EXCELLENCE IN ECOLOGY

18

O. Kinne, Editor

Jonathan J. Cole

Freshwater ecosystems and the carbon cycle

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FRESHWATER ECOSYSTEMS AND THE CARBON CYCLE

Introduction (Otto Kinne, Matthias Seaman)

Jonathan J. Cole: A Laudatio
(Colin S. Reynolds)

18

Publisher: International Ecology Institute
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Germany

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Contents

Introduction

Otto Kinne, Matthias Seaman

International Ecology Institute, Nordbünte 23, 21385 Oldendorf/Luhe, Germany

About the Book

In Excellence in Ecology Book 18, Jonathan Cole, winner of the ECI Prize 2003 in Limnetic Ecology, reviews the differences in turnover of dissolved and particulate organic carbon between marine and freshwater ecosystems, as well as the importance of allochthonous inputs — particularly of terrestrial detritus — for carbon metabolism and food webs in lakes and rivers. The author discusses the importance of bacterial vs. primary production for the exchange of matter across ecosystems — such as the efflux of CO_2 from lakes to the atmosphere — and concludes with an appraisal of the paramount significance of lake sediments as a long-term sink for organic carbon of terrestrial origin.

Jon Cole is a former President of the American Society of Limnology and Oceanography (ASLO), and one of the world's leading limnologists. His achievements are summarized in the Laudatio by the Chairman of the Jury, Prof. Colin Reynolds (see pp. XV–XVI).

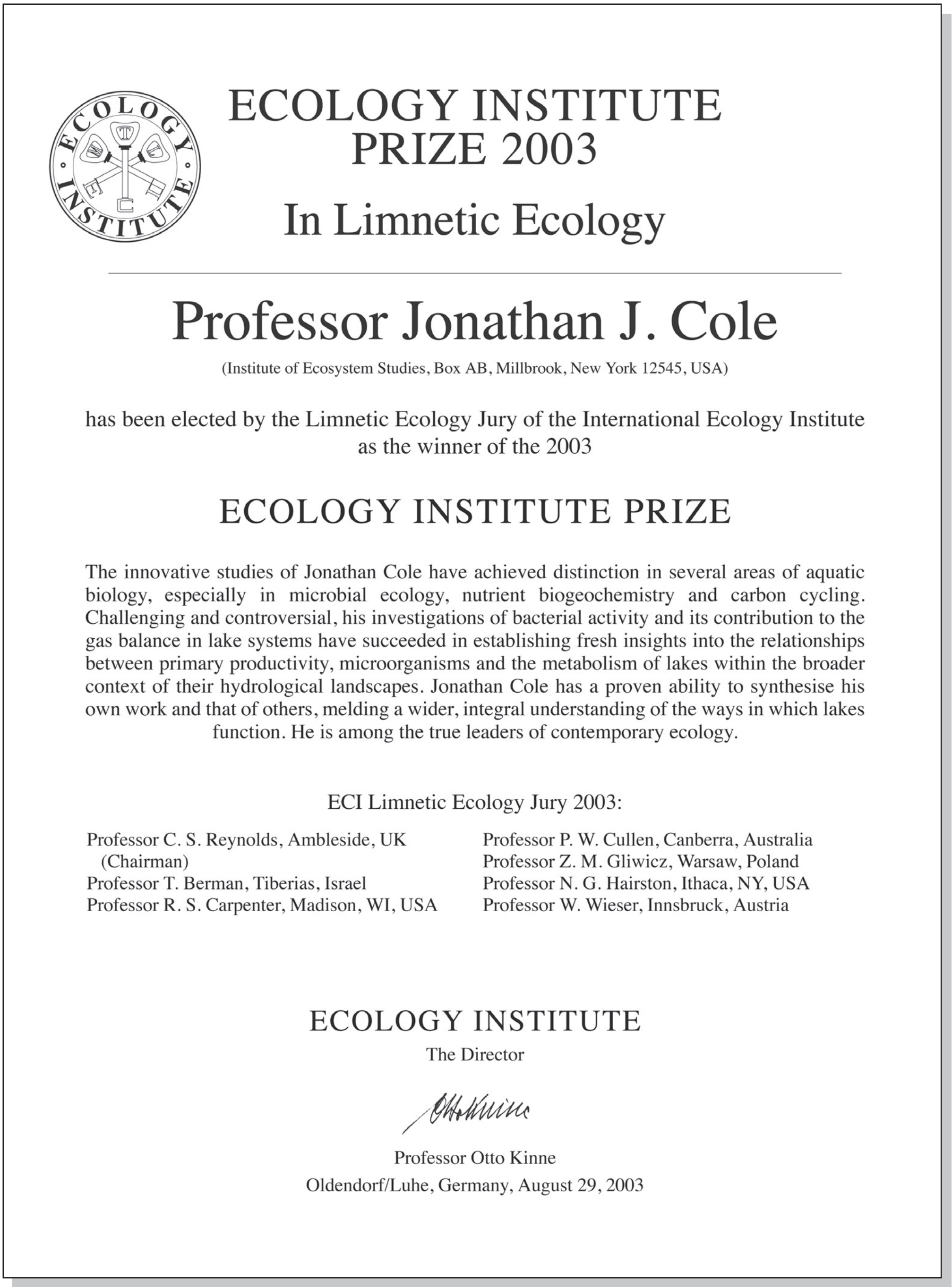
About the International Ecology Institute

The International Ecology Institute (ECI) was founded by Otto Kinne in 1984. It is a non-profit-making organization of research ecologists, sponsored by Inter-Research Science Publisher. The ECI's aims and activities are given in detail at www.int-res.com/ecology-institute/eci-home/. The ECI strives to achieve its aims by setting out awards to honor outstanding scientists: the ECI Prize (with associated EE Books) and the IRPE Prize. The Institute also supports postgraduates in eastern European countries via the Otto Kinne Foundation (OKF).

ECI and IRPE Prizes. The ECI Prize honors the sustained high performance of outstanding research ecologists. It is awarded annually, in a rotating pattern, for the fields of marine, terrestrial and limnetic ecology. We realize that the division into such general fields is not entirely satisfactory; however, so far it has worked quite well. Laureates are elected by a jury of seven ECI members appointed by the ECI Director.

The IRPE (International Recognition of Professional Excellence) Prize honors a young (not more than 40 years of age) research ecologist who has published uniquely independent, original and/or challenging papers representing an important scientific breakthrough and/or who must work under particularly difficult conditions. The prize recipients are elected by the ECI Jury mentioned above.

OKF. The Otto Kinne Foundation supports promising young environmental scientists in eastern European countries. It aids postgraduates — without distinction of race, religion, nationality, or sex — by providing financial assistance for research projects, educational travel, and purchase of scientific equipment or published information. Details are available from the President of the Foundation: Dr. Anna F. Pasternak, P. P. Shirshov Institute of Oceanology, Russian Academy of Sciences, Nakhimovskii prospekt 36, Moscow 117 851, Russia (Email: pasternakanna@hotmail.com).



ECOLOGY INSTITUTE PRIZE 2003

In Limnetic Ecology

Professor Jonathan J. Cole

(Institute of Ecosystem Studies, Box AB, Millbrook, New York 12545, USA)

has been elected by the Limnetic Ecology Jury of the International Ecology Institute as the winner of the 2003

ECOLOGY INSTITUTE PRIZE

The innovative studies of Jonathan Cole have achieved distinction in several areas of aquatic biology, especially in microbial ecology, nutrient biogeochemistry and carbon cycling. Challenging and controversial, his investigations of bacterial activity and its contribution to the gas balance in lake systems have succeeded in establishing fresh insights into the relationships between primary productivity, microorganisms and the metabolism of lakes within the broader context of their hydrological landscapes. Jonathan Cole has a proven ability to synthesise his own work and that of others, melding a wider, integral understanding of the ways in which lakes function. He is among the true leaders of contemporary ecology.

ECI Limnetic Ecology Jury 2003:

Professor C. S. Reynolds, Ambleside, UK (Chairman)
Professor T. Berman, Tiberias, Israel
Professor R. S. Carpenter, Madison, WI, USA
Professor P. W. Cullen, Canberra, Australia
Professor Z. M. Gliwicz, Warsaw, Poland
Professor N. G. Hairston, Ithaca, NY, USA
Professor W. Wieser, Innsbruck, Austria

ECOLOGY INSTITUTE
The Director

Professor Otto Kinne
Oldendorf/Luhe, Germany, August 29, 2003

Nominations. Nominations for ECI and IRPE Prizes (accompanied by the nominee's CV, list of publications, and a statement why, in the opinion of the nominator, the nominee qualifies for the prize) are invited from research ecologists worldwide. They should be sent to the chairperson of the respective ECI Jury (see www.int-res.com/ecology-institute/call-for-nominations/) or, alternatively, to the ECI's director, who will then forward them to the chairperson. Eligible are all ecologists engaged in scientific research (except the ECI's director, the Jury's chairperson, and previous Laureates; Jury members nominated will be replaced by other ECI members). The Jury selects prize winners using the nominations received as well as their own knowledge of top performers and their own professional judgement.

Nominations for OKF Fellows, to be addressed to Dr. Anna F. Pasternak (address given above) and accompanied by a letter of support as well as a brief documentation of the nominee's performance, are invited from scientists worldwide.

ECI Prize Winners and Their Books

Tom Fenchel (Helsingør, Denmark), 1986, marine ecology
(Jury Chair: John Gray, Oslo, Norway)
Book 1: Ecology – Potentials and Limitations (published 1987)

Edward O. Wilson (Cambridge, MA, USA), 1987, terrestrial ecology
(Jury Chair: Sir Richard Southwood, Oxford, UK)
Book 2: Success and Dominance in Ecosystems: The Case of the Social Insects (published 1990)

Gene E. Likens (Millbrook, NY, USA), 1988, limnetic ecology
(Jury Chair: William D. Williams, Adelaide, Australia)
Book 3: The Ecosystem Approach: Its Use and Abuse (published 1992)

Robert T. Paine (Seattle, WA, USA), 1989, marine ecology
(Jury Chair: Tom Fenchel, Helsingør, Denmark)
Book 4: Marine Rocky Shores and Community Ecology: An Experimentalist's Perspective (published 1994)

Harold A. Mooney (Stanford, CA, USA), 1990, terrestrial ecology
(Jury Chair: John L. Harper, Penmaenmawr, UK)
Book 5: The Globalization of Ecological Thought (published 1998)

Robert H. Peters (Montreal, PQ, Canada), 1991, limnetic ecology
(Jury Chair: Jürgen Overbeck, Plön, Germany)
Book 6: Science and Limnology (published 1995) Authors: The late F. H. Rigler and R. H. Peters

David H. Cushing (Lowestoft, UK), 1992, marine ecology
(Jury Chair: John Costlow, Beaufort, NC, USA)
Book 7: Towards a Science of Recruitment in Fish Populations (published 1996)

Paul R. Ehrlich (Stanford, CA, USA), 1993, terrestrial ecology
(Jury Chair: Harold A. Mooney, Stanford, CA, USA)
Book 8: A World of Wounds: Ecologists and the Human Dilemma (published 1997)

Colin S. Reynolds (Ambleside, UK), 1994, limnetic ecology
(Jury Chair: William D. Williams, Adelaide, Australia)
Book 9: Vegetation Processes in the Pelagic: A Model for Ecosystem Theory (published 1997)

Ramon Margalef (Barcelona, Spain), 1995, marine ecology
(Jury Chair: Ernest Naylor, Menai Bridge, UK)
Book 10: Our Biosphere (published 1997)

John H. Lawton (Ascot, UK), 1996, terrestrial ecology
(Jury Chair: Ilkka Hanski, Helsinki, Finland)
Book 11: Community Ecology in a Changing World (published 2000)

Z. Maciej Gliwicz (Warsaw, Poland), 1997, limnetic ecology
(Jury Chair: Winfried Lampert, Plön, Germany)
Book 12: Between Hazards of Starvation and Risk of Predation: The Ecology of Offshore Animals (published 2003)

Richard T. Barber (Beaufort, NC, USA), 1998, marine ecology
(Jury Chair: B.-O. Jansson, Stockholm, Sweden)
Book 13: (cancelled)

Ilkka Hanski (Helsinki, Finland), 1999, terrestrial ecology
(Jury Chair: F. A. Bazzaz, Cambridge, MA, USA)
Book 14: Habitat Loss and its Biological Consequences (published 2005)

Stephen R. Carpenter (Madison, WI, USA), 2000, limnetic ecology
(Jury Chair: Wolfgang Wieser, Innsbruck, Austria)
Book 15: Regime Shifts in Lake Ecosystems: Pattern and Variation (published 2003)

Louis Legendre (Villefranche-sur-Mer, France), 2001, marine ecology
(Jury Chair: Richard T. Barber, Beaufort, NC, USA)
Book 16: Scientific Research and Discovery: Process, Consequences and Practice (published 2004)

Michel Loreau (Paris, France), 2002, terrestrial ecology
(Jury Chair: Paul Ehrlich, Stanford, CA, USA)
Book 17: The Challenges of Biodiversity Science (published 2010)

Jonathan Cole (Millbrook, NY, USA), 2003, limnetic ecology
(Jury Chair: Colin Reynolds, Ambleside, UK)
Book 18: Freshwater Ecosystems and the Carbon Cycle (published 2013)

Bo Barker Jørgensen (Bremen, Germany), 2004, marine ecology
(Jury Chair: Victor Smetacek, Bremerhaven, Germany)
Book 19: (cancelled)

Robert D. Holt (Gainsville, FL, USA), 2005, terrestrial ecology
(Jury Chair: Michel Loreau, Paris, France)
Book 20: On The Conceptual Unification of Ecology: An Unfinished Agenda (tentative title; in preparation)

Winfried Lampert (Plön, Germany), 2006, limnetic ecology
(Jury Chair: Nelson G. Hairston, Jr., Ithaca, NY, USA)
Book 21: Daphnia: Development of A Model Organism in Aquatic Ecology (published 2011)

Daniel Pauly (Vancouver, Canada), 2007, marine ecology
(Jury Chair: Bo Barker Jørgensen, Bremen, Germany)
Book 22: Gasping Fish and Panting Squids: Oxygen, Temperature and The Growth of Water Breathing Animals (published 2010)

Monica Turner (Madison, WI, USA), 2008, terrestrial ecology
(Jury Chair: Robert D. Holt, Gainsville, FL, USA)
Book 23: Lessons from Landscape Ecology (tentative title; in preparation)

Brian Moss (Liverpool, UK), 2009, limnetic ecology
(Jury Chair: Morten Søndergaard, Copenhagen, Denmark)
Book 24: Liberation Ecology: The Reconciliation of Natural and Human Cultures (published 2012)

Paul Falkowski (New Brunswick, USA), 2010, marine ecology
(Jury Chair: Victor Smetacek, Bremerhaven, Germany)
Book 25: Inheriting The Earth: The Imperative for Understanding How Earth's Systems Operate (tentative title; in preparation)

Georgina Mace (London, UK), 2011, terrestrial ecology
(Jury Chair: Michel Loreau, Montreal, QC, Canada)
Book 26: Biodiversity Conservation in a Rapidly Changing World (tentative title; in preparation)

Alan Hildrew (London, UK), 2012, limnetic ecology
(Jury Chair: Brian Moss, Liverpool, UK)
Book 27: From Natural History to Ecosystem Process: Threads and Webs in Fresh Water Communities (tentative title; in preparation)

Antje Boetius (Bremen, Germany), 2013, marine ecology
(Jury Chair: Tom Fenchel, Helsingør, Denmark)
Book 28: Marine Carbon Matters: Connecting Ocean Geochemistry and Biodiversity (tentative title; in preparation)

IRPE Prize Winners

Not in all years did the Jury elect an IRPE Prize winner. The nominations received were either too few or not sufficiently strong

Colleen Cavanaugh (The Biological Laboratories, Harvard University, Cambridge, MA 02138, USA), 1986, marine ecology.
(Jury Chair: John Gray, Oslo, Norway)

Karel Šimek (Hydrobiological Institute, Czech Academy of Sciences, 370 05 České Budějovice, Czech Republic), 1991, limnetic ecology.
(Jury Chair: Jürgen Overbeck, Plön, Germany)

Richard K. Grosberg (Department of Zoology, University of California, Davis, CA 95616, USA), 1992, marine ecology.
(Jury Chair: John Costlow, Beaufort, NC, USA)

Nikolai V. Aladin (Zoological Institute, Russian Academy of Sciences, St. Petersburg 199034, Russia), 1993, terrestrial ecology.
(Jury Chair: Harold A. Mooney, Stanford, CA, USA)

Stephen J. Hawkins (Centre of Environmental Sciences, University of Southampton, UK), 1995, marine ecology.
(Jury Chair: Ernest Naylor, Menai Bridge, UK)

Susan Harrison (Division of Environmental Studies, University of California, Davis, CA 95616, USA), 1996, terrestrial ecology.
(Jury Chair: Ilkka Hanski, Helsinki, Finland)

Jef Huisman (Department of Biological Sciences, Gilbert Hall, Stanford University, Stanford, CA 94305, USA), 1997, limnetic ecology.
(Jury Chair: Winfried Lampert, Plön, Germany)

Philip Boyd (NIWA Centre for Chemical and Physical Oceanography, Department of Chemistry, University of Otago, Dunedin 9001, New Zealand), 1998, marine ecology.
(Jury Chair: B.-O. Jansson, Stockholm, Sweden)

Kevin J. Gaston (Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2NT, UK), 1999, terrestrial ecology.
(Jury Chair: F. A. Bazzaz, Cambridge, MA, USA)

Ruben Sommaruga (Institute of Zoology and Limnology, University of Innsbruck, Technikerstr. 25, 6020 Innsbruck, Austria), 2000, limnetic ecology.
(Jury Chair: Wolfgang Wieser, Innsbruck, Austria)

David M. Post (Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06520 USA), 2003, limnetic ecology.
(Jury Chair: Colin Reynolds, Ambleside, UK)

Markus G. Weinbauer (Laboratoire d'Océanographie de Villefranche-sur-Mer, France), 2004, marine ecology.
(Jury Chair: Victor Smetacek, Bremerhaven, Germany)

Andrew Hector (Institute of Environmental Sciences, University of Zürich, Switzerland), 2005, terrestrial ecology.
(Jury Chair: Michel Loreau, Paris, France)

M. Jake Vander Zanden (Center for Limnology, University of Wisconsin, Madison, Wisconsin, USA), 2006, limnetic ecology.
(Jury Chair: N. G. Hairston Jr., Ithaca, NY, USA)

Marcel M. M. Kuypers (Max Planck Institute for Marine Microbiology, Bremen, Germany), 2007, marine ecology.
(Jury Chair: Bo B. Jørgensen, Bremen, Germany)

Campbell O. Webb (Harvard University Herbaria, Cambridge, MA, USA), 2008, terrestrial ecology.
(Jury Chair: Robert D. Holt, Gainesville, FL, USA)

Francesca Malfatti (University of California at San Diego, USA), 2010, marine ecology.
(Jury Chair: Victor Smetacek, Bremerhaven, Germany)

Jérôme Chave (Laboratoire Evolution et Diversité Biologique EDB, Toulouse, France), 2011, terrestrial ecology.
(Jury Chair: Michel Loreau, Montreal, QC, Canada)

Sujay S. Kaushal (University of Maryland, College Park, MD, USA), 2012, limnetic ecology.
(Jury Chairman: Brian Moss, Liverpool, UK)

Anne K. Salomon (Simon Fraser University, Burnaby, BC, Canada), 2013, marine ecology.
(Jury Chairman, Tom Fenchel, Helsingør, Denmark)

Ecology Institute Staff 2013 (in brackets: year of appointment)*

Director and Founder: Professor O. Kinne, Nordbünte 23, 21385 Oldendorf/Luhe, Germany

Marine Ecology

Prof. F. Azam, La Jolla, CA, USA (1985)
Prof. J. Cebrian, Dauphin Island, AL, USA (2009)
Prof. S. W. Chisholm, Cambridge, MA, USA (1993)
Prof. P. Falkowski, New Brunswick, NJ, USA (2010)
Prof. T. Fenchel, Ebeltoft, Denmark (1985)
Dr. N. S. Fisher, Stony Brook, NY, USA (1985)
Prof. B. B. Jørgensen, Århus, Denmark (2004)
Prof. D. M. Karl, Honolulu, HI, USA (2006)
Prof. L. Legendre, Villefranche-sur-Mer, France (2002)
Prof. E. Naylor, Menai Bridge, UK (1984)
Prof. S. W. Nixon, Narragansett, RI, USA (1989)
Prof. R. T. Paine, Seattle, WA, USA (1990)
Prof. D. Pauly, Vancouver, BC, Canada (2007)
Dr. T. Platt, Dartmouth, NS, Canada (1984)
Dr. F. Rassoulzadegan, Villefranche-sur-Mer, France (1997)
Prof. V. Smetacek, Bremerhaven, Germany (1993)
Prof. A. Underwood, Sydney, Australia (2005)
Prof. B. B. Ward, Princeton, NJ, USA (2006)
Dr. M. Weinbauer, Villefranche-sur-Mer, France (2004)

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*Following their receipt of the ECI Prize document, ECI laureates are invited to join the institute's staff

Terrestrial Ecology

Prof. T. N. Ananthakrishnan, Chennai, India (1984)
Prof. R. Barbault, Paris, France (2007)
Prof. F. A. Bazzaz , Cambridge, MA, USA (1998)
Prof. F. S. Chapin, III, Fairbanks, AK, USA (1986)
Dr. P. Ehrlich, Stanford, CA, USA (1994)
Prof. M. Gadgil, Bangalore, India (1985)
Prof. G. Glatzel, Vienna, Austria (1995)
Prof. I. Hanski, Helsinki, Finland (1993)
Prof. A. Hector, Zürich, Switzerland (2006)
Prof. Robert D. Holt, Gainesville, FL, USA (2005)
Prof. Ch. Körner, Basel, Switzerland (2006)
Prof. E. Kuno, Kyoto, Japan (1986)
Prof. J. Lawton, Heslington, UK (1997)
Prof. M. Loreau, Moulis, France (2003)
Prof. G. Mace, London, UK (2011)
Prof. A. P. Møller, Paris, France (1995)
Prof. H. A. Mooney, Stanford, CA, USA (1991)
Prof. C. Nilsson, Umeå, Sweden (2006)
Prof. B.-E. Saether, Trondheim, Norway (2000)
Prof. D. Schimel, Boulder, CO, USA (1998)
Dr. M. Shachak, Sede Boker, Israel (1989)
Prof. M. G. Turner, Madison, Wisconsin, USA (2005)
Dr. D. H. Wall, Fort Collins, CO, USA (2005)
Prof. E. O. Wilson, Cambridge, MA, USA (1988)

Limnetic Ecology

Prof. N. V. Aladin, St. Petersburg, Russia (1994)
Prof. J. Cairns, Blacksburg, VA, USA (1998)
Prof. S. R. Carpenter, Madison, WI, USA (2000)
Prof. J. J. Cole, Millbrook, NY, USA (2004)
Prof. J. I. Furtado, London, UK (1985)
Prof. Z. M. Gliwicz, Warsaw, Poland (1998)
Prof. N. G. Hairston, Ithaca, NY, USA (1998)
Dr. J. E. Hobbie, Woods Hole, MA, USA (1986)
Prof. E. Kamler, Warsaw, Poland (1993)
Prof. W. Lampert, Plön, Germany (1993)
Prof. G. E. Likens, Millbrook, NY, USA (1989)
Prof. K. Lillelund, Hamburg, Germany (1985)
Dr. D. M. Livingstone, Duebendorf, Switzerland (2009)
Prof. B. Moss, Liverpool, UK (2009)
Prof. T. J. Pandian, Madurai, India (1985)
Prof. E. Pieczynska, Warsaw, Poland (1993)
Prof. M. Power, Berkeley, CA, USA (2006)
Dr. C. S. Reynolds, Kendal, UK (1995)
Prof. D. W. Schindler, Edmonton, Alberta, Canada (2006)
Dr. T. Simé-Ngando, Aubière, France (2009)
Prof. R. Sommaruga, Innsbruck, Austria (2008)
Prof. M. Søndergaard, Hillerød, Denmark (2009)
Prof. R. Sterner, St. Paul, MN, USA (2005)
Prof. L. Tranvik, Uppsala, Sweden (2005)
Prof. J. G. Tundisi, São Paulo, Brazil (1990)
Prof. D. Uhlmann, Dresden, Germany (1989)
Prof. M. Yamamuro, Tokyo, Japan (2009)

Jonathan J. Cole: Recipient of the Ecology Institute Prize 2003 in Limnetic Ecology. A Laudatio

Colin S. Reynolds

Freshwater Biological Association and Centre for Ecology and Hydrology,
LA22 0LP Ambleside, Cumbria, UK

Jonathan Cole's work has achieved distinction in several areas. His studies on the bacteria in aquatic ecosystems have elucidated many of the linkages between bacterial activity and the production and mortality of phytoplankton, illuminating, in particular, the pathways by which the primary products of algal photosynthesis are delivered to and cycled within the food web. A series of thoughtful reviews have provided definitive empirical statements about the interactions among algae and bacteria, becoming landmark reference points as well as comprehensive syntheses of the earlier literature.

Jonathan and his colleagues have also engaged in whole-lake manipulations involving experimental adjustments of food webs, nutrient loads and the constraints governing metabolism at the ecosystem scale. Exciting experiments address the relative importance of autochthonous sources (carbon fixed by plant production in the lake) and allochthonous sources (carbon delivered from outside to the lake) in supporting the consumer food web. This work has had considerable implications for the ways in which the biogeochemical role of nutrients is regarded, especially with respect to imbalances in the fulfillment of other resource demands.

A further focus of Jonathan's attention has been carbon dioxide exchange in lakes and seas. Whereas high photosynthetic rates under favourable conditions are capable of stripping carbon dioxide from solution and of furnishing reduced carbohydrate skeletons for the anabolic assembly of biomass, Jonathan and his collaborators showed that this is rather the exception. Many lakes and rivers are normally close to the air-saturation point with respect to carbon dioxide concentration, meaning that they are frequently de-gassing CO_2 to the atmosphere. Far from being a net sink for atmospheric CO_2, these lakes are either relatively neutral in their net fluxes or tend to net heterotrophy in oxidising organic carbon formed outside the lake. Jonathan has reminded us that lakes are not isolated entities, but hydraulic sumps for their watersheds. He has taught us that to understand the dynamics and metabolism of lakes, it is essential to view them in the context of their terrestrial landscapes.

Jonathan's ability to assimilate information into context, to synthesise facts into a broader understanding, has been an enduring feature of his scientific career. He passed his early postgraduate days as a research fellow at Cornell University, before moving on to the Institute of Ecosystem Studies at Millbrook, NY, USA. This laboratory has supported renowned aquatic ecologists, including J.E. Hobbie and G.E. Likens, with whom Jonathan worked closely on the highly regarded research projects centered on Hubbard Brook. Inspired by his senior colleagues, Jonathan nevertheless quickly established his own insights and an ability to synthesise disparate research findings into clear hypotheses about the functional aspects of ecosystems. His destiny to become a leader was not long in fulfillment and, supported by such able colleagues as Nina Caraco, George Kling, Tim Kratz and Michael Pace, he has inspired and led a veritable adventure in limnological research.

Jonathan plays an active part in the running of the Institute in Millbrook. He has a significant role in national activities and committees, and in refereeing and editing work for several leading journals. He has worked tirelessly in support of the American Society of Limnology and Oceanography and was elected as its next President in 2002. Jonathan has taught numerous courses at the IES and at Yale University. He has supervised several graduate students to completion of their theses and advised a number of post-doctoral fellows from outside the USA, helping them to build their reputations. All attest to his inspiration and generosity in helping others.

After addressing the scientific attributes and credentials of the 2003 Laureate, it is relevant to say something about the task of the Jury. We received 14 nominations, each on behalf of a well-known limnologist with an illustrious track record. We organised the ballot in 2 stages. Jonathan comfortably topped both ballots, giving us an unambiguous outcome, and the Jury was unanimous in recognising the high esteem in which his work is held.

As one of the outstanding contributors to modern limnology and as one of the true leaders of contemporary ecology, Jonathan has all the qualities that the ECI Prize seeks to celebrate. Challenging and controversial in his ideas, intent in his scholarship, proven in leadership skills, innovative and influential in shaping modern limnology, Jonathan Cole is a most deserving and appropriate winner of the ECI Prize.

DEDICATION

This book is dedicated to the memory of Darwin Cabin. The cabin was built by the Congregation of the Sacre Coeur around 1930. It was used as a retreat by the faculty and administration of the University of Notre Dame until about 1970, when it was turned over to the University of Notre Dame Environmental Research Center (UNDERC) to house researchers and teachers. I began using Darwin Cabin in the early 1990s when I joined Steve Carpenter, Jim Kitchell, Jim Hodgson, and Mike Pace on what became a long collaboration on a series of projects located at UNDERC. We all stayed and cooked together in this crowded cabin during our weeks at UNDERC. The porch of Darwin Cabin was the birthplace of many ideas. Some of these were good and viable ideas, and they led to the research covered in this book and elsewhere. Others were, well, just ideas. The invention, incubation, and winnowing of these ideas on the Darwin porch over bourbon and beer have been some of my best times as a professional scientist. Sadly, due to an overzealous concern for safety, Darwin was demolished in 2010.

Darwin Cabin in 2009, a year before it was demolished. The famous porch is on the opposite side, facing Tenderfoot Lake. Photo by J. Hodgson

1 PREFACE

The carbon song of a buried Bog Man

This book is about the carbon cycle in fresh waters, with an emphasis on lakes and lake-like rivers. To begin, I wish to introduce you to two Danes — the reason will become clear shortly. About 2500 years ago, an iron-age man living in what is now Denmark was killed by hanging and then thrown into a small, boggy lake. In 1953, his remarkably well-preserved body was discovered and ultimately examined by scientists from several disciplines, including anthropologists and forensic doctors. His internal organs were well preserved, as were his stomach and intestinal contents, which revealed the composition of his final meal — a porridge of grain and seeds. This freshwater mummy, now called 'Tollund Man' (Fig. 1), is on display in a special museum in Silkeborg, not far from Aarhus. His face has very recognizable features and one can see, or at least easily imagine, the sense of his facial expression. In fact, Tollund Man looks very similar to Dr. Morten Søndergaard as a younger man. Morten Søndergaard is a silicone-age Danish limnologist and oceanographer who has worked extensively on the carbon cycle in fresh waters.

Fig. 1. Tollund Man, an iron-age Dane preserved in the sediments of a bog and now housed in a museum in Silkeborg, Denmark. Photograph reprinted with permission of the Silkeborg Kulturhistoriske Museum

While mummified bog people are not commonplace, they are distributed widely across Northern Europe and Russia, as described by I. V. Glob (Glob 1969). I do not know if Dr. Glob was attracted to bog people because of his name. At least, as an American would pronounce it, ‘glob’ is pretty close to the noise a boot makes as it sinks into deep, organic-rich mud of the kind in which Tollund Man was found. I do know that there are no reports of this kind of remarkable, long-term preservation of mummies in the ocean. This ‘extreme preservation’ (I am indebted to Dr. John Downing for coining this term in a talk) seems restricted to either the driest deserts, or to lakes and bogs. For desert mummies, be they Pharaohs in Egypt or sea lions in Antarctica, the lack of water is the usual explanation for the preservation. However, water is plentiful both in bogs and in the ocean.

I bring up Tollund Man and Morten Søndergaard for several reasons. First, the existence of mummified bog people in some freshwater environments alerts us that the way organic matter is cycled in fresh waters is different than in salt waters, a subject that is threaded throughout this book. Second, in 1986, Morten Søndergaard and his long-term colleague, Bo Riemann, wrote an important book on the carbon cycle (C cycle) in lakes (Riemann and Søndergaard 1986). Some of the research for that book was in progress while I was at Cornell completing my Ph.D. thesis on aspects of carbon in freshwaters, and it influenced my early career. In fact, my first international trip as a professional scientist (well, I was a post-doctoral researcher) included a visit to the Salten Skov Limnological Field station to give a lecture, to interact with Bo Riemann and Morten Søndergaard, and to learn first-hand about some of the material that ultimately went into their book. It was on that trip that I visited Tollund Man in the flesh, so to speak, in the museum at nearby Silkeborg. Third, the Riemann and Søndergaard (1986) book is very much a product of its time. Most limnologists (including Riemann and Søndergaard), especially those interested in biogeochemistry, had adopted what is now seen in retrospect as an overly oceanographic model of how the C cycle in lake ecosystems worked.

The overly oceanographic view of lake ecosystems

By ‘overly oceanographic’, I mean that limnologists previously considered that, for lakes, the only important input of readily reactive organic C came from primary production (largely planktonic) within the lake. These in-lake sources of organic material are called autochthonous sources. Perhaps this hermetic view of the C cycle was a cultural holdover from some of the earliest limnological work. For example, Forbes’ famous work written in 1887, 'The lake as a microcosm', took this view and teachers still subject grade school children to it when they have them watch a sealed aquarium which contains a fish and a few sprigs of *Elodea*. Limnologists, of course, had known for some time that dissolved organic C (DOC) of terrestrial origin entered lakes in large quantities, but they thought of it then as a physically important but biologically inert, or at least refractory, substance. The imported sources of organic material are called allochthonous sources. Limnologists were keenly aware that DOC affected the color of lake water, which in turn affected heating and stratification. DOC does certainly affect the physical properties of lakes, but limnologists did not fully appreciate that this terrestrially derived material was also highly biologically active. They also did not fully appreciate that large quantities of particulate organic C (POC) entered lakes as both aeolian and fluvial vectors and that this POC could also interact with the food web (Gasith and Hasler 1976, Bowman 1988, Cole et al. 1989). Starting in the 1980s, some limnologists observed that these external (i.e. allochthonous) inputs could affect the metabolic balance of lakes (Salonen et al. 1983, Arvola and Tulonen 1998), but most tended to think that net-heterotrophic lakes (those in which respiration exceeded gross primary production [GPP]) were rare and restricted to very highly-colored boggy systems (perhaps like the one in which Tollund Man was deposited) or what Wetzel (2001; quoting earlier work) called 'dystrophic' lakes.

Limnologists who worked in streams (Fisher and Likens 1973) and rivers (Peterson et al. 1985), which receive much higher allochthonous loads than lakes and are more obviously connected to their watersheds, realized more quickly that the terrestrial C could affect metabolic and organic matter balances, and food webs (Webster and Meyer 1997b). The stream and lake literature, however, seemed to be on different trajectories during the 1980s.

The advent in the early 1980s of techniques which could measure the rate at which bacteria synthesized new biomass (secondary production; Fuhrman and Azam 1982, Kirchman et al. 1985, Riemann and Søndergaard 1986, Smith and Azam 1993) revealed some systems in which pelagic bacterial production was co-equal or even greater than primary production (Scavia et al. 1986). The observations in Lake Michigan, that bacterial production was greater than primary production, stimulated a lively debate with interesting outcomes. Strayer (1988) tried to reconcile these results by demonstrating that secondary production is not inherently constrained by primary production, even in a system in which autochthonous primary production is the only significant organic C input. This argument is both eye-opening and true, but probably not the root cause of the observed high rates of bacterial production (BP). Cole and Caraco (1993) tried to explain the phenomenon by construct-ing a food web in which bacteria consumed other bacteria, creating several trophic levels within the microbial loop — a plausible explanation, but again not the likely one. While secondary production is not inherently limited by C supply, heterotrophic respiration certainly is (Cole and Pace 1995, Jahnke and Craven 1995). After further study on the rates of bacterial respiration (BR), or growth efficiencies [BP / (BP + BR)], it became obvious that in many freshwater and marine systems BR is simply too high to explain if the only source of labile organic C is autochthonous primary production (del Giorgio and Peters 1994, del Giorgio et al. 1997, Cole 1999, Roland and Cole 1999).

Net heterotrophy and terrestrial carbon inputs

A consistent pattern emerged which (I would argue) changed limnologists' thinking over the C cycle in lakes in particular, and also influenced thinking over the C cycle in the ocean (summarized nicely in del Giorgio and Williams 2005). Techniques have improved for measuring metabolism in bottles and in free water, including (among many): automated sensors for dissolved oxygen and/or CO_2; new methods using ambient isotopes, such as the triple oxygen isotope method (i.e. Luz and Barkan 2000); and optodes. The explosion in technical capacity led to a greater interest in measuring both metabolism and, more simply, the actual concentrations of metabolic gases relative to saturation values. With the spike in interest, it was revealed that whole system respiration (R) often exceeds GPP in a large range of freshwater and marine environments. The only way to explain this excess R is to have the some of the external, terrestrial supply of organic matter actively respired within the water body (Salonen et al. 1983, 1992, Cole et al. 2000, Staehr and Sand-Jensen 2007). Support for this view also came from the growing field of photochemistry. Researchers working in the ocean and in lakes showed that sunlight affects the chemistry of DOC. Some showed that UV radiation oxidizes DOC directly to CO_2 (Graneli et al. 1996); others showed that large molecules are cleaved into smaller ones, and these smaller molecules are more labile to microbial attack (Lindell et al. 1995, Reche et al. 1999, Pace et al. 2012). All these discoveries changed the view that terrestrial DOC was refractory. DOC is far less refractory when subjected to the well-lit surface waters of a lake or river than it is buried in lightless soils. From the point of view of the C cycle, an aquatic system, especially one with a long residence time that sees some sunlight, is a window in the terrestrial landscape (Cole 1999).

