

# APPLIED AND ENVIRONMENTAL MICROBIOLOGY

VOLUME 74 • JULY 2008 • NUMBER 14

**L. Nicholas Ornston**, *Editor in Chief* (2011)  
*Yale University*

**Daniel J. Arp**, *Minireview Editor* (2009)  
*Oregon State University*

**Axel A. Brakhage**, *Editor* (2011)  
*HKI and University of Jena*

**Daniel Cullen**, *Editor* (2012)  
*USDA Forest Products Laboratory*

**Harold L. Drake**, *Editor* (2012)  
*University of Bayreuth*

**Katharine J. Gibson**, *Editor* (2011)  
*DuPont Experiment Station*

**Lone Gram**, *Editor* (2011)  
*Danish Institute for Fisheries Research*

**Mansel W. Griffiths**, *Editor* (2010)  
*University of Guelph*

**Jo Handelsman**, *Editor* (2010)  
*University of Wisconsin*

**Sophia Kathariou**, *Editor* (2012)  
*North Carolina State University*

**Michael J. Larkin**, *Editor* (2012)  
*The Queen's University of Belfast*

**Laura G. Leff**, *Editor* (2011)  
*Kent State University*

**Frank E. Löffler**, *Editor* (2013)  
*Georgia Institute of Technology*

**Charles R. Lovell**, *Editor* (2010)  
*University of South Carolina*

**Ellen L. Neidle**, *Editor* (2012)  
*University of Georgia*

**Douglas H. Ohlendorf**, *Editor* (2011)  
*University of Minnesota*

**Matthew R. Parsek**, *Cover Editor* (2009)  
*University of Washington*

**Donald W. Schaffner**, *Editor* (2010)  
*Rutgers, The State University of  
New Jersey*

**Alfred M. Spormann**, *Editor* (2011)  
*Stanford University*

**Marylynn V. Yates**, *Editor* (2009)  
*University of California—Riverside*

**Jizhong Zhou**, *Editor* (2013)  
*University of Oklahoma*

## EDITORIAL BOARD

Yousef Abu Kwaik (2008)

Luis A. Actis (2008)

Eric Altermann (2009)

Gary Andersen (2010)

Thomas Andlid (2010)

Adam Arkin (2009)

Beate Averhoff (2010)

Andrea Azcarate (2009)

Felix J. Baerlocher (2009)

Michael Bagdasarian (2009)

Bert Bago (2010)

Christopher E. Bagwell (2008)

Alan Bakalinsky (2009)

Katherine H. Baker (2009)

József Baranyi (2010)

Tamar Barkay (2008)

Douglas H. Bartlett (2008)

Florian Bauer (2009)

Gwyn A. Beattie (2008)

Harry Beller (2009)

Tahia Benitez (2008)

Andrew K. Benson (2009)

Peter L. Bergquist (2009)

Colin Berry (2008)

Tom Besser (2010)

Arvind A. Bhagwat (2009)

K. Johanna Bjorkroth (2010)

Rafael Blasco (2010)

David E. Block (2010)

Paul L. E. Bodelier (2008)

Antje Boetius (2008)

Eckhard Boles (2009)

Paola Bonfante (2009)

Violaine Bonnefoy (2010)

Kathryn J. Boor (2010)

Katherine A. Borkovich  
(2009)

James Borneman (2008)

Dulal Borthakur (2009)

Thomas L. Bott (2009)

Kostas Bourtzis (2009)

Gesche Braker (2008)

Michael G. Bramucci (2008)

Byron Brehm-Stecher (2010)

Frederick Breidt, Jr. (2010)

Neil C. Bruce (2010)

George Bullerjahn (2010)

William Burkhardt III (2010)

H. J. Busscher (2010)

Mark P. Buttner (2009)

Murulee Byappanahalli (2009)

Douglas R. Call (2010)

Terri A. Camesano (2009)

Russell W. Carlson (2010)

Michael J. Carter (2010)

Jinru Chen (2008)

Wilfred Chen (2009)

Michael L. Chikindas (2010)

John D. Coates (2008)

Luca Cocolin (2010)

James Cole (2010)

Mary Lynne Perille Collins (2008)

