

# Overview: the links that bind aquatic ecosystems

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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.

Ashley Moerke, amoerke@lssu.edu Allison Roy, roy@kutztown.edu Co-editors

# Overview: the links that bind aquatic ecosystems

# Dominic T. Chaloner<sup>1</sup>

Department of Biological Sciences, University of Notre Dame, Notre Dame, Indiana 46556 USA

## Roger S. Wotton<sup>2</sup>

Division of Biosciences, University College London, London WC1E 6BT UK

**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.,

<sup>2</sup> r.wotton@ucl.ac.uk

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  $\leq 7\%$ , on average, of the citations in those articles were to marine or estuarine

<sup>&</sup>lt;sup>1</sup> E-mail addresses: dchalone@nd.edu

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-cite	ed papers	50 most-rece	ent 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  $\sim \frac{1}{2}$  of the studies, whereas new data were generated from experimental manipulations or field sampling, often complemented by literature surveys, in the other 1/2. 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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Authors         Year         Jound*         Subject         Teal         Pert         Explore         Holton         Perto         Cospo         Holton         Perto         Cospo         Holton         Perto         S           Reelungia         1973         UC         Reduction (DOM)         11         2         F, M         P         F         5         5           Reburgia         1977         UC         Reduction (DOM)         13         7         F, M         P         15         5         5           Heggia         198         UC         Reduction (DOM)         21         10         15 <td< th=""><th></th><th></th><th></th><th></th><th>Times cited</th><th>ted</th><th></th><th></th><th></th><th></th><th></th></td<>					Times cited	ted					
197410Pagic bacterial1143 $E, M$ $P$ $E$ 1975MEMicrobiolNicrobiol812 $E, M$ $P$ $E$ 11977LOBenitrobiol812 $E, M$ $P$ $E$ 11977LOBenitrobiol200 $P$ $E, F, M$ $P$ $E$ 11984CJTASBenitrobiol201 $E, F, M$ $P$ $E$ $E$ 1988LOCMA78 $24$ $E, F, M$ $P$ $E_S$ 1988LONuterinitizion $23$ $23$ $E, M$ $P$ $E$ 108LONuterinitizion $23$ $23$ $E, M$ $P$ $E_S$ 108LONuterinitizion $23$ $23$ $E, M$ $P$ $E$ 111991LONuterinitizion $23$ $24$ $14$ $P$ $E, M$ $P$ 141991LONuterinitizion $23$ $12$ $E, F, M$ $P$ $E_S$ 15Nuterinitizion $23$ $12$ $E, F, M$ $P$ $E$ $E_S$ 16Nuterinitizion $23$ $12$ $E, F, M$ $P$ $E_S$ 1991NEPacific bacterial $29$ $12$ $E, F, M$ $P$ $E_S$ 1992MEPLOPacific bacterial $29$ $12$ $E, F, M$ $P$ $E_S$ 1993LOPacific bacterial $29$ $12$ $E, F, M$ $P$ $E_S$ 199	Authors	Year	Journal <sup>a</sup>	Subject	Total	Per y	Ecosys	Habitat	Method	Con	
1975MIEWith discrimination methane812 $F,M$ $P,B$ $E$ 11977LORecruit altacture1204 $E,M$ $P,B$ $E$ 11977LORentinic and paragic1204 $E,M$ $P,B$ $L$ 1988LOSentinica and consumption26110 $E,F,M$ $P,B$ $L$ 1988LOZooplankton feeding78 $4$ $E,M$ $P$ $E$ 1988LONutrient limitation23 $29$ $E,M$ $P$ $E$ 1988LONutrient limitation23 $29$ $E,M$ $P$ $E$ 1988LONutrient limitation23 $29$ $E,M$ $P$ $E$ 1991LOSooplankton27414 $E,M$ $P$ $E_S$ 1991MEPalogic bacterial290 $12$ $E,F,M$ $P$ $E_S$ 1991MEPalogic bacterial297 $17$ $E,F,M$ $P$ $E_S$ 1993LOParticulate organic242 $14$ $E,M$ $P$ $E_S$ 1993MEBenthic bacterial297 $17$ $E,F,M$ $P$ $E_S$ 1993MEBenthic bacterial297 $14$ $E,F,M$ $P$ $E_S$ 1993MEBenthic bacterial297 $17$ $E,F,M$ $P$ $E_S$ 1993MEBenthic bacterial70 $4$ $E,F,M$ $P$ $E_S$ 1994 </td <td>Paerl</td> <td>1974</td> <td>ΓO</td> <td>Pelagic bacterial</td> <td>114</td> <td>З</td> <td>F, M</td> <td>Р</td> <td>Е</td> <td>S</td> <td></td>	Paerl	1974	ΓO	Pelagic bacterial	114	З	F, M	Р	Е	S	
	Paerl	1975	ME	uptake of DOM Microbial attachment	81	7	F, M	Ъ	Щ	S	
	Reeburgh and Heggie	1977	ΓO	Benthic and pelagic methane	120	4	F, M	P, B	LS	D	
	Bird and Kalff	1984	CJFAS	consumption Pelagic bacterial abundance and	261	10	Е, Ғ, М	Ъ		S	
	DeMott	1988	ΓO	cnioropnyu <i>a</i> Zooplankton feeding	78	4	F, M	Р	Е	D	