What about streams?

In this book about the C cycle in fresh waters, I focus on the several fates of terrestrially-derived C in lake ecosystems and how this external input affects the C cycles of both lakes and some lake-like rivers. As such, this book is an example of 'carbocentric limnology' (Prairie 2008). While I will mention a few lake-like large rivers, I will only refer to streams in passing. There is a vast literature about the fates of terrestrial organic matter and metabolism in small streams. Conceptual models for organic C sources to lotic and lentic ecosystems differ but are converging with new findings. Historically, streams and small rivers were viewed as heterotrophic ecosystems dominated by allochthonous inputs with food webs supported by detrital carbon (Hynes 1970, Fisher and Likens 1973, Vannote et al. 1980, Leroux and Loreau 2008). Lake food webs were viewed as supported primarily by aquatic primary production (Lindeman 1942, Riemann and Søndergaard 1986), although the importance of organic carbon inputs to lake carbon budgets was also recognized (Richey et al. 1978). While in small, shaded streams terrestrial detritus is the dominant basis of the food web (Hall et al. 2001), more recent work in a wider array of streams has shown the surprisingly large importance of autochthonous carbon fixation to the food webs (Webster and Meyer 1997a, Robertson et al. 1999, McCutchan and Lewis 2002, Bunn et al. 2003). In lakes, recent work supports the argument of Wetzel (1995) of significant utilization of allochthonous carbon by microbial and animal consumers. These changes in perspective are also consistent with growing evidence of cross-ecosystem subsidies in a wide range of habitats including streams, rivers, lakes, islands, and riparian terrestrial environments (Polis et al. 1997, Power and Dietrich 2002, Fausch et al. 2002, Marcarelli et al. 2011). Thus, stream food webs are perhaps less dependent on terrestrial organic matter than previously thought, while lake food webs are more dependent on it. I will look more at these evolving paradigms in Chapter 3, but this book will not attempt to cover much of the work on stream C cycling.

I have narrowed the scope of this book to 3 areas. Chapter 2 covers the role that inland waters (rivers, streams, and lakes) play in the C cycle at global to regional scales. Chapter 3 examines the theory that terrestrial organic matter can subsidize lake food webs and looks in depth, with data, at the patterns and magnitudes of this subsidy. Chapter 4 examines why terrestrial subsidies to lake food webs is a controversial topic and tries to resolve the controversy. Finally, Chapter 5 briefly reviews present understanding of the storage of organic C in lake sediments and what is known (and not known) about how these systems preserve organic matter at such high rates.

2 THE ROLE OF INLAND WATERS IN THE GLOBAL AND REGIONAL CARBON BALANCE

This chapter examines the 'big picture' and asks in what way, at what time scales, and by how much, inland waters participate in the C balances of their watersheds, regions, and the globe. Continental aquatic environments (lakes, rivers, streams, and ground water) bury organic matter in sediments, exchange CO_2 and CH_4 with the atmosphere, and transport both inorganic and organic C to the ocean. Despite the small surface area of inland waters, 25 to 50% of global, terrestrial net ecosystem production is either transported or buried, or respired in these waters. This chapter starts with a framework for thinking about C balances in connected ecosystems and then reviews current knowledge about the magnitudes of the important fluxes.

The algebra of ecosystem carbon budgets

To look at C budgets in a general way, and to see how the components are inter-related, I use the terminology given in Lovett et al. (2006) and Cole et al. (2007) (Table 1). There are many choices, but the terminology used in these papers is clear and also the oldest, and comes originally from Woodwell and Whittaker (1968) (but see Chapin et al. 2006 for some alternative terminology).

For the Earth in its entirety (or its analog, Biosphere-II; Weyer et al. 2000; or a sealed aquarium), the C budget is simply one of reallocation of C among pools. The only input to the organic pool is from GPP; the return to CO_2 comes from respiration (R) and abiotic oxidations. Storage (S) is simply the balance between GPP and oxidations. Imports (I) and exports (E) are not relevant at this scale; the mass balance of C occurs entirely within the boundaries of the global ecosystem. Any change in S has a concomitant change in CO_2. The entire planet Earth is essentially sealed for C; the ecosystems that comprise the planet are not sealed. These component ecosystems exchange CO_2 with the atmosphere and hydrologic fluxes with other systems. Thus local, within-ecosystem changes in S are not necessarily reflected in local changes in CO_2, especially as the time frame is broadened. Furthermore, for many ecosystems and the majority of freshwater systems, I and E (organic

Table 1. Terms and definitions in ecosystem organic carbon balances. Most of the terms are discussed in the section, *Algebra of ecosystem carbon budgets*. Some terms not mentioned in the text are nevertheless common in carbon budgets and included in this table for completeness

Acronym	Component	Definition	Note
GPP	Gross primary production	All photosynthesis in an ecosystem independent of its fate	Also called 'autochthonous input'
R	Respiration	Respiration of both autotrophs and heterotrophs	Also called 'total respiration'
NEP	Net ecosystem production	GPP – R	May be positive or negative. Sometimes called 'NCR' (net community respiration)
R_h	Heterotrophic R	R of all consumer organisms	
$R_{h\text{-}T}$	R_h of terrestrial organic matter	Consumer R supported by imported organic C	
$R_{h\text{-}GPP}$	R_h of autochthonous GPP	Consumer R supported by local GPP	$R_h = R_{h\text{-}T} + R_{h\text{-}GPP}$
R_a	Autotrophic R	R of all autotrophs	$R = R_a + R_h$
I	Imported organic C	C imported from outside the ecosystem boundaries	Also called 'allochthonous input'
S	Storage	Increase or decrease in organic C within the ecosystem	Includes sediments, biomass, etc. *S* can be positive or negative. Some studies use the term 'burial'
E	Export	Organic C which exits the ecosystem	
NPP	Net primary production	GPP – R_a	Organic C of autochthonous origin, potentially available to heterotrophs, or to *S* or *E*
I_{CO2}	Dissolved CO_2 imported in ground water	Exported terrestrial respiration	
I_{HCO3}	Dissolved bicarbonate imported in ground water	'Hidden' terrestrial respiration and weathering	

imports and exports across ecosystem boundaries) can be significant. Consider a lake that is accruing some sediment. The organic C inputs are:

$$\mathrm{GPP} + I \tag{1}$$

The outputs are:

$$\mathrm{R} + E + \Delta S \tag{2}$$

Since inputs must equal outputs, then

$$\mathrm{GPP} + I = \mathrm{R} + E + \Delta S \tag{3}$$

Rearranging,

$$\mathrm{GPP} - \mathrm{R} = E + \Delta S - I \tag{4}$$

By definition, net ecosystem production (NEP) = GPP − R, thus

$$\mathrm{NEP} = E + \Delta S - I \tag{5}$$

This set of equations (Eqs. 1 to 5) can be universally applied to any ecosystem, with a few caveats. There may be abiotic oxidation of organic matter. In terrestrial systems, fire can be a major one (Randerson et al. 2006). For some ecosystems, S can be negative. For example, the organic C in old peat in some parts of the Arctic is presently being respired as the climate warms (Wieder 2001, Waddington et al. 2002, Hardie et al. 2009). One needs to be careful and consistent with the sign convention and explicit about what is included in the R term. There are a few more terms that are often encountered in this literature. $\mathrm{R_a}$ is the respiration of autotrophs. While difficult to measure, $\mathrm{R_a}$ is an important term in theory. Net primary production (NPP) is equal to GPP − $\mathrm{R_a}$ and is the fraction of primary production potentially available to consumers. $\mathrm{R_h}$ is the respiration of heterotrophs, including all consumers and microorganisms. R is the sum of $\mathrm{R_h}$ and $\mathrm{R_a}$ (Table 1).

The equations can be applied to the total mass of C or can be used for the key metabolic gases, CO_2 and O_2. In aquatic systems, 3 things need to be measured: (1) the change in concentration or mass of these gases in the water; (2) their export or import across the air–water interface; and (3) where significant, the difference between hydrologic import and export. While both the change in concentration and atmospheric flux terms can be important over the short term (hours to days), if the time scale is long (months to years) the net gas flux usually dominates NEP. A long enough time scale might be an annual cycle of dissolved CO_2 or O_2 in a lake; or it might be only a few hours in a roily stream. At these time scales, for these cases, the change in concentration of gas from the start to finish is often close to zero. That is, the change in storage is small. Thus a ‘long’ record of the net gas flux for a year can give a very good measure of NEP, again with a few caveats. The net gas flux has to be large compared to any of the dissolved gas imported in fluvial or groundwater inputs (Carignan et al. 1998, Stets et al. 2009). The longer the water residence time of the system, the less this importation is a concern. In this section, I will focus just on what can be gleaned from the net gas flux, or more simply, the extent to which the metabolic gases in surface waters are out of equilibrium with the atmosphere.

To make this explanation simple, I start with O_2. Because CO_2 is a reactive gas, one has to deal with the entire carbonate system in water to account for CO_2. So it is simpler to start with O_2. If a system exports O_2 to the atmosphere over a sustained period of time, it must be producing O_2. This implies several things about the system: GPP > R; NEP is positive; and $E + \Delta S$ is a positive number. That is, the system either exports or stores some organic matter. If a system imports O_2 from the atmosphere over time, R > GPP; NEP is negative; and $E + \Delta S$ must be $<I$. Unless previously stored organic C is being actively oxidized, the only way that this condition is met is if terrestrially imported organic matter (I) is being respired, and I is greater than the sum of E and ΔS. So, NEP can be calculated from either the balance of organic C (from I, E and ΔS) or from the balances of the metabolic gases.

To calculate NEP from the oxygen balance, one needs to know the flux of O_2 across the air–water interface at time intervals short enough to capture the significant dynamics in the changes in O_2 concentrations. The advent of reliable automated *in situ* instruments (sondes) has facilitated this (e.g. Cole et al. 2000, Hanson et al. 2003, Sand-Jensen and Staehr 2009 and many others). One also needs to know the total amount of O_2 in the system over depth (e.g. moles O_2 m^{-2}), but only at the start and end of the measurement period. The gas flux depends on 2 components: (1) the departure from the saturation concentration of the gas in the surface water; and (2) the physical rate of gas exchange across the air–water interface, often called the 'piston velocity'. The piston velocity can be visualized as the height of the water column that exchanges gas with the atmosphere per unit time. This piston velocity is specific for a given gas at a given temperature:

$$\text{Flux } O_2 = k_{O2} \times ([O_2] - [O_{2sat}]) \qquad (6)$$

where $[O_2]$ is the concentration of O_2 in the surface water and $[O_{2sat}]$ is the concentration in surface water if it were in equilibrium with the overlying atmosphere. $[O_2]$ comes from measurements; $[O_{2sat}]$ is calculated from temperature, barometric pressure and altitude (Benson and Krause 1980). k_{O2} is the piston velocity for O_2 at a given temperature. One can spend a lot of time worrying about k. For now, I consider its broader implications with simple and approximate values. k_{O2} in lakes is often near 0.5 to 1 m d^{-1} (Cole and Caraco 1998, Cole et al. 2010) and $[O_{2sat}]$ is about 240 µM. Eq. (6) shows that net exchange depends both on the piston velocity and on the difference between $[O_2]$ and $[O_{2sat}]$. It is illustrative to rewrite the flux equation as:

$$\text{Flux } O_2 = k_{O2} \times [O_2] - k_{O2} \times [O_{2sat}] \tag{7}$$

Written this way, it is more obvious that even at saturation there is gross exchange of oxygen with the atmosphere. That is, the gas exchange is never 0; the magnitude of the gross exchange depends only on the piston velocity and the absolute values of $[O_2]$ and $[O_{2sat}]$. That gas exchange is dynamic in both directions and independent of the water-side concentration becomes critical when one is modeling the exchanges of isotopes. This dynamism does not affect the net flux of gases but does affect specific isotopes (e.g. Hendricks et al. 2005, Cole et al. 2006).

Imagine that $[O_2]$ varies between 60 and 110% (which is about the range seen across most surface waters) of $[O_{2sat}]$ and that k_{O2} ranges from 0.5 to 1. The resulting net gas flux varies from −100 to +50 mmol O_2 m^{-2} d^{-1}; part of this range is shown in Fig. 2. At the low end of oxygen saturation, this flux implies that at least 1.2 g of organic C is respired for each square meter of

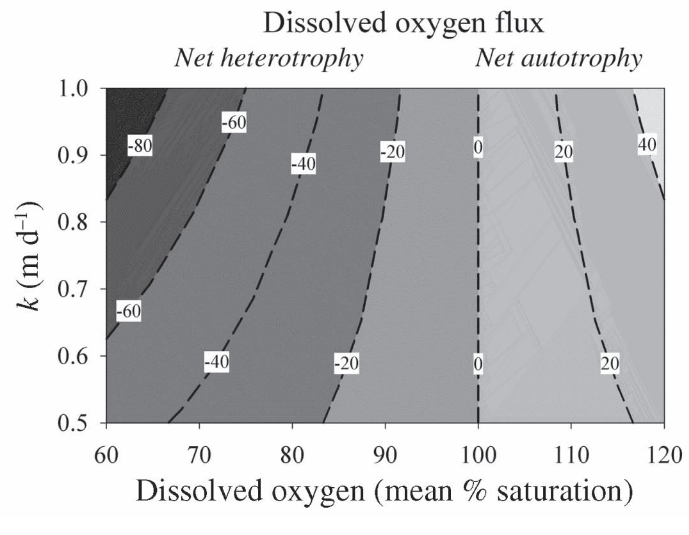

Fig. 2. The flux of oxygen across the air–water interface in aquatic systems. The x-axis shows representative values for surface-water dissolved oxygen in percent saturation. Lakes are typically in the range of 80 to 110%; many rivers are in the range of 70 to 90%. The y-axis shows possible values for the piston velocity (k). Lakes typically have k-values between ~0.5 and 0.75 m d^{-1}; rivers have k-values from ~0.7 to 1 m d^{-1}. The contour lines are the resultant daily gas flux (mmol m^{-2} d^{-1}). Negative values are the influx of oxygen into the lake; positive values are the efflux of oxygen from the lake. Assuming 250 ice-free days per year, the −20 contour line represents an annual CO_2 efflux of 60 g C m^{-2} yr^{-1}

lake per day beyond what was fixed by autochthonous photosynthesis. At the high end, the flux implies that 0.6 g of organic C is sequestered (either as ΔS) or exported (E) resulting from the excess of photosynthesis over respiration. On any given day, fluxes like these can be caused by temporal imbalances in GPP and R. If they persist over time, they inform us that (if flux is negative) imported organic C (from I) is being respired. Surface waters are rarely very far out of atmospheric equilibrium for O_2 over an entire year, but it is common to see lakes that sustain levels of between 90 and 95% of saturation. Further, mean piston velocities over time are usually closer to 0.5 m d^{-1}. If these conditions are sustained, even these small departures from atmospheric equilibrium imply a substantial flux, and organic C subsidy from land, of between 25 to 50 g C m^{-2} yr^{-1}. The subsidy is the portion of the terrestrial input that is respired. The input of organic C from land is usually much larger than this respiratory subsidy, with the residual either exported or buried (Caraco and Cole 2004). Clearly the respired portion cannot be smaller than the subsidy. Consider a typical temperate lake with a mean depth of 5 m and residence time of 1 yr and groundwater DOC concentrations of 20 mg C l^{-1} (which could also be written as 20 g C m^{-3}). The average input of terrestrial DOC to this system is then 20 g C m^{-3} × 5 m yr^{-1} = 100 g C m^{-2} yr^{-1}. If NEP were −50 g C m^{-2} yr^{-1}, the implication would be that about half of the C in the incoming DOC was respired and half, exported (or buried; Fig. 2). That more than one-third (and up to one-half) of the terrestrially derived DOC is metabolized in a year is quite consistent with the budgetary studies on lakes (Dillon and Molot 1997, those reviewed by Caraco and Cole 2004, and recent work in Sweden: Koehler et al. 2012, Weyhenmeyer et al. 2012)

Inorganic carbon balance and other complications

The above analysis demonstrates that the metabolic balance affects the concentration and flux of dissolved oxygen, but not that the flux of dissolved oxygen (or CO_2) depends exclusively on the metabolic balance. A lake, river or stream can import water that is far out of atmospheric equilibrium with respect to O_2 or CO_2 (I_{CO2} in Table 1). For example, ground water in many wetlands can be anoxic or hypoxic. This anoxic ground water may contain a substantial oxygen demand as reduced ions (especially of iron and sulfur) that have the potential to consume oxygen once it is available. If the residence time of the receiving aquatic system is short, this input can have a large effect on the resulting flux of oxygen between the receiving systems and the atmosphere. At atmospheric equilibrium and normal temperatures, water holds about 240 µM O_2. If the incoming water is anoxic, and the conditions are the same as in the DOC analysis in the previous section, the effect on the lake's O_2 economy is minor. On an average day, the input of anoxic ground water is only 0.27% of the lake's volume and would cause, at most (e.g. with no gas exchange), depression of about 0.6 µM, which is difficult to measure. If one thought of this in terms of O_2 flux, this importation of anoxic ground water would cause an influx of O_2 of about 0.3 mmol O_2 m^{-2} d^{-1}, which is small compared to the fluxes usually seen (Fig. 2). The input of the reduced Fe or S ions could be much more substantial. Similarly, incoming ground water can have very high concentrations of free CO_2 from the sum of aerobic and anaerobic processes in the soil. $p\mathrm{CO}_2$ in inflowing ground waters often exceeds 4000 µatm (or 140 µM CO_2, roughly 10-fold higher than atmospheric equilibrium). Taking the same conditions, if the lake had 14 µM CO_2 (e.g. near atmospheric equilibrium), the ground water might cause a sustained increase in $p\mathrm{CO}_2$ in the system of about 0.4 µM. The implied flux difference is about 0.2 mmol m^{-2} d^{-1}, again small.

Displaced terrestrial metabolism

Setting aside these fluvial inputs of gas (or gas deficits), the main cause of departures from atmospheric equilibrium is metabolism in the receiving aquatic system. Clearly this assumption needs site-specific evaluation. On the other hand, the departure from equilibrium must be due to metabolism, either in the receiving aquatic system or its watershed. That is, the terrestrial watershed exports some of its respiration in water, and can be expressed in the currency of either inorganic C or O_2. Thus, a lake or river or stream that is a source of CO_2 to the atmosphere is either a conduit for terrestrial respiration, or is subsidized by the import of terrestrial organic matter, which is respired in the aquatic system (Kling et al. 1991).

The export of dissolved bicarbonate from land to water represents 'hidden' terrestrial respiration. The dissolved inorganic C (DIC) that enters a water body from land is often dominated by the HCO_3^- ion rather than by free CO_2. Dissolved bicarbonates are formed principally by the dissolution of carbonate and aluminosilicate minerals by CO_2 and water. The CO_2 involved in these reactions comes largely from the respiration of the terrestrial biosphere (Meybeck 1993, 2004), thus:

Carbonate weathering

$$\mathrm{CO_2 + H_2O + CaCO_3 \rightarrow Ca^{++} + 2HCO_3^-} \tag{8}$$

$$\mathrm{CaMg\ (CO_3)_2 \rightarrow Ca^{++} + Mg^{++} + 4HCO_3^-} \tag{9}$$

Silicate weathering

$$2\,CO_2 + 3H_2O + CaSiO_3 \rightarrow Ca^{++} + 2HCO_3^- + H_4SiO_4 \qquad (10)$$

$$2\,CO_2 + 3H_2O + MgSiO_3 \rightarrow Mg^{++} + 2HCO_3^- + H_4SiO_4 \qquad (11)$$

Many geochemists keep track of more and more specific weathering reactions; these are very useful in tracing the source of the HCO_3^- (Suchet et al. 2003, Probst 2005). If carbonate weathering is the source of the bicarbonate, then half the C in the bicarbonate was originally CO_2 respired in the soil. If silicate weathering is the source, then all C in the bicarbonate originated as soil CO_2. Globally, about half the weathering is from bicarbonate and half from silicate, meaning that 75% of the bicarbonate-C transported in aquatic systems is really soil respiration in disguise (Stallard 1998).

The precipitation of carbonates is also a source of CO_2 to the water column. Just as the dissolution of $CaCO_3$ by CO_2 is a sink for CO_2, carbonate formation and its subsequent precipitation is a source of CO_2. It is the carbonate weathering Eqs. (8) & (9) in reverse. The solubility product of calcium carbonate is low and can be exceeded by large inputs of either Ca^{++} or $CO_3^=$ or, more commonly by an increase in pH. This increase in pH is often caused by photosynthetic drawdown of CO_2. In hard-water lakes, for example, intense photosynthesis in macrophyte stands results in these plants becoming encrusted in carbonate. It is argued that in some lakes, carbonate precipitation can contribute significantly to the supersaturation of CO_2 in the water column (McConnaughey et al. 1994, Stets et al. 2009). The building of coral reefs or the sinking of coccolithophorids in the ocean is also a source of CO_2 to the surface water where this carbonate was formed. Coral reefs build carbonate for long periods of time; carbonate bearing particles that sink, even if they dissolve in deep water, do not re-enter the surface water for millennia. Thus, the CO_2 that was formed with the carbonate in the oceanic surface water cannot re-equilibrate with that carbonate. In lakes it is less clear if the formed carbonate is a seasonal transient or a long-term storage, so its role in the CO_2 economy of the surface water is less certain (Stets et al. 2009).

Fates of terrestrial net ecosystem production in aquatic-system global magnitudes

Organic carbon burial

Lakes contain some of the largest reservoirs of organic C on the continents. In fact, the sum of the sedimentary organic stores for just 8 of the world's lakes for which there are complete estimates (total sediment inventory rather than just surface concentration) suggests that there is about an order of magnitude more organic C in these lakes alone than in the entire global inventory of soils plus terrestrial vegetation (Alin and Johnson 2007; my Table 2). The tectonic lakes in particular, have sedimentary deposits that are ~2 km thick and contain 100- to 1000-fold more organic C than do their terrestrial watersheds. For large glacial lakes, which are much younger with thinner sediments, the effect is less dramatic. Nevertheless, these glacial lakes contain nearly as much organic C as do their watersheds, even though the watersheds are much larger than the lakes (Kortelainen and Pajunen 2000). Alin and Johnson (2007) estimate the total annual C burial in very large lakes globally to be 0.007 Pg C yr^{-1}, which is a very small annual flux for a global scale. Older estimates for burial rates in large lakes range from 0.006 to 0.011 Pg C yr^{-1} (Mulholland and Elwood 1982, Dean and Gorham 1998, Stallard 1998, Einsele et al. 2001). So, for the world's largest lakes there is a low annual burial rate, but a vast amount of C storage that persists, especially in the case of the large tectonic lakes, for hundreds of thousands of years.

Several studies have estimated the rate of organic C accumulation in lakes during the Holocene (reviewed in Cole et al. 2007). While the methods and assumptions differ quite a bit between studies, all agree that small lakes, in aggregate, accumulate the majority. Estimates range from about 0.03 to 0.07 Pg C yr^{-1}. One of the big differences among the various estimates is the area assigned to small lakes. Because of the difficulties in mapping the nu-

Table 2. Inventory of organic C (in Pg C) in the sediments of 8 of the world's largest lakes and their watersheds. If these values are correct, the sum of the organic C in just these 8 lakes is much larger than the total inventory in continental soils or land vegetation; the inventory of organic C in African rift lakes alone far exceeds what is estimated to be in terrestrial soils. From the data of Alin and Johnson (2007)

Lake	Sediments	Watershed	Ratio lake: watershed
Tanganyka	14 000	4.4	3273
Malawi	5000	1.5	3729
Baikal	4500	1.0	441
Biwa	3.8	0.07	53
Superior	2.3	4.8	0.5
Erie	2.1	1.3	1.6
Michigan	1.7	2.7	0.6
Ontario	0.3	1.3	0.2
Sum	24 000		
Global soil		1580	
Global vegetation		610	

merous small and very small lakes and ponds, these systems have either been excluded or underestimated in most early studies. Using new satellite photography and a geomorphometric modeling approach based on the Pareto distribution, Downing et al. (2006) suggest that natural lakes occupy about 4.2 × 10^6 km^2, an area about 50% larger than that used by Einsele et al. (2001) and other authors. Further, Downing et al. (2006) argue that the smallest lakes (<10 km^2) are where most of this difference occurs. In fact, if Downing et al. (2006) are correct, the average lake in the world is quite small, <2 ha. Applying the rather high organic C burial rate of 40 g C m^{-2} yr^{-1} used by Einsele et al. (2001) for lakes <500 m^2 and using the Downing et al. 2006 estimate of area increases the global estimate to 0.14 Pg C yr^{-1}. Clearly this estimate has high uncertainty and more research is needed into the burial rates in different sizes of lakes. The use of the Pareto distribution by Downing et al. (2006) is challenged by Seekell and Pace (2011), who suggested that this approach may overestimate the global abundance of small lakes.

Reservoirs

Man-made impoundments and ponds tend to have very high rates of sedimentation (Fig. 3). These systems range in size from small farm ponds of

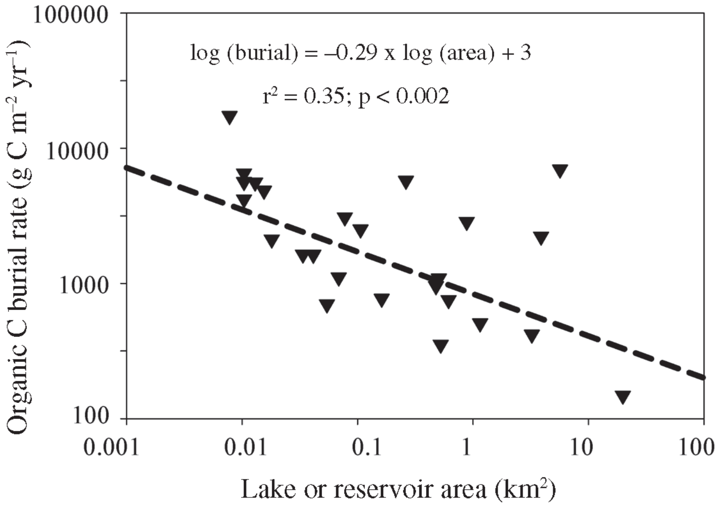

Fig. 3. The relationship between the burial of organic C in sediments and the area of man-made impoundments (lakes or reservoirs). Each point represents a different lake or reservoir. Although r^2 is low (0.35), the log-log regression (dotted line) is significant ($p < 0.002$). Redrawn from the data in Downing et al. (2008)

<1 ha, to large hydroelectric reservoirs >2000 km^2, and the construction of these large systems continues to increase over time (St Louis et al. 2000; www.icold-cigb.net/). The rate of C burial is inversely proportional to the area of the system (Fig. 3). There are several estimates of the burial of organic C in these systems, but again, there is a great deal of heterogeneity as to what was included and how the estimates were made. The older published values suggest a rate near 0.2 Pg C m^{-2} yr^{-1} (reviewed in Cole et al. 2007). The largest uncertainty is the area occupied by reservoirs and the relationship between reservoir size and sedimentation rate. For example, St Louis et al. (2000), in a study of gas flux from reservoirs, used a value of 1500×10^3 km^2 for the area behind impoundments. This value appears to be greatly inflated and seems to include large natural lakes that have some degree of damming on their outlets. Mulholland and Elwood (1982), Dean and Gorham (1998) and many subsequent authors used 400×10^3 km^2. Most of the older global estimates include the myriad of very small man-made farm ponds throughout the world. Stallard (1998) uses 664×10^3 km^2, a value which may include some farm ponds but excludes paddy lands which he treats separately (see next paragraph). Downing et al. (2006) estimate small farm ponds explicitly (again using the Pareto distribution approach) at 77×10^3 km^2 and actually provide a lower areal estimate for dammed impoundments (260×10^3 km^2). Applying the rate of C burial in reservoirs used by Einsele et al. (2001) of 500 g C m^{-2} yr^{-1} arrives at a global value of 0.17 Pg C yr^{-2}, very close to older estimates. On the other hand, the available data suggest that both bulk sediment accumulation rates and organic C content of sediments increase with decreasing area of reservoirs. Downing et al. (2006) estimate that small farm ponds alone accumulate some 0.15 Pg C yr^{-1}. Using the lower estimate for the impoundment area of non-farm ponds provided by Downing et al. (2006) and multiplying this by the average C burial rate in impoundments gives a value of 0.14 Pg C yr^{-1} in impoundments or a total reservoir burial of about 0.3 Pg C yr^{-1} globally. Tranvik et al. (2009) estimate burial in impoundments at 0.6 Pg C yr^{-1}.

Stallard (1998) examined rice paddys and other paddy culture systems that are also aquatic environments, which had not been included in the global C balance. Using several scenarios, Stallard (1998) suggests that as much as 1 Pg C yr^{-1} may be stored in paddys alone. The farm pond area of Downing et al. (2006) probably includes the area of paddy culture. However, Stallard (1998) used a much higher rate of C burial (based on data) for these paddy systems than Downing et al. (2006) used for ponds in general. It is likely then, that small farm ponds, if paddys are included, may produce an estimate higher or even much higher than that of Downing et al. (2006) or Tranvik et al. (2009).

Rivers

Over time, rivers cut and recut their main channels. The conventional wisdom is that there is no true net sediment accumulation within rivers themselves. I know of no global estimate for the deposition of sediments in the flood plains of rivers. Thus, for the global balance I score the net sedimentation in rivers as simply >0.

Export to the ocean

In the treatment here, only rivers transport C. This assumes that any C transported from lakes or streams is accounted for in riverine delivery to the ocean. It is likely that the sediment transported by those rivers that flow into endorheic regions is accounted for in sediment burial in those regions. So, our riverine transport value may be on the conservative side if these assumptions are not true.

Organic carbon. There are numerous reports of the global transport of organic C from rivers to the sea. Most of these are reviews of older literature and are not independent estimates. Stallard (1998) citing Meybeck (1987) and Sarmiento and Sundquist (1992) gives the DOC and POC fluxes as 0.23 and 0.30 Gt C yr^{-1}, respectively, a good representation of the older literature. Ludwig et al. (1996) used a new empirical approach and came up with similar but slightly smaller values, 0.21 and 0.19 Gt yr^{-1} for DOC and POC, respectively. Harrison et al. (2005) used a more spatially explicit approach for DOC and estimated a similar 0.17 Gt C yr^{-1}. Harrison et al. (2005) utilised a relatively simple model (NEWS-DOC) that uses wetland area, and consumptive water use in each river basin. The newest estimate for riverine POC is that of Beusen et al. (2005) at 0.197 Gt C yr^{-1}. Beusen et al. (2005) use a complex multiple linear regression that includes land use, slope, soil conditions and climatic factors. It is encouraging that these newer and independent approaches yield similar data and estimates that are not far from older approaches, which were based on inventories of the world's larger river systems. On the other hand, as Richey (2004) notes, they essentially all rely on the same ultimate C concentrations and river discharge data. Clearly more data are needed.

Inorganic carbon. There are 2 things of interest with the transport of HCO_3^-: (1) the total magnitude, and (2) the fraction derived from carbonate versus silicate weathering. This is because in accounting for the fates of atmospheric CO_2, the C derived from the dissolved $CaCO_3$ needs to be subtracted. The older literature, again nicely summarized by Stallard (1998), gives total DIC flux as 0.29 Pg C yr^{-1}, about evenly divided between silicate weathering and carbonate weathering. So, half the DIC from carbonate weathering came from the old carbonate rock, which is not counted in this balance leaving the atmospheric portion at 0.22 Pg C yr^{-1}. Ludwig et al. (1996) estimated that total DIC discharge is 0.32 Pg C yr^{-1}, of which 0.23 Pg C yr^{-1} are 'atmospheric' and the residual 0.09 Pg are from the carbonate C resulting from limestone dissolution. Intriguingly, Stallard (1998) does not cite the Ludwig et al. (1996) paper as the source of his DIC estimate, but does cite the paper in another context. It is hard to know if these two studies (i.e. Stallard 1998 and Ludwig et al. 1996) are independent. In the most recent and independent estimate, Hartmann (2009) reviewed some of the more recent estimates and included a new approach based on weathering models. The values (for atmospheric CO_2 in HCO_3^- transport) cluster between about 0.14 and 0.17 Pg C yr^{-1} (Table 3). The newer estimates suggest that more than half the exported HCO_3^- comes from the weathering of silicate minerals, which means a larger fraction of this export represents a CO_2 sink (hidden respiration) from land.

Gas exchange

Lakes. A majority of the lakes that have been sampled are supersaturated in CO_2 and are therefore sources of CO_2 to the atmosphere (Cole et al. 1994, Sobek et al. 2005). For global fluxes, the early estimates of about 0.15 Pg C m^{-2} yr^{-1} were arrived at by simply multiplying an area for global lakes by the mean value for (pCO_2 water − pCO_2 air) and by a ballpark estimate for

Table 3. Flux (in Pg C yr^{-1}, percentages in parentheses) of dissolved inorganic carbon (largely bicarbonate) from land to the sea, via rivers, depending on rock type weathered (silicate or carbonate); after data in Hartmann (2009)

Source		Silicates	Carbonates	Total
Gaillardet et al. (1999)		0.14 (48.6)	0.15 (51.4)	0.29
Amiotte-Suchet et al. (2003)		0.15 (59.9)	0.10 (40.1)	0.26
Hartmann (2009)	(A)	0.15 (63.0)	0.09 (37.0)	0.24
	(B)	0.17 (65.6)	0.09 (34.4)	0.26
	(C)	0.16 (65.6)	0.08 (34.4)	0.24

(A) Best model; (B) assuming basalt weathering (after Dessert et al. 2003); (C) assuming no contribution from plutonic or metamorphic rocks the gas piston velocity of 0.5 m d^{-1} (Cole et al. 1994). Although the data set for lakes in Cole et al. (1994) was fairly large, around 2260 estimates from 1835 different lakes, newer data sets are larger (e.g. Sobek et al. 2005). Further, both Cole et al. (1994) and Sobek et al. (2005) (which subsumes the data set of Cole et al. 1994 and increases it to 4902 lakes) are heavily biased in north temperature and boreal systems. Furthermore, Cole et al. (1994) used a conservative estimate of total lake area of 2×10^6 km^2, which is about half the global lake area arrived at by Downing et al. (2006; 4.2×10^6 km^2). Duarte et al. (2008), in a study of $p\mathrm{CO}_2$ in saline lakes, found a much higher $p\mathrm{CO}_2$ on average than for freshwater lakes, and note that the piston velocity was enhanced due to the high pH and greater wind speeds than over small freshwater lakes. They estimate a flux of 0.11 to 0.15 Pg C yr^{-1} for saline lakes alone and suggest a global estimate of 0.28 to 0.32 Pg C yr^{-1}. Alin and Johnson (2007) made a separate estimate for just very large lakes (>500 km^2) of 0.09 Pg C yr^{-1}. The data set of Sobek et al. (2005) shows that $p\mathrm{CO}_2$ is inversely proportional to lake size, suggesting that smaller lakes emit a disproportionately large amount of CO_2 per unit area. Recently, Y. Prairie and colleagues estimated the CO_2 flux from global lakes by size class. Included in that analysis are the relationships between $p\mathrm{CO}_2$ and lake size, piston velocity and lake size, and the newer estimates of lake area by size class. Y. Prairie (pers. comm.) estimates a global flux of 0.53 Pg C yr^{-1}. Marotta et al. (2009) expanded on the data set of Sobek et al. (2005) by including a large number of tropical systems. Marotta et al. (2009) found higher $p\mathrm{CO}_2$ in these systems than in the northern latitudes that dominate the earlier data sets and arrive at another global estimate of 0.44 Pg C yr^{-1}.

Increased interest in gas flux from lakes has also resulted in some re-evaluation of what was earlier reported as dominant patterns. In a study of shallow, macrophyte-rich lakes in the Mackenzie delta, Tank et al. (2009) found that most of these lakes were undersaturated with CO_2 during the summer and likely net sinks for atmospheric CO_2 for the annual cycle. Clearly, as more data are collected and limnologists learn more about the large number of factors that control lake CO_2, the global and regional estimates will continue to change. However, it is clear that the exchange of CO_2 between lakes and the atmosphere is large enough to command further interest at the global scale.