Michael T. Collins (2010)

James M. Cregg (2009)

Patricia Cruz (2010)

Tom Curtis (2010)

Lori L. Daane (2008)

Rolf Daniel (2009)

Steven L. Daniel (2008)

Michelle Danyluk (2010)

Atin R. Datta (2010)

Frank B. Dazzo (2010)

Angelo DePaola, Jr. (2009)

Anne Desjardins (2008)

Ronald P. de Vries (2008)

Thomas J. DiChristina (2008)

Alan DiSpirito (2008)

Jan Dolfing (2010)

Daniel P. Dougherty (2009)

Irina S. Druzhinina (2008)

Nicole Dubilier (2010)

Siobain Duffy (2010)

Peter Dürre (2008)

Nancy DuTeau (2008)

Richard Eaton (2010)

Leo Eberl (2008)

T. S. Edrington (2010)

Henry L. Ehrlich (2010)

Christopher Elkins (2008)

David Emerson (2009)

Scott A. Ensign (2008)

K.-D. Entian (2010)

Slava Epstein (2010)

Danilo Ercolini (2009)

David Faguy (2008)

Joseph O. Falkinham III (2010)

Brian Federici (2009)

Juan Ferré (2009)

Matthew W. Fields (2008)

Turlough Finan (2010)

Steven E. Finkel (2010)

Madilyn Fletcher (2008)

Christopher Francis (2010)

James A. Fraser (2009)

Herbert L. Fredrickson  
(2010)

Masao Fukuda (2009)

Clay Fuqua (2008)

Manuela Giovannetti (2009)

Heidi Goodrich-Blair (2009)

Lawrence Goodridge (2009)

Joerg Graf (2008)

Irene R. Grant (2010)

Jean Guard-Bouldin (2010)

Mary Lou Guerinot (2008)

Martin W. Hahn (2010)

Ken Hammel (2010)

Theo A. Hansen (2010)

Hauke Harms (2010)

Steven Harris (2008)

Valerie J. (Jody) Harwood  
(2009)

Terry C. Hazen (2010)

Qiang He (2010)

Zhili He (2010)

Hermann Heipieper (2008)

Alfredo Herrera-Estrella  
(2008)

Russell T. Hill (2008)

Dallas G. Hoover (2009)

David J. Hopper (2010)

Hor-Gil Hur (2009)

Fumio Inagaki (2010)

Douglas Inglis (2009)

Karl-Erich Jaeger (2008)

Janet K. Jansson (2010)

Lee-Ann Jaykus (2009)

Tom Jeffries (2008)

Paul R. Jensen (2008)

Peter Jensen (2008)

Carlos A. Jerez (2008)

Mike Jetten (2010)

D. Barrie Johnson (2008)

Yves Jouanneau (2009)

Ari Jumpponen (2009)

Juan Luis Jurat-Fuentes  
(2009)

David Kaplan (2010)

Levente Karaffa (2009)

Charles W. Kaspar (2010)

Jay D. Keasling (2008)

James E. Keen (2010)

Martin Keller (2009)

John J. Kelly (2009)

Robert M. Kelly (2008)

Angela Kent (2010)

Lee Kerkhof (2009)

Philip J. Kersten (2010)

David L. Kirchman (2008)

Mary Jo Kirisits (2010)

Maia Kivisaar (2010)

Staffan Kjelleberg (2008)

Martin G. Klotz (2008)

Allan Konopka (2008)

Joel E. Kostka (2010)

George Kowalchuk (2009)

Lee Krumholz (2009)

Indira Kudva (2010)

Kirsten Kuesel (2010)

Timothy M. LaPara (2009)

Laurie LaPat-Polasko (2009)

Gisèle LaPointe (2010)

Jared Leadbetter (2010)

Yin-Won Lei (2010)

Mary Beth Leigh (2010)

Jeffrey T. LeJeune (2009)

Michael Lemke (2008)

Celeste Linde (2008)

Markus Linder (2008)

Nic D. Lindley (2010)

John T. Lisle (2009)

Wen-Tso Liu (2010)

Jon Lloyd (2010)

G. T. Macfarlane (2008)

Robert Mach (2009)

