

APPLIED AND ENVIRONMENTAL MICROBIOLOGY

VOLUME 76 • FEBRUARY 2010 • NUMBER 3

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

Lone Gram, *Editor* (2011)
Technical University of Denmark

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

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

Volker Müller, *Minireview Editor*
(2014)
Goethe University Frankfurt am Main

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

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

Matthew R. Parsek, *Cover Editor* (2014)
University of Washington

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

Janet L. Schottel, *Editor* (2013)
University of Minnesota

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

Marylynn V. Yates, *Editor* (2014)
University of California—Riverside

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

EDITORIAL BOARD

Yousef Abu Kwaik (2011)
Luis A. Actis (2011)
Eric Altermann (2012)
Gary Andersen (2010)
Thomas Andlid (2010)
Beate Averhoff (2010)
Andrea Azcarate-Peril (2012)
Charles Bacon (2012)
Michael Bagdasarian (2012)
Bert Bago (2010)
Christopher E. Bagwell (2011)
József Baranyi (2010)
Tamar Barkay (2011)
Florian Bauer (2012)
Gwyn A. Beattie (2011)
Sebastian Behrens (2012)
Harry Beller (2012)
Peter L. Bergquist (2012)
Tom Besser (2010)
Arvind A. Bhagwat (2012)
Valeria Bianciotto (2012)
Indranil Biswas (2012)
K. Johanna Bjorkroth (2010)
Rafael Blasco (2010)
Paul Bodelier (2012)
Harry Boer (2012)
Eckhard Boles (2012)
Violaine Bonnefoy (2010)
Kathryn J. Boor (2010)
Katherine A. Borkovich
(2012)
James Borneman (2011)
Kostas Bourtzis (2012)
Gesche Braker (2011)
Michael G. Bramucci (2011)
Byron Brehm-Stecher (2010)
Frederick Breidt, Jr. (2010)
Neil C. Bruce (2010)
Alison Buchan (2011)
Robert Buchanan (2012)
George Bullerjahn (2010)
William Burkhardt III (2010)
H. J. Busscher (2010)
Mark P. Buttner (2012)
Murulee Byappanahalli (2012)
Douglas R. Call (2010)
Michael J. Carter (2010)

Jinru Chen (2011)
Shicheng Chen (2011)
Wilfred Chen (2012)
Yi Chen (2011)
Yuhuan Chen (2012)
Michael L. Chikindas (2010)
Luca Cocolin (2010)
James Cole (2010)
Michael T. Collins (2010)
Doug Cossar (2012)
James M. Cregg (2012)
Patricia Cruz (