linkages among aquatic ecosystems exist because water defines them all. We think integration of research across aquatic ecosystems is important, realistic, and has much potential. However, many gaps exist in our knowledge, and the success of the kind of holistic research needed to fill those gaps depends upon the involvement and support of the entire community of aquatic scientists.

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