Reservoirs and impoundments. St Louis et al. (2000) present a review of CO_2 emissions from reservoirs and provide an estimate of global CO_2 efflux from them of about 1 Pg C yr^{-1}. This number is too large for several reasons. St Louis et al. (2000) used a definition of impoundment than included natural lakes whose level was managed. Their global reservoir area is much larger than other estimates (discussed above). Cole et al. (2007) used the areal rate of CO_2 flux from St Louis et al. (2000) with a more reasonable global reservoir area of 450 × 10^6 km^2 and arrived at a flux of 0.28 Pg C yr^{-1}. This value is lower still if the newer reservoir area from Downing et al. (2006) is used, down to 0.17 Pg C yr^{-1}. Nevertheless, such an approach does not include any relationships with reservoir age or size. This value may change in the future. Recently, Roland et al. (2010) looked at gas flux from very large tropical reservoirs in the Cerrado region of Brazil and found considerably lower flux values than those listed by St Louis et al. (2000).

Large rivers. The 2 estimates I know of for global riverine gas exchange agree somewhat in magnitude but were arrived at very differently. Cole and Caraco (2001) accumulated data on pCO_2 for 46 large river systems, distributed world-wide. The data set included 7638 individual records from which pCO_2 was calculated. Battin et al. (2009) reviewed data on whole system metabolism (GPP, R, and NEP) for 37 large river systems. Both estimates were scaled up to the global level by multiplying the simple mean areal rate by the global area for rivers. Battin et al. (2009) use 0.295 × 10^6 km^2 for the area of large rivers; Cole and Caraco (2001) estimated total stream plus river area as 0.74 × 10^6 km^2 by assuming channel area is equal to 0.5% of watershed area. For just the large rivers, based on the metabolic data, Battin et al. (2009) obtain a mean NEP (i.e. GPP – R) of −1.6 g C m^{-2} d^{-1}, or an emission of 605 g C m^{-2} yr^{-1}. Cole and Caraco (2001) get a mean net gas flux of 407 g C m^{-2} yr^{-1}. These estimates for large rivers compare quite well considering the differences in approach (0.3 Pg C yr^{-1} from Cole and Caraco 2001 and 0.18 Pg C yr^{-1} from Battin et al. 2009). Battin et al. corrected their river estimate downward in an online corrigendum to 0.07 Pg C yr^{-1}. This new estimate is hard to accept because the gas flux from the Amazon alone is much higher than this.

Streams. The Cole and Caraco (2001) estimate attempted to include streams but did a poor job of it because they had pCO_2 data only from large rivers and did not have an explicit area for streams. If the areal gas flux rate from Cole and Caraco (2001) is applied to the area of large rivers used by Battin et al. (2009), a global flux of 0.12 Pg C yr^{-1} is obtained for large rivers; streams, by difference, would be 0.18 Pg C yr^{-1}.

Small streams are typically more highly supersaturated in CO_2 than are rivers and have far higher gas piston velocities (Wanninkhof et al. 1990, Hall and Tank 2003). Battin et al. (2009) provide a global NEP estimate for streams based on the same metabolic approach they used for rivers and an estimate for stream area of 0.275 × 10^6 km^2; and arrive at NEP = 0.32 Pg C yr^{-1}. It is likely that the estimate for stream area is quite conservative as most first-order streams do not show up on either maps or in GIS databases.

Total fluvial gas emissions. Summing Battin et al. (2009, corrected) for CO_2 efflux from streams and large rivers obtains 0.5 Pg C yr^{-1}, about 50% higher than the estimate of Cole and Caraco (2001). Richey et al. (2002) argue that the Amazon alone has a gas emission of >0.3 Pg C yr^{-1}. It is a little unclear if Richey et al. (2002) are referring here to the Amazon proper or to the entire drainage network. Either way, this high value for the Amazon suggests that the global estimate for fluvial gas flux is higher than 0.5 Pg C yr^{-1}. Richey (2004) speculates that the value is near 1 Pg C yr^{-1} globally.

Putting the pieces together

With the magnitudes of these fluxes in hand, what can be concluded about the fate of terrestrial (continental) NEP in inland waters? How do these aquatic pieces fit together? Table 4 presents the summary values to start the discussion. Atmospherically-derived C (sensu Meybeck 1993) meets several fates in the fluvial-lacustrine network. Terrestrially-derived organic C is either respired, exported, buried, or transported. Terrestrially-derived inorganic C is either degassed, or transported as either CO_2 or HCO_3^-. All of these fates come at the expense of terrestrial NEP. This can be looked at in 2 ways, depending on how terrestrial NEP was assessed. If terrestrial NEP was arrived at by looking at the accumulation rate of soil and biomass on dry land, then true terrestrial NEP must be larger than that estimate by the amount of the summed aquatic (lateral) losses. If terrestrial NEP was arrived at by inverse modeling of the atmospheric CO_2 concentrations, then true terrestrial (e.g. dry land) NEP is smaller than that estimated by the sum of the lateral losses; in this case, continental NEP is unaffected.

It is obvious that these values are known very imprecisely and on-going work has lowered or increased specific estimates in some cases. Nevertheless, the summed magnitude is on the order of 2 Pg C yr^{-1} with a little less than half of this (0.9 Pg C yr^{-1}) being transported to the ocean in rivers. The remainder is either buried in lake or reservoir sediments or degassed as CO_2 in streams, lakes or rivers. Terrestrial NEP is estimated to be between about 1 and 4 Pg C yr^{-1} (Randerson et al. 2002). What can be concluded is that a large fraction, perhaps about half or more, of terrestrial NEP meets a fate in inland waters. It can also be concluded that the magnitude of terrestrial NEP that leaves 'dry' land is about twice as large as the fraction of this that reaches the ocean.

Table 4. Aquatic fluxes in the continental carbon balance. In some cases the revisions or departures were published since Cole et al. (2007); in other cases these values were not used by Cole et al. (2007)

Ecosystem and flux type	Cole et al. (2007)	Significant revisions or departures from Cole et al. (2007)	Notes	Source
Burial				
Lake sediments	0.05	0.14	More smaller lakes	Downing et al. (2006)
Reservoir sediments	0.18	>0.6	Rice paddies after Stallard (1998)	–
Transport				
Organic C (rivers)	0.45	–	–	–
Inorganic C (atmospheric)	0.26	0.17	Uses weathering models	Hartmann (2009)
Emissions				
Lake CO_2	0.11	0.3 to 0.53	Saline lakes added; small lakes revaluated	Tranvik et al. (2009), Marotta et al. (2009), Duarte et al. (2008)
River CO_2	0.23	Possibly >1	Includes Amazon and other tropical rivers	Richey et al. (2002), Tranvik et al. (2009)
Reservoir CO_2	0.28	0.28 to 0.17	Changed reservoir area	Downing et al. (2006)
Small streams CO_2	?	0.12	Probably too low	Battin et al. (2008)
Estuary CO_2	0.12	–	Needs revision	–
TOTAL	1.68	~2.5 to 3	As large as continental NEP	–

Uses and misconceptions of the global aquatic carbon balance

Syntheses like the one above and its antecedents have emboldened limnologists to tackle aquatic C cycling questions in a global context. And this, as Martha Stewart[1] might say, is a good thing. If the magnitude in the aggregate of gas flux or sediment burial is as large as some terrestrial or oceanic pro-

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[1] Martha Stewart was the TV and magazine doyenne of American good living in the 1990's. She has expanded into a major brand name in recent years.

cesses, research into its regulation, other consequences, or even improving the global estimate, seem worthwhile and warranted. On the other hand, there are some patently incorrect ways, or at least inappropriate comparisons, that limnologists are often tempted to draw. It is worth examining two of these here.

The 'missing terrestrial carbon sink' is underwater

This is likely not true. The 'missing terrestrial C sink' is the difference between anthropogenic CO_2 emissions and the sum of oceanic CO_2 uptake and the accumulation of CO_2 in the atmosphere (see Hobbie et al. 1984). For most of the Holocene, atmospheric CO_2 was roughly constant. During the industrialized period and maybe starting before this, which some call the Anthropocene, the combustion of peat and fossil fuels and the cutting of forests caused a rise in atmospheric CO_2. This rise (about 3.1 Pg C yr^{-1}) is quite a bit smaller than the anthropogenic emissions of CO_2 (about 6 Pg C yr^{-1}) because some CO_2 diffuses into the ocean (about 1.5 Pg C yr^{-1}) and some is sequestered on land in places where there is net growth or net accumulation of organic soils. The magnitudes of both the accumulation in the atmosphere and the uptake by the oceans are known with reasonably good precision. It is not presently possible to directly measure the net sequestration of CO_2 on land at a global scale. Its presumed magnitude is the difference between the other terms (i.e. $6 - 3.1 - 1.5 = 1.4$). A great deal of terrestrial research is directed towards finding this ~1.4 Pg C yr^{-1} on land (Reay et al. 2008). Because the aquatic fate of terrestrial NEP is as large or larger than this missing sink, it is tempting to claim that this is the missing sink or a significant part of it. There are several things wrong with this claim. First, the missing sink has to have increased from near 0 in the pre-industrial period to its present magnitude over the past 150 years or so. At present, the evidence that most of the aquatic C fluxes have increased is scant. Clearly sedimentation in rice paddies and man-made reservoirs represent new stores of C created during the Anthropocene. If sedimentation in impoundments is as large as estimates by Stallard (1998) or Tranvik et al. (2009), it is conceivable that indeed, part or even most of the missing sink is in the organic sediments of reservoirs and especially in rice paddies. Another very new idea is that lateral fluxes from land into rivers have also been increased by human activity. Regnier et al. (2013) suggest that, in addition to human-caused sedimentation, rivers have also significantly increased their flux of CO_2 to the atmosphere as a result of human activities. Further, Regnier et al. (2013) suggest there has been an increase, albeit a modest 0.1 Pg C yr^{-1}, in the transport of C from land to sea by rivers. Nevertheless, while it is possible that the key to the missing sink is in aquatic habitats, one has to be careful about how this claim is made and over what time frame.

Lakes are almost as important to the global carbon balance as the ocean

This is another misconception. The organic C added to the sediment of lakes each year (0.07 to 0.14 Pg C yr^{-1}) is co-equal with long-term sediment accumulation of organic C in the ocean (0.12 Pg C yr^{-1}; Siegenthaler and Sarmiento 1993). This is a striking result because the area of lakes is about 1% of that of the oceans. However, in the modern, anthropogenically perturbed, C balance, the oceans take up 1 to 2 Pg C yr^{-1} as CO_2 which dissolves from the elevated $p\mathrm{CO}_2$ of the atmosphere into the ocean. Further, the sediments in most lakes (excepting deep tectonic systems) exist for only tens of thousands of years before some process, such as glaciation, ploughs these sediments up. The ocean sediments endure for tens of millions of years until they are subducted due to the spreading of the continental plates. Thus, the comparison would be more appropriate if it were restricted to only organic C and to the Holocene, but pre-industrial, period.

Summary of the role of inland waters in the global carbon balance

A large fraction of continental NEP meets a fate in lakes, streams, rivers and reservoirs. While the magnitudes are not well constrained, many are large enough to affect the estimates of NEP at a global scale. Furthermore, if the time scale of several millennia is considered, these aquatic fates of NEP can be the dominant ones. For example, over millennia, forest biomass can be considered as being at roughly a steady state, and the soil is the major terrestrial reservoir for C sequestration. Looked at this way, the export of organic C in water that drains the land is large in comparison. Total organic C in soil is estimated at about 2150 Pg (Sundquist and Visser 2005) with about 560 Pg in terrestrial vegetation (Houghton 2005). If all this organic C accumulated during the last interglacial period, the rate is at around 0.23 Pg C yr^{-1}. Clearly, at some non-glaciated locations, it took longer or much longer to accumulate (net) this material, so this estimate is at the upper end of the rate. Thus, the long-term accumulation on land is comparable to the accumulation of lake sediments and somewhat lower than the export of organic C to the ocean. So, lake sediments clearly matter to the global C balance when one takes a time frame of several millennia.

3 PATTERNS AND MAGNITUDES OF TERRESTRIAL SUBSIDIES: ARE FISH MADE OF TREES?

An introduction to allochthony

The food that supports a given food web can be produced by photosynthesis from within same system as the food web (autochthonous organic matter) or can be imported from outside of the boundaries of that system (allochthonous organic matter). The terms ‘allochthonous’ and its antonym ‘autochthonous’ may represent difficult concepts, but they can have considerable value. In June 2004, during a spelling contest in South Bend, Indiana, one of the young contenders, Akshay Buddiga, fainted when given the word ‘autochthonous’, according to an article in the Associated Press. He recovered. David Tidmarsh, without fainting, spelled it correctly and won USD $17 000. ‘Allochthony’ comes from the Greek ‘kthonos’, which means ‘earth’ or ‘ground’, and ‘allo’, which means ‘somewhere else’. For the purposes of this book, allochthonous organic matter was created by photosynthesis on land whereas autochthonous organic matter was created by local photosynthesis (by phytoplankton, periphyton or macrophytes) within the water body of interest. Allochthony has several other uses in diverse fields including sociology (e.g. Koonings 2003) and geology (meaning rock or minerals that formed elsewhere than where they are deposited).

In aquatic ecology we mean something quite specific to organic matter sources for aquatic ecosystems. *Allochthony* is the proportion of organic carbon flow into an aquatic compartment from terrestrial photosynthetic sources (France 1997, Carpenter et al. 2005, Karlsson et al. 2007). The alternative is *autochthony* which is the proportion of organic carbon flow into an aquatic compartment from aquatic photosynthetic sources. Examples of a compartment could be: the standing stock of DOC; the biomass of a consumer; or, the respiration of all consumers.

To provide a concrete example of allochthony, consider the Amazon River, which is a rather special place. During the annual flood the river rises more than 10 m in many areas and inundates the surrounding forest. At this time the tops of canopy trees just clear the river’s surface and the shorter terrestrial vegetation is completely under water. The trees and other plants of these flooded forests are well adapted to this fluctuating water level and, for the most part, survive these floods. With tens of thousands of square kilometers of seasonally flooded forest, it is not surprising to learn that there are species of fish that exploit this underwater, but otherwise terrestrial, habitat.

A famous example is the tambaqui (*Colossoma macropomum*; Fig. 4), a large (up to 30 kg) cousin of the piranha, which has crushing teeth that it uses to break open the terrestrial nuts and fruits on which it lives. This fish has other names, among them Pacu and Cachama, but sometimes these common names refer to other, also herbivorous Amazonian fish in other genera (*Metynnis*, *Piaracutus* and a few others). Few species of fish are primarily herbivores. The tambaqui is not only an herbivore, but one specialized to eat terrestrial fruits and nuts. The tambaqui, and some other Amazonian species, get their food directly from the forest, rather than the river, and the tambaqui is capable of digesting and assimilating terrestrial plant material (Oliveira et al. 2008, Anderson et al. 2009). Stable isotope analyses of C and N suggest that the tambaqui gets somewhere between 55 and 95% of its biomass C during the high-water season from fruits and seeds from forest trees (Oliveira et al. 2006a,b). The base of the food web for the tambaqui during flood stage is terrestrial, rather than aquatic primary production. The carbon in the biomass of these fish was fixed into organic matter by trees on land. In this sense the tambaqui is made of trees; the tambaqui is made of *allochthonous* organic matter.

Aquatic food webs supported by terrestrial organic matter are not only found in the Amazon. The phenomenon is widespread, if somewhat counterintuitive, and one that goes against the grain of traditional limnology. In an important essay, Forbes (1887) described lakes as microcosms and pictured them as more or less self-contained, somewhat like a sealed, schoolroom aquarium. That a sealed aquarium can be self-sustaining does not imply that lakes function this way. In fact, this hermetic view of lakes has hampered limnologists' understanding of how lakes actually function. Aquatic ecosys-

Fig. 4. A tambaqui, grilled and ready to eat. Photo courtesy of S. Tomasz

tems are not self contained, but are intricately connected to their terrestrial watersheds, receiving both the nutrients that sustain plant life and some of the organic matter that sustains, or at least subsidizes, aquatic consumers. The strong connection to the terrestrial watershed is more obvious in streams and rivers. For example, in the Hudson River — a fjord that does not flood its forest — the main source of essential plant nutrients is not recycling from consumers, but input from the watershed. Further, most (>90%) of the organic matter in the Hudson comes from the terrestrial watershed rather than from photosynthesis by plants and algae that live in the river (Howarth et al. 1996, Cole and Caraco 2006). This terrestrially-derived organic matter is not directly available to the fish in the Hudson (alas, there are no tambaqui there). It is first utilized by bacteria and some invertebrates, forming a food web that is based, in part, on terrestrially derived detritus. The Hudson River fish consume the members of this food web along with members of a food web that is based on the local primary production of macrophytes, benthic algae and phytoplankton.

Allochthony in lakes

In the rest of this Chapter I review what has been reported in the literature about the magnitudes and patterns allochthony in lakes, with some reference to lake-like, deep rivers.

While ‘autochthony’ might be lucrative to spellers (see ‘An introduction to allochthony’ above), the ideas of autochthony and allochthony present a useful framework for thinking about aquatic ecosystems and their connection to land. Cross-ecosystem subsidies to food webs can alter metabolic balances in the receiving (subsidized) system and free the food web, or particular consumers, from the energetic constraints of local primary production (Polis et al. 1997). Ever since Elton (1927) started compiling the first diagrams on food webs, ecologists have generally viewed these food webs as being fueled exclusively by local (autochthonous) primary production. This view, while no longer universal, is still pervasive today, and I argue, incorrect, or at least not always applicable.

How allochthony is studied

As shown in Chapter 2, the loading of allochthonous material to some lakes can be equal to, or larger than, the loading from autochthonous primary production. In many lakes respiration is greater than gross primary production

(R > GPP), which implies that at least some of the terrestrial organic matter is catabolized within the lake. If all of the GPP is respired (that is, no autochthonous organic matter is either buried or exported), then the total magnitude of the respiration of terrestrially derived organic matter (R_T) would be equal to NEP when NEP is negative (e.g. NEP = GPP − R; Chapter 2). If, instead, buried and exported organic matter is a mixture of autochthonous and allochthonous sources (a much more likely scenario), then R_T can be much larger than NEP, independently of the sign of NEP.

Several approaches are used to assess allochthony in lakes. These include the use of ambient stable or radioisotopes, biomarkers, diet studies (especially in fishes), and experiments that manipulate isotopes at the ecosystem or mesocosm scale. These approaches have their strengths and weaknesses. Ambient isotope analysis would seem, at first, to be the most powerful approach with the fewest assumptions, but often the ultimate sources or 'end-members' are not sufficiently separated to draw clean conclusions. Further, the higher the target organism's trophic position, the more difficult it becomes to establish what is at the base of its food web (Rasmussen 2010). Biomarkers, usually specific fatty acids, are difficult to measure and to interpret (Alfaro et al. 2006). For example, the presence of fatty acids such as C16:1n-7 or C20:5n-3 in a fish would suggest that diatoms were ultimately important in the food web that built this fish. However, this biomarker does not indicate quantitatively how important diatoms were and what else was at the base of the fish's food-web. Most researchers who use biomarkers consider the approach to be qualitative or semi-quantitative. Diet studies are good to the extent that what is in the diet and where that came from can be identified. Manipulative experiments with isotopes can increase the contrast between terrestrial and aquatic end-members, but create temporal and spatial complexities that can be difficult to resolve. Finally, all of the approaches have uncertainties that may not be easy to address.

I review the state of our knowledge about the allochthony of key consumers or compartments in lakes, starting in this section with organisms (from the top consumers downwards to bacteria) and ending in the next section with the standing stocks of particulate and dissolved organic matter (DOM and POM).

Fishes

There are many studies of the diets of lake fishes, based on gut contents. In general, littoral fishes contain numerous terrestrial organisms in their guts. For example, in a long-term (21 yr) study of largemouth bass (*Micropterus* *salmonoides*) in a small (1.7 ha) lake in the north temperate zone of the USA (Paul Lake), Hodgson and Hansen (2005) found that terrestrial insects comprised about 10% and terrestrial vertebrates about 12% of the biomass of the bass diets. While the dominant diet items in these fish were benthic aquatic invertebrates (41.3%) and fish (35%), more than a fifth of what an average bass consumes in this small lake is of terrestrial origin. While these values are for the entire lake, note that Paul Lake is small with a great deal of littoral habitat. We might expect a much lower consumption of terrestrial organisms in larger systems with less littoral area and a relatively smaller interface with the surrounding watershed; we might not be correct in this thinking. Working in a somewhat larger (12 ha) lake in Germany, Großer Vätersee, Mehner et al. (2005) calculated that about 84% of the diet of bleak (*Alburnus alburnus*) consisted of terrestrial insects (see Table 5).

Research results on how important terrestrial prey items are to fish vary widely over lakes and fish taxa. Francis and Schindler (2009) used gut analysis to show a very interesting pattern that explained part of this variability. In what was both a detailed study of several lakes in the Pacific Northwest (USA) as well as a literature review for many more lakes in North America, Francis and Schindler (2009) found that in undeveloped lakes (lakes with no shoreline urbanization) the diets of trout (*Oncorynchus* spp.) averaged 50% terrestrial insects (ranging up to 100%), while in developed lakes it was only 2% (Fig. 5). The pattern suggests that terrestrial insects are an important, but variable, component of fish diets in undeveloped lakes; a small amount of urbanization can eliminate the utilization of terrestrial prey. In this study, when only 10% of the shoreline was developed, terrestrial prey was nearly absent from the diets of most fishes (Fig. 5). The study also revealed differences among fish taxa, with trout receiving the largest contribution from terrestrial insects and yellow perch, the least (Francis and Schindler 2009).

Direct diet studies like the ones mentioned above potentially give a minimal estimate for the importance of terrestrial subsidies to fish. That is, in addition to consuming terrestrial organisms directly, fish consume zooplankton, benthic invertebrates, and other fish, all of which may have been subsidized to some extent by terrestrial organic matter. Thus, fish may get some terrestrial carbon indirectly. To establish the level of allochthony in the fish of interest, the total amount of terrestrial photosynthesis that supported the fish needs to be calculated. Diet studies alone cannot accomplish this, but diet studies combined with bioenergetic models and either isotope analyses or biomarkers can determine the allochthony of the diet items. Several examples are provided below.

Whitefish in Lake Annecy, France. Lake Annecy is a relatively large (28 km^2), deep (z_{max} = 65 m) oligotrophic lake in southeast France, with an

Table 5. Estimates of allochthony in fish. The column labeled 'Allochthony?' gives the study's conclusion about the qualitative or quantitative importance of terrestrial organic matter to these fishes

Source	Target fish	Allochthony?	System	Approach
Dudgeon (1983)	5 fish species (4 Cyprinidae, 1 Chiclidae)	33 to 100% of diet was terrestrial plants	Reservoir, Hong Kong	Diet study
Forsberg et al. (1993)	35 diverse species	C4 plants = 2.5 to 17% of fish biomass. Phytoplankton probably dominate	Amazon River	Ambient ^{13}C
Jones et al. (1998)	*Salmo salar, Salvelinus alpinus, Gasterosteus aculeatus*	About 50% terrestrial	Loch Ness	Ambient ^{13}C, ^{15}N
James et al. (2000)	*Galaxias brevipinnis*, *Oncorhynchus* sp., *Salmo trutta*	Epiphytes dominate food source. Some terrestrial input for *Galaxias* and juvenile *Salmo*	Lake Coleridge, NZ	Diet, model, Ambient ^{13}C
Fisher et al (2001)	Many species	Allochthonous sources important during flood; less so in summer	Missouri River backwater lakes	Diet, model, Ambient ^{13}C, ^{15}N
Lewis et al. (2001)	18 fish species	Dominance by algal sources. Low food-web supply from flood plain vegetation	Orinoco flood plain	Ambient ^{13}C, ^{15}N
Grey et al. (2002)	*Salvelinas alpinus*	<20% allochthonous	Loch Ness	Diet, Ambient ^{13}C, ^{15}N
Wantzen et al. (2002)	33 fish species	13 to 30% (for some spp.) from C4 plants in flood plain	Coquiero Lake, Brazil	Ambient ^{13}C, ^{15}N
Bunn et al. (2003)	10 species	Mostly algal. No strong evidence for terrestrial support	Waterholes in Cooper Creek, Australia	Ambient ^{13}C, ^{15}N
Darnaude (2005)	Flat fish, 5 species	High for *Solea solea*; low for *Arnoglossus laterna*	Rhone River plume	Diet, Ambient ^{13}C, ^{15}N
Mehner et al. (2005)	*Alburnus alburnus*	85% of diet = terrestrial insects	Small lake in Germany	Diet study
Hoffman et al. (2007)	Juvenile *Alosa sapidissima*	>65% in wet years, 10 to 50% in dry years	Mattaponi River	Ambient ^{13}C, ^{15}N

Table 5. (continued)

Source	Target fish	Allochthony?	System	Approach
Nonogaki et al. (2007)	Loricariid catfish	These fish eat wood. ~100% allochthonous, varies seasonally	Pantanal wetlands, Brazil	^{13}C in otolith
Francis and Schindler (2009)	Trout, several species	Terrestrial prey alone averages 50% in undeveloped lakes, highly variable	56 North American Lakes; littoral habitat	Diet study with large data base
Weidel et al. (2008)	*Lepomis macrochirus, Perca flavescens, Micropterus salmoides, Gasterosteus aculeutas, Pimephales promelas, Notemigonus chrysoleucas*	Allochthony ranges from 38% to 65%. Varies with taxa and eutrophication	Four lakes in northern Wisconsin	Whole-lake ^{13}C additions, diet studies and models
Perga et al. (2009)	*Coregonus lavaretus*	High allochthony	Lake Annecy, France	Non-essential fatty acid biomarker
Solomon et al. (2011)	Cyprinidae, *Lepomis macrochirus*, *Micropterus salmoides*	10 to 60% depending on taxa and lake	Four lakes in northern Wisconsin	Ambient ^{2}H, ^{13}C and ^{15}N, Bayesian model
Karlsson et al. (2012)	*Perca fluviatilis*	57%	Upper Bear Lake, Sweden	Ambient ^{2}H and ^{13}C

important local whitefish (*Coregonus larvatus*) fishery. In their early life stages whitefish are typically planktivorous and feed largely on zooplankton. Perga et al. (2009) hypothesized that the base of the food web supporting whitefish production were diatoms from the spring bloom that were consumed by *Daphnia* sp., which were subsequently consumed by *C. larvatus*. Perga et al. (2009) used non-essential fatty acids as biomarkers to test this hypothesis. They chose this approach because essential fatty acids are preferentially retained in both zooplankton and fish and, therefore, cannot be used as reliable trophic tracers. Their initial hypothesis was not supported. While diatom biomarkers were seen in abundance in *Daphnia*, in *C. larvatus*, they found little of the diatom marker but a great deal of a biomarker derived from terrestrial detritus (C24:0). This marker was low in *Daphnia* but high in copepods, both of which are found in the guts of *C. larvatus*.

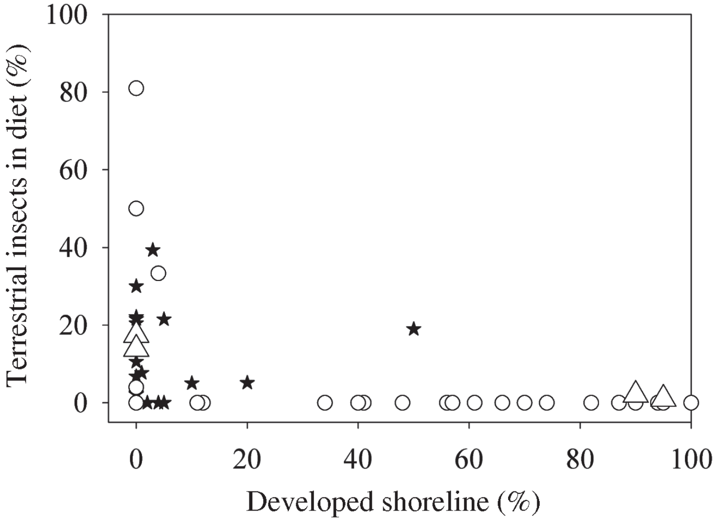

Fig. 5. Fish diets vary with development on the shoreline. Francis and Schindler (2009) combined multiple, detailed measurements from 4 lakes in the Pacific Northwest (open triangles) with a literature survey of data from the Pacific Northwest (open circles) and a broader literature survey of data from North America (stars). The plot shows the percentage of terrestrial insects in the diets of trout as a function of the percentage of the lake's shoreline that has urban development. Redrawn from the data of Francis and Schindler (2009), the data were kindly provided by Dr. T. Francis

Perga et al. (2009) concluded that an important pathway leading to the production of whitefish is terrestrial detritus, consumed directly or indirectly by copepods, which are then consumed by the fish. Unfortunately Perga et al. (2009) were not able to put a quantitative estimate of allochthony in this study, but were able to conclude that the terrestrial subsidy is large.

Small lakes in the upper mid-West, USA. To estimate the total contribution of allochthony to fishes, Weidel et al. (2008) made use of a series of whole-lake ^{13}C additions to several lakes in the upper mid-West, USA. These are the lakes of the University of Notre Dame Environmental Research Center (UNDERC). I will discuss the details of these ^{13}C addition experiments, along with their strengths and weaknesses, in Chapter 4. For one of the lakes (Crampton Lake), a 26 ha, clear-water lake with a diverse fish assemblage, Weidel et al. (2008) conducted a particularly intensive study. Since both the autochthonous primary production of the upper mixed layer, and its invertebrate consumers, were labeled with ^{13}C, Weidel et al. (2008) combined diet studies, measurements of ^{13}C in the fishes, and bioenergetic modeling to determine the fraction of current (e.g. the season in which the measurements were made) autochthonous primary production that contributed to the fishes.

The most interesting result is that for most of the fishes in this lake, the majority of the C supporting their growth did not come from contemporaneous primary production. Young-of-year yellow perch (*Perca flavescens*) and bluegills (*Lepomis macrochirus*) had the highest proportion of autochthonous C (~56%), largely because they consumed zooplankton that was closely linked to phytoplankton production. For older and larger fish (these species plus largemouth bass, *Micropterus salmoides*) contemporaneous autochthonous production accounted for 40 to 50% of their growth. In this lake, the direct consumption of terrestrial prey items was a minor component of the fish diets. Weidel et al. (2008) concluded that terrestrial inputs and detritus of both terrestrial and possibly autochthonous origin supported most of the fish growth. Weidel et al. (2008) were very careful in the way they worded their conclusions. The ^{13}C experiments labeled only the primary production that occurred after the label was added. Detritus of autochthonous origin produced in prior years or even months or weeks ('old autochthony') before the ^{13}C addition was therefore not labeled. Later work, using ambient isotopes of ^{13}C, ^{15}N and ^{2}H, convinced limnologists that input from old autochthony (Solomon et al. 2008) is, at most, only minor in this lake and others. So I have named the *y*-axis in this plot (Weidel et al. 2008) as the fraction of allochthonous origin (Fig. 6). Similar studies, with lower intensity and detail, were performed for fishes in several other lakes at UNDERC that also had ^{13}C additions (Carpenter et al. 2005, Cole et al. 2006). Despite major differences in the fish communities among these lakes, Weidel et al. (2008) found a strong correlation between fish allochthony (or, non-current autochthony) and the ratio of chromophoric DOM (CDOM) to chlorophyll-*a* (chl-*a*, Fig. 6). CDOM can be used as a crude index of terrestrial inputs, since most CDOM is of terrestrial origin. Chl-*a* can be used as an index of autochthonous primary production. For one of these lakes (Peter Lake), we have data both for when the lake was enriched with N and P and had high chl-*a*, and for when the lake was not. The same species of fishes (pumpkin seeds *Lepomis gibbosus*, golden shiners *Notemigonus crysoleucas* and sticklebacks *Gasterosteus aculeutas*) in Peter Lake are far less allochthonous (~38%) during eutrophication than without nutrient additions (~65%; Fig. 6). The large shift in allochthony in response to nutrient enrichment suggests to me that the method of analysis was sound.

Both the degree of allochthony and the way a fish may acquire terrestrial C can change over life-history stages. Using the ^{13}C additions and bioenergetic modeling, Cole et al. (2006) showed these developmental changes for large-mouth bass in Paul Lake. Small, young-of-year fish were the most autochthonous, acquired much of their C from zooplankton, and essentially none from terrestrial insects. One year plus (1+) fish fed largely on the ben-

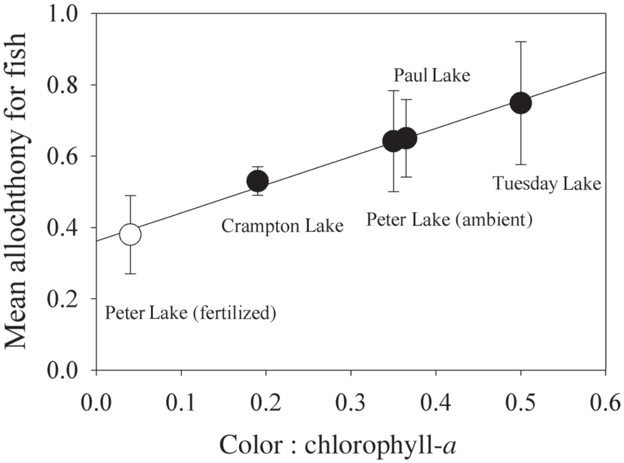

Fig. 6. Terrestrial support of fish, estimated from several whole-lake ^{13}C additions. Peter Lake appears twice because in one year (○) it was fertilized with N and P to eutrophy it. All of the other lakes are in their ambient state (filled circles). The *x*-axis is the mean ratio of color (chromophoric dissolved organic matter [CDOM]; from absorbance at 440 nm) to chlorophyll-*a* for each lake and year. Redrawn from the data of Weidel et al. (2008)

thic prey and to a lesser degree on terrestrial prey, and were intermediate in their allochthony. Adult fish were the most allochthonous, largely due to being quite piscivorous as well as feeding heavily on terrestrial prey (Fig. 7).

What regulates terrestrial subsidies of f ishes? The existing studies (Table 5) reveal a great deal of variability in the allochthonous support of fishes. In some cases (e.g. loricarid catfish in flood plain lakes in the Pantanal) the fish are 100% allochthonous (these fish eat wood); in other cases (e.g. Arctic char), less than 20%. It is unfortunate that most of the existing estimates are qualitative rather than quantitative. Two of the most likely factors that are expected to influence terrestrial food support provided to fishes might also vary widely with the system. These are (1) the relative amount of allochthonous material loaded into the system compared to primary production, and (2) lake size. These 2 factors are generally, but not always, correlated. For example, small, forested lakes often have low primary production and high terrestrial loading; large lakes with long residence times, or highly eutrophic lakes, should be at the opposite end of the spectrum. Also, in small lakes with a great deal of terrestrial interface, fish might have a greater opportunity to consume terrestrial prey than in larger, more circular-shaped lakes.

Another important factor is the type of fish present. Young gizzard shad (*Dorosoma cepedianum*) are zooplanktivorous but as adults eat detritus in the sediments. Several laboratory studies have shown that gizzard shad can

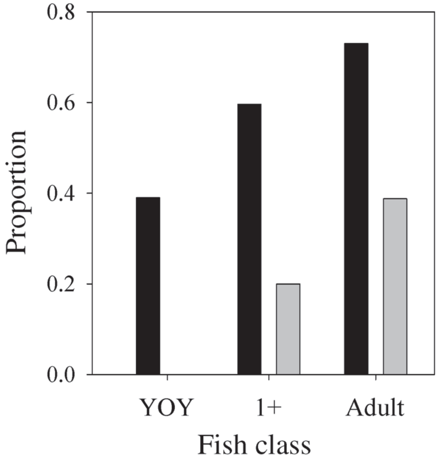

Fig. 7. Terrestrial support of fish in Paul Lake (redrawn from the data in Cole et al. 2006). Shown is the proportion of largemouth bass supported by terrestrial organic matter (*y*-axis) from all pathways (black bars) and the proportion coming directly from consuming terrestrial prey (grey bars). The fish classes are young-of-year (YOY), juvenile fish (1+) and adults

assimilate organic matter from both autochthonous and allochthonous sources (Smoot and Findlay 2000, Pilati and Vanni 2007, Zeug and Winemiller 2008, Pilati et al. 2009). Using the stable isotope deuterium (^{2}H), Babler et al. (2011) found that the allochthonous support of gizzard shad averaged about 34% among a series of 11 lakes or reservoirs in the mid-West. The large variation in the terrestrial food support provided to these fish (0 to 68% among these lakes and the different model scenarios used) was mostly explained by lake size. The gizzard shad in smaller lakes were significantly more allochthonously supported than those in larger lakes and the correlation was relatively strong (r^2 from 0.42 to 0.76 depending on the scenario used). The biomass of gizzard shad per unit area (used as an index of their secondary production) was positively and significantly correlated with autochthonous primary production and negatively correlated with the terrestrial support of the fish. Babler et al. (2011) suggest, from these data, that autochthonous detritus and the benthic organisms it supports is better food for gizzard shad than allochthonous detritus and the food web it supports. But, in systems in which primary production is low and allochthonous loading is high (generally the smaller lakes in this data set), a large fraction of gizzard shad biomass is supported, directly or indirectly, by terrestrial inputs.