Eugene L. Madsen (2008)

Walter F. Mahaffee (2008)

Mike Manefield (2008)

Helene Marquis (2009)	George-John Nychas (2009)	Verena Seidl (2009)	Jan van Beilen (2008)
Robert E. Marquis (2008)	Mark R. O'Brian (2009)	Gordon Shephard (2010)	Jos Vanderleyden (2010)
Terence L. Marsh (2008)	Kevin P. O'Connell (2008)	Wenyuan Shi (2008)	Alain Vertes (2010)
Andrew P. Martin (2008)	Ronald S. Oremland (2009)	Simon D. Silver (2008)	Anne K. Vidaver (2008)
Maria Esperanza Martinez-Romero (2010)	Mark Osborn (2010)	Anne Simon (2008)	Gerrit Voordouw (2008)
Jan Martinussen (2008)	Joerg Overmann (2010)	Pascal Simonet (2009)	Adrián A. Vojnov (2010)
Juergen Marxsen (2008)	Rebecca Ehrlich Parales (2008)	Randall S. Singer (2009)	Carmen Wachter (2010)
Luke Masson (2008)	Matthew A. Parker (2008)	Brajesh Singh (2010)	Michael Wagner (2010)
Harold D. May (2010)	John H. Paul (2008)	Kaarina Sivonen (2008)	Irene Wagner-Döbler (2008)
Alejandro Mazzotta (2008)	Jakob Pernthaler (2009)	Joan L. Slonczewski (2008)	Suzanne Walker (2009)
J. Vaun McArthur (2008)	M. Julia Pettinari (2008)	Kornelia Smalla (2009)	Judy D. Wall (2009)
Timothy R. McDermott (2008)	Flynn Picardal (2010)	Hauke Smidt (2008)	Peng G. Wang (2009)
Katherine McMahon (2009)	Roger W. Pickup (2010)	Patricia A. Sobecky (2010)	Todd Ward (2010)
Brian McSpadden-Gardner (2010)	James L. Pinckney (2008)	John Spear (2010)	Kazuya Watanabe (2008)
Rick Meinersmann (2009)	Anton F. Post (2010)	Andrew Spiers (2010)	Bart Weimer (2010)
Aubrey F. Mendonca (2009)	Rolf Prade (2009)	Dirk Springael (2009)	Ronald Weiner (2008)
Jianghong Meng (2009)	Jim I. Prosser (2008)	Ewald Strobotnik (2008)	Elizabeth M. Wellington (2010)
Eric S. Miller (2008)	Cheryl L. Quinn (2009)	Eric Stabb (2010)	Alan Welman (2009)
Robert V. Miller (2008)	John P. Quinn (2009)	Lucas J. Stal (2009)	Andrew S. Whiteley (2008)
Patricia D. Millner (2009)	Jos M. Raaijmakers (2008)	Alfons J. M. Stams (2010)	Marvin Whiteley (2010)
Donald K. Milton (2009)	Fredrick A. Rainey (2008)	Robert J. Steffan (2010)	Giovanni Widmer (2008)
Kiwamu Minamisawa (2008)	Gerald R. Reeck (2010)	Craig Stephens (2009)	Martin Wiedmann (2008)
William W. Mohn (2008)	Bernd Rehm (2009)	John Stolz (2010)	Steve Wilhelm (2009)
Sylvain Moineau (2008)	Gregor Reid (2009)	Wolfgang Streit (2009)	Joanne Willey (2008)
Istvan Molnar (2008)	Walter Reineke (2010)	Herbert Strobel (2008)	Rolf-M. Wittich (2008)
Melanie Mormile (2010)	Geoffrey D. Robson (2008)	Joseph Sturino (2010)	Mark J. Wolcott (2010)
Volker Müller (2010)	Neil Rowan (2008)	Marcelino Suzuki (2010)	K. Eric Wommack (2009)
Peter Muriana (2008)	Edward G. Ruby (2010)	Ken Takai (2010)	Thomas K. Wood (2008)
Yuji Nagata (2009)	Michael J. Sadowsky (2010)	Gerald W. Tannock (2008)	Randy Worobo (2010)
István Nagy (2010)	Badal C. Saha (2010)	Ron Teather (2010)	Michael Wyman (2009)
Cindy H. Nakatsu (2010)	Andrew D. Sails (2010)	Tuula Teeri (2008)	Dong Xu (2008)
Diane G. Newell (2010)	Sima Sariaslani (2009)	Andreas Teske (2009)	Jian Xu (2010)
Walter G. Niehaus, Jr. (2010)	Brian Sauders (2010)	Chris M. Thomas (2009)	Luying N. Xun (2008)
Brendan A. Niemira (2009)	Patrick D. Schloss (2009)	Michael G. Thomas (2009)	Chuanlun Zhang (2009)
Hideaki Nojiri (2009)	Andreas Schmid (2008)	Ian P. Thompson (2008)	Erwin G. Zoetendal (2009)
Kenneth M. Noll (2008)	Janet Schottel (2008)	Tim Tolker-Nielsen (2009)	Angeles Zorreguieta (2010)
Norbert Nowotny (2009)	Andreas Schramm (2010)	Eva M. Top (2009)	
	Kate M. Noll (2008)	Effie Tsakalidou (2010)	
	Bernhard Seiboth (2008)	Masataka Tsuda (2009)	