1988LOComparative actions of phytoplankton603 $F, M$ $P$ $LS$ ace1991LOBernhic NH4* $274$ 14 $F, M$ $P$ $LS$ al.1991ESTBernhic NH4* $50$ $3$ $E, F, M$ $P$ $LS$ 1991MEParation such phytoplankton $274$ $12$ $E, F, M$ $P$ $LS$ 1991MEParation such production and growth $290$ $12$ $E, F, M$ $P$ $LS$ 1992MEPSPalagic bacterial growth $290$ $17$ $E, F, M$ $P$ $LS$ 1993LOParation and growth $297$ $17$ $E, F, M$ $P$ $LS$ 1993LOParation and growth $292$ $14$ $F, M$ $P$ $LS$ 1993LOParation and growth $292$ $14$ $E, F, M$ $P$ $LS$ 1993LOParation and arrowth $292$ $14$ $E, F, M$ $P$ $LS$ 1993MEBernhic bacteria and andren $61$ $4$ $E, M$ $P$ $LS$ 1994NATStorkhometry production $70$ $4$ $E, F, M$ $P$ $LS$ 1994NATStorkhometry of production $199$ $R$ $E, F, M$ $P$ $LS$ 1994NATStorkhometry of production $129$ $R$ $E, F, M$ $P$ $LS$ 1994NATStorkhometry of production $129$ $R$ <	Hecky and	1988	ΓO	And selectivity Nutrient limitation	628	29	F, M	Р	LS	D	
ace1991LOacterial use of phytoplankton27414 $F, M$ $P$ LSal.1991ESTButhic NH $^+$ 503 $E, F, M$ B $E, LS$ 1991MEPelagic bacterial23012 $E, F, M$ B $L_S$ 1991MEPelagic bacterial23012 $E, F, M$ P $L_S$ 1992MEPSPelagic bacterial23012 $E, F, M$ P $L_S$ 1993LOPelagic bacterial24214 $F, M$ P $L_S$ 1993LOParticulate organic24214 $F, M$ P $L_S$ 1993ECOBenthic bacterial70 $4$ $E, F, M$ B $L_S$ 1993ECOBenthic bacterial70 $4$ $E, F, M$ B $L_S$ 1993ECOBenthic bacterial61 $4$ $F, M$ $B$ $L_S$ 1994LOMaterial flux and61 $4$ $F, M$ $B$ $L_S$ 1994NATSolicitometry of129 $B$ $E, F, M$ $P$ $B$ 1994NATSolicitometry of129 $B$ $E, F, M$ $P$ $E, F, M$ $B$ 1994NATSolicitometry of129 $B$ $B$ $E, F, M$ $P$ $E, F, M$ $E$ 1994NATSolicitometry of129 $B$ $B$ $E, F, M$ $P$ $E, F, M$ $E$ 1995JPRPlankton $P$	Kilham and	1988	ΓO	or pnytopiankton Comparative ecology	60	б	F, M	Р	LS	S	
al. $1991$ EST $Borthic NH_4^+$ $50$ $3$ $E, F, M$ $B$ $E, LS$ $1991$ ME $Pelagic bacterial23012E, F, MPLS1992MEPSPelagic bacterial23017E, F, MPLS1993LOPelagic bacterial29717E, F, MPLS1993LOParticular organic24214F, MPLS1993MEBenthic onerry704E, F, MBLS1993MEBenthic bacteria andatticulationerly704E, F, MBLS1993ECOBenthic bacteria andproduction684E, F, MBLS1994LOMaterial flux andproduction614E, F, MPLS1994NATStorichometry ofplanktonic1298E, F, MPLS1994NATStorichometry ofplanktonic1298E, F, MPS1994PATStorichometry ofplanktonic1298E, F, MPS1994PATStorichometry ofplanktonic1298E, F, MPS1995JPRPlanktonicplanktonic956E, F, MPS1995JPRPlanktonicplanktonic95<$	песку Baines and Pace	1991	ΓO	or pnytopiankton Bacterial use of phytoplankton	274	14	F, M	Ъ	LS	D	
191MEParticipation activity growth23012E,F,MPLS192MEPSPelagic bacterial growth29717E,F,MPLS193LOParticulate organic metationships24214F,MPLS193LOParticulate organic metation24214F,MPLS193MEBenthic bacterial production704E,F,MBLS193ECOBenthic bacterial production704F,MBLS194LOMaterial flux and planktonic614F,MPLS194NATStoichiometry of planktonic1298E,F,MPLS194PNATStoichiometry of 	Seitzinger et al.	1991	EST	${ m DOM}$ Benthic ${ m NH_4}^+$	50	С	E, F, M	В	E, LS	D	
1992MEPSPelagic bacteria and plankton29717E, F, MPLS1993LOParticulate organic relationships24214F, MPLS, S1993MEBenthic bacterial production704E, F, MBLS, S1993MEBenthic bacterial 	White et al.	1991	ME	sorption Pelagic bacterial production and	230	12	Е, Ғ, М	Ч	LS	D	
1993LOParticulate organic matter24214F, MPLS, S1993MEBenthic bacterial production704E, F, MBLS1993ECOBenthic bacterial macrobenthos704E, F, MBLS1994LOMaterial flux and planktonic614F, MPLS, S1994NATStoichiometry of planktonic1298E, F, MPLS1994NATStoichiometry of planktonic1298E, F, MPSnd1995JPRPelagic bacteria and 	Sanders et al.	1992	MEPS	growth Pelagic bacteria and plankton	297	17	E, F, M	Ч	LS	S	
1993MEstoichiometry broduction704E, F, MBLS1993ECOBenthic bacterial production704F, MBLS, S1994LOMaterial flux and planktonic614F, MPLS1994NATStoichiometry of planktonic1298E, F, MPLS1994NATStoichiometry of planktonic1298E, F, MPSnd1995JPRPelagic bacteria and plankton956E, F, MPLS, S	Hecky et al.	1993	ΓO	relationships Particulate organic matter	242	14	F, M	Ъ		D	
1993ECOProduction macrobenthos684F, MBLS, S1994LOMaterial flux and planktonic614F, MPLS1994NATStoichiometry of plankton1298E, F, MPSnd1995JPRPelagic bacteria and plankton956E, F, MPLS, S	Sander and	1993	ME	stoichiometry Benthic bacterial	70	4	Е, Ғ, М	В	LS	S	
1994LOmacrobenthos macrobentho614F, MPLS1994NATStoichiometry of plankton1298E, F, MPSnd1995JPRPelagic bacteria and plankton956E, F, MPLS, S	Kaltt Schallenberg	1993	ECO	production Benthic bacteria and	68	4	F, M	В	LS, S	D	
1994 NAT Stoichiometry of 129 8 E, F, M P S plankton interactions 1995 JPR Pelagic bacteria and 95 6 E, F, M P LS, S plankton abundance	and Kalff Baines et al.	1994	ΓO	macrobenthos Material flux and planktonic	61	4	F, M	Ч	LS	D	
1995 JPR Pelagic bacteria and 95 6 E, F, M P LS, S plankton abundance	Elser and Hassett	1994	NAT	production Stoichiometry of plankton	129	œ	Е, Ғ, М	Ъ	S	D	
	del Giorgio and Scarborough	1995	JPR	interactions Pelagic bacteria and plankton abundance	95	Q	Е, Ғ, М	Ъ		D	