The work of Francis and Schindler (2009), Weidel et al. (2008) (Figs. 5 & 6) and Babler et al. (2011) shows how some of the variance in the terrestrial food support of fishes plays out across different systems. In a several-year study of the Mattaponi River, Hoffman et al. (2007) give some insight as to how this variability plays out in a single system. Using ^{13}C and ^{15}N, Hoffman et al. (2007) found that American shad (*Alosa sapidissima*) was sometimes heavily terrestrially supported (> 80%) and sometimes less so (near 20%). The Mattaponi receives terrestrial material mostly when river flow is high.

Hoffman et al. (2007) found a good relationship between river discharge (integrated over the 10 d prior to sampling) and allochthony in American shad (Fig. 8). I do not think that Hoffman et al. (2007) are suggesting that shad turnover their tissues on a 10 d time frame. Rather, the high and low flow periods tend to be seasonal and the 10 d integration simply smoothes out daily variability in discharge. At high discharge (and by inference high loading of terrestrial organic matter), the shad are highly allochthonous; at low discharge (and by inference, longer residence times), autochthonous primary production is relatively more important for the shad. This seems like a reasonable pattern.

Benthic invertebrates

There are very few studies that address the allochthonous support of benthic invertebrates in lakes or even deep rivers. The literature for shallow rivers and streams is very well developed on this topic and multiple approaches have been used. A good example is the study of Rasmussen (2010), who compiled ^{13}C data from the Sainte Marguerite River, Quebec (Canada) and used it in a novel gradient approach. In essence, Rasmussen (2010) used a regression of δ^{13}C-DIC (as reflected in benthic algae) and components of the food web over the length of the river. δ^{13}C-DIC changes progressively with

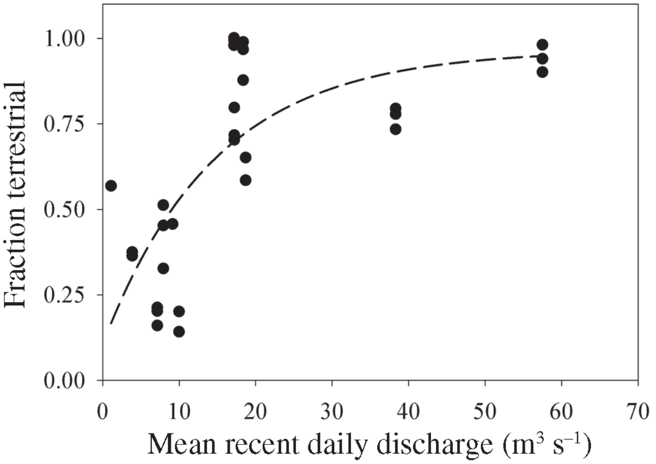

Fig. 8. Terrestrial support of American shad in the Mattaponi River in Virginia. Using ambient ^{13}C and ^{15}N and a mixing model, Hoffman et al. (2007) calculated terrestrial support of shad collected at different times in the river. The resulting terrestrial support is plotted against an integrated measure of prior discharge (the mean discharge for the 10 d prior to sampling). Redrawn from the data in Hoffman et al. (2007)

distance downstream and this change is propagated into benthic algae and subsequently the invertebrates that consume them. δ^{13}C-DIC values in something eating entirely material of terrestrial origin would not change over the length of the river. By examining different feeding guilds of invertebrates, Rasmussen (2010) showed that herbivores known to consume mostly algae (e.g. specialist organisms like some families of Ephemeroptera [Baetidae, Heptageniidae and Ephemerellidae] and Trichoptera [Brachycentridae, Glossosomatidae, Helicopsychidae], and small amphipods), are the group that is least supported by terrestrial organic matter (Fig. 9). Shredders (organisms including some families of Trichoptera [Limnephilidae, Lepidostomatidae], and the dipteran, *Tipula*) and several families of Plecoptera (Pteronarcyidae, Nemouridae, Leuctridae) are the most allochthonous (Fig. 9). In this system the shredders are about 80% supported by terrestrial organic matter while the herbivores are only near 15%. Filter-feeders and collector-gatherers are intermediate (around 40%). The approach of Rasmussen (2010) is a clever and novel one but it illustrates a well-known feature in streams. The type of invertebrates present will affect allochthony. In addition, the amount of benthic algal production versus terrestrial input can directly affect allochthony and select for different invertebrate groups. It is unfortunate that the gradient approach will not work in a single lake; it may be possible to apply it to a population of lakes but so far it has only been used for pelagic components (see Mohamed and Taylor 2009, Wilkinson et al. 2013a,b).

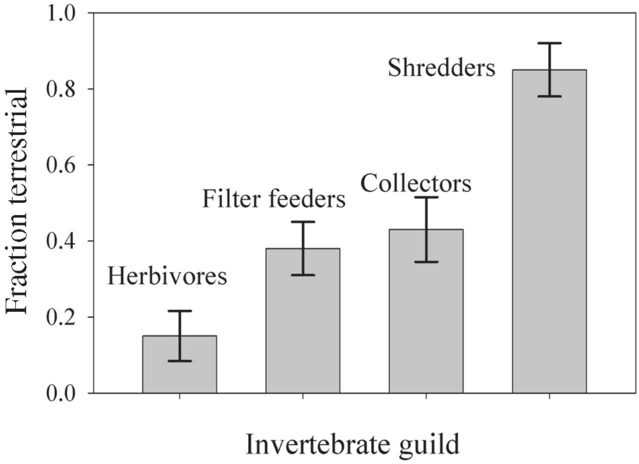

Fig. 9. The fraction of biomass of benthic invertebrates supported by terrestrial organic matter in the Ste. Marguerite River, Quebec. The fraction terrestrial was calculated using ^{13}C and a longitudinal gradient approach which is explained in detail in Rasmussen (2010). Drawn from data presented in Rasmussen (2010)

Lake Findley, Washington, is a small (11.4 ha), deep (z_{max} = 25 m) oligotrophic lake that receives a large amount of terrestrial material from the surrounding coniferous forest. Using a simple mixing model and ambient ^{13}C levels, Rau (1980) calculated that the source of C in chironomids is about 47 to 51% terrestrial. This early study was not a particularly sophisticated one in that there was no direct measurement of the isotopic signature of phytoplankton. Rather, the δ^{13}C of phytoplankton was estimated from the $\delta\ ^{13}$C-DIC and a generic estimate of photosynthetic fractionation, which could be criticized as too depleted (−34‰). On the other hand, using the same data and mixing model, Rau (1980) found that chaoborids in the same lake were entirely dependent on autochthonous primary production (e.g. phytoplankton). If the estimate isotopic signature of the phytoplankton were too depleted, it is unlikely that Rau (1980) would have gotten this result for chaoborids. France (1997, 1998), working in 4 lakes in Ontario, found that most benthic invertebrates had ^{13}C levels that were intermediate between those of terrestrial vegetation and the epiphyton. While France did not give actual estimates for allochthony, it can be calculated from his data. Based on the means and on the most enriched ^{13}C value (least allochthonous) shown in France (1997), I computed the fraction allochthonous using a simple 2 member mixing model (where X is the fraction terrestrial and is the only unknown; Table 6).

$$^{13}\text{C\_Invertebrate} = {}^{13}\text{C\_Terrestrial} \times X + {}^{13}\text{C\_Epiphytes}\ (1 - X) \qquad (12)$$

Rearranging,

$$X = ({}^{13}\text{C\_Invertebrate} + {}^{13}\text{C\_Epiphytes}) \,/\, ({}^{13}\text{C\_Terrestrial} + {}^{13}\text{C\_Epiphytes}) \qquad (13)$$

Table 6. Using the data of France (1998) for boreal lakes in Ontario, I calculated the fraction terrestrial (allochthony) using the mean of the distribution of δ^{13}C in each invertebrate group (mean ^{13}C) and the most enriched (lowest possible allochthony). The end-members in this calculation are terrestrial at −28‰ (which has a narrow distribution in France's data) and epiphytic algae (mean: −15‰, with a broader distribution)

Invertebrate group	δ^{13}C (‰) Mean	δ^{13}C (‰) Most enriched	Fraction terrestrial Mean	Fraction terrestrial Least possible
Trichoptera	−25	−18	0.77	0.23
Odonata	−26	−21	0.85	0.46
Diptera	−26.5	−22	0.88	0.54
Ephemerata	−27	−24	0.92	0.69
Amphipoda	−25	−22	0.77	0.54

For these invertebrates the fraction allochthonous is lowest in Trichoptera (77% based on the mean, but 26% based on the lowest possible) and highest in Ephemeroptera (>90% based on the mean, and about 70% based on the lowest possible). There are problems with the simple calculation for both of the France studies. The data were read from a graph and I have not taken into account the variability in the benthic algal end member among systems. Further, we are assuming here that these are the only 2 ultimate food sources and that neither phytoplankton nor macrophytes are significant food. While obviously over-simplified, the study of France (1998) does suggest that terrestrial food sources may be quite significant across a range of invertebrate groups in lakes. Lake Biwa is the largest freshwater lake in Japan, with an area of 674 km^2. Karube et al. (2010) investigated the food sources for benthic mollusks in the littoral areas of the lake, near tributaries that drain very different sections of the watershed with different land uses. Karube et al. (2010) considered terrestrial sources (represented by POM in river flow), epiphytic algae, and pelagic POM. They assumed that pelagic POM represented phytoplankton in this system. Using ^{13}C and ^{15}N, Karube ran models in Isosource for snails (*Semisculcopira* spp.) and bivalves (*Unio douglasiae biwae*) collected at various locations. Both the gastropods and the bivalve showed a high degree of spatial variation in the fraction terrestrial, reflecting the very different inputs from the tributaries. The snail was dominated, in general, by pelagic POM sources, but the bivalve was dominated by pelagic sources (Fig. 10). However, both the snail and much more so the bivalve had significant terrestrial subsidies at some sites, ranging up to ca. 60% for the bivalve and 24% for the snails.

In many cases, especially in soft-water lakes, the δ^{13}C of the terrestrial vegetation can be quite close to that of phytoplankton and sometimes also to

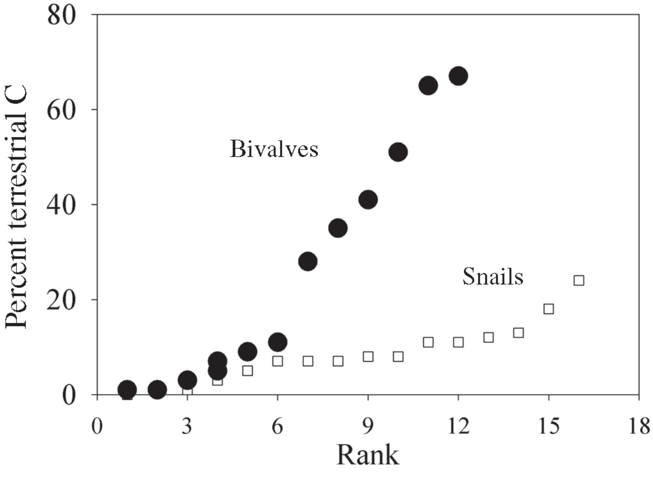

Fig. 10. The percentage of terrestrial C in bivalves (●) and snails (□) from different littoral locations in Lake Biwa, Japan. Drawn from data in Karube et al. (2010)

that of benthic algae. The similarity in the isotopic signatures of terrestrial and aquatic food sources makes it difficult to distinguish which source is supporting the food web. The design of a series of whole-lake additions of inorganic ^{13}C attempted to overcome this problem, as explained in the 'Fishes' section above. Solomon et al. (2008) used these experiments to examine sources of food for benthic invertebrates. As in the case for fishes, the best-studied lake in this regard is Crampton Lake (Solomon et al. 2008) but estimates are also available for several other lakes in the experimental series (Carpenter et al. 2005, Cole et al. 2006). Solomon et al. (2008) found that the terrestrial food support of benthic invertebrates increased with increasing DOC and decreased with increasing chl-*a*. Thus, the ratio of DOC (or CDOC) to chl-*a* was a reasonable predictor of the allochthonous support of the macrobenthos. As explained in the Fishes section, the ^{13}C experiments are a direct measure of the support from current autochthonous production and Solomon et al. (2008) were very careful to report it this way. As with the fish data, and for the same reasons, I have reported non-current autochthony here simply as 'allochthony'. In Crampton Lake, odonates were significantly more tightly connected to current autochthonous production (75%) than were chironomids at the same depth (1.5 m; 40%). Nevertheless, both groups were significantly supported by terrestrial C (25% for odonates, 60% for chironimids). Solomon et al. (2008) found that one of the factors affecting allochthony is the taxon of the invertebrate. To compare across lakes where other ^{13}C addition experiments had been performed, Solomon et al. (2008) had to use odonates because these were the only taxon common to all the lakes, for which there was sufficient data. As noted above, in Crampton Lake odonates had the least amount of terrestrial food support. Across the lakes, the terrestrial food support of odonates ranged from about 80% in Peter and Tuesday Lakes to very low levels (<5%) in Peter Lake when it was experimentally fertilized. The degree of allochthony tracked well with the ratio of color (CDOM; absorbance at 440 nm) to chlorophyll (Fig. 11A) and with the ratio of gross primary production (GPP) to the total load of organic matter from GPP and terrestrial input (I_T; Fig. 11B).

Crayfish can be an important part of the benthos in lakes and changes in crayfish populations can affect entire food webs (Lodge et al. 1994). In the Pacific Northwest (USA), *Pacifastacus leniusculus* is present in many lakes. Using ambient ^{13}C levels, Larson et al. (2011) studied terrestrial food subsidies for this species in a series of 11 lakes. In the smallest lakes (about 0.1 km^2) the food subsidy for *P. leniusculus* was nearly 100% terrestrial; in the largest lakes (nearly 500 km^2—Lake Tahoe) the food subsidy for *P. leniusculus* was nearly 100% autochthonous. As we saw with fishes (Francis et al. 2011), human development on the shoreline diminished the terres-

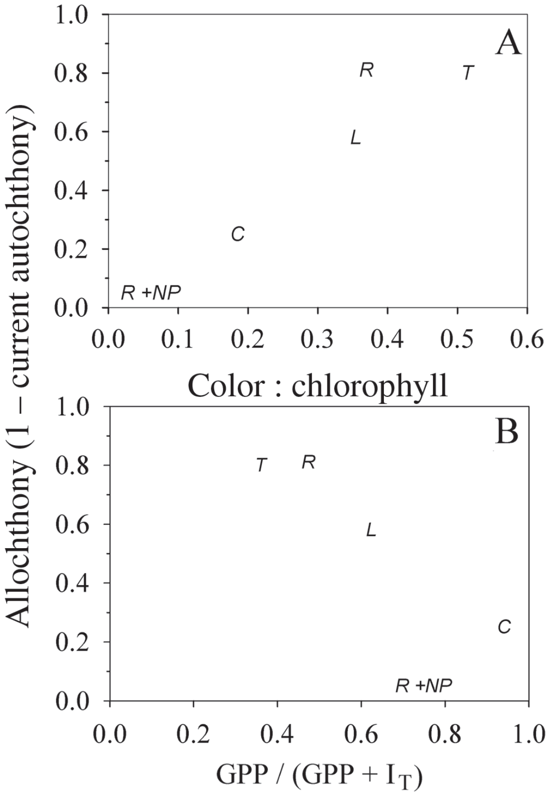

Fig. 11. Terrestrial support of benthic invertebrates in 4 lakes in northern Michigan, based on results from whole-lake ^{13}C addition experiments. The *y*-axes are the fraction of support by terrestrial inputs (allochthony). (A) Allochthony plotted against the ratio of water color (a measure of CDOM) to chlorophyll-*a*. (B) Allochthony plotted against the ratio of autochthonous gross primary production (GPP) to GPP plus the input of terrestrial organic matter (I_T). The lakes are: C — Crampton, L — Paul, R — Peter, T — Tuesday, and R+NP — Peter Lake in 2001 with the addition of N and P to increase phytoplankton. Redrawn from the data in Solomon et al. (2008)

trial food support of crayfish (Larson et al. 2011), especially for the smaller lakes. In the larger lakes, where autochthonous supplies naturally dominate for crayfish, the effect of urbanization was less severe.

The sources of food for the food web of the Hudson River, including several benthic invertebrates, was recently examined by Cole and Solomon (2012). They used stable isotopes of C, N and H along with a Bayesian isotope mixing model and considered four possible food sources: terrestrial inputs, phytoplankton, benthic algae and submersed macrophytes. The benthic invertebrates in this study included the zebra mussel (*Dreissena polymorpha*); oligochaetes (mostly in the genus *Limnodrilus*), chironomids (several genera combined including *Coelotanypus, Tanytarsus*, and *Polypedilum*), amphipods (*Gammarus fasciatus*) and polychaetes (unidentified species in two genera: *Scolecolepides* and *Manayunkia*). Since its arrival 1990's, the zebra mussel is the dominant benthic invertebrate in the system and actually comprise >90% of the metazoan biomass in the freshwater parts of the Hudson (Strayer and Smith 2001). Cole and Solomon (2012) estimated that the zebra mussel is made of about 40% terrestrial material.

Table 7. Estimates of the terrestrial C support of benthic invertebrates in lakes

Source	Benthic invertebrate	Allochthony	System	Method
Rasmussen (2010)	By feeding guilds	10% in herbivores, 80% in shredders	Ste. Marguerite River, Quebec. Varies by guild.	^{13}C gradient approach
Rau (1980)	Chironomids	47 to 51%	Findley Lake, Washington	Ambient ^{13}C mixing model
France (1998)	Many feeding guilds	77 to 92% (mean), 23 to 69% (low)	Boreal lakes, Ontario. Varies by guild	^{13}C (poorly constrained)
France (2000)	Leeches	50 to 100%	Boreal lakes, Ontario. Varies with DOC	^{13}C
Karube et al. (2010)	Benthic mollusks	0 to 24% in gastropods, 0 to 75% in bivalves	Lake Biwa. Littoral sites with different tributaries	^{13}C, ^{15}N and Isosource
Solomon et al. (2008)	Chironomids	60%	Crampton Lake (oligotrophic clear water)	Whole-lake ^{13}C addition
Solomon et al. (2008)	Odonates	25 to 58%	Wisconsin lakes	Whole-lake ^{13}C addition
Solomon et al. (2008)	Odonates	<5%	Peter Lake (with added N and P)	Whole-lake ^{13}C addition
Solomon et al. (2011)	Chironomids, odonates	High for both; 20 to 80% depending on lake	4 northern Wisconsin lakes	Ambient ^{2}H, ^{13}C, ^{15}N, Bayesian model
Larson et al. (2011)	Crayfish	High (up to 85%) in small lakes; low (<10%) in largest lakes. Mean ~55%	14 lakes in the western USA from 0.1 to 500 km^2. Urbanization lowers allochthonous support	Ambient ^{13}C with mixing model
Karlsson et al. (2012)	Chironomids	63%	Upper Bear Lake, Sweden	Ambient ^{2}H and ^{13}C
Batt et al. 2012	Snail (*Helisoma trivolvis*)	21%	Ward Lake, northern Michigan	Ambient ^{2}H, ^{15}N and ^{13}C Bayesian model
Cole and Solomon (2012)	Chironomids, zebra mussels, oligochaetes	40 to 60%	Tidal, freshwater Hudson River	Ambient ^{2}H, ^{15}N and ^{13}C, Bayesian model
Cole and Solomon (2012)	Amphipods, polychaetes	0 to 20%	Tidal, freshwater Hudson River	Ambient ^{2}H, ^{15}N and ^{13}C, Bayesian model

Oligochaetes and chironomids were also highly terrestrial (60% and 40% respectively). Amphipods which were collected from littoral rocks were estimated to be supported largely by benthic algae and only a small (<20%) contribution from terrestrial sources. Similarly the polychaetes showed essentially no terrestrial support at all. The Hudson study shows that in one system with diverse habitats and diverse fauna, there can be a large range of terrestrial support among benthic invertebrate taxa. However, as secondary production of benthic invertebrates in the Hudson is dominated by the zebra mussel, and the zebra mussel is comprised of about 40% terrestrial material, it is obvious that a terrestrial subsidy is important to the total secondary production of benthic invertebrates of the Hudson. A big surprise in the Hudson study was that submersed macrophytes, which are abundant, were not an important resource to any of the benthic invertebrates studied, except possibly the polychaetes (Cole and Solomon 2012). The estimate for the polychaetes, however, has very large uncertainty so I can only say here that support by macrophytes is possible, not certain.

Zooplankton

Zooplankton would seem to be the least likely organisms to be subsidized by terrestrial inputs. These organisms can be highly selective feeders, even choosing one taxon of phytoplankton over another (e.g. Teegarden et al. 2001; and many other studies). Being pelagic (mostly, but see Rautio and Vincent 2007), these organisms do not ‘chew’ or scrape large chunks of terrestrial detritus in the way that some benthic invertebrates do. It is possible, but the evidence is scant, that zooplankton can assimilate dissolved organic matter by osmotrophy. Speas and Duffy (1998) suggest the process occurs in *Daphnia*, but is not significant to its C balance. It is thus likely that zooplankton predominantly use terrestrial organic matter by consuming particles of direct or indirect terrestrial origin. These could be particles (dust) that either entered the lake from land or are formed by either bacterial uptake or flocculation of DOM of terrestrial origin (von Wachenfeldt and Tranvik 2008). Some zooplankton can directly consume particles as small as bacteria (Peterson et al. 1978, Ojala et al. 1995); others possibly consume protozoa that have themselves consumed bacteria.

From a literature search, I was able to find 20 studies that report an explicit quantitative assessment of terrestrial food support in the zooplankton and an additional 6 studies that report only a qualitative assessment (Table 8). There are a small number of other studies that have analyzed pelagic food webs in lakes without any mention of allochthonous inputs.

Table 8. Allochthony estimates for zooplankton in lakes (and one lake-like river, the Hudson); expanded from Cole et al. (2011). Shown are the study, the target organisms, the system or systems studied, the methodological approach and whether or not the study supports the hypothesis that some zooplankton in the system showed more than a 20% (or high for qualitative statement) subsidy from terrestrial organic matter. ϕT zooplankton: percentage of zooplankton biomass formed from terrestrial organic matter

Source	ϕT zooplankton	System	Approach	Support
Quantitative estimates				
Meili et al. (1996)	~40% in cladocerans, 25 ± 20% in *Eudiaptomus*	A humic lake, Sweden	Ambient ^{13}C	Yes
Jones et al. (1998), Grey et al. (2001)	~40 to 50% in copepods and cladocerans. Seasonal variation	Loch Ness, Scotland; 2 separate studies	Ambient ^{13}C, ^{15}N	Yes
Cole et al. (2002, 2006)	<10%	2 small Wisconsin lakes experimentally fertilized; 2 separate studies	Whole lake ^{13}C addition	No
Karlsson et al. (2003)	9 to 77% (mean 53%)	15 sub-arctic lakes	Ambient ^{13}C with model	Yes
Carpenter et al. (2005)	22 to 73% across lakes and 3 models	3 humic Wisconsin lakes, not fertilized	‘Whole’ lake ^{13}C addition	Yes
Matthews and Mazumder (2006)	40 to 50% in *Holopedium gibberum*, 15 to 40% in *Leptodiaptomus tyrelli*, 50 to 60% in *Epsichura nevadensis*	Council Lake, British Columbia, Canada	Ambient ^{13}C, ^{15}N and experiments	Yes
Pace et al. (2007)	2% in *Leptodiaptomus minutus*, 30% in *Holopedium gibberum*	30 ha clear-water Wisconsin lake	Whole lake ^{13}C addition and model	Yes
Karlsson et al. (2007)	37% in copepods, 42% in cladocerans	13 lakes, northern Sweden	Ambient ^{13}C	Yes
Taipale et al. (2009)	29 to 53%	Shallow Finnish lake	Whole lake ^{13}C addition and model	Yes
Mohamed and Taylor (2009)	9 to 23%	27 Ontario lakes	Ambient ^{13}C and regression model	Yes
Kankaala et al. (2010)	0 to 80%; mostly near 40%	5 Finnish lakes	Ambient ^{13}C and ^{15}N. Combines allochthonous with bacteria and green sulfur bacteria	Yes
Berggren et al. (2010)	23% (7 to 45% depending on model run)	Lake Ortrasket, large, boreal lake (7.3 km^2)	Microbial model	Yes

Caraco et al. (2010)	21 to 57%. Higher for cladocerans than for copepods	Hudson River	Ambient ^{14}C with ^{2}H, ^{13}C and ^{15}N	Yes
Cole et al. (2011)	20 to 40% in *Daphnia* spp., *Holopedium gibberum* and *Leptodiaptomus minutus*	2 Wisconsin lakes	Ambient ^{2}H, ^{13}C and ^{15}N over depth; IsoSource model	Yes
Francis et al. (2011)	<5%	25 lakes, Pacific NW, USA	Ambient ^{13}C and ^{15}N	No
Solomon et al. (2011)	20 to 80% depending on taxa and lake	4 Wisconsin lakes; multiple taxa	Ambient ^{2}H, ^{13}C and ^{15}N Bayesian model	Yes
Rautio et al. (2011)	Seasonally varying. >60% in *Daphina umbra* from Jan to Aug, less for cylopoids	Lake Saanjarvi, Finland	Ambient ^{13}C and ^{15}N Complicated food web mixing models tried	Yes
Karlsson et al. (2012)	47% for zooplankton. Higher for cladocerans and cyclopoid copepods (~60%) than for calanoids (25%)	Upper Bear Lake, Sweden	Ambient ^{2}H,^{13}C, ^{15}N	Yes
Cole and Solomon (2012)	40% for *Bosmina freyi*; 20% for copepods	Hudson River, New York	Ambient ^{2}H,^{13}C, ^{15}N; Bayesian model	Yes
Batt et al. (2012)	9% for *Skistodiaptomus oregonensis*. 18% for *Chaoborus* sp.	Ward Lake, Michigan. Eutrophic lake at UNDERC	Ambient ^{2}H,^{13}C, ^{15}N; Bayesian model	No
Wilkinson et al. (2013a)	*Chaoborus* spp. mean among lakes: 36%, range: 4 to 82%; cladocerans mean: 35%, range: 5 to 76%; copepods mean: 20%, range: 3 to 50%	40 lakes (*Chaoborus* spp.) and 17 lakes (cladocerans and copepods) in Michigan and Wisconsin from dystrophic to eutrophic. Includes epilimnetic and metalimnetic phytoplankton	Ambient ^{2}H,^{13}C; Bayesian model	Yes
Qualitative estimates				
Bunn and Boon (1993)	Likely low	Australian pond	Ambient ^{13}C and ^{15}N	No
del Giorgio and France 1996	Low	Canadian lakes	Ambient ^{13}C	No
Sobczak et al. (2002)	Low	San Joaquin River	Mass balance	No
Karlsson et al. (2004)	High for cladocerans	15 sub-arctic lakes	Ambient ^{15}N	Yes
Perga et al. (2009)	High for copepods; low for *Daphnia sp.*	Lake Annecy, France	Fatty acid biomarkers	Yes
Lee et al. (2011)	*Daphnia longispina* high and *Acanthodiaptomus pacificus* low	Lake Shirakomaike, Japan	^{13}C, ^{15}N over depth	Yes

One could argue these should also be included in Table 8. For example, there is a beautiful study of Lake Baikal (Yoshii et al. 1999) and another one for a eutrophic lake in Japan (Yoshioka et al. 1994), both of which were able to produce perfectly acceptable food-web models using stable isotopes, without considering terrestrial inputs, even conceptually. Neither of these studies are evidence for complete autochthony; they simply did not consider allochthonous inputs at all. A similar study is available for Lake Kinneret, but in this case allochthonous sources are mentioned, but not analyzed. Zohary et al. (1994), in trying to explain the ^{13}C composition of Lake Kinneret zooplankton, mention terrestrial organic matter in passing, because a food source isotopically like terrestrial C might help to solve the problem they are discussing (the $\delta^{13}C$ of the zooplankton is too low to be explained by the prey items in the lake). However, Zohary et al. (1994) dismiss this idea without analysis because an earlier model suggests that terrestrial organic matter is a very small source of ^{13}C to Kinneret. Thus, I did not include in Table 8 these studies or any similar ones that did not explicitly consider the allochthonous support provided to zooplankton.

For the quantitative estimates, most (17 of 20, or 85%) estimate that at least some taxa of zooplankton in these systems are supported by 20% or more (sometimes much more) C input from terrestrial detritus. Among the qualitative assessments, 3 of 5 suggest that the allochthonous support provided to zooplankton is large, while 2 studies suggest it is not. Clearly, most (but not all) of the studies that have looked for the allochthonous support of zooplankton in lakes have found something to report. Of course, consensus among authors does not mean that they are necessarily correct. The variability in the allochthony estimates among lakes forms a consistent pattern which I find convincing. There is a lot of variability in the results given in Table 8 — across systems, among studies, and among taxa. Most studies estimate that the majority of the food of zooplankton is derived from phytoplankton, but in many of the systems 20 to 40% comes from terrestrial primary production. The lowest quantitative estimates come from 2 kinds of studies: (1) whole-lake ^{13}C additions to UNDERC lakes being experimentally eutrophied (Cole et al. 2002, 2006), and (2) analysis of ambient ^{13}C and ^{15}N levels from a series of 25 urban lakes in the Pacific Northwest (USA) (Francis et al. 2011). Pace et al. (2007) found a predictive relationship between the ratio of CDOM:chl-*a* and the fraction terrestrial in zooplankton. That is, in systems with either high chl-*a* and low organic color (eutrophic lakes and oligotrophic clear water lakes) allochthony was lower than in lakes with high organic color and low chl-*a* (Fig. 12).

It is possible that plotting all of the estimates for zooplankton allochthony against the ratio of color to chl-*a* would sort out some of the large variability

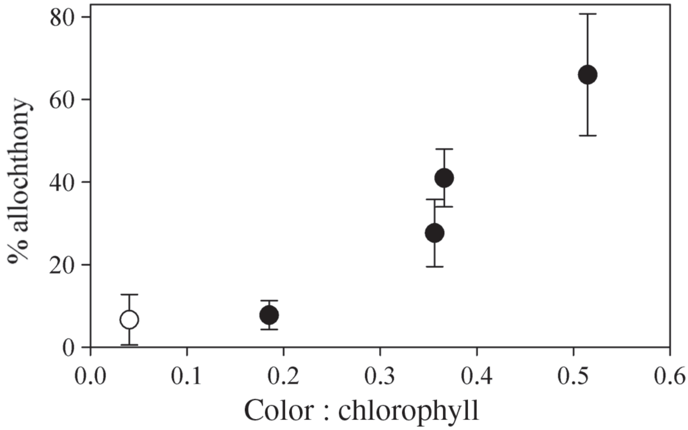

Fig. 12. The fraction of zooplankton biomass that is terrestrial (% allochthony) from a series of lakes in northern Wisconsin which vary in the ratio of color to chlorophyll (○, ●). The open symbol is from Peter Lake when it was experimentally eutrophied by adding N and P (modified from Pace et al. 2007). The estimates come from a series of whole lake ^{13}C addition experiments (Carpenter et al. 2005, Cole et al. 2006)

within the canon of the studies. Unfortunately, we do not have the ancillary data for most of the lakes. It is also likely that many factors affect the utilization of terrestrial detritus by zooplankton. Further, it is certainly not difficult to criticize many of the studies in Table 8 on methodological grounds. In fact, there is a controversy in the literature that is largely methodological which I will discuss in the next chapter (Chapter 4). I will note here that 4 new studies have now used multiple isotopes under ambient conditions (^{2}H, ^{13}C and ^{15}N) in the same lakes for which the ^{13}C additions were performed. Cole et al. (2011) used these 3 isotopes for 2 of the lakes (Paul and Crampton), along with a relatively simple isotope mixing-model (IsoSource; Phillips and Gregg 2003). Cole et al. (2011) considered as possible ultimate sources surface phytoplankton, deep phytoplankton (at the metalimnion), benthic algae and terrestrial vegetation. They found that no matter what combination of these sources were included, the zooplankton in Paul and Crampton Lakes would have to have appreciable terrestrial subsidies in order to explain its isotopic composition. This approach produced allochthony estimates for the zooplankton that were as high as or higher than those from the ^{13}C addition experiments. Solomon et al. (2011) used an earlier data set, and included 4 of the ^{13}C-addition lakes. Solomon et al. (2011) used a more sophisticated Bayesian mixing model that better accounted for uncertainty, both in the consumers and in the end-members. Solomon et al. (2011) also found that estimates of allochthony for the zooplankton were similar or higher than those arrived at by the ^{13}C additions. Batt et al. (2012) used this approach of Solomon et al. (2011) in a small, naturally eutrophic lake and calculated a very low allochthony contribution to the calanoid zooplankton (about 10%). Karlsson et al. (2012) used the ambient stable isotopes ^{2}H and ^{13}C in a lake dominated by terrestrial inputs and found a modest terrestrial food support in calanoids (25%) and quite high terrestrial food support in both cladocerans (58%) and cyclopoids (60%).

While zooplankton can clearly be selective feeders, the data in Table 8 suggest that this selectivity can be overwhelmed when phytoplankton (of the right size and shape) are compared to the right-sized particles of terrestrial origin. The Hudson River presents an interesting case. The Hudson River is lake-like in that it is freshwater (the upper 200 km or so), relatively deep for a river (mean depth 8 m) and has zooplankton taxa such as *Bosmina freyi* and *Mesocyclops* sp. that are typically found in lakes. The Hudson River is not like most lakes in that it is tidal and the water column is not stratified. Caraco et al. (2010) used ambient stable isotopes (^{13}C, ^{15}N and ^{2}H) along with ambient ^{14}C. The Hudson and some other rivers have particulate organic C (POC) that is very old (^{14}C-depleted; Raymond et al. 2004). This ^{14}C-depleted POC is of terrestrial origin and 1500 to 5000 years old depending on flow and time of year (Cole and Caraco 2001, Raymond and Bauer 2001). There is a great deal more terrestrially-derived seston in the river than particulates of phytoplankton origin (more on this later). Further, because of intense grazing by the zebra mussel (*Dreissena polymorpha*), much of the existing phytoplankton consists of large diatoms, diatom chains, or filamentous greens. So a great deal of the standing stock of phytoplankton is too large to be consumed by the dominant cladoceran, *Bosmina freyi,* and even too large for many of the small copepods. In addition, the particles most ^{14}C-depleted (old) are small and in a size range perfect for zooplankton consumption (Fig. 13).