**Thomas E. Shenk**, *Chairman, Publications Board*  
**Barbara S. Slinker**, *Production Editor*

**Barbara M. Goldman**, *Director, Journals*  
**Ellie Ghatineh**, *Assistant Production Editor*

*Applied and Environmental Microbiology* (ISSN 0099-2240), a publication of the American Society for Microbiology (ASM), 1752 N St., N.W., Washington, DC 20036-2904, is devoted to the advancement and dissemination of applied knowledge as well as ecological knowledge, both applied and fundamental, concerning microorganisms. Instructions to authors are published in the January issue each year; reprints are available online and from the Journals Department. *Applied and Environmental Microbiology* is published twice monthly, one volume per year. Nonmember print subscription prices (per year) are: \$1,260, U.S.; \$1,375, Canada (plus 6% GST, or 14% GST+HST where applicable); \$1,359, Europe; \$1,392, Latin America; \$1,396, rest of world. Member print subscription prices (per year) are: \$164, U.S.; \$279, Canada (plus 6% GST, or 14% GST+HST where applicable); \$263, Europe; \$296, Latin America; \$300, rest of world. Single copies are: \$100, nonmember; \$50, member (Canadians add 6% GST, or 14% GST+HST where applicable). For prices of electronic versions, contact the Subscriptions Unit, ASM. Correspondence relating to subscriptions, defective copies, missing issues, and availability of back issues should be directed to the Subscriptions Unit, ASM; correspondence relating to reprint orders should be directed to the Reprint Order Unit, ASM; and correspondence relating to disposition of submitted manuscripts, proofs, and general editorial matters should be directed to the Journals Department, American Society for Microbiology, 1752 N St., N.W., Washington, DC 20036-2904. Phone: (205) 737-3600.

Claims for missing issues from residents of the United States, Canada, and Mexico must be submitted within 3 months after publication of the issues; residents of all other countries must submit claims within 6 months of publication of the issues. Claims for issues missing because of failure to report an address change or for issues "missing from files" will not be allowed.

Periodicals postage paid at Washington, DC 20036, and at additional mailing offices.

POSTMASTER: Send address changes to *Applied and Environmental Microbiology*, ASM, 1752 N St., N.W., Washington, DC 20036-2904.

Made in the United States of America. Printed on acid-free paper. doi:10.1128/AEM.74.14.2008 CODEN: AEMIDF

Copyright © 2008, American Society for Microbiology. All Rights Reserved.

The code at the top of the first page of an article in this journal indicates the copyright owner's consent that copies of the article may be made for personal use or for personal use of specific clients. This consent is given on the condition, however, that the copier pay the stated per-copy fee through the Copyright Clearance Center, Inc., 222 Rosewood Drive, Danvers, MA 01923, for copying beyond that permitted by Sections 107 and 108 of the U.S. Copyright Law. This consent does not extend to other kinds of copying, such as copying for general distribution, for advertising or promotional purposes, for creating new collective works, or for resale.