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Continued.	
TABLE 2.	

				Times cited	ited				
Authors	Year	Journal <sup>a</sup>	Subject	Total	Per y	Ecosys	Habitat	Method	Con
Elser et al.	1995	AME	Pelagic bacterial	68	5	F, M	Р	н	D, S
Maranger and	1995	MEPS	Pelagic viral	113	8	F, M	Ρ	LS, S	D
Amon and	1996	ΓO	apundance Pelagic bacterial use	347	25	F, M	Р	E, S	D, S
benner del Giorgio and France	1996	ΓO	or DOM Zooplankton and POM isotopic	89	9	Е, Ғ, М	4	LS, S	D
Malinsky- Rushansky and Leorand	1996	MEPS	composition Pelagic bacteria use of plankton	44	б	F, M	Ч	Щ	D
West and King del Giorgio	1996 1997	EST NAT	Fish communities Pelagic respiration	39 335	3 26	E, F, M E, F, M	P, B P	S LS	S D, S
et al. Hassett et al.	1997	ГО	Production Plankton stoichiometric	68	IJ	Е, Ғ, М	Ч	S	D
Myers et al.	1997	CJFAS	Interactions Spatial scale of fish	83	9	F, M	Ρ, Β	S	D
Sommaruga et al.	1997	AEM	Effects of solar radiation on	84	9	F, M	Ч	ш	S
Methé et al.	1998	ΓO	pacteriopiankton Pelagic bacterial	89	~	F, M	Р	LS, S	D
Glöckner et al.	1999	AEM	Bacterioplankton	383	35	F, M	Р	S	D, S
Guildford and Hecky Ball and Vallf	2000	O1	Phytoplankton nutrient limitation Eactors influencing	152	15	F, M	Ч	S	S
Havens et al.	2001	EP	picophytoplankton Autotrophic	62 49	νŋ	F, M E, F, M	Р Р, В	LS	D, S D
Hillebrand	2002	J-NABS	succession Controls of autotrophic	68	6	F, M	В	MA	S
Repeta et al.	2002	GCA	Benthic and pelagic	45	9	F, M	Р, В	S	S
Shurin et al.	2002	EL	Strength of trophic	245	31	F, M	Р, В	MA	D
Simon et al.	2002	AME	Organic aggregate formation	188	24	Е, Ғ, М	Р, В	ΓS	S
Mei and Danovaro	2004	ГО	Benthic virus production	44	Г	F, M	В	LS, S	S
			1						