In the tidal, freshwater parts of the Hudson River the zooplankton have depleted ^{14}C-signals similar to that of the POC and especially the smaller-sized POC fraction (Fig. 14). The phytoplankton is only slightly depleted in ^{14}C and reflects the ^{14}C content of the DIC. In fact, in the units of Δ^{14}C or carbon ‘age’, phytoplankton and DIC will be identical. (Δ^{14}C corrects the ^{14}C content of sample for fractionation using the ^{13}C content of that sample and is used as the basis for the ^{14}C age calculation; Bauer et al. 2004). Similarly, the macrophytes and modern terrestrial plants in the Hudson are not at all depleted in ^{14}C, and are the same age as the DIC. One has to conclude that the zooplankton consume organic matter that is clearly not of autochthonous origin (e.g. not phytoplankton, not macrophytes, not benthic algae). The ^{14}C of the zooplankton is consistent with consumption of the small particles of POC that are clearly of allochthonous origin. While Caraco et al. (2010) are certain that these particles are of allochthonous origin, they were not able to

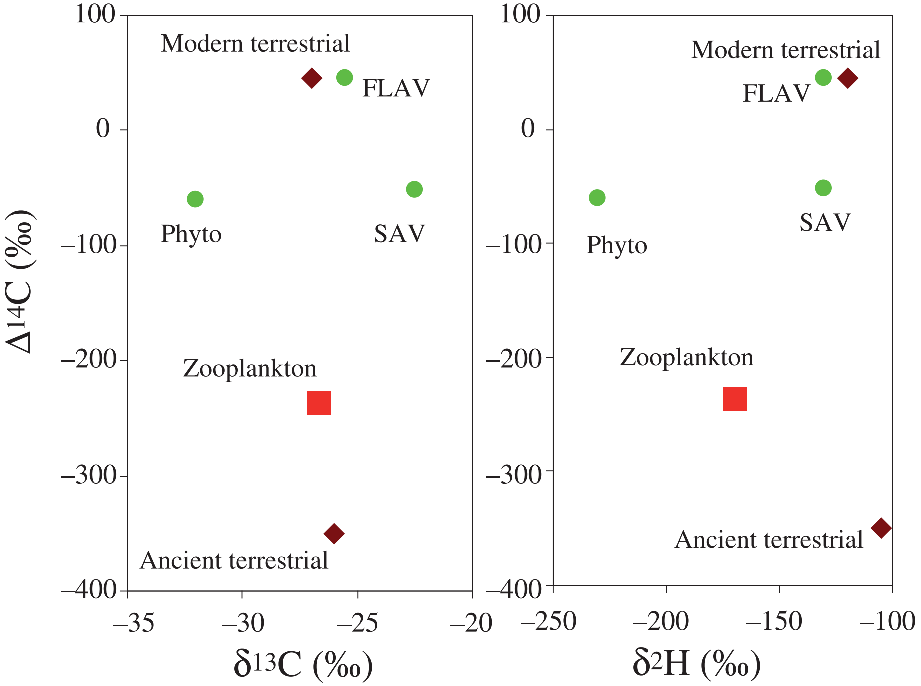

Fig. 13. Isotope analysis bi-plots for the Hudson River (modified from Caraco et al. 2010). The *y*-axes are $\Delta^{14}C$. On this scale, 0‰ represents modern, atmospheric C and values above 0 reflect radiation from bomb tests. Negative values of $\Delta^{14}C$ represent material that is depleted in ^{14}C and is old. Note that $\Delta^{14}C$ includes a correction for fractionation. The red square marked 'Zooplankton' represents multiple samples of *Bosmina freyi* and of mixed, small copepods; Phyto: phytoplankton; SAV: submersed aquatic vegetation; and FLAV: floating leaved aquatic vegetation

be certain about the exact origin of them. The possibilities include: old soils of post-glacial origin, very old organic matter from shale in the watershed, and anthropogenic additions of hydrocarbons. If shale or oil were the source, these particles would be ^{14}C 'dead' since these materials are more than 50 000 years old (and likely much older). If post-glacial soil were the source, the oldest material would be about 9000 years old and the average about 3400. To 'make' the measured ages of the POM in the river, it takes more 9000 year-old C than 50 000 year-old C. Thus Caraco et al. (2010) estimate that the allochthony contribution to the zooplankton is between 21 and 57%. Because it seems unlikely that there is enough organic C from shale entering the river, the higher percentage is probably more plausible. Further, this estimate of allochthony includes only the aged, terrestrial fraction. Zooplankton may also be consuming modern terrestrial C so the terrestrial subsidy could be higher. We will revisit the Hudson River in Chapter 4.

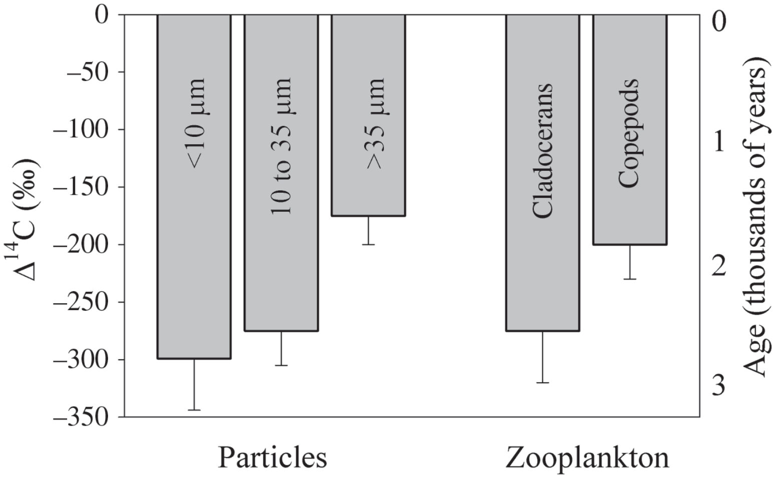

Fig. 14. $\Delta^{14}C$ (left axis) and calculated age before present, for size-fractioned POC and 2 groups of zooplankton in the Hudson River (from Caraco et al. 2010). $\Delta^{14}C$ is corrected for fractionation of ^{13}C and is used as the basis of calculating radiocarbon age. See www.esapubs.org/archive/ecol/E091/170/appendix-A.htm

Caraco et al. (2010) note that the cladoceran samples are more depleted in ^{14}C than are the copepods. This difference makes sense in that copepods are thought to be more selective feeders and *Bosmina* tends to consume small particles. Most of the phytoplankton in the Hudson consist of large diatoms or filaments, as many of the smaller-sized cells have been removed by intense grazing by the zebra mussel (see Caraco et al. 1997, Strayer et al. 1999, Cole and Caraco 2006). Thus, the particles available to *Bosmina* are now largely of terrestrial origin and apparently quite old. The results of Caraco et al. (2010) are supported by a subsequent study of the Hudson River food web using stable isotopes of C, H and N and a Bayesian isotope mixing model (Cole and Solomon 2012). Cole and Solomon (2012) estimate that *Bosmina* consists of about 40% and copepods consist of 30% (Table 8).

Lake Saanajarvi is a modest sized (0.7 km^2), relatively deep ($z_{\max}$= 24 m) lake in Finland with relatively low concentrations of DOC (~2 mg C l^{-1}). The lake is ice-covered for about 8 months of the year and stratified for only about 2 months, during summer. Rautio et al. (2011) investigated the allochthonous contribution to the dominant zooplankton species (*Daphnia umbra, Eudiaptomus graciloides, Cyclops abyssorum*) over the course of a full annual cycle. Using ^{13}C levels and mixing models with different assumptions, Rautio et al. (2011) found an interesting pattern. For *Daphnia*, allochthony peaked towards the end of the ice-covered period, reaching values close to 100%. Allochthony declined through the ice-free phase, averaging 20 to 40% (depending on the scenario in the model), and reached the lowest values, near 0%, just before ice-in. Both *Eudiaptomus* and *Cyclops* were essentially 100% autochthonous throughout the ice-covered period and increased in allochthony (40 to 70% for *Eudiaptomus*, depending on the model; 20 to 40% for *Cyclops*) throughout the ice-free season. Rautio et al. (2011) indicate that the copepods are largely metabolically inactive during the winter; while in that season *Daphnia* is not growing rapidly, but is turning over tissue. Rautio et al. (2011) conclude that when autochthonous C is in low supply, allochthonous C may help the cladocerans to get through an otherwise lean time. Such lean times may be long in boreal lakes, which are ice-covered with very low photosynthesis for months at a time. Looking at their results, I am impressed by the high degree of allochthony (>20% by all the models) for all 3 species during the ice-free season. Nevertheless, under the ice may be an environment in which allochthony could be particularly important.

Allochthony of bacteria and sources of carbon for respiration

The respiration of terrestrial carbon. Numerous studies have shown that free-living, pelagic bacteria are capable of degrading and growing on ambient DOM in lakes (reviewed by Tranvik 1992). This DOM is made from a mixture of sources. Very few studies have attempted to determine the extent to which lake bacteria grow on or degrade the allochthonous fraction of the DOM. McCallister and del Giorgio (2008) used a novel approach whereby they collected the CO_2 respired by pelagic bacteria in a series of incubation experiments. The method is complex but has been well described and well tested in an earlier study (McCallister et al. 2006). Using 8 lakes in Quebec, McCallister and del Giorgio (2008) found that the $\delta^{13}C$ signature of this respired CO_2 varied between −32.5 and −28‰. Using a mixing model and estimates of the algal C isotopic signature in each lake, they calculated that terrestrial C supports from 3 to >70% of the bacterial respiration among the lakes. McCallister and del Giorgio (2008) found a strong ($r^2 = 0.71$, $p < 0.0005$) negative correlation between the fraction of bacterial respiration that is supported by terrestrial organic matter, and chl-*a*. There is also a significant, but weaker, positive relationship between the terrestrial support provided to bacterial respiration and the ratio of DOC:chl-*a* ($r^2 = 0.47$, $p < 0.01$).

The approach of McCallister and del Giorgio (2008) is sophisticated, but is open to the criticism that the samples are highly manipulated. In this system the ambient DIC is removed, which greatly increases the sensitivity of the measurements. Karlsson et al. (2007) used a simpler, but less sensitive, approach in a series of 13 lakes in Sweden. They incubated lake water for up to 4 days, observed the changes in the $\delta^{13}C$ of DIC over time, and analyzed these data using 'Keeling plots' (Karlsson et al. 2007). Among the lakes, most of the DIC produced by respiration used terrestrial DOM as the substrate. The observed range was from about 72 to 87% terrestrial DOM in the different lakes. The most uncertain aspect of this study is that the algal end-members were estimated from literature values and may not be correct. Karlsson et al. (2007) used a quite negative estimate for the $\delta^{13}C$ of algae (–40.2‰); if the actual algal signature were less depleted (which is likely), the allochthony of the respired DIC would be even larger.

Terrestrial carbon in bacterial biomass. The above studies show that terrestrial organic matter supports a significant amount of microbial respiration in lakes. What about the production of bacterial biomass? Making use of the same lakes in the upper mid-West (USA) that were used for the ^{13}C addition experiments (see 'Fishes' above), Kritzberg et al. (2004, 2005, 2006) investigated whether newly formed bacterial biomass was labeled (and hence derived from current autochthonous photosynthesis) or not (and therefore derived from the background terrestrial DOC). To do this, Kritzberg and colleagues first filtered the water to remove essentially all organisms, re-inoculated it with a small amount of water containing bacteria from the lakes and then incubated this water either in dialysis bags *in situ* in the study lakes or in bottles in the laboratory. These experiments were first performed in 2 lakes (Peter and Paul), and then expanded to 2 more (Kritzberg et al. 2004, 2006). Both incubation approaches gave similar results. The regrown bacteria were enriched in ^{13}C, demonstrating that some of the substrate they used was of algal origin. Depending on the experiment and the lake, 35 to ca. 70% of bacterial growth was attributed to terrestrial C and 30 to 60% to algal C. Since the DOC pool consisted overwhelmingly of terrestrial C (>85%), these experiments demonstrated that pelagic bacteria actually grow preferentially on algal-derived DOC. Kritzberg et al. (2004) calculated an electivity coefficient (P) as the ratio of the autochthonous fraction used by bacteria to that present in the water.

$$P = (\mathrm{autofrac_B} / \mathrm{allofrac_B}) / (\mathrm{autofrac_{DOC}} / \mathrm{allofrac_{DOC}}) \qquad (14)$$

where: $\mathrm{autofrac_B}$ and $\mathrm{allofrac_B}$ are the fraction that bacteria are made of autochthonous or allochthonous C, and $\mathrm{autofrac_{DOC}}$ and $\mathrm{allofrac_{DOC}}$ are the fraction that DOC is made of autochthonous or allochthonous C.

If $P = 1$, there is no preference; $P < 1$ demonstrates a preference for terrestrial C; $P > 1$ indicates a preference for algal C. There was a fair bit of variance among the lakes. For Paul Lake, P averaged 7 (SD 5); for Peter Lake, P averaged 4 (SD 1). Clearly, the bacteria in these lakes 'prefer' or use algal C in a greater ratio than its supply. Nevertheless, Kritzberg et al. (2004, 2005, 2006) demonstrated that about half of the C used by the pelagic bacteria in these lakes was of terrestrial origin. In further analyses of the ^{13}C-enriched lakes, Kritzberg et al. (2006) found that, as for fish and zooplankton, bacteria were more allochthonously supported when the ratio of CDOM to chl-*a* was high. With only 4 lakes, it is hard to use this as a predictive relationship, but the correlation makes a lot of sense. Further, Peter Lake, when it was experimentally eutrophied, had the highest chl-*a* concentration in the lake and the lowest allochthony for bacteria (about 45%) and Tuesday Lake, which has high DOC and low chl-*a*, the highest allochthony for bacteria (>75%; Fig. 15). There are some interesting implications from this work. It is often thought that the C bacteria move up the food web is entirely of terrestrial origin (see Jansson et al. 2007). The work of Kritzberg et al. suggests that bacteria may be only about half made up of terrestrial organic C. Secondly, the work of Kritzberg et al. (2005) and others (del Giorgio and Cole 1998) suggests that bacterial growth efficiency (BGE = BP / (BR + BP)) is relatively low and especially low at low values of BP. Kritzberg et al. (2005) measured BP and BR in a suite of 10 lakes over a wide range of DOC concentrations (from 2.1 to 20 mg C l^{-1}). BGE ranged from about 0.05 to 0.3 and much of that variation can be explained by either the chl-*a* levels, or by BP itself. That is, at high BP (which occurs under more-eutrophic conditions), BGE is high. The variation in BR is less than the variation in BP across this

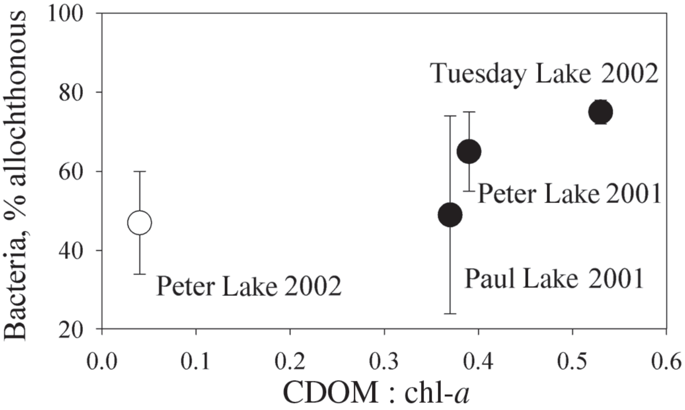

Fig. 15. Terrestrial support of bacteria in a series of lakes. Kritzberg et al. (2006) used the whole-lake ^{13}C additions described in this chapter and in Chapter 4, and incubations to determine the fraction of C of algal and terrestrial origin that comprised bacterial biomass. The lakes and years are shown; in 2002, Peter Lake (○) was deliberately eutrophied with added N and P to increase algal biomass. The *x*-axis is the ratio of chromophoric DOM (CDOM) to chlorophyll-*a*. Redrawn from the data in Kritzberg et al. (2006)

gradient. When BGE is low, it means that very little of the C assimilated by bacteria is turned into biomass; most of the assimilated C is respired. Further, some fraction (from 25 to 60%) of BP is supported by autochthonous C. This means that, although bacteria may respire a large amount of allochthonous C, they may not pass a great deal of it up the food web. Using this information in a model, Cole et al. (2006) argued that, due to the low values of BP and BGE, and the fact that BP was not entirely made of allochthonous C, the DOM to bacteria to zooplankton pathway was not large enough to explain the allochthonous nature of the zooplankton in these lakes. This conclusion remains controversial because in many ways it seems that this likely pathway (DOM to bacteria to zooplankton) should be more important.

Particulate and dissolved organic matter (POM and DOM)

In the above section we have seen that organisms of all kinds in lakes: fish, benthic invertebrates, zooplankton, and bacteria, often bear a terrestrial isotopic or fatty acid signature in their biomass. The inorganic C produced by the respiration of either bacteria or the entire biota of a whole lake also carries a terrestrial signal. With the exception of fishes, some of which consume terrestrial insects (and sometimes reptiles and rodents; see Hodgson and Hansen 2005), the way that terrestrial organic matter enters the food web is via the dissolved and particulate organic materials that enter the system from land. In the lake, both POM and DOM are potentially mixtures from a number of sources including phytoplankton, benthic algae, macrophytes and terrestrial inputs. The make-up of the POM can be gleaned from its isotopic composition and sometimes other tracers (specific biomarkers, for example). These tools also work for DOM, but in this case some of the optical properties can also be useful (e.g. McKnight et al. 2001, Cory and McKnight 2005).

What is in the seston?

If some zooplankton are significantly subsidized by terrestrial organic matter, one would expect that terrestrial organic matter might comprise a significant fraction of the POM in lakes. The limited literature available on the allochthony of POM in lakes shows a range of values from nearly entirely autochthonous to nearly entirely allochthonous. Mohamed and Taylor (2009) examined a series of 27 lakes in Ontario. Using just the surface water, they reasoned that the POM was a mixture of C of phytoplanktonic and terrestrial origins. The $\delta^{13}C$ of the phytoplankton moiety, they argued, should vary with the $\delta^{13}C$ of CO_2 (the substrate for photosynthesis), while the ^{13}C of terrestrial origin should be nearly invariant, near the typical $\delta^{13}C$ terrestrial value of about −28 ‰. The argument is based on the idea that photosynthetic fractionation (ε; the contrast between the $\delta^{13}C$ of phytoplankton and the ^{13}C of dissolved CO_2) should be relatively constant, but that the $\delta^{13}C$ of CO_2 will vary with alkalinity and other factors such as pH and the origin of the DIC in individual lakes. If POM were entirely of terrestrial origin a plot of $\delta^{13}C$-POC versus $\delta^{13}C$-CO_2 would have a slope of zero and be at the terrestrial value (about −28‰). If POM were entirely algal, the plot would have a slope of 1. A slope between 0 and 1 is indicative of a mixture of the 2 sources. Mohamed and Taylor (2009) found that the average terrestrial portion of the POC for the suite of lakes was between 25 and 38%. The range among the different lakes (as opposed to the range of the estimate of the average for all the lakes) depends on the details of the model adopted. The POC in the individual lakes in this series range from >90% allochthonous to <5% allochthonous and average 51% allochthonous, with a very large standard deviation among lakes (35%). Karlsson et al. (2003, 2007) have data for POM in a series of 15 lakes from northern Sweden and, using $\delta^{13}C$, concluded that the POC pool was dominated by C of allochthonous origin. In this work, Karlsson et al. (2003) independently estimated the $\delta^{13}C$ of phytoplankton for these lakes using the $\delta^{13}C$ of CO_2 of each lake, the biovolume of the phytoplankton in those lakes, and a relationship between photosynthetic fractionation and cell volume from the literature (Popp et al. 1998). This approach lead to estimates of rather large negative values of ε (−25 ‰ or more) and very negative $\delta^{13}C$ values for phytoplankton, and consequently a large estimate of the allochthony of POC (93 ± 7% allochthonous across the data set). Changing ε from −25‰ to −18 ‰ drops the estimate to 86% allochthonous and the variance is higher among lakes (SD = 19%). I took the data from Karlsson et al. (2003) and analyzed it in accordance with the approach of Mohamed and Taylor (2009), which does not require assuming a particular value of ε. The analysis reveals that the $\delta^{13}C$ of POC is not well correlated with the $\delta^{13}C$ of CO_2 (Fig. 16). The regression is not significant ($p = 0.14$) and the 95% confidence limits of the slope overlap 0 (slope = 0.187 ± 0.25). If the POC were 100% autochthonous, the slope would be 1; if 100% allochthonous, the slope would be 0. The regression approach suggests that 100% allochthonous is actually a reasonable estimate for this group of lakes taken together. Karlsson (pers. comm.) calculated the allochthony of POC for his data from a different suite of lakes using a similar approach and came up with a mean of 75% (data from Karlsson et al. 2007). So, in the more eutrophic Ontario lakes POC was only partially alloch-

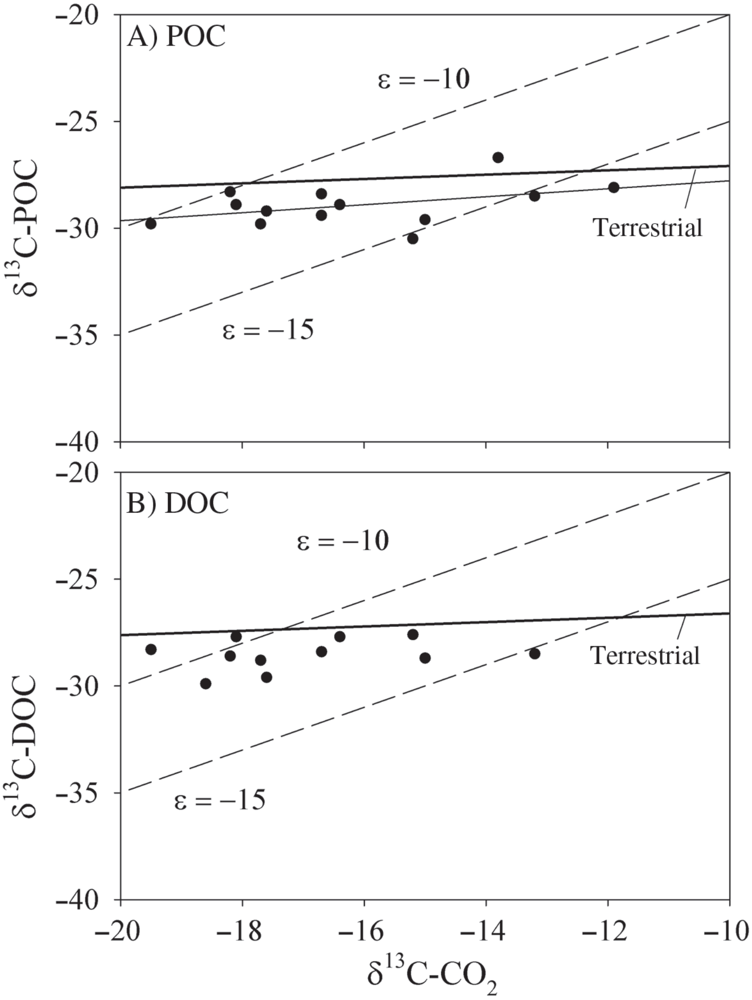

Fig. 16. Plots of the δ^{13}C of (A) POC and (B) DOC against the δ^{13}C of the δCO_2 moiety of DIC. These plots follow the format of Mohamed and Taylor (2009) and Rasmussen (2010); the data used here are from Karlsson et al. (2003, 2007) and J. Karlsson (pers. comm.). Each point represents a different lake in Sweden. If the DOC (or POC) were entirely of terrestrial origin, the δ^{13}C of DOC (or POC) would not vary with that of CO_2 and would be near the terrestrial value of about −28‰ (solid line, both panels). If DOC (or POC) were produced entirely from autochthonous photosynthesis, we would expect the δ^{13}C of DOC (or POC) to track that of CO_2. Depending on the value for ε, the line for 100% autochthonous contribution would have different intercepts. For both panels, lines are shown for ε = −10 and −15‰. ε is the difference between δ^{13}C in organic matter and in the CO_2 moiety of DIC. In (A) the additional thin solid line is the regression of the δ^{13}C of POC versus the δ^{13}C of CO_2. These plots suggest that for this data set there is little contribution to the POC or DOC from autochthonous photosynthesis and that most of the POC and DOC are of terrestrial origin

thonous, in the Swedish data set, dominated by brown water and oligotrophic lakes, POC was highly (>75% and up to perhaps 100%) allochthonous.

Working on Loch Ness, Grey et al. (2001) also argued that most of the POC was of terrestrial or riverine origin rather than from autochthonous primary production. Grey et al. (2001) do not quantify the degree of allochthony, but provide enough data to make the calculation since they give measured values of the ^{13}C of phytoplankton and of a range of terrestrial plants. Using these, I calculate the POC is 74 to 94% allochthonous. This calculation is sensitive to the value chosen for the terrestrial end-member. I used the mean of the most enriched values they reported (for 2 genera, *Fraxinus* spp. and *Pteridium* spp.; −26.4 and −25.4 ‰, respectively); using the mean of all the plants (a more depleted value of −27.7‰) results in a mean allochthony of the POC of >100%.

Darren Bade reported measurements of the C isotope ratios in the DIC, DOM and POM for a series of lakes in Northern Wisconsin and the Upper Peninsula of Michigan (Bade et al. 2004, 2007). In this data set, 32 lakes were sampled, most of them once, several of them 2 or 3 times. Using the approach of Mohamed and Taylor (2009), I have plotted Bade's measurements of ^{13}C concentrations in the POM against the ^{13}C concentrations of CO_2 (calculated from the $\delta^{13}C$ of DIC along with temperature and pH) (Fig. 17). The regression is not significant ($p = 0.4$) and the slope (−0.06 ± 0.16, 95% CI) overlaps zero with a y-intercept (−31.2 ± 4.07‰) that overlaps the terrestrial end-member. As in the other data sets, this one also suggests that for the suite of lakes, the POC is mostly allochthonous and could be entirely allochthonous. If we calculate allochthony for the individual values with the assumption that $\varepsilon = -15‰$ for all 41 data points in the 32 lakes, the mean allochthony for POC is 80% with a large standard deviation (46%). Individual lakes in this scenario range from >90% allochthonous (13 of 41 samples) to <10% allochthonous (2 lakes, both eutrophic). If we increase ε to −18‰, the allochthony of POM would be slightly higher (mean ± SD 82 ± 35%) and 15 of the 41 samples are >90% allochthonous, with only one lake <10% allochthonous (Fig. 17).

Recently, Wilkinson et al. (2013b) used the stable isotopes of both C and H to examine the composition of POM and DOM in a series of 40 lakes in the Upper Peninsula of Michigan and nearby northern Wisconsin. Wilkinson et al. (2013b) made use of the variation in the $\delta^{2}H$ of water among lakes to perform a gradient analysis similar to that of Mohamed and Taylor (2009) who used ^{13}C. Wilkinson et al. (2013b) found that whether $\delta^{2}H$ or $\delta^{13}C$ was used, the POM in the lakes showed the same pattern and that POM on average among the lakes is about 55% terrestrial. The lakes in this study were chosen to represent a large range of conditions and trophic levels, from dark

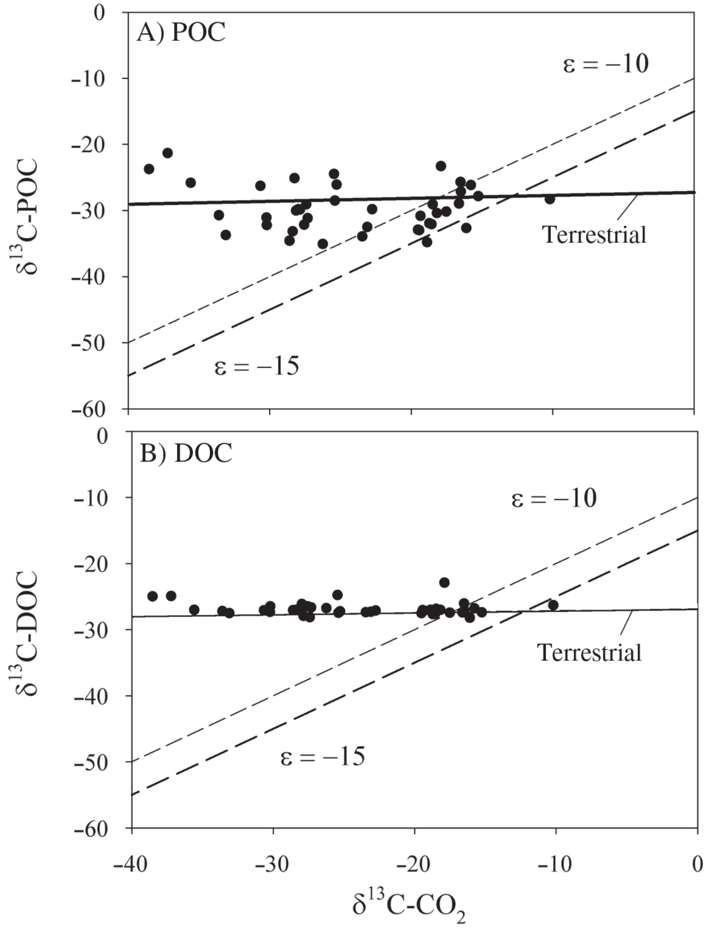

Fig. 17. Plots (as in Fig. 16) for data from lakes in northern Michigan from Bade et al. (2007) and Bade (2004). Each point is a different lake and again (as in Fig. 16) there is no evidence that either (A) POC or (B) DOC are strongly influenced by autochthonous primary production. On average, terrestrial sources dominate these pools on average for this lake district

water bogs to highly eutrophic lakes. POM in the individual lakes ranged from being nearly entirely of autochthonous origin to about 100% allochthonous. In only the most eutrophic lakes was POM dominated by autochthonous sources. Interestingly, the estimated fraction terrestrial of POM from the subset lakes in this data set that had deep water O_2 maxima, was well correlated with that of the epilimnetic POM, but slightly less enriched in terrestrial sources (12 to 88% terrestrial for the metalimnion). Thus, both epilimnetic and metalimnetic POM appears to be dominated by terrestrial sources in many of the lakes in this data set.

POM of the whole-lake ^{13}C experiments

From the results of the whole-lake ^{13}C experiments, my colleagues and I used 3 different models to estimate a range for the terrestrial contribution to the POM (Carpenter et al. 2005). When Peter Lake was fertilized with N and P, the POM was nearly entirely autochthonous; only 0 to 7% was of terrestrial origin. In the other lakes (including Peter) without nutrient enrichment, the terrestrial contribution to the POM ranged from a low of about 40% in Paul Lake to about 60% in Tuesday Lake.

The ^{13}C-addition experiments have their complications (see Chapter 4), so we also computed the allochthony of POM using ambient stable isotopes in the small lakes we worked on at the University of Notre Dame Environmental Research Center–UNDERC. Because it is difficult to physically separate phytoplankton from seston, it is difficult to separately know the isotopic signatures of phytoplankton and the other components of the POM. An intriguing indirect way to measure the phytoplankton signature, and to simultaneously examine the sources of organic matter to POM, is to use deuterium (^{2}H). The fractionation of H uptake during photosynthesis is very large when water is not limiting. In phytoplankton and benthic algae the organic H is about 150 to 160‰ depleted compared to the H in H_2O; this fractionation (ε_H) is both relatively invariant among habitats (Doucett et al. 2007, Caraco et al. 2010, Cole et al. 2011, Solomon et al. 2011) and easy to measure in dilution-regrowth experiments. Terrestrial plants, although somewhat variable in ^{2}H, are much more enriched than phytoplankton. Again, the terrestrial sources can be measured in a straightforward way. If it is assumed that POM is a mixture of terrestrial and phytoplankton organic matter, we can solve for the fraction allochthonous (ϕ_T). That is, the δ^2H signature of POM (δ^2H-POM) is described by the fraction of POM that is terrestrial (ϕ_T, an unknown); the fraction of POM that is made of phytoplankton ($1 - \phi_T$; also an unknown) and the δ^2H content of phytoplankton and δ^2H of terrestrial sources (both knowns).

$$\delta^2\text{H-POM} = \phi_T \times \delta^2H_T + (1 - \phi_T) \times \delta^2H_P \tag{15}$$

where δ^2H_T and δ^2H_P are the deuterium ratios for terrestrial material and phytoplankton respectively.

Rearranging, we see that:

$$\phi_T = (\delta^2H_{POM} - \delta^2H_P) / (\delta^2H_T - \delta^2H_P) \tag{16}$$

So, the fraction terrestrial (or algal) that comprises the POM can be calculated with just the deuterium values. Since organic materials like leaves, wood, soil and phytoplankton do not vary greatly in their C:H ratios, δ^2H can also be used to estimate the $\delta^{13}C$ content of phytoplankton (assuming there is a known value for the terrestrial end-member). In this case the knowns are ϕ_T, $\delta^{13}C_{POM,}$ and $\delta^{13}C_{T,}$ and the only unknown is $\delta^{13}C_P$:

$$\delta^{13}C_P = (\delta^{13}C_{POM} - \phi_T\, \delta^{13}C_T) / (1 - \phi_T) \tag{17}$$

An analogous set of equations can be used to compute the ^{15}N signature of phytoplankton; the caveat here is that the C:N ratio of phytoplankton is likely different (and lower) than that of terrestrial input so the calculation is either more tenuous or needs a correction for the relative C:N ratios of the algal and terrestrial inputs. One caution with this algebraic approach is that if the POM is nearly entirely of terrestrial origin, and there is variability, one can get unstable answers. Comparing this approach to actual samples of phytoplankton suggest it works best when ϕ_T of POM is <85% and poorly when ϕ_T of POM is >85% (G. Wilkinson, pers. comm.).

Using the ^2H approach and all of the POM isotope data from the UNDERC lakes, it can be seen that the POM in these lakes is largely allochthonous, and somewhat variable in time and highly variable among lakes (Fig. 18). This approach estimates a somewhat higher allochthony in the POM (50 to 80%) than found in the ^{13}C experiments. In one naturally eutrophic lake in this region (Ward Lake), the POM was only 9% allochthonous. Using a more sophisticated approach with 3 isotopes, Batt et al. (2012) estimate the allochthony of the POM at 43%, considerably higher than the simple ^2H estimate of 9%. This ^2H approach is sensitive to the value used for the terrestrial end-member and more work is needed to refine it. Further, while there is a fairly large data set for Paul and Crampton Lakes, there are only a few points for the other lakes. The data and approach are nevertheless strongly suggestive that in the more oligotrophic lakes, POM is largely allochthonous (but variable over time) and in the eutrophic lakes, POM is more autochthonous.

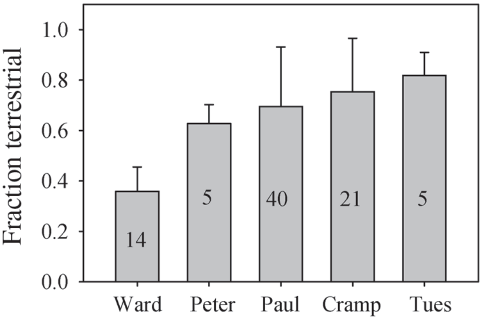

Fig. 18. The terrestrial fraction (e.g. allochthony) of POM in 5 lakes in northern Michigan. The mean fraction terrestrial was calculated from δ^2H and from the mixing model described in the text in the section *POM of the whole-lake ^{13}C experiments* and in Eqns (15) & (16). The data are from Cole et al. (2011), the UNDERC data base and R. Batt (pers. comm., for Ward Lake). The number of samples is shown in each bar; error bar = +SD

In the Hudson River it is sometimes possible to collect nearly pure algal samples with the right sized plankton net, and then remove the non-algal particles under a dissecting scope. This allows the direct measurement of the ^{13}C, ^{15}N and ^{2}H of the phytoplankton. Using a Bayesian isotope mixing model (Solomon et al. 2011), and 4 possible food sources (terrestrial, phytoplankton, benthic algae, and submersed macrophyte) it was found that the POM was comprised mostly of terrestrial material (>75%) with most of the remainder from phytoplankton (Cole and Solomon 2012; Fig. 19)

What is in the DOM?

Some of the same isotopic approaches used for POM have also been used for DOM. In the Swedish data set (discussed in 'What is in the seston' above),

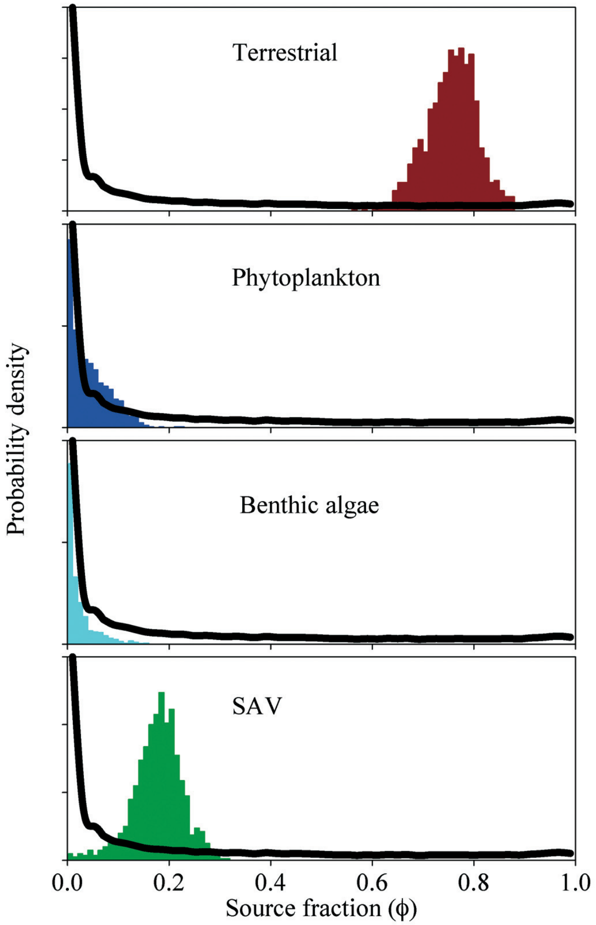

Fig. 19. The composition of particulate organic matter (POM) in the seston of the Hudson River. Three isotope analyses (δ^2H, $\delta^{15}N$, and $\delta^{13}C$) and a Bayesian mixing model (Solomon et al. 2011) were used to calculate the contribution of 4 possible sources of POM (terrestrial, phytoplankton, benthic algae and submersed aquatic vegetation [SAV]). Φ is the fraction for each source and the *y*-axis shows the probability density for each fraction. The thick black line is the assumed prior distribution for these probabilities. The data show that POM in the Hudson is composed mostly of terrestrial material with small contributions from benthic algae and phytoplankton. Re-drawn from the data of Cole and Solomon (2012)

using the estimates of ε from Karlsson et al. (2003), the allochthony of the DOM averages 95.9 ± 4.9% for that series of lakes. Changing ε from −25 ‰ to −18‰ changes this to 93 ± 9%. Using the regression approach of Mohamed and Taylor (2009) again results in a non-significant regression against the $\delta^{13}C$ of CO_2, and a low slope that is not statistically different from 0 (slope = 0.105 ± 0.35). This result is consistent with an entirely allochthonous origin of the DOM in the Swedish lakes. The same data set of Bade et al. (2004, 2007) discussed in the POM section can be used for the DOM as well (Fig. 16B). Using the approach of Mohamed and Taylor (2009) I find that the DOM in these 32 lakes is likely entirely of allochthonous origin. The regression is not significant ($p = 0.36$); the slope (0.021 ± 0.05) is not different from zero and the y-intercept (−27.3 ± 1.1) is identical to the terrestrial end-member value. In all but one of the lakes, terrestrial organic matter comprises more than 90% of the DOM no matter what value of ε between −12 and −20‰ is used.

The study of Wilkinson et al. (2013b), discussed on the POM section, also calculated the terrestrial fraction of DOM using both $\delta^{2}H$ and $\delta^{13}C$. Using either isotope the DOM from the epilimnion of all of these lakes appears to be entirely terrestrial, ranging from about 75% to about 100% with a mean among lakes of 102 ± 13%. In the subset of lakes that had O_2 maxima, the DOM was still dominated by terrestrial sources, but had a lower terrestrial component (range from 25 to 100%) and a mean among lakes of 66%.

Bade et al. (2007) used the whole-lake ^{13}C experiments and a model that took account of the difference in the standing stock of DOC to evaluate the allochthonous and autochthonous contributions to DOC. While the ^{13}C experiments have problems, these experiments are inherently more sensitive than using ambient isotopes alone. Bade et al. (2007) made a time-varying set of differential equations to examine the terrestrial and algal source of the DOC in these lakes.

$$\mathrm{d}[\mathrm{DO}^{13}\mathrm{C}] / \mathrm{d}t = \mathrm{PP}_{13\mathrm{C}} + T_{13\mathrm{C}} - R_{13\mathrm{C}} - L_{13\mathrm{C}} \tag{18}$$

where $[\mathrm{DO}^{13}\mathrm{C}]$ is the concentration of ^{13}C-DOC and the terms on the right side are the inputs of ^{13}C from primary production (PP) and terrestrial matter inputs (T) and the outputs of ^{13}C in respiration (R) and losses (L) to the combination of photo-oxidation and outflow or seepage. To solve this equation, Bade et al. (2007) had to estimate a number of parameters that are poorly known. Nevertheless, they were able to solve for the algal and terrestrial contributions to the DOC over time. The contributions of DOC of algal origin ranged from a low of about 5% in Tuesday Lake (the lake with the highest DOC) to 40% in Peter Lake during 2002, when that lake was experimentally eutrophied. Paul and Peter Lakes (2001, no nutrients added) had intermediate values of 22 and 17% respectively. The values from this model of the allochthonous contribution to these lakes are higher than those estimated from ambient isotopes but show the same trend. Unless the lake is eutrophic, the DOC pool is dominated by terrestrial sources.

Summaries

In this Chapter a lot of detailed information is presented on estimates in the literature of the terrestrial fraction of organisms and organic matter pools in lakes. In this section, I try to provide brief summaries in broad categories followed by some thoughts about where the field should go next.

Fishes. The section on fishes gives some examples showing the importance of terrestrial organic matter to fish. The strongest statement that can be made is that the potential exists for a significant allochthonous support of lake fishes. Different studies have suggested numerous factors that may regulate the degree of the terrestrial subsidy to fishes among lakes and over time within a single system, and I do not see a consensus in the existing literature. It is highly likely that there truly is a great deal of variance across water body types and among fish taxa; it is also likely that some of the variability is only apparent and due to methodological differences. Nevertheless, fish can acquire terrestrially derived material several ways: Direct consumption of terrestrial vegetation (as in the case of the tambaqui); consumption of sediments containing terrestrial detritus as in the case of gizzard shad; direct consumption of terrestrial organisms; consumption of aquatic invertebrates; or, consumption of other fish that have consumed terrestrial material or that have consumed other organisms that do (the likely case for herring in the Hudson River). In the more eutrophic systems fishes tend to be supported largely by autochthonous resources. In the brown water systems, we see variation among taxa and systems with significant support for some taxa from allochthonous resources.

Benthic invertebrates. To summarize what is known about terrestrial support of benthic invertebrates in lakes, it must be noted that there are relatively few studies that explicitly address allochthonous support for lake benthic invertebrates (Table 7). Many more studies have examined the extent to which benthic invertebrates depend on either pelagic or benthic primary production rather than on allochthonous versus autochthonous sources (Vadeboncoeur et al. 2002). However, of the few studies that have looked explicitly at terrestrial food sources for benthic invertebrates, most have found significant amounts. The terrestrial subsidy varies with: the invertebrate taxa studied, the amount of terrestrial inputs; with the trophic richness of the lake, with lake size, the taxa of invertebrate studied; and with the degree of human development near the shoreline.

Zooplankton. To summarize the zooplankton work, most of the studies that have explicitly looked for a terrestrial C signal in zooplankton have found one. A few studies have found or asserted that there is essentially no evidence for a terrestrial subsidy to zooplankton. The existing literature suggests that the fraction allochthonous varies widely, but is often in the range of 20 to 40% with a few studies much higher. Many, but not all, of the studies report a greater degree of allochthony into cladocerans than into other groups (copepods, for example; Table 8). This makes sense; as filter feeders most cladocerans would be less selective than particle capture feeders. The highest degree of allochthony appears to be in small lakes with high DOC, boreal lakes with long seasonal ice cover and systems (e.g. Hudson River) with a large particle load of terrestrial origin. The lowest allochthony is in eutrophic systems or ones with high ratios of chl-*a* to CDOM (Table 8).

Pelagic bacteria. Since there are so few studies that have attempted to measure the allochthonous versus autochthonous sources used by pelagic bacteria, it is difficult to draw a meaningful summary. This is clearly an area ripe for new research. The work in lakes (E. Kritzberg and colleagues in the several papers cited) suggest that bacteria use allochthonous and autochthonous sources about equally despite the overwhelming dominance of allochthonous material in the ambient DOM pool. DOM of terrestrial origin supports a large fraction of microbial respiration where it has been investigated.

Particulate organic matter. Using various approaches one can show that the standing stock of POM in lakes is often comprised of a mixture of phytoplankton and terrestrial sources and that phytoplankton may not be the majority of this mixture, especially in oligotrophic, humic lakes and some rivers. This means that zooplankton and other organisms that feed on pelagic particles are confronted with a situation in which many of the particles encountered are not of algal origin. I draw 2 conclusions for the POM results. First, it would be unwise to equate the isotopic signature of POM with that of phytoplankton unless one is relatively certain (as in the open ocean or a large, eutrophic lake) that the POM is truly of algal origin. Second, it seems likely that even with some selectivity, zooplankton will wind up at ingesting some terrestrial particles.

Dissolved organic matter. In summary, the DOM, like the POM, appears to be comprised of a mixture of autochthonous and allochthonous sources, but tends to be much more dominated by allochthonous sources, at least for the lakes for which we have data. These lakes tend to be small, oligotrophic and nutrient-poor. The lakes with the highest algal contribution in the Bade data set are Peter Lake under experimental eutrophication (40%) and, from the ambient isotopes (e.g. Fig. 17b), Trout Lake, which is a relatively large (>1500 ha) oligotrophic lake. Of the 40 lakes in those studied by Wilkinson et al. (2013b), Trout Lake also had the highest contribution of algal material to the DOM. The lakes examined by Wilkinson et al. (2013b) included several eutrophic lakes which also had a larger algal contribution to the DOM than the average lake in that data set. Nevertheless, the ratio of color to chl-*a* explained only 20% of the variance in the fraction of DOM made up of terrestrial material in the Wilkinson data set. So, we are not yet in a good position to predict the variation in the terrestrial fraction for DOM among lakes. We can say that the terrestrial fraction of DOM is large with 50 to 80% common in small lakes.

Conclusions, considerations, and looking forward

Some things are better known than others

So, what is known about terrestrial subsidies to lake food webs and where should the field go from here? Clearly some components are better known than others. For example, I think I am on firm ground when I say that there is strong evidence that DOM in lakes is largely of terrestrial origin and POM reflects a mixture of terrestrial and aquatic sources. On the other hand, little is known about the sources of organic matter for pelagic bacteria. Better methods are needed to separate bacteria from water in sufficient quantities to be able to measure their isotopic or biomarker signatures. The existing studies are based on attempts to regrow bacteria under realistic conditions, and even so there are very few studies. It is surprising that there are almost no assessments of the allochthonous or autochthonous characterization of lake sediments. Karlsson et al. (2012), based on both δ^2H and δ^{13}C estimated that the sediments on one lake were about 75% of terrestrial origin. There may be spatial variation in the composition of the sediments as well. Lake Constance is a large and complex lake that sits at the borders of Austria, Germany and Switzerland. Using stable isotopes of C and N, along with mineralogical composition, Fuentes et al. (2013) estimated that for one site, near the entrance of two major rivers, that 73% of the sedimentary organic matter was of terrestrial origin. In the same study, a site in the central basin was 34% terrestrial. It would be informative to look at lakes over a range of conditions, to look within individual lakes over time, including paleo time, and space, and to consider separating the sediment material by size class. The isotopic study of sediments is not straightforward, especially when using δ^2H, because the contribution of inorganic materials to the signal is unknown. New methods that separate the organic and inorganic fraction would help enormously here.

Uncertainty in food sources is a big problem

The uncertainty for what supports the rest of the food web (zooplankton, fishes and benthic invertebrates) is much higher than that for DOM and POM, and lower than that for bacteria. There are a large number of studies for metazoan consumers (Tables 5, 7 and 8). We have patterns in the estimates of allochthony among lakes, for these consumers, that make intuitive sense. The terrestrial fraction is largest in small lakes with high loading of terrestrial organic matter and lowest in eutrophic lakes and large lakes. We also have a number of problems that make any one of the estimates highly uncertain. In theory a researcher can measure the stable isotope ratio (or biomarker concentration) in a large enough number of samples of some consumer to reduce the coefficient of variance. The variability in the food sources presents a different problem. The mixing models at best are only correct if the researchers properly considered the possible food sources. One can come to erroneous conclusions by either omitting a significant food source or by including a food source that seems correct isotopically, but is actually not consumed.

Even if the potential food sources are known or can be imagined, there is a question about how well the food source can be characterized. For stable isotopes, there are two problems: poorly quantified variation (for example among all the possible terrestrial inputs) and the difficulty in directly measuring some sources (e.g. phytoplankton). For tracers such as fatty acids and other biomarkers there is the problem of not yet being able to be quantitative. Combining isotopes and biomarkers is an area for growth. Martin Berggren (pers. comm.) has a submitted manuscript which does just that for zooplankton in a series of 18 lakes in Quebec. While combining tracers is definitely a step forward, it does not solve the problem of unknown variability in the terrestrial and aquatic food sources. Bayesian mixing models can inform us about the effect that variability in the isotopic signatures of food sources has on the uncertainty of our estimates of how important they are to consumers. However, no model can inform us as to what the true or important variability is. For example, do we need to know the isotopic signatures of all of the vegetation in a lake's watershed, or just those of the major trees? Would a sample of incoming ground water DOM be more informative? As another example, not all phytoplankton are ideal food sources. Do we need to understand isotopic differences among different groups of phytoplankton to determine their importance as a food source? I am not proposing a solution here, but suggest that we wrestle with this problem.

Are terrestrial inputs true subsidies to the aquatic food web?

Although the literature on terrestrial support of aquatic organisms often uses the word ‘subsidy’ it is not clear at all that ‘use’ and ‘subsidy’ are equivalent. That is, one can demonstrate, with the appropriate caveats, that some fraction of the tissues of a given aquatic organism consists of material of terrestrial origin. However, this does not imply that adding more terrestrial material to the lake will result in greater growth of that organism, as the word ‘subsidy’ would imply. In fact, over a gradient of increasing terrestrial loading, growth might actually decrease. In an intriguing model, Jones et al. (2012) suggest that the production of zooplankton tends to increase with increased loading of terrestrial organic matter while the production of benthic animals tends to decrease. This model needs to be tested with data. To really look at what Jones et al. (2012) call the ‘subsidy versus subtraction’ quandary one needs data on both the terrestrial fraction of key organisms, and their secondary production. Having both types of data is rare in the present literature on allochthony. S. Jones, S. Solomon and B. Weidel are in the process of collecting these kinds of data.

Looking at the lake literature on allochthony broadly, it is clear that the most contentious issue is the terrestrial subsidy of zooplankton. The hypothesis that zooplankton obtain some of their organic nutrition from land has generated a great deal of rather polarizing disagreement. In the next chapter (Chapter 4) I look in detail at this controversy. For me, this controversy has made it a fun time to be a limnologist. Because of this controversy there is a lot of new work on terrestrial subsidies to zooplankton. I know of several excellent papers that are currently submitted or in preparation that address this topic. There are undoubtedly many more in the works now of which I am unaware. I will predict that the best papers are yet to come.

4 THE ALLOCHTHONY CONTROVERSY

For scientists who work on the food webs of small streams it is simply a given fact that the food web is subsidized by terrestrial inputs. Stream invertebrates are usually described as feeding 'guilds' based on how they access organic matter (e.g. scrapers, shredders, filter-feeders), some of which specialize on terrestrial leaves. Stream ecologists are impressed that, with so much terrestrial organic matter available, many invertebrates show strong preferences for autochthonously produced organic matter, and consume it in greater proportion than would be expected by abundance alone (Marcarelli et al. 2011). Nevertheless, stream invertebrates and the fish that eat them, are still subsidized, often heavily, by terrestrial inputs (Rasmussen 2010). In fact, this clear knowledge of allochthony has even made it into books for children (Fig. 20).

On the other hand, science is no stranger to controversy, and the study of allochthonous subsidies to *lake* food webs is no exception. As I hinted in the prior chapter, the idea that terrestrial organic matter is a significant subsidy in lakes is quite controversial (Reynolds 2008). This controversy is greatest for zooplankton. In this chapter I will examine the arguments for and against terrestrial subsidies to lake food webs (including some lake-like rivers) focusing largely, but not exclusively, on zooplankton.

Why is there a controversy?

There are at least 4 disparate causes or threads for a controversy in this area. Two threads relate to the historical understanding of lake systems and the nature of terrestrial organic matter. First, limnologists have in the back of their minds the oceanographic model of lakes that I discussed in Chapter I. In the open ocean, which receives very little terrestrial detritus relative to autochthonous primary production, zooplankton (and the rest of the food web) consumes phytoplankton or the detritus derived from phytoplankton.

Second, limnologists have an old idea that organic matter of terrestrial origin is 'refractory.' Before it is exported, terrestrial organic matter resides for some time in the soil, ground water, and the streams that drain land. The 'refractory' theory argues that what was not degraded in the soil or in transport must be quite resistant to further decay. The proponents of this view tend to miss 2 points: (1) refractory is a relative term, not an absolute one. Given enough time, terrestrial organic matter will decompose; and (2) the conditions for decomposition in a well-lit lake are quite different from those

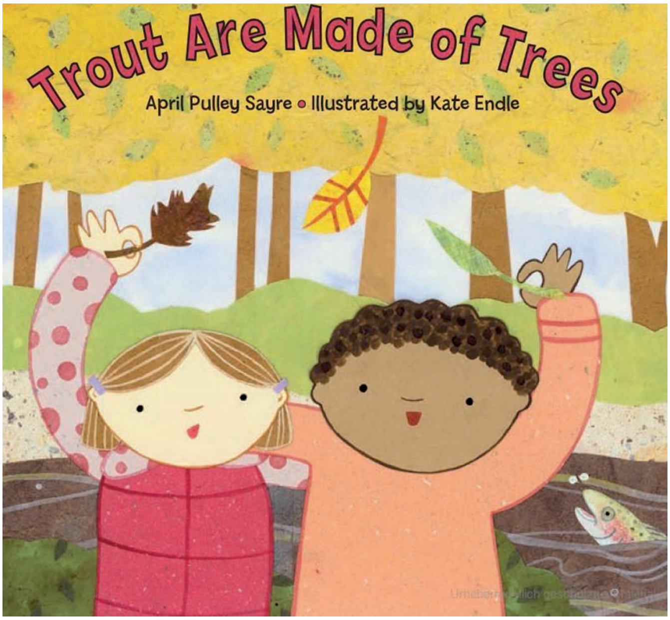

Fig. 20. Book cover of Sayre and Encle (2008) *Trout are made of trees,* Charlesbridge Publishing. Children, fishermen, stream ecologists, and even the rarified membership of the North American Benthological Society (now the Society for Freshwater Science) have embraced, since long ago, the idea of significant terrestrial subsidies to aquatic food webs. In lakes, however, this concept is highly controversial

in the dark, often dry, soil where sorption to particles can also impart resistance to microbial attack. The evidence, from laboratory work to whole-ecosystem metabolism balances, demonstrates unequivocally that terrestrial organic matter does decompose at significant rates in lakes (Tranvik 1992, Arvola and Tulonen 1998, Jonsson et al. 2007).

The third thread combines behavioral and physiological arguments and really focuses on zooplankton. While it is easy to imagine how benthic invertebrates or littoral zone fish might have easy access to terrestrial detritus or terrestrial insects (t-prey), it is harder to envision how planktonic crustaceans would access these sources. Limnologists also know that zooplankton in the laboratory are often highly selective feeders, even choosing among algal species. With these selective abilities, why would the zooplankton bother to eat low-grade, terrestrial detritus?

The fourth thread relates to the difficulties in demonstrating that any aquatic consumer (zooplankton, benthic invertebrate, fish) is, or is not, unequivocally supported in part by terrestrial primary production. To quantify how terrestrially-supported an aquatic organism might be, a tracer is needed that is (1) different in kind (a specific fatty acid, for example) or abundance (some stable isotopes) between terrestrial and aquatic sources, and (2) is preserved in the food web. Gut-contents analysis from diet studies on fish and invertebrates can provide evidence to support the tracer studies. Zooplankton studies are limited to the tracers alone and, in some cases, rearing or diet modeling studies (Rautio et al. 2011). Because of the first 3 threads, unless an ironclad case for allochthony is made (especially for zooplankton in lakes), there will, and probably should, be skeptics.

In Chapter 3 I reviewed data that suggest that 85% of the studies examining the allochthonous support of zooplankton in lakes have found that it is common and often as large as 50% of the carbon consumed by them (Table 8; see Cole et al. 2011). On the other hand, several authors looking at similar kinds of data come up with a different conclusion. For example, Francis et al. (2011, p. 371) state '[our] results suggest terrestrial support of lake zooplankton production is trivial' and '… it appears that allochthonous support of zooplankton production has been vastly overstated'. Another example comes from Brett et al. (2011, p. 21197) who state that terrestrial particulate organic carbon '… makes a minor contribution to zooplankton production.' How can scientists differ so much in their interpretation? A lot of this comes down to 3 issues: (1) the methods used to approach the problem, (2) semantics about what constitutes trivial and significant, and (3) which lakes have been studied.

Whole-lake ^{13}C additions: pros, cons, and resolutions

If you wanted to know if an aquatic organism made use of terrestrial C, the most direct way would be to use ^{13}C to trace terrestrial and aquatic C flows to consumers. This approach can work under the right conditions and some examples were shown in Chapter 3 (see e.g. Tables 5, 7, and 8). Ultimately what is needed is a demonstrable and reliable separation between the isotopic signatures of terrestrial and aquatic primary production. Unfortunately, this separation is rarely achieved for a majority of lakes. Often there is a great deal of overlap between the δ^{13}C signatures of aquatic and terrestrial primary producers, along with a large range among the aquatic group. Nevertheless, the result is that the δ^{13}C for aquatic primary producers and especially phytoplankton is often quite close to that for the terrestrial end-member. Dense stands of macrophytes or benthic algae tend to be less depleted in ^{13}C than phytoplankton; thus δ^{13}C is often more useful in separating these sources than for separating phytoplankton from terrestrial sources such as C-3 plants. On the other hand, macrophytes can be isotopically similar to terrestrial C-4 plants (Caraco et al. 2010), once again making the distinction difficult. Further, an enriched benthic algal or macrophyte signal and the more depleted signatures of terrestrial sources or phytoplankton can add to the confusion because the benthic sources and phytoplankton can wind up both higher and lower, isotoptically, than the terrestrial end members. This ambiguity makes mixing models that use ambient $\delta^{13}C$ alone difficult to apply to a wide variety of lakes. Another problem is that it is not always possible to achieve a good physical separation of pure phytoplankton from the seston (the latter is usually a mixture of aquatic and terrestrial sources) making it difficult, or impossible, to directly measure the phytoplankton C signature in many cases (see Hamilton et al. 2005).

To overcome some of these problems, my colleagues and I pioneered the use of what we called ‘whole-lake ^{13}C additions’, in which we greatly enriched the $\delta^{13}C$ of the DIC in the epilimnia of several lakes without changing the concentration of the lake DIC significantly (Cole et al. 2002). We reasoned that, coupled with time-dynamic models of ^{13}C in various pools, we could provide a better estimate of allochthony than by using ambient ^{13}C alone and traditional isotope mixing models (Pace et al. 2004, 2007, Carpenter et al. 2005, Cole et al. 2006). In these experiments we labeled the upper mixed layers of 6 small lakes (1.7 to 26 ha) at the University of Notre Dame Environmental Research Center (UNDERC) in the Upper Peninsula of Michigan. Because we labeled only the epilimnia of the lakes (as opposed to the entire water column), it might be incorrect to call these ‘whole lake’ experiments.

As an aside, in addition to the food web results (below) we learned a number of interesting things from the whole-lake ^{13}C experiments, and I list a few highlights here. The enriched ^{13}C enabled us to better constrain estimates of the gas piston velocity, *k* (Cole et al. 2010). We demonstrated that pelagic bacteria incorporate about a 50:50 mixture of terrestrial and algal sources (Kritzberg et al. 2004, 2005, 2006) despite the fact that the standing stock of DOC is very much dominated by terrestrial sources, unless the lake is eutrophic (Bade et al. 2007). The ^{13}C additions allowed us to obtain reasonably direct estimates of photosynthetic fractionation by phytoplankton, which showed that these vary a lot and tend to be smaller than the frequently assumed –20‰. In fact the range is 0 to 15‰ among the lakes (Bade et al. 2006). On the geochemical side, in one of the lakes, which was made quite eutrophic by adding nutrients, the ^{13}C additions made it possible to examine both chemically enhanced diffusion and isotopic fractionation during this process, and put constraints on some of the key parameters (Bade et al. 2006).

The main point of the whole-lake ^{13}C additions was to quantify the allochthonous and autochthonous food sources flowing into the lake food webs under a range of conditions. The experiments were useful, but far more complex to interpret than we initially expected. All of the experiments were successful in elevating the δ^{13}C of DIC and enriching both the phytoplankton and the benthic algae in the upper mixed layer by large amounts (Cole et al. 2006, Pace et al. 2007). This success is both a strength and weakness of the approach. On the one hand, we created large increases in the ^{13}C signatures of photosynthetic organisms growing within the upper mixed layer during the time of ^{13}C enrichment. On the other hand, we did not label any photosynthesis that occurred below the upper mixed layer or that occurred prior to the time we started adding the ^{13}C. If the zooplankton fed significantly on primary production below the thermocline (discussed below), our experiment could underestimate the autochthonous support; we call this the 'deep feeding' problem. If the zooplankton was supported significantly by detritus of phytoplanktonic origin produced in the weeks between ice-out and when we started the ^{13}C additions, we would again underestimate autochthony. We call this the 'old autochthony' problem. So, our critics are correct that these 2 factors create the potential for bias in the methods for the whole-lake ^{13}C experiments (Brett et al. 2009, Francis et al. 2011). The question is: Are these potential biases realized in a significant way?

Old autochthony

This potential problem only exists for the whole-lake ^{13}C experiments; in the absence of isotopic enrichment this problem does not exist at all. A straightforward way to address it is to analyze the food web again in the same lakes using only ambient isotopes, an analysis greatly enhanced in recent years by the additional use of deuterium (δ^2H) as a food web tracer (Doucett et al. 2007). Using ambient isotope analysis for δ^{13}C, δ^{15}N and δ^2H, we performed food web analyses using different combinations of the isotopes and mixing models and using data from different lakes and years (Cole et al. 2011, Solomon et al. 2011). We estimated the allochthonous support of zooplankton (Cole et al. 2011) or zooplankton and benthos (Solomon et al. 2011) to be as high as or higher than that estimated from the whole-lake ^{13}C additions. This strongly indicates that the 'old allochthony' issue is a minor one, at best, in these systems (Fig. 21). These strong results were hinted at by a more indirect approach from the Dual Isotope Flow model (DIF), which we used to analyze the ^{13}C additions (Cole et al. 2006). Because seston sinks through the water column relatively quickly, the POC that originated from the phytoplankton prior to the addition is not likely to reside in the water column for long. The DIF model attempts to calculate all the inputs and outputs

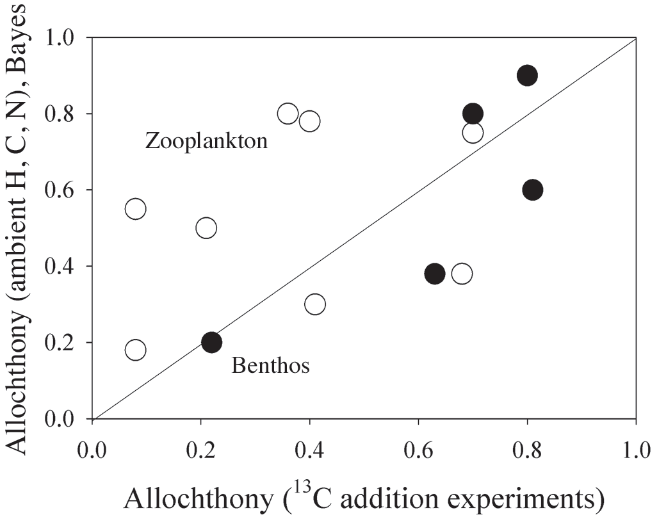

Fig. 21. Estimates of the allochthonous support of zooplankton (○) and benthic invertebrates (●) in a series of lakes using 2 methods: whole-lake ^{13}C additions (x-axis) and modeling ambient isotope ratios (δ^{13}C, δ^{15}N and δ^{2}H) using a Bayesian isotope mixing model. The solid line shows 1:1. Redrawn from the data of Solomon et al. (2011)

from each of 12 'pools', including POC (see Cole et al. 2006). In the model the settling rate of the POC is determined by the settling rates of its components (live phytoplankton, phytoplankton in zooplankton feces, POC of terrestrial origin, tPOC) and needs to fit the mass balance of the POC and the dynamics of the ^{13}C labeling of the POC. In the various lakes the sedimentation of POC works out to be (in the model) from about 0.2 to 0.5 per day. With the upper mixed layer in these lakes being <4 m, the residence time of old POC is relatively brief. So, for these lakes, at least for zooplankton, the 'old autochthony' problem is not likely significant and can be dismissed.

Deep feeding

Unlike the 'old autochthony' problem, 'deep feeding' could influence the estimates of autochthony made from either whole-lake ^{13}C additions or from ambient isotopic approaches that do not account for the phytoplankton growing deep in the water column. In theory, ^{13}C additions to the upper mixed layer would exaggerate the 'deep feeding' problem because the ^{13}C in the upper mixed layer (and the algae that use it) would be far more enriched than the ^{13}C and algae below the mixed layer. Even in the absence of a ^{13}C addition, there still can be a large contrast between the ^{13}C of the DIC in surface and deeper waters — with deeper waters generally more depleted in ^{13}C than surface waters — due to an excess of respiration over primary production. If the phytoplankton are actually growing in these deep poorly illuminated waters (as opposed to settling there from above), phytoplankton could be more depleted in ^{13}C than the surface phytoplankton and this difference be important in calculating the sources of food for zooplankton. Using ambient isotope (δ^{13}C, δ^{15}N and δ^{2}H) analyses over depth for 2 of the lakes in which were performed ^{13}C additions, Cole et al. (2011) found little depletion in ^{13}C for either the phytoplankton or POM over depth within the oxic portions of the lakes. Further, POM from deeper waters is slightly more depleted in δ^{2}H than is POM in surface waters in these two lakes. The mixing models show that whether or not zooplankton feed at depth, they still obtain a significant amount of organic matter from terrestrial sources (Fig. 22). That is, no com-

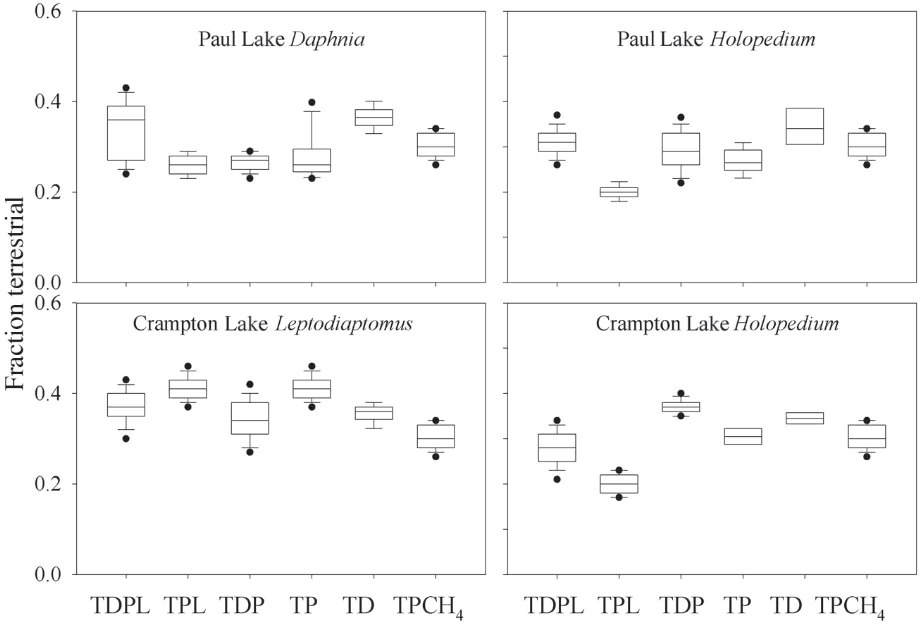

Fig. 22. Terrestrial food-source support (*y*-axis) of zooplankton consumers in Paul and Crampton Lakes at UNDERC (The University of Notre Dame Ecological Research Center near Land O' Lakes, Wisconsin). The fraction terrestrial (*y*-axis) is calculated using 3 isotopes (δ^{13}C, δ^{15}N and δ^{2}H) and a mixing model (IsoSource). Different combinations of end-members were tested (*x*-axis). T — terrestrial, P — phytoplankton from the upper mixed layer, D — phytoplankton from the metalimnion, L — benthic algae, and CH$_4$ — a rough estimate of methanotrophic organic matter. 'TPL' means that 3 sources (T, P and L were tested), 'TD' means that only T and D were tested. The boxplots represent the distribution of possible mixing solutions and show the median (centre line), standard deviation (whiskers); upper and lower quartiles (box limits) and the 5th and 95th confidence limits (points). Note that no matter which sources were tested, the fraction terrestrial is significantly above 0 for both lakes and all 3 taxa of zooplankton. Redrawn from Cole et al. (2011)

bination of epilimnetic and metalimnetic phytoplankton can explain the isotopic signature of the zooplankton.

Zooplankton surely feed in the metalimnia of some lakes, and when they do, this can confound attempts to use stable isotopes, especially C, to assign ultimate food sources (Francis et al. 2011). So, one can reasonably ask, why, in the whole-lake ^{13}C additions to the UNDERC lakes, was deep feeding not significant? For 'deep feeding' to be significant, zooplankton captured in the upper mixed layer of the lake would have to get a significant part of its food from deep in the water column. Two conditions are needed for deep feeding to be important: there must be a significant diel vertical migration (DVM) of zooplankton; and there must be a significant source of autochthonous food at depth, for example, a deep chl *a* maximum (DCM). During the ^{13}C addition experiments, the DCM appeared in some lakes (notably Peter Lake), for a few weeks over the years of the experiments. It was an inconsistent feature and when present, it often occurred well into anoxic water. Estimates of DVM in some of the lakes suggest that the DVM is small, averaging less than 1 m (Farrell and Hodgson 2012) (Table 9). Historical data on DVM in Paul Lake reveals that the mean daytime (deeper water) position of the zooplankton almost never reaches the upper part of the thermocline. This indicates that DVM is insufficiently large in Paul Lake to allow for epilimnetic zooplankton to feed in the metalimnion during daytime (Brosseau et al. 2012). It is certainly possible that migration could occur without a diel cycle but we have no evidence for it in this lake. Paul and Peter Lakes were both used in the whole-lake ^{13}C experiments and zooplankton were found to be labeled quite differently and much less labeled than the epilimnetic phytoplankton.

Table 9. Diel vertical migration (DVM) of the zooplankton in Peter and Paul Lakes. Depth-difference scores for the year 2008 are given. Using vertical profiles of zooplankton abundance during day and night, the mean daytime and night-time positions were calculated; *z*-difference is the difference between day and night time position. Negative values indicate normal DVM (migration to shallower depths at night) and positive scores indicate reverse DVM. Distances are in meters. Note that the largest DVMs were less than 1 m in both lakes for all taxa at this time (data from Farrell and Hodgson 2012)

Zooplankton category	*z*-difference (m)	
	Paul Lake	Peter Lake
Cyclopoid copepod	–0.67	–0.19
Calanoid copepod	0.04	0.26
Daphnia spp.	–0.09	–0.55
Copepod nauplii	–0.16	–0.08

The small DVM in these lakes makes it highly unlikely that the epilimnetic zooplankton could have fed significantly on metalimnetic (and therefore unlabeled) phytoplankton. The ^{13}C-labeling of the zooplankton is consistent with the consumption of a mixture of algal terrestrial organic matter. Further, when East Long Lake and Peter Lake were made eutrophic by the addition of nutrients, allochthony to the zooplankton essentially disappeared (Cole et al. 2002, Carpenter et al. 2005, Cole et al. 2006, Pace et al. 2007). It could be that both the deep-feeding and old-autochthony problems were somehow eliminated by adding nutrients. It is more likely that in these 2 lakes, which do not have persistent DCMs and in which zooplankton DVM is very small, the zooplankton are significantly subsidized by terrestrial organic matter. Crampton Lake is clear, oligotrophic, lacks a distinct DCM, and is oxic nearly to the bottom. In this lake the ^{13}C experiments estimated that the terrestrial C support provided to the cladoceran *Holopedium* was modest (about 30%), while that provided to *Leptodiaptomus* was almost zero (Pace et al. 2007). It needs a fairly complex model of both the deep feeding and old autochthony problems to explain these results. For example, if *Holopedium* accessed deep phytoplankton but *Leptodiaptomus* did not, then DVM may be able to explain these results. A simpler and more plausible explanation is that *Holopedium* is subsidized by terrestrial organic matter, *Leptodiaptomus* (in this case) less so. Further, the ambient stable isotope analysis of Crampton Lake found even higher allochthony to both *Holopedium* and *Leptodiaptomus* than that estimated by the ^{13}C addition experiments (Cole et al. 2011). It is difficult to explain how either deep feeding or old allochthony could cause a lower estimate of allochthony for a ^{13}C addition than for an analysis of ambient isotopes.