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				Times cited	ited				
Authors	Year	Journal <sup>a</sup>	Subject	Total	Per y	Ecosys	Habitat	Method	Con
Price and Sowers	2004	PNAS	Temperature effects on microbial metabolism	111	19	F, M	P, B	LS	S
Mermillod- Blondin and Rosenhero	2006	AS	Effects of ecosystem engineering on henthos	16	4	Е, Ғ, М	В	ш	D
Piña-Ochoa and Álvarez- Cobelas	2006	BGC	Denitrification	35	6	Е, Ғ, М	В	MA	D
Seitzinger et al.	2006	EA	Denitrification	91	23	Е, Ғ, М	В	LS	S
Smith	2006	ΓO	Effects of nutrients on phytoplankton	45	11	Е, Ғ, М	Ъ	LS	S
Sommer and	2006	OEC	Controls on phytonlankton	20	IJ	F, M	Ρ	E, LS	D
Ventura	2006	MEPS	Zooplankton elemental	13	б	F, M	Ъ	LS	D, S
Bancroft et al.	2007	EL	composition Effects of ultraviolet light	34	11	F, M	Р, В	MA	S
Elser et al.	2007	EL	Nutrient limitation of primary	139	46	F, M	Р, В	MA	S
Filippini and Middelboe	2007	FME	Pelagic and benthic viral abundance	12	4	Е, Ғ, М	Ρ, Β	S	D, S
Hillebrand et al.	2007	PNAS	Controls of producer diversity	31	10	F, M	Р, В	MA	D
Sterner et al. Hillebrand	2008 2009	JP JP	Seston stoichiometry Grazer control of periphyton biomass	6 0	ωα	F, M F, M	B	LS MA	o v
<sup>a</sup> Journal abbreviations: AEM = Applied Environ CJFAS = Canadian Journal of Fisheries and Aquatic ( EST = Estuaries, FME = Federation of European J Phycology, JPR = Journal of Plankton Research, J-N Marine Ecology Progress Series, ME = Microbial Ec United States of America	iations: AEM Journal of Fi <sup>2</sup> ME = Fede Journal of Pla ogress Series, nerica	I = Applied E isheries and Aq ration of Euro ankton Researc , ME = Microł	<sup>a</sup> Journal abbreviations: AEM = Applied Environmental Microbiology, AME = Aquatic Microbial Ecology, AS = Aquatic Science, BGC = Biogeochemistry, IFAS = Canadian Journal of Fisheries and Aquatic Sciences, EA = Ecological Applications, ECO = Ecology, EL = Ecology Letters, EP = Environmental Pollution, ST = Estuaries, FME = Federation of European Microbiology Societies Microbiology Ecology, GCA = Geochimica et Cosmochimica Acta, JP = Journal of tycology, JPR = Journal of Plankton Research, J-NABS = Journal of the North American Benthological Society, LO = Limnology and Oceanography, MEPS = arine Ecology Progress Series, ME = Microbial Ecology, NAT = Nature, OEC = Oecologia, PNAS = Proceedings of the National Academy of Sciences of the American Benthologia, PNAS = Proceedings of the National Academy of Sciences o	<i>i</i> , AME = Aqu gical Applicatic es Microbiolog e North Ameri re, OEC = Oec	atic Microbial ms, ECO = Ecc y Ecology, GC can Benthologi ologia, PNAS	Ecology, AS = <sup>1</sup> logy, EL = Ecolc A = Geochimics cal Society, LO = = Proceedings of	Aquatic Science gy Letters, EP 1 et Cosmochir - Limmology ar the National 1	, BGC = Biog = Environmen nica Acta, JP nd Oceanograp Academy of Sc	eochemistry, tal Pollution, = Journal of hy, MEPS = iences of the

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TABLE 2. Continued.

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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), upstreamdownstream (e.g., Mulholland et al. 1995) and surfacesubsurface 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

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 analyzing (e.g., Geographical Information Systems) such data, especially at larger and smaller scales. Powerful database tools (e.g., Web of Science<sup>TM</sup>) 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, collectorgatherers (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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