The idea that the metalimnion provides significant nutrition to epilimnetic zooplankton is interesting and one that should get more attention (Francis et al. 2011). In a recent and very intriguing experiment, Armengol et al. (2012) labeled the metalimnion of a small (1.3 ha) lake (Laguna El Tejo, near Cuenca, Spain) with ^{15}N-NH$_4$ in order to investigate the zooplankton use of metalimnetic resources. Although the tracer addition was imperfect in that there was some ^{15}N-NH$_4$ accidentally added to surface waters, the experiment was successful in that the seston of the metalimnion became quite labeled, about 90 ‰ enriched compared to surface water seston. Zooplankton captured in the epilimnion during either day or night were no more enriched in ^{15}N than was epilimnetic seston (Fig. 23). There was only a slight ^{15}N increase in the zooplankton captured in the metalimnion where the seston was most enriched. In the metalimnion the zooplankton ranged, depending on the depth, from 20 to 80‰ depleted in ^{15}N compared to seston at the same depths. It is very obvious from these results that neither the zooplank-

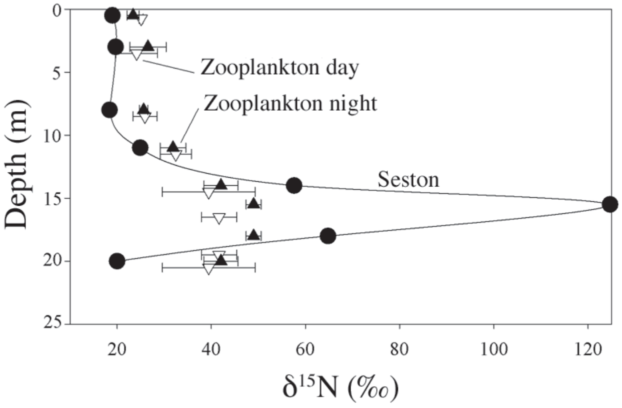

Fig. 23. Results of a metalimnetic injection of $^{15}N\text{-}NH_4$ to a small lake in Spain (redrawn from the data of Armengol et al. 2012). The filled circles show the $\delta^{15}N$ of seston; the inverted open triangles show the $\delta^{15}N$ of zooplankton collected during daytime (mean and SD); and the filled triangles show the $\delta^{15}N$ of zooplankton collected over depth during nighttime (mean and SD). The results of this experiment do not support the hypothesis that zooplankton collected in the epilimnion at any time of day used metalimnetic algae as a food source. The data were kindly provided by J. Armengol

ton in the epilimnion or metalimnion consumed much of the highly labeled metalimnetic algae. Further, there was no diel increase in the ^{15}N of zooplankton captured by vertical hauls in the epilimnion. Armengol et al. (2012) suggest that metalimnetic algae is not a very significant food source for most of the zooplankton in this lake. Armengol et al. (2012) chose this lake because it has a very large night time increase in cladocerans (particularly *Diaphanosoma brachyurum*) in the epilimnion which they expected was the result of DVM. The ^{15}N experiment revealed that this cladoceran, despite large increases in numbers in the epilimnion at night, was also not labeled with the metalimetic ^{15}N. The authors hypothesized that the large night time increase in *Diaphanosoma brachyurum* was the result of horizontal migration from littoral areas and not an upwards migration from deeper waters.

Under the leadership of G. Wilkinson, my colleagues recently labeled the metalimnion of Peter Lake with ^{13}C-DIC (Wilkinson et al. unpubl.). This study was successful in that the ^{13}C of DIC in the metalimnion was enriched by about 80‰. The added ^{13}C was entirely contained within a stratum about 2 m deep and within 5 days was well mixed horizontally throughout the lake. No enrichment of either the epilimnion or the hypolimnion occurred; these conditions were maintained for about 60 days until mixing occurred in late August. The $\delta^{13}C$ of POM in the metalimnion increased, but little or no increase was seen in zooplankton collected in the epilimnion; some enrichment was seen in zooplankton collected in the metalimnion. As in the Armengol et al. (2012) study, the ^{13}C addition to the metalimnion of Peter Lake did not support the hypothesis that the metalimnion is a significant food resource for zooplankton in the epilimnion. At the time of the writing of this book, the full analysis of these data is still underway.

In lakes, POM is generally more enriched in ^{15}N (unlike the situation for δ^{13}C) as depth increases. In Lake Superior, for example, the δ^{15}N of surface-water POM ranges from ca. −3 to ca. +1‰; at depth these values increase to +3 to +4‰. With an expected trophic fractionation of about 2.5 to 3‰ (Vanderklift and Ponsard 2003), zooplankton that fed in the surface would have quite different δ^{15}N values from that which fed in deep water (about 0 to +4‰ if it fed entirely on surface POM; and +6 to +7‰ if it fed entirely at depth). Keough et al. (1996) reports δ^{15}N values of zooplankton (diaptomid copepods) as averaging about 3‰, consistent with surface sources. These zooplankton also apparently consume surface particles and do not rely on particles at depth, based on the nitrogen isotopes. In the same study, some mixed zooplankton samples were more enriched (range 5.4 to 6.8‰), consistent with a mixture of surface and deep sources, perhaps relying more on deeper sources. Sierszen et al. (2006) took mixed samples of zooplankton that were dominated by *Holopedium*, *Bythotrephes* and *Daphnia* and found δ^{15}N values (ca. −1‰) did not vary with depth of the station. Again, these values are inconsistent with feeding on deep particles. Similarly, the δ^{13}C for these samples did not deplete with increasing depth of the sampling station for these taxa. In contrast, *Diporeia* showed marked depletion of ^{13}C and marked enrichment of ^{15}N over increasing sample depth. So, the Lake Superior data suggest that while most taxa are not feeding significantly at depth, some are, notably *Diporeia* (which may be consuming benthic production). I am not trying to argue here that the zooplankton in Lake Superior are in any way supported by terrestrial inputs. The above studies do not address that question. Rather, I am pointing out that despite the well-documented large DVM in this lake, the isotopic evidence for most taxa indicates that feeding is only significant in the upper waters.

In the small, oligotrophic UNDERC lakes, the isotopic composition of zooplankton is consistent with a terrestrial δ^{15}N signal. The phytoplankton in the surface water are more enriched in ^{15}N than terrestrial sources and N at depth is even more enriched in ^{15}N (see below). The zooplankton are not enriched enough in ^{15}N for phytoplankton, either in the surface or at depth, to be their sole N source (Cole et al. 2011). Thus, looking more broadly at N isotopes could be very helpful in resolving the controversy about the food sources for zooplankton in lakes and the role of deep feeding.

Some strong evidence for a terrestrial subsidy to zooplankton

For the small lakes in northern Wisconsin-Upper Michigan, both the whole-lake ^{13}C addition and ambient isotopic approaches agree that components of the food web, and zooplankton in particular, are significantly subsidized by terrestrial inputs (Solomon et al. 2011). Of the other studies listed in Table 8 (Chapter 3), most have 2 flaws: (1) they do not have independent estimates of the isotopic composition of the phytoplankton; and (2) they do not consider that the phytoplankton in the metalimnion (or at the DCM) may be isotopically distinct from the phytoplankton in the epilimnion. It is often the case that the zooplankton are somewhat more depleted in ^{13}C than is the POM from the upper mixed layer. This has lead to several ideas including: (1) the support of zooplankton, or other consumers, by methanotrophic bacteria (which are very depleted in ^{13}C; Jones et al. 2008, Deines et al. 2009); (2) the zooplankton feed on metalimnetic phytoplankton that is more depleted in ^{13}C than is the phytoplankton or photosynthetic bacteria from the surface waters (del Giorgio and France 1996); and (3) the POM in the surface water or the metalimnion is actually a mixture of phytoplankton and terrestrial sources (and perhaps other sources in some lakes) and that the phytoplankton moiety may be more depleted in ^{13}C than the POM mixture (Caraco et al. 2010, Cole et al. 2011). Nevertheless, the 2 flaws, especially if the study used only ^{13}C as the tracer, makes the conclusions of some of the studies in Table 8 uncertain.

For the 2 studies (Cole et al. 2011, Karlsson et al. 2012) that provide estimates of allochthony based on δ^2H alone, the deep feeding issue is basically moot. In dimictic lakes there is only a small difference in the δ^2H of water over depth. This is caused by evaporation in surface waters favoring the lighter isotope. Deeper waters, unaffected by evaporation, become lower in δ^2H than surface waters between spring and fall mixing. The effect is small, amounting to only a few del units. Thus, phytoplankton that grow in deep waters use water for photosynthesis which has less ^2H than surface waters and have slightly more negative values of δ^2H than phytoplankton that grow in surface waters. While δ^2H is not useful in distinguishing between meta- and epilimentic phytoplankton as food sources, δ^2H can be used to distinguish between either meta- or epilimnetic phytoplankton and terrestrial sources. In fact, if the mixing model uses metalimnetic algae and terrestrial organic matter as the possible sources, the terrestrial fraction will be larger than the mixing model that uses epilimnetic algae and terrestrial sources. So, whether or not zooplankton were sampled over depth, the metalimnetic phytoplankton either increase or do not affect the calculation of allochthony when δ^2H is the basis of the calculation.

While the results of some of the studies in Table 8 (Chapter 3) might be considered uncertain, some of them present extremely strong evidence for the terrestrial food support of the zooplankton. The study of the Hudson River (Caraco et al. 2010) is one of these. One of the potential problems in the lake studies that use only ^{13}C, discussed in detail in the previous section, is the idea that zooplankton may obtain some nutrition from algal growth deep in the water column. Suppose we examined the isotopic compositon of zooplankton in a system which lacked stratification and thus, had no metalimnion at all. The tidal-freshwater portion of the Hudson has a well-mixed water column, no persistent stratification, and thus, has no metalimnion. Caraco et al. (2010) used ambient ^{14}C in addition to the stable isotope to determine the source of food for zooplankton in the Hudson. In that study there is really no other possibility except that the zooplankton consumes a significant amount of small ^{14}C-depleted particles of ultimately terrestrial origin. These are the only items in the Hudson system that are as depleted in ^{14}C as the zooplankton (Fig. 13). The Hudson ^{14}C results are particularly strong. Nevertheless, some in the field have argued, I think without carefully reading the paper, that other explanations are possible. Let's look at these in question and answer form.

Could the zooplankton seem 'old' because the phytoplankton uses DIC that is ^{14}C depleted? No. The ^{14}C of DIC is barely depleted. In the units of Δ^{14}C, phytoplankton and DIC will have the same apparent age, because Δ^{14}C corrects for ^{13}C (see Bauer et al. 2004) and cannot explain the low values of Δ^{14}C of the zooplankton. The zooplankton have a ^{14}C age of >1000 years old while the phytoplankton, because of the slight depletion in the DIC have a ^{14}C age of only about 100 years old (Caraco et al. 2010).

Could the zooplankton consume bacteria that use old DOC? This is possible. On the one hand, McCallister et al. (2004) performed incubations and found that bacteria regrown on Hudson River DOC were 'old' in 2 of 4 trials and 'young' in the other 2 trials. On the other hand, nearly all of the DOC samples measured in the Hudson have been 'modern' DOC (e.g. not depleted in ^{14}C; Bauer et al. 2004, Raymond et al. 2004). Either way, if bacteria were the source of the ^{14}C-depleted organic matter to zooplankton via the terrestrial DOC pathway, the ultimate source would still be allochthonous.

Could the zooplankton obtain the ^{14}C depleted organic C from oil or coal pollution entering the Hudson? We cannot completely rule this out but it would be a remarkable result. The POM in the Hudson is ^{14}C depleted but has C:N ratios similar to soils and is not as N-deficient as coal or oil. Certainly oil and maybe coal enter the Hudson; it is an industrially active river. It is hard to imagine that coal or oil could be a significant part of the POM pool, and harder to imagine that zooplankton consume it. Finally, this coal and oil is clearly allochthonous.

One could argue that the ^{14}C result is hard to reproduce in other systems. Not every river has old POM in it (Raymond et al. 2004). Also, ambient ^{14}C is both difficult and expensive to analyze. Cole and Solomon (2012) conducted an extensive follow-up study in the Hudson using data sets from other years in which only δ^{13}C, δ^{15}N and δ^{2}H values were available; the results were very similar to those of Caraco et al. (2010). The multi-isotope study of the Hudson used the 3-isotope Bayesian isotope mixing-model of Solomon et al. (2011) and considered 4 basal resources to the Hudson food web: phytoplankton, terrestrial inputs, submersed aquatic vegetation and benthic algae (Cole and Solomon 2012). The model uses an uninformed prior distribution in which there is equal likelihood that any of the 4 basal resources support a given consumer. There are a number of ways to do this but we followed the methods of Solomon et al. (2011) and Semmens et al. (2009), both of which use a log-ratio transformation that centers the prior distribution on the geometric mean (Fig. 24). These priors have a mean of 25% but a median of 9% and a mode that approaches zero (Fig. 24). The model uses informed priors for 2 key parameters: (1) the fraction of H that comes from water (as opposed to food sources); and (2) the trophic fraction for N, which is a function of assumed trophic level and the value for fractionation per trophic level. The details are in Solomon et al. (2011), but the point here is that the model attempts to solve the possible mixtures of sources to fit all 3 isotopes in each consumer, and at the same time fit the dietary water and trophic fractionation parameters. Further, the model takes into account the inherent uncertainty in each source for each isotope (Moore and Semmens 2008). Some exemplar results are shown in Fig. 24 and in Cole and Solomon (2012). The amphipods were collected from littoral habitats. The Bayesian model results showed that they are supported largely by benthic algae (Fig. 24). Both *Bosmina freyi* (a pelagic cladoceran) and the zebra mussel (a benthic filter feeder) are, in contrast, supported by a mixture of phytoplanktonic and terrestrial food sources. In Fig. 25 I show a summary diagram of the distributions of the food source contribution to a range of organisms and pools, from Cole and Solomon (2012). Note that the POM is about 75% terrestrial and that the 2 zooplankton organisms in the data set show a mixture of terrestrial and phytoplanktonic sources. The terrestrial input to *Bosmina* is about 40% and to the copepod, about 30%. These estimates are quite close to the estimates of Caraco et al. (2010) using ambient ^{14}C (see above). In the Hudson data set some other organisms (e.g. zebra mussels and oligochaetes) are strongly subsidized by the terrestrial inputs. Others (e.g. amphipod, polychaete) show a stronger connection to benthic primary production. The fishes tend to show a mix of all the sources, as higher consumers tend to integrate the basal sources. Interestingly, the herring, which eat a mixture of

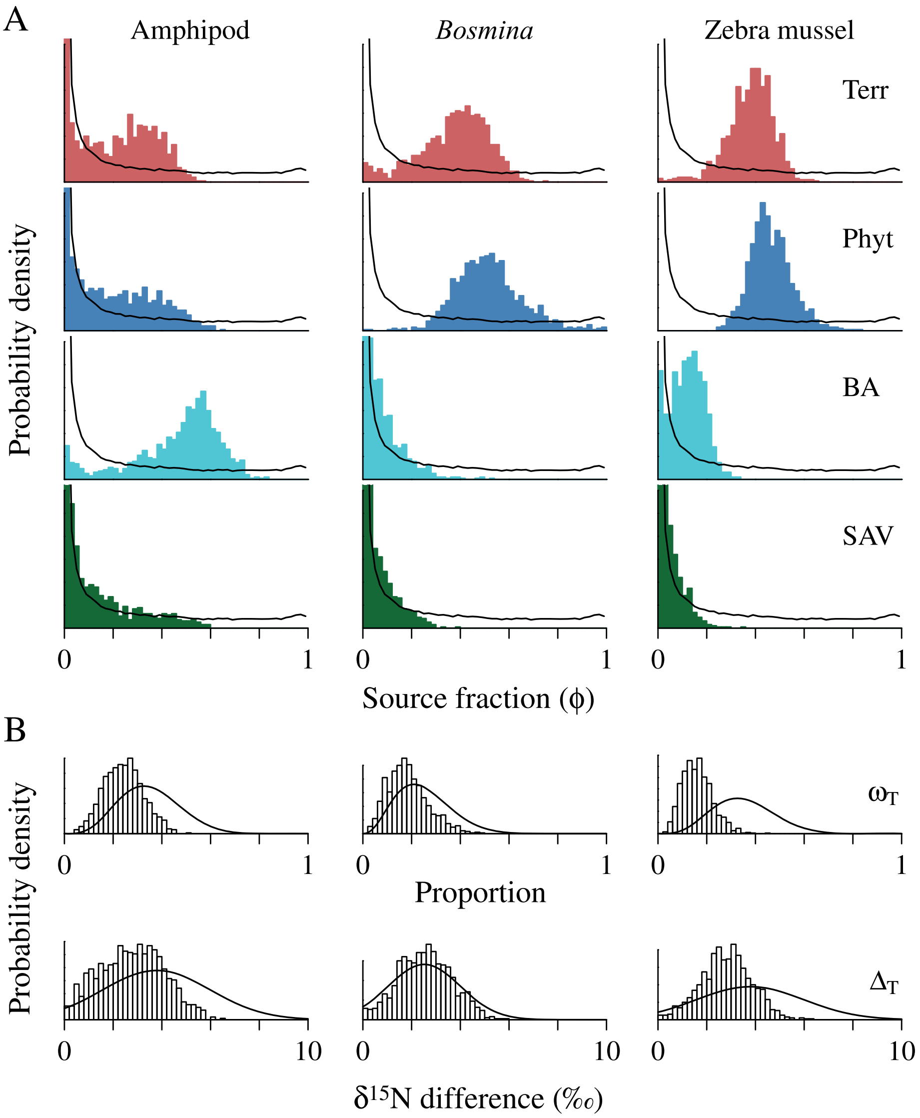

Fig. 24. Results for a 3-isotope Bayesian mixing model applied to the Hudson River. The histogram in each of the 3 columns of panels represents the full data for three different organisms. (A) Probability density functions for the 4 sources (terrestrial — red; phytoplankton — blue; benthic algae [periphyton] — turquoise; and submersed macrophytes — green). The prior distribution is shown with the black line. In Bayesian terminology the 'prior distribution' is the assumed probability distribution before any data are used. The histograms represent the probability density function of the posterior distribution (i.e. the result). (B) The upper row shows the fraction of the deuterium (^{2}H) signal that comes from water, as opposed to food sources (ω_T) and the bottom row shows the trophic shift (ΔT) for ^{15}N. As in (A), the black line represents the prior distribution and the histograms the posterior distribution. Redrawn from the data in Cole and Solomon (2012)

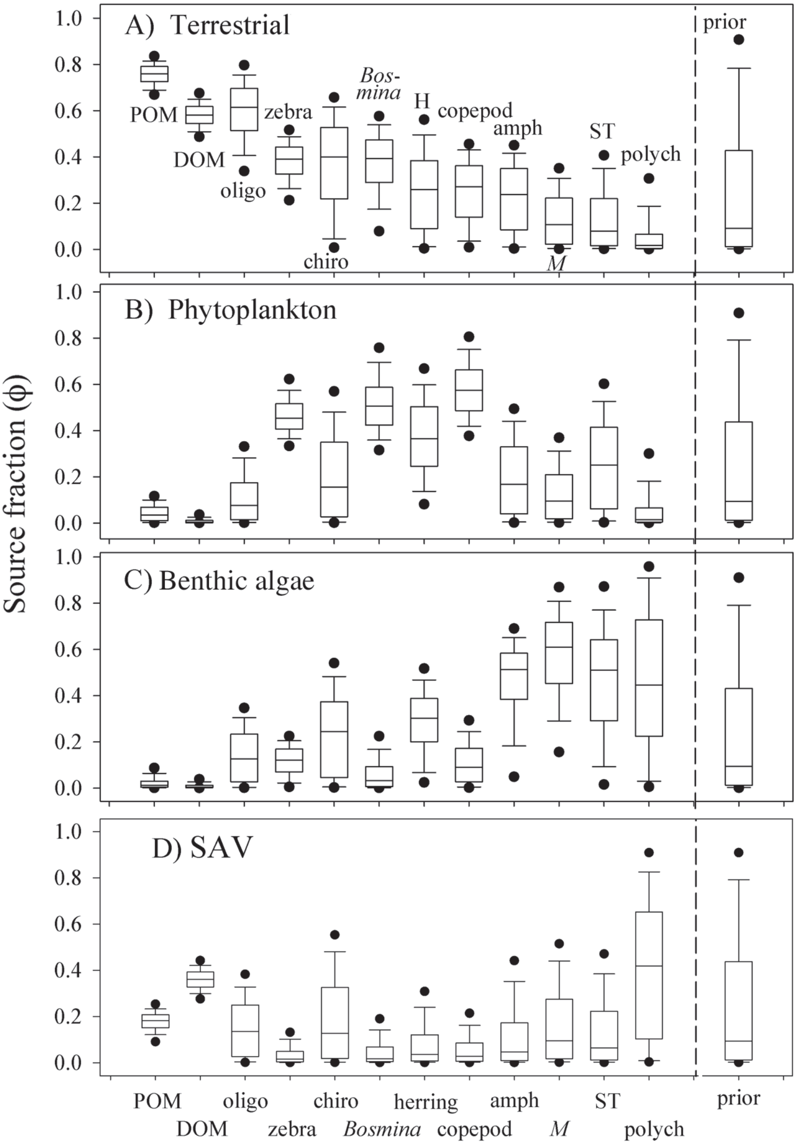

Fig. 25. Summary results of the 3-isotope Bayesian mixing model applied to the Hudson River for 10 consumers, POM and DOM. This graph (taken from similar data to that of Fig. 24) shows the distributions of the fractions of the 4 possible food sources for each organism and compartment. The box plots show the median (mid-line), upper and lower quartiles (box limits), standard deviation (whiskers) and the 5 and 95% confidence limits (points). Redrawn from the data in Cole and Solomon (2012). The consumers are: oligochaetes (oligo), zebra mussels (zebra), chironomids (chiro), *Bosmina freyi* (*Bosmina*), herring (H), copepods, amphipods (amph), *Morone* spp. (M), Spottail shiners (ST; *Notropis hudsonius*), and polychaetes (polych)

zooplankton and benthic sources in this river (K. Limburg pers. comm.), reflect a mixture of terrestrial and phytoplanktonic sources (probably due to the consumption of zooplankton) and benthic algal sources (due to the consumption of benthic invertebrates such as amphipods, which have a strong reliance on benthic algae).

The Hudson zooplankton are more enriched in material from phytoplankton than is the seston. This indicates that zooplankton preferentially select the algal portion from the seston. Nevertheless, at 30% (copepods) and 40% (cladocerans), there is still a significant terrestrial subsidy.

Upper Bear Lake is typical of small, humic lakes in boreal Sweden. Like many lakes with high DOC, the loading of organic C to Upper Bear Lake is dominated by terrestrial inputs. Karlsson et al. (2012) measured both benthic and pelagic primary production and estimate their sum as 3.4 mg C m^{-2} d^{-1}; the allochthonous loading is about 1000-fold larger (3000 mg C m^{-2} d^{-1}). Consequently, ecosystem respiration exceeds gross primary production by about 30-fold (Karlsson et al. 2012). Clearly, terrestrially supplied organic matter is respired in this lake. Using $\delta^{13}C$ and $\delta^{2}H$, Karlsson et al. (2012) calculated the terrestrial and autochthonous support provided to key benthic and pelagic consumers in this lake, based on each isotope alone. One of the objections to calculations that use multiple isotopes simultaneously is that the model assumes that the different elements (C, N and H for example) are moving together and have the same sources. They may not. Further, there are different problems associated with different elements. For $\delta^{13}C$, is it often difficult to distinguish terrestrial inputs from phytoplankton, but benthic algae and macrophytes are often quite distinct. For $\delta^{2}H$, benthic algae and phytoplankton are usually nearly identical, but quite different from terrestrial sources. Further, for $\delta^{2}H$ a portion of an organism's H comes directly from water, rather than from the food it consumes. This 'dietary water' is an issue for only $\delta^{2}H$ and not for $\delta^{13}C$ (Solomon et al. 2009). Using either isotope, Karlsson et al. (2012) found nearly identical terrestrial food subsidies to zooplankton (Fig. 26). Calanoid copepods had modest terrestrial support (about 25% with either isotope) but both cyclopoid copepods and cladocerans had terrestrial support of near 60% estimated with either isotope (Fig. 26). Given the very different problems and uncertainties with the 2 isotopes, the close agreement in the allochthony estimate is very strong evidence of the terrestrial support of zooplankton.

The majority of studies that have examined terrestrial support to zooplankton have been done in oligotrophic lakes with high DOC (Chapter 3, Table 8). To be thorough, one should also ask if the same techniques that lead to consistently large estimates of allochthony in high-DOC low-productivity lakes also give a reasonable estimate in naturally eutrophic lakes. I have already discussed the results of the ^{13}C addition experiments in artificially eutrophic lakes (above), but what happens in a naturally eutrophic lake? Ward Lake is a neighbor of Peter, Paul and Tuesday Lakes in the Upper Peninsula of Michigan. It is naturally eutrophic with luxuriant macrophyte growth, surface chl-*a* of 8 to 10 µg l^{-1} and a metalimnetic chlorophyll maximum that sometime reaches more than 50 µg l^{-1} (Batt et al. 2012). Batt and co-workers employed a Bayesian isotope mixing model modified from that of Solomon et al. (2011) and used the stable isotope ratios of C, H an N to evaluate the autochthonous and allochthonous resources used by key consumers in Ward Lake. Batt et al. (2012) found very low allochthonous support of zooplankton in this lake. For the dominant zooplankton species, *Skistodiaptomus oregonensis*, epilimnetic and metalimnetic phytoplankton accounted for 59 and 29%, respectively, of its resource use. The remaining 17% was made up from a combination of terrestrial and benthic resources. For *Chaoborus* spp., the results were similar, with 46 and 26% coming from epilimnetic and metalimnetic phytoplankton, respectively, and the remaining 25% split between benthic and terrestrial sources. So, the same techniques that reveal high allochthony in zooplankton in low-productivity, high-DOC lakes, reveal low allochthony in naturally eutrophic lakes.

Using the same gradient of lakes that Wilkinson et al. (2013b) used for POC and DOC (see Chapter 3), Wilkinson et al. (2013a) sampled 40 lakes

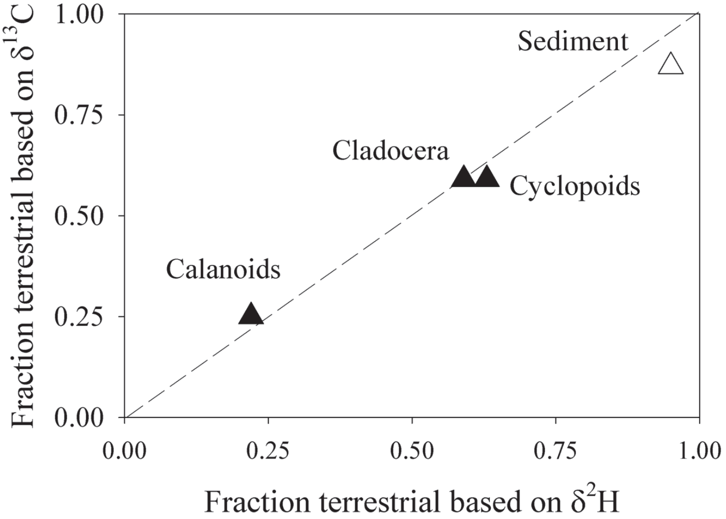

Fig. 26. Estimates, using 2 isotopes separately, of the terrestrial support of zooplankton in a boreal lake in Sweden (Upper Bear Lake). Filled triangles are 3 groups of zooplankton; the open triangle is lake sediments. The *x*-axis shows an estimate based only on δ^2H; the *y*-axis estimate is based only on δ^{13}C. The line is 1:1. Redrawn from the data in Karlsson et al. (2012)

for zooplankton, and obtained samples of *Chaoborus* for all of the lakes and crustacean zooplankton for 18 of them. Of the 18 lakes with zooplankton, Wilkinson et al. obtained 15 samples of cladocerans and 17 samples of copepods. Wilkinson et al. used both ^{13}C and ^{2}H to estimate terrestrial support to *Chaoborus*, cladocerans, and copepods. For those lakes that had deep chlorophyll maxima (15 of the 40) Wilkinson et al. (unpubl.) also used mixing models that included both epilimnetic and metalimnetic sources. The lakes were chosen to span a wide range of conditions and ranged from dystrophic to highly eutrophic. Eight of the lakes had chl-*a* concentrations above 10 μg l^{-1}; and 4 lakes above 20 μg l^{-1}. The estimates of allochthonous support of *Chaoborus*, based on ^{2}H, ranged from 4 to 82% and of crustacean zooplankton, from 1 to 76%. For both *Chaoborus* and the crustacean zooplankton, about half the lakes had allochthonous support of more than 30%. For the lakes that had deep chlorophyll maxima, including both the epilimnetic and metalimnetic sources did not change the estimates of terrestrial support to *Chaoborus*. For lakes that had both copepods and cladocerans, cladocerans tended to have larger terrestrial support than copepods. This study cannot tease out the separate importance of metalimnetic and epilimnetic sources, but it does show that whether or not metalimnetic resources are being used, there is, nevertheless, a significant terrestrial subsidy in many of the lakes. Among the lakes, allochthonous support was highest in small lakes with high DOC and color and low chlorophyll. Allochthonous support of zooplankton was positively correlated with the fraction of terrestrial material in POM (adjusted $r^2 = 0.54$) and negatively, but more weakly correlated with total phosphorus (adjusted $r^2 = 0.11$). Several other variables in combination were good predictors of zooplankton allochthony. These included the ratio of color:TP (adjusted $r^2 = 0.46$), the ratio of color:chl-*a*, and DIC (adjusted $r^2 = 0.51$) among others. Lake area was negatively correlated with terrestrial support of *Chaoborus* and this variable alone explained 49% of the variance. The results of Wilkinson et al. (2013a) suggest that terrestrial support of zooplankton is highly variable among lake types but likely widespread in small lakes with high DOC.

Laboratory evidence that zooplankton can consume terrestrial particles

To summarize, the evidence from field studies, largely based on stable isotopes (one study used ^{14}C, and one used specific fatty acids) suggests that in lakes and lake-like rivers, aquatic organisms, including zooplankton, are supported significantly by terrestrial inputs. Some studies are stronger than others and many gaps in our understanding remain. If the field studies are to be believed, it should be possible to demonstrate that zooplankton can both consume and grow on (directly or indirectly) terrestrially-derived organic matter sources at least in combination with autochthonous sources. There are 3 possible ways that a zooplankter could access terrestrial organic matter: (1) by direct assimilation of terrestrial DOM; (2) by consuming bacteria (or the protozoan consumers of those bacteria) that has assimilated terrestrial DOM; (3) by consuming particles of terrestrial origin that either entered the lake or were formed there by flocculation of terrestrial DOM. Which of these pathways might be either important or unlikely is the subject of a lot of debate. Direct uptake of DOM is reported to occur for *Daphnia*, from laboratory studies, but the process is not likely significant to its carbon balance (Speas and Duffy 1998). So, this pathway exists but there is no strong evidence that it is ever important. There are numerous studies from both the field and the laboratory showing the capabilities of zooplankton, particularly cladocerans, to ingest bacteria (Peterson et al. 1978, Pace 1988, Tranvik 1989), and some evidence to suggest that bacteria can supply a significant amount of the organic matter ingested by *Daphnia* (Work et al. 2005, Karlsson et al. 2007, Sawstrom et al. 2009). It is also well known that many zooplankton species can, and do, consume heterotrophic flagellates that feed on bacteria. So, there are well-documented mechanisms to move DOM, via bacteria, into zooplankton. What is in question about this pathway is how quantitatively significant it is, and under what conditions (see e.g. Kritzberg et al. 2004, Cole et al. 2006).

Two recent studies show that cladocerans in the laboratory are capable of growth from feeding on terrestrial particles. Masclaux et al. (2011) attempted to grow 2 cladoceran species (*Daphnia longispina* and *Simocephalus vetulus*) in the laboratory on a diet of pollen from 3 genera of trees (*Alnus, Populus*, and *Cedrus*). Both cladoceran species were able to grow on a diet of *Populus* and *Cedrus* pollen, but grew at rates about half that obtained on a good algal food source (*Scenedesmus obliquous*). *Daphnia*, but not *Simocephalus*, also grew on a diet of *Alnus* pollen, again at about rates that were half optimal. While treating *Cedrus* pollen by sonication did not increase growth rates, pre-incubating the pollen with fungi and bacteria resulted in nearly optimal growth of both cladoceran species. Masclaux et al. (2011) concluded that while fresh pollen may not support much growth of zooplankton, pollen conditioned by microbial colonization might be a significant subsidy to zooplankton. It is also interesting that even without the fungal treatment, pollen in the dark could support zooplankton growth that was nearly half the optimal rate. Half optimal growth rates are still substantial rates of growth to be supported on this apparently recalcitrant terrestrial material and in the absence of algal photosynthesis. Working in a small oxbow lake, Masclaux et al. (2013) demonstrated the actual importance of pollen to some zooplankton. Using a combination of fatty acid and stable isotope analyses, Masclaux et al. (2013) estimate that pollen represents about 90% of the C supplied to *Scapholeberis* sp. and 66% to *Chydorus* sp. On the other hand, phytoplankton were the major contributors of C to both *Bosmina* sp. (79%) and calanoid copepods (99%).

Brett et al. (2009) attempted to grow *Daphnia magna* in the laboratory on a diet of alder leaves (*Alnus*) ground into particles of about the size range that *Daphnia* would ingest. As with the pollen experiment, alder leaves alone were a poor food for *Daphnia*; reproduction did not occur and growth rate was about 20% of growth rate on an optimal food source (*Cryptomonas ozolinii* in this case). Brett and co-workers then gave *Daphnia* mixtures of the alga and leaves while keeping the total amount of added C constant. In this case, growth and reproduction when the terrestrial component was 80% of the total, was not statistically different from growth on the alga alone (Fig. 27). This experiment suggests that terrestrial particles may assist growth and reproduction, but that something essential is provided by the alga. Brett et al. (2009) demonstrated that a large fraction of the fatty acids, independent of the relative mixture of terrestrial and algal organic matter, came from the alga. In lakes, zooplankton would never experience terrestrial organic matter in isolation; they would almost always encounter some algae. This study demonstrates the potential for a significant terrestrial subsidy to zooplankton in the presence of an algal component (which would almost always be present in any system that supported zooplankton).

In a recent and elegant expansion of this type of work, Taipale et al. (2013) grew *Daphnia magna* in the laboratory on a variety of diets consisting of many combinations of specific cultured algae, specific cultures of freshwater bacteria, and terrestrial particles derived from the grass, *Phragmites australis*. Taipale et al. (2013) ground the *P. australis* finely and then allowed it to incubate in lake water in the dark for 2 months to simulate the sort of degraded terrestrial particles (t-POC) that zooplankton might encounter. To increase their ability to detect isotopic difference among sources, the authors also labeled the algal cultures with ^{13}C and ^{15}N in some of the experiments. Further, Taipale et al. (2013) also used specific fatty acids and sterols to actually quantify the food sources for *Daphnia*. As I mentioned above, most prior work with biomarkers has been qualitative rather than quantitative. As expected, t-POC alone was a poor food source for *Daphnia*; on a diet of 100% t-POC, *Daphnia* were smaller than when fed on any other single food source. However, on mixtures of 75% t-POC and 25% *Cryptomonas marsonii*, growth rates and reproduction were as high as on a diet of 100% algae (a mixture of *C. marsonii*, *Chlamydomonas* sp., and

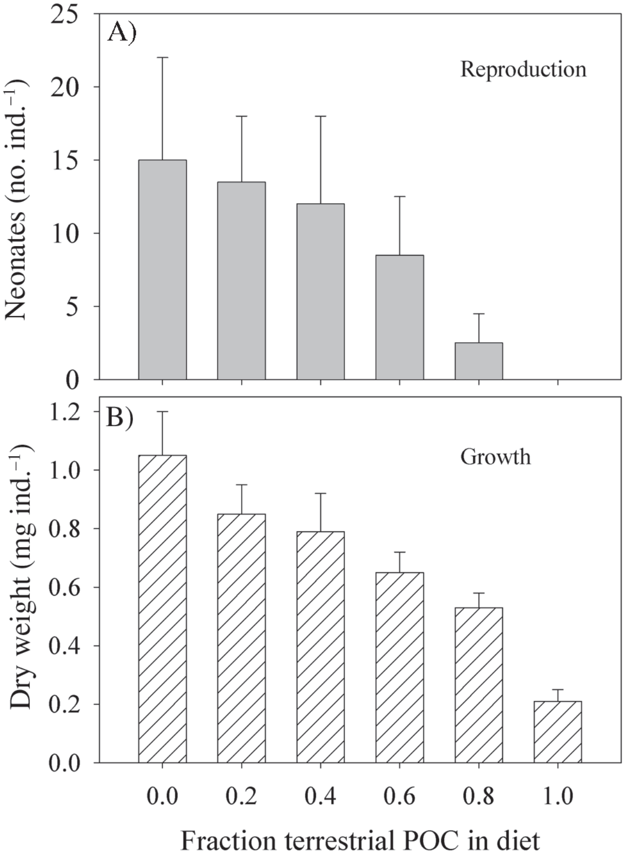

Fig. 27. (A) Reproduction and (B) growth of *Daphnia magna* on mixtures of terrestrial particles (alder leaves) and an alga food source (*Cryptomonas ozolinii*). The food quantity was kept constant and the *x*-axis shows the fraction of this that was terrestrial. Thus, 1.0 means that no algae were added; 0.0 means the diet was entirely algal. Note that on a diet of only 20% algae (and 80% alder leaves), both growth and reproduction of *Daphnia* were robust, with growth at about half the rate on the pure algal diet. Redrawn from the data of Brett et al. (2009)

Scenedesmus gracilis). Further, in batch experiments, t-POC supplied 68 to 71% of the assimilated C (based on ^{13}C) in mixtures that were 95% t-POC and 5% algal. As the proportion of t-POC in the diet was lowered, the fraction of C from t-POC dropped steeply and in a non-linear fashion. For example, at 50% t-POC and 50% *Scenedesmus*, t-POC contributed only 26% of the C. Nevertheless, even at 5% t-POC and 95% *Scenedesmus*, 5% of the assimilated C came from t-POC. This laboratory experiment proves that *Daphnia* can assimilate terrestrial C. Further, this work agrees qualitatively with the recent field study of Wilkinson et al. (2013b) who found that the fraction of terrestrial organic matter in zooplankton varied directly with the fraction of terrestrial material in the seston.

Is terrestrial support of lake food webs only in the eye of the beholder?

The simple answer to this question is, ‘No.’ The combined evidence from the field in terms of stable isotopes (many studies); radiocarbon (one study; Caraco et al. 2010) and fatty acids (one study; Perga et al. 2009) suggest that zooplankton, at least under some conditions, do obtain terrestrial organic matter. The evidence from the laboratory suggests that several pathways potentially allow zooplankton to access terrestrial organic matter (see above). There are several key unanswered questions. (1) Under what conditions do zooplankton get significant subsidies from the watershed? (2) Which mechanisms are the important ones that provide terrestrial organic matter to zooplankton? And (3), Is this use of terrestrial organic matter actually a ‘subsidy’ or is it merely a dilution (Jones et al. 2012)? Until more research comes in, I can provide only a set of personal speculations. The answer to the first question, I think, is quite simple, and nicely explained by Marcarelli et al. (2011). Most organisms are highly selective and where possible attempt to select the food with the highest nutritive qualities. Usually the autochthonous resource is the better one. However, when autochthonous resources are rare and terrestrial sources abundant, many organisms will obtain some of their nutrition from the terrestrial resource. This idea is very well supported by the studies of Cole and Solomon (2012) and Karlsson et al. (2012), which both show that zooplankton selectively consume algae but nevertheless obtain significant support from the more abundant terrestrial resources. There may also be an interaction with the kinds of consumers present. Filter feeders are probably less capable of strong electivity than are consumers that select individual particles. The cases in the literature (see Table 8 in Chapter 3) in which some cladocerans appear to be more terrestrially supported than a calanoid copepod from the same system could be an example of this principle. Jansson et al. (2007) make a good case that ‘basal resources’ in lakes have multiple sources. One part comes from the primary production in the lake and another part comes from the bacteria that use DOM. The DOM, in turn, may be derived from either allochthonous or autochthonous sources. This also seems a reasonable conceptual model if it can be demonstrated that bacteria vary in their reliance on terrestrially derived DOM.

Based on the weight of evidence of multiple studies and approaches, it is highly likely that terrestrial food subsidies are significant to aquatic organisms, including zooplankton, in some freshwater lakes and rivers. The allochthony controversy has missed its mark. The question should not be whether or not a subsidy exists, but under what conditions, how widespread the occurrence is, in what kinds of systems, and for which kinds of organisms, is it important. There is ample evidence that terrestrial organic matter enters the aquatic food web. There is also a great deal to yet work out for how terrestrial organic matter enters the aquatic food web. There are intriguing mysteries here. For example, do zooplankton obtain their terrestrial signal from the DOM to bacteria pathway, or by direct consumption of terrestrial particles? Both pathways are possible, based on experiments in the laboratory, but which pathways occur and to what extent, in nature? The controversy has another interesting dimension. While numerous studies presented in the previous chapter (Chapter 3, Table 8) show significant terrestrial support of zooplankton, there are several repeating groups of people who get these results. These are: ‘The Loch Ness Monsters’ (Roger Jones, Jonathan Grey, Darren Sleep and others who worked together on Loch Ness but then dispersed to work on other systems — during the Loch Ness Diaspora — or who worked with the Loch Ness folks elsewhere, such as Mila Rautio); ‘The Swedish Axis of Isotopes’ (including Mats Jansson, Jan Karlsson, Lars Tranvik, Jenny Ask, and their numerous students and postdocs who have worked largely in Swedish lakes) and ‘The Trophic Cascaders’ (myself, along with Steve Carpenter, Mike Pace, Jim Kitchell, Jim Hodgson and our many former and current students and postdocs — notably here Grace Wilkinson, Ryan Batt, Chris Solomon, Brian Weidel from the USA and Emma Kritzberg and David Bastviken from Sweden) who worked together for many years on small lakes on the Wisconsin-Michigan border. On the other hand, many of the major critics of the idea of the allochthonous support of zooplankton all have a Seattle connection (Michael Brett, Daniel Schindler, Tessa Francis and the folks they have worked with on this). There are now many more scientists working on this topic outside of these groups, and it will be interesting to see how the controversy plays out as it reaches more scientists.

5 WHY IS THERE SO MUCH ORGANIC CARBON IN THE SEDIMENTS OF LAKES?

Of Deans and Danes

This chapter is about the burial of organic C in the sediments of lakes. This is an interesting topic for several reasons. First, this burial is quite large (Stallard 1998, Alin and Johnson 2007). There is about as much organic C in the sediments of lakes as in the entire remainder (e.g. soils, vegetation) of the terrestrial biosphere (Fig. 28). Carbon burial in lake sediments is also increasing in modern time with clear anthropogenic effects of agriculture, land-use changes, and nutrient inputs (Heathcote and Downing 2012). Most interesting for us here is that the mechanisms that promote C preservation in lake sediments are poorly understood at present. While oceanography is theory-rich in explaining C burial in marine sediments, limnological theory is not well developed. In Chapter 1 we met Tollund Man, a well-preserved Dane in a bog who met his end about 2500 years ago. There are many other examples of what John Downing calls 'extreme preservation' events in freshwaters (Downing 2009). A favorite is the case of Mabel Smith Douglas, the

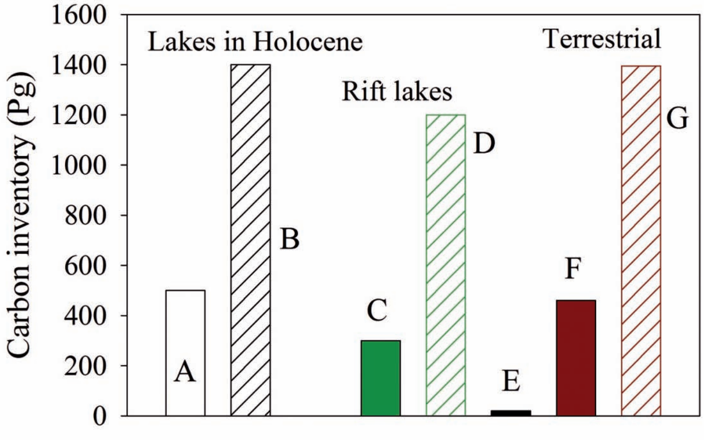

Fig. 28. Carbon stores in lakes and in the terrestrial biosphere. Each bar represents the total amount of organic C (in Pg) stored in various components of the biosphere and for different time periods. (A) and (B) are 2 estimates of the C storage in lakes during the Holocene. (A) is based on old estimates of lake area (Cole et al. 2007); (B) uses the larger estimate of the global area of small lakes and the higher organic matter content in small lakes (Downing et al. 2006, Tranvik et al. 2009). (C) is for Lake Malawi and (D) for all the African Rift lakes (from Alin and Johnson 2007). (E) is the carbon in reservoir sediments (Stallard 1998), (F) and (G) represent the total terrestrial C store in biomass (F) and soils (G) (both from Houghton 2005)

first Dean of the New Jersey College for Women. She disappeared while rowing a boat on New York's Lake Placid in 1933. Her remarkably well-preserved body was found by SCUBA divers in 1963, according to the New York Times (Sept. 26, 1963). The divers said that the body showed no signs of decomposition. Interestingly, the death was ruled accidental despite the rope that was found around her neck attached to a 50-pound anchor. Foul play aside, it is intriguing how the sediments in fresh waters, but not those in salt water, can be such a good environment for preservation. Beyond Danes and Deans, this chapter investigates the phenomenon of C preservation in lake sediments and explores what we know about its causes.

The marine hypotheses for carbon burial

Oceanographers have been having an active debate for decades on the processes that lead to carbon preservation in marine sediments. To make this as simple as possible there are 2 major hypotheses: (1) the oxygen-exposure-time hypothesis; and (2) the sorptive-preservation hypothesis. The former asserts that it is the lack of oxygen in sediments that allows organic C to be preserved: the latter argues that organic C is preserved because of its close association with clay. The 2 are well explained in Hartnett et al. (1998).

Marine sediments, and the sedimentary rock formed from them, represent the largest pool of organic C on earth. Although contemporaneous rates of C burial in marine sediments are not large (about 0.12 Pg C yr^{-1}), they are continuous. That is, until subduction occurs at the continental margins, organic C accumulates at this average; and even after subduction, some of the C is preserved in sedimentary rock. This enduring process leads to an enormous, very long-term (hundreds of millions of years), sink for atmospheric CO_2. In contrast, C accumulation on land is relatively short-lived and reaches a steady state after a few centuries. So, while the C pool on land is reasonably large, it tends to not increase much for extended periods.

Because C preservation in marine sediments is so large, it has been well studied (Hedges and Keil 1995). The C content of marine sediments is actually quite low (usually less than 0.1% organic C by weight). The reason that marine C accumulation is large is that there is a lot of sediment. Most of the ocean bottom is in contact with well-oxygenated water, even at abyssal depths. However, there are a few exceptional, small areas in the deep ocean where sediments are in contact with anoxic water. Early observations of the deepest spots in the ocean, such as the Cariaco Basin, revealed much higher than mean oceanic concentrations of organic matter (2 to 5%; Thunell et al. 2000 and references therein) and anoxic or hypoxic water (Richards and

Vaccaro 1956). These observations led some researchers to suggest that a low oxygen concentration was the cause of the high rates of C preservation at these especially deep sites. The counter-argument is that the low oxygen concentration is the result of high deposition of organic C and that a low oxygen level, per se, does not control C burial. Further, other basins with low or no oxygen, like the Black Sea, have low accumulations of organic C in sediments (Calvert et al. 1991). The sorptive-preservation hypothesis argues that a low oxygen concentration is not the key factor in C burial. Rather, the sorption of organic compounds to clays accounts for their long-term preservation (Mayer 1994, Mayer et al. 2004). In this hypothesis, the presence of clay with free sorption sites is the key factor. That this debate in the ocean, on such a fundamental issue, has not yet been resolved is fascinating.

The organic content of lake sediments is much higher than that of typical marine sediments. When I joined the Woods Hole Oceanographic Institute as a post-doctoral researcher in the Geology Department, I went to work with Dr. Susumu ‘Sus’ Honjo. He was measuring the sedimentation rate of particles all over the ocean, with high-tech sediment traps. Sus wanted me to write a proposal to work in the Panama Basin because he had an excellent set of sediment traps there (Honjo et al. 1982) and because this site had ‘high’ organic C in the sediments (about 1% by weight). We wanted to see how the sediment flux (sinking particles) changed into sediment during very early diagenesis (Cole et al. 1987). When we first discussed this I said that 1% organic C content did not sound high to me. I told Sus that I had worked on lakes during my thesis work and many lakes had organic C contents of 20% and higher. Sus told me that I must mean 20‰, not percent. We eventually worked out this argument but it pointed out that, in terms of the organic content of sediments, lakes and the ocean can be very different.

What controls carbon burial in lakes?

Lake size

There is a well-known relationship between lake area and the organic content in the sediments. For example, Rowan et al. (1992) compiled data from 80 lakes in Canada plus a handful from Europe and Africa (Fig. 29). There is a highly significant ($p < 0.001$) negative relationship between organic content (as a percentage of dry weight) and lake area (Fig. 29). Log (Lake size) explains about 54% of the variation in log (organic content). In this data set the average lake has an organic content of about 30%, which would correspond to an organic C content of about 15%. The smallest lakes in this data

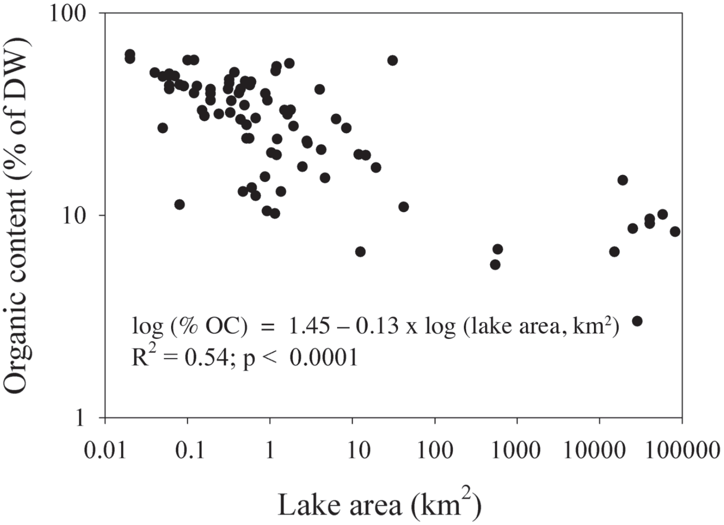

Fig. 29. The relationship between lake size and the organic content of surface sediments. The plot of log (lake area) versus log (sediment organic matter) is highly significant ($p < 0.001$) and lake area explains about half ($r^2 = 0.54$) of the variance in sediment organic matter. Redrawn from the data in Rowan et al. (1992)

set (about 2 ha) have organic contents near 60% (Fig. 29). The 13 lakes in this data set that are 15 ha or smaller have a mean organic content of 45% with a standard deviation of only 12%. So, we can see that lakes tend to have much higher sedimentary organic content than does the ocean, and increasingly smaller lakes have increasingly larger organic C contents.

Burial efficiency and its possible controls

Why is there so much organic C in the sediments of lakes and especially small lakes? Could large differences in inputs to the sediments be the cause? Surface particles have a much longer time to decompose during transit through the deep ocean water-column than through shallow lakes (Pace et al. 1987). Both primary production and external inputs can also be lower in the ocean than in some lakes. To remove the direct effect of inputs, oceanographers often look at burial efficiency (BE). BE is the fraction of input to the sediment surface that is ultimately buried. BE can be measured by comparing the accumulation rate of organic C in sediments (from cores) to either the input of sediment-forming material (estimated from sediment traps) or, more commonly, to sediment respiration. The idea here is that the incoming C is either buried or respired and that the sum of burial and respiration is equal to that input. So the total amount of organic C that reaches the sediment is the sum of the burial rate (B) plus the respiration rate (R). Then burial efficiency is expressed as:

$$\mathrm{BE} = B / (B+R) \tag{19}$$

BE can be expressed as a ratio or, more commonly, as a percentage.

Do lakes tend to have high or low BE compared to the ocean and how does BE vary among lakes? Sobek et al. (2009) examined BE in a suite of 11 lakes and at multiple sites within these lakes. The overall mean BE was 48%, i.e. nearly half of the organic matter that reaches the lake bottom is ultimately sequestered into sediments. This is much higher than BE at most oceanic sites, where it is usually under 20% and often under 5% (Betts and Holland 1991, Hartnett et al. 1998). Sobek et al. (2009) then stratified the lakes and sites within the lakes, as ones likely to have high allochthonous inputs (i.e. near-shore sites and small lakes) and sites not likely to have high allochthonous inputs, based on nearness to shore. The high allochthonous sites had a mean BE of 67%; the autochthonous sites had a mean burial efficiency that was lower, but still high by marine standards (23%). Sobek et al. (2009) produced an intriguing graph by plotting BE against calculated oxygen exposure time, and separating the autochthonous from allochthonous sites (Fig. 30). The plot shown here was assembled by Sebastian Sobek and

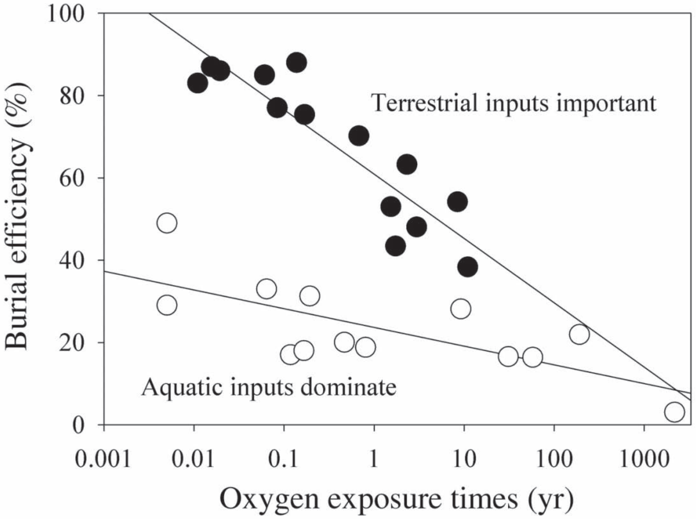

Fig. 30. The relationship between sediment burial efficiency and oxygen exposure time in the sediments of lakes. The open circles show lakes or sites in a lake that are dominated by autochthonous inputs (from aquatic primary production); the filled circles show lakes or sites dominated by allochthonous inputs (from terrestrial primary production). The plot combines data from Sobek et al. (2009, 2011), kindly provided by S. Sobek

kindly sent to me for use in this book. This plot combines the data from his 2009 review (Sobek et al. 2009) with newer data from another paper (Sobek et al. 2011) on Lake Kinneret. The pattern is striking. BE increases as oxygen exposure time gets shorter, but the line is much steeper for sites and lakes where terrestrial inputs are high. That is, in the presence of terrestrial inputs, the effect of low oxygen concentration is more pronounced (Fig. 30). The pattern in Fig. 30 suggests that at least 2 factors are important in explaining BE, oxygen exposure time and the influence of terrestrial material.

A simple predictive model of sediment organic content

The Sobek et al. (2009) plot (Fig. 30) could help to explain why smaller lakes tend to have higher organic contents in their sediments. Small lakes, at many locations, would tend to receive relatively more allochthonous inputs and small lakes are more likely to be stratified for long periods. However, the Sobek plot is far from conclusive evidence that either oxygen or allochthonous inputs are the key cause of the variation in the carbon content of lake sediments. Using data from 40 Swedish lakes, Hakanson and Peters (1995) tried to construct a simple predictive model that would explain the variation in the organic content of the upper layer of sediments (Fig. 31). The statisti-

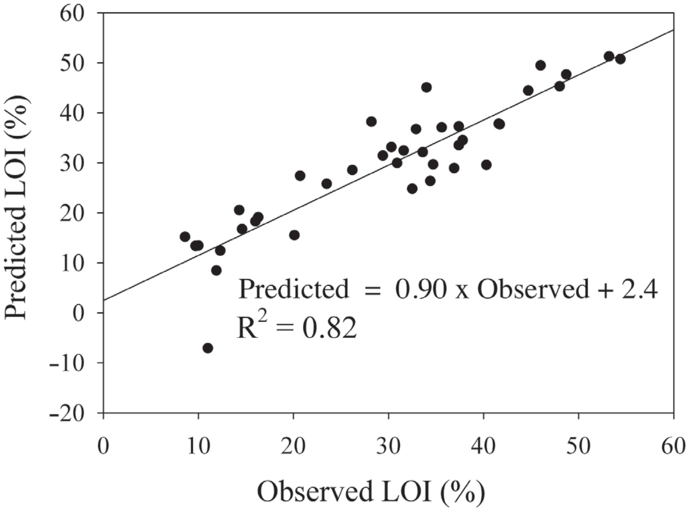

Fig. 31. A model of the carbon content of lake sediments. The plot shows the predicted organic matter content (as loss on ignition or LOI) observed in 39 lakes (*x*-axis) and the modeled value for the same lakes (*y*-axis). The model is explained in the text. Significantly, the model does not use dissolved oxygen in the prediction. Redrawn from Hakanson and Peters (1995)

cal model explains 82% (adjusted R^2) of the variance in the observed data and has a slope near unity and an intercept near zero. Interestingly, the Hakanson-Peters model does not use dissolved oxygen or oxygen exposure time as predictors. Instead, it uses the ratio of watershed to lake area; relative depth (a measure of the mean slope of the lake bottom), pH and water color (Fig. 31). While the prediction is good, it does use a lot variables, so the adjusted R^2 is not spectacularly high. Again, this is also not strong evidence that the oxygen level is unimportant, because oxygen is probably correlated with both pH and relative depth. Further, water color and the ratio of watershed to lake area could be proxies for allochthonous loading.

Experimental approaches

Whole lake experiment. An experiment that manipulated bottom water oxygen concentrations in lakes could shed some light here. Engstrom and Wright (2002) studied 10 lakes in Minnesota, of which 5 lakes were aerated to control P release, and 5 lakes were not. The aeration was long-term (5 to 15 yr) and Engstrom and Wright obtained sediment cores from prior- and post-aeration periods (Fig. 32). Interestingly, there was no decrease (on average) in the organic C content of the aerated lakes compared to the non-aerated lakes (Fig. 32). In fact, no lake in either group decreased in organic C content in the sediments. This study had only a few lakes and the authors do not report how effective the aeration was. That is, they do not tell us the concentrations of oxygen near the sediment–water interface. So this study, like some of the others, is intriguing but somewhat inconclusive.

Laboratory experiments. There are a large number of laboratory studies that have examined either the rates of bacterial growth or the mineralization of organic C under oxic and anoxic conditions. A general pattern is that, over the short term (hours to weeks), there is not a great deal of difference in mineralization rates with labile substrates. As a marine example of this type of work, Andersen (1996) labeled diatom cells (*Skeletonema costatum*) with ^{14}C and exposed these to sea-water microcosms that were either oxic or anoxic. Using evolved $^{14}C\text{-}CO_2$ as a measure of mineralization, Andersen (1996) found that 58% of the added diatoms was mineralized in the aerobic treatment, while 48% was mineralized in the anaerobic treatment, after an 80 d incubation. Given the errors, these means are not likely statistically different. With marine levels of sulfate, there is still a huge pool of electron acceptors in this anoxic water. Looking at the data another way, Andersen (1996) measured the amount of original $PO^{14}C$ that remained as particles. The oxic and anoxic treatments had nearly identical amounts of remaining

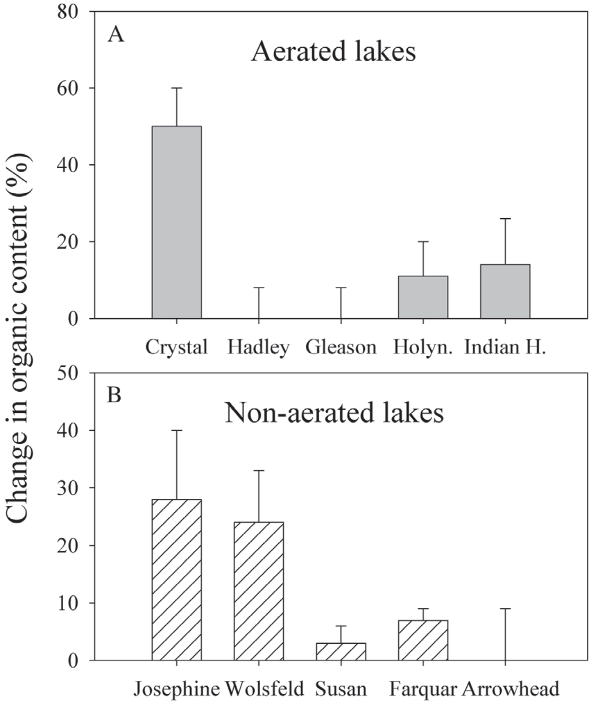

Fig. 32. The effect of experimental aeration on sediment organic C in 10 lakes in Minnesota. Shown is the change in the organic content of surface sediments of (A) 5 lakes that were aerated for several years and (B) 5 lakes that were not aerated. Redrawn from Engstrom and Wright (2002)

substrate (31 and 37%, respectively). That is, the sum of ^{14}C-CO_2 and ^{14}C-DOC lost from the original particles over 80 d was about the same. The difference, although small, is that the DOC was mineralized more rapidly in the aerobic treatment.

How do oxic and anoxic decomposition rates compare in fresh waters and on less labile substrates? Bastviken et al. (2001) compared the growth rate of bacteria in waters from several lakes in Sweden, in which they created either oxic or anoxic conditions. These authors watched the regrowth of bacteria in dilution-regrowth experiments. While the different lakes and lake strata had dramatically different bacterial growth rates, within a lake or stratum there was essentially no difference between the oxic and anoxic treatments. Bacteria grew just as quickly in the presence or absence of oxygen. In this study the authors did not measure bacterial respiration. The inference is that bacteria probably mineralized more substrate in the anoxic treatments to maintain similar growth rates because of the lower energy yields under the anoxic conditions. In a companion paper using the same system, Bastviken et al. (2004) showed that the bacterial production, measured as the incorporation of ^{3}H-leucine, also did not differ between the anoxic and oxic treatments in these lakes. Thus, both the cell counts and the biochemical measure of growth rate give the same qualitative picture; the absence of oxygen is not slowing down bacterial growth.

In a still more realistic experiment, Bastviken et al. (2004) measured decomposition rates in sediment slurries from 2 Swedish lakes, one eutrophic (Maarn) and one humic and oligotrophic (Lillsjon). For each lake they created replicate oxic and anoxic treatments (by bubbling with different gases) and measured the total amount of both CO_2 and CH_4 that was produced over time (Fig. 33). In the eutrophic lake, there was barely a difference in decomposition rates between oxic and anoxic treatments (Fig. 33). In the humic lake, the rate of decomposition under oxic conditions was about twice as fast as that under anoxic conditions. The pattern in this experiment supports the correlation observed by Sobek et al. (2009) and shown in Fig. 29. That is, there is a clear effect of anoxia and that effect is stronger with less labile substrates, such as terrestrial inputs.

Other factors

I have shown that 2 factors, low oxygen levels and allochthonous inputs, are associated with high C burial across many, but not all, of the studies to date. Are there other factors to consider? Gudasz et al. (2010) combined a large

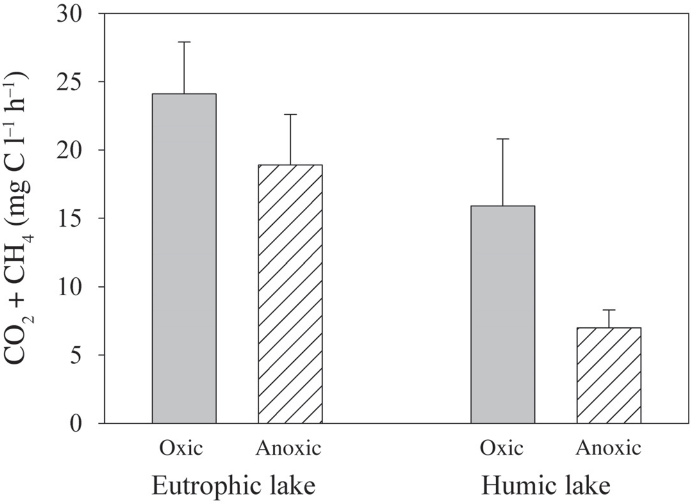

Fig. 33. The rate of sediment mineralization (as the sum of the production of CO_2 and CH_4) in the sediments of a eutrophic lake (Maarn, left pair of bars) and a humic lake (Lillsjon, right pair of bars). In each case the hatched bar shows the results for anoxic incubations while the grey bar show those for oxic incubations. Drawn from data reported in Bastviken et al. (2003)

literature survey with their own new data from lakes in Sweden and found a strong relationship ($r^2 = 0.43$, $n = 574$) between log (temperature) and (sediment mineralization) rates in boreal lakes. There are several intriguing things in this relationship. First, the mineralization rates increase as a power law with increasing temperature, with a slope of about $10^{0.034}$, or a Q_{10} of about 2. Then, in experimental work, Gudasz et al. (2010) incubated sediments from contrasting lakes over a range of temperatures and came up with almost the identical relationship as in the cross-system correlation. A very eutrophic lake with autochthonously-dominated sediments had the same Q_{10} as a highly humic lake with allochthonously-dominated sediments. The bacterial production in these lakes is also highly correlated to sediment mineralization (Gudasz et al. 2012). Thus, both sediment mineralization and bacterial production are about equally influenced by temperature. By examining these temperature relationships along with estimates of burial efficiency, Gudasz et al. (2010) argue that global warming will lead to greater mineralization of sediment organic C, and lower C burial, in boreal lakes and that this increase will occur even in the face of increased C loading to lake sediments from processes such as increasing eutrophication (Heathcote and Downing 2012). Gudasz (2011) compared the effect of temperature on organic C mineralization in lake sediments to what is known about terrestrial soils. The lake sediments are more sensitive to temperature increases than are soils (higher Q_{10}; Gudasz 2011).

Why are lakes hotspots for organic carbon burial?

A brief summary of what we have learned so far. Clearly, lakes tend to have high concentrations of organic C in their sediments — bury a lot of organic C — and in this respect are disproportionately important compared to the small area of the planet they occupy (Alin and Johnson 2007, Cole et al. 2007). This makes lakes ‘hotspots’ of C sequestration (McClain et al. 2003). While the store of organic C in sediments is very large, the annual increment (the burial rate) is low (Kortelainen et al. 2004, Buffam et al. 2011). For northern regions rich in lakes, it works out there is about as much organic C in lake sediments as in the watersheds of the lakes. One of the key reasons for this is simply that lake sediments endure for tens of millennia or more, while forest biomass and soils are dynamic at the decadal to century time step, sometimes increasing rapidly, sometimes decreasing rapidly. The experimental and correlative studies suggest that both low oxygen concentrations and allochthonous inputs tend to be correlated with higher burial rates among different lakes. One aspect of a low oxygen level that has not been explicitly investigated in lakes is its effect on the activity of benthic invertebrates. Invertebrates can be critical in breaking large particles into small ones that are more easily attacked by bacteria. To the extent that a low oxygen level excludes most invertebrates, this could have a profound effect on sediment mineralization rates.

Two contrasting hypotheses, and Shakespeare. The lake studies agree with the marine studies in that oxygen exposure is one important control on organic C burial in sediments. The lake studies have advanced the idea, not discussed extensively in the marine literature, that terrestrial inputs tend to increase C preservation. As far as I know, there are no studies on lakes that directly address the other major marine theory, that of sorptive preservation. If the evolving model is correct, it suggests 2 contrasting and testable hypotheses. (1) Let's call the first idea the 'selective preservation of allochthonous inputs hypothesis.' If the allochthonous material simply degrades more slowly, we would expect that the concentration of terrestrially-derived materials should be greater in the sediments than in the material reaching the sediments. The alternative is more complex. Let's call this second idea the 'allochthonous protection hypothesis.' If sediment mineralization is slower in the presence of allochthonous materials, but the concentration of allochthonous material in the sediments is not higher than that which reaches those sediments, the inference has to be that allochthonous material protects the more labile autochthonous materials from being degraded. Shakespeare's gravediggers in Hamlet address this hypothesis, albeit for soil, in Act V, Scene I:

> Hamlet: '*How long will a man lie i' the earth ere he rot?*'
> Gravedigger: '*I' faith, if he be not rotten before he die—*
> *as we have many pocky corses now-a-days that will*
> *scarce hold the laying in —he will last you some eight*
> *year or nine year: a tanner will last you nine year.*'
> Hamlet: '*Why he more than another?*'
> Gravedigger: '*Why, sir, his hide is so tanned with his*
> *trade, that he will keep out water a great while, and your*
> *water is a sore decayer of your whoreson dead body.*
> (indicates a skull) *Here's a skull now. This skull has lain*
> *in the earth three-and-twenty years.*'

It seems unlikely that terrestrial DOM sorbed to otherwise labile particles would 'keep out water' but there might be something to the gravediggers practical wisdom that sorbed DOM interferes with microbial enzyme attachment on algal particulates.

There is some evidence for the ‘selective-preservation’ hypothesis from the PhD work of von Wachenfeldt (2008). At the time of this writing the key paper on this topic (Paper IV, ‘Preferential sequestration of allochthonous organic matter in boreal lake sediments’) has not been published, but it is likely that it will be soon. Von Wachenfeldt and his co-workers (L. Tranvik and D. Bastviken) compared various measures of both particulate flux and surface sediments in a series of 12 lakes in Sweden. They examined C:N ratios of the particulate material, and in extracts of sediments, they used 3-dimensional fluorescence spectroscopy and evaluated this with parallel-factor analysis (PARAFAC). The PARAFAC model allows the analysis of multidimensional matrices of fluorescence data (Bro and de Jong 1997, McKnight et al. 2001, Stedmon et al. 2003, Stedmon and Bro 2008) and can be used to develop indices of the allochthonous or autochthonous natures of the extract. Von Wachenfeldt (2008) found that all of the indices of allochthonous character increased in the sediments compared to those in the sinking particles. Conversely, most but not all of the autochthonous indices decreased in the sediments compared to those in the sinking particles. In these lakes, the bulk of sedimenting organic matter is of allochthonous origin and arose from the flocculation of terrestrially derived DOM (von Wachenfeldt and Tranvik 2008). Thus, sediments are enriched in terrestrially derived materials compared to the input into the sediments. These results support the idea that allochthonous material degrades more slowly than autochthonous material. On the other hand, von Wachenfeldt studied humic lakes where the particulates were dominated by terrestrial material. It would be interesting to see this analysis repeated in lakes that had a larger autochthonous fraction in the sinking flux and lower concentrations of DOM. I have not found evidence for the allochthonous protection hypothesis, but there is very little work that compares the allochthonous versus autochthonous character of sediment-forming particles. The von Wachenfeldt work is very intriguing. Nevertheless, the approach is a bit indirect. It depends on fluorescent analysis of extracts from sediments and some complex modeling of the results. Perhaps other tracers, for example δ^2H ratios, which have proven useful in the plankton, could be adapted to sediments. There are some issues with just measuring organic δ^2H in the presence of clays that contain water of inclusion (R. Doucett pers. comm.) but the method has been used with very reasonable results in lake sediments with low clay content (Karlsson et al. 2012). C. Gudasz and J. Karlsson are actively working on this problem, so look for papers by them and others in the near future. Of course it is possible that both the selective-preservation and allochthonous-protection mechanisms operate simultaneously. It will be exciting to see this problem sorted out.

Conclusions

I have shown that terrestrial C has important effects on lakes and lake-like rivers that receive this material from land. Inputs from land make lakes function quite differently from the ocean in many respects and an 'oceanographic' view of lakes that isolates them from their watersheds is not appropriate (Chapter 1). I have examined the large role that inland waters play in regional C budgets, and even in the global balance of C (Chapter 2). Allochthonous inputs affect the metabolic balance of lakes, and tend to push them towards net heterotrophy and the efflux of CO_2 from lakes into the atmosphere (Chapter 2). Further, these terrestrial inputs subsidize at least some components of the food webs of both lakes and rivers (Chapters 3 and 4). The idea of a terrestrial subsidy to lake food webs is an evolving story and remains surprisingly controversial (Chapter 4). In the final chapter, Chapter 5, I reviewed the mounting evidence that allochthonous inputs may enhance the burial of organic C in lake sediments and may be selectively preserved in these sediments in comparison to autochthonous inputs. The mechanisms that allow for large stores of organic C to accumulate in lake sediments are not yet fully worked out.

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Some of this work, particularly that on the terrestrial support of aquatic food webs, has been surprisingly controversial and there is no doubt that exchanges with our critics both in person and in the literature have improved and sharpened the research. These skeptical critics include Daniel Schindler, Tessa Francis and Michael Brett, in particular. There is nothing better for science than a good, loud, public disagreement.

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Most of the members of the NCEAS working group on *Integrating the Terrestrial and Aquatic Carbon Cycle*, also known as 'the usual suspects'. Starting at the back, left to right: Jack Middelburg, Carlos Duarte, Bill McDowell, Lars Tranvik, and Rob Striegl. Front row left to right: Jon Cole, John Downing, Pirkko Kortelainen, and Yves Prairie. Members not shown in the picture are Nina Caraco and John Melack. Photo by L. Afree

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About the Author and the Book


Jonathan Cole

Since the 1970s, Jonathan Cole has distinguished himself as an influential limnologist. His work is focused on microorganisms and carbon cycling in freshwater ecosystems, recently with particular attention to the exchange of carbon between freshwater and terrestrial systems, as well as with the atmosphere. He has been co-editor of and contributor to several important books on aquatic ecosystem research. In addition to his outstanding scientific work, Jon Cole plays a leading role as a manager of science, serving on numerous scientific committees, such as various panels of the National Science Foundation (USA). He has been very active in the American Society of Limnology and Oceanography (ASLO; recently renamed the Association for the Sciences of Limnology and Oceanography) as an organizer of special sessions at ASLO annual meetings, and he was President of ASLO from 2004 to 2006.

In EE Book 18, Jon Cole examines the role of freshwater ecosystems in the global carbon cycle and subsequently focuses on terrestrial subsidies to lake food webs. He analyzes the complex mechanisms responsible for converting allochthonous carbon into CO_2 efflux to the atmosphere, and discusses the importance of lake sediments as the planet's principal hotspots of carbon sequestration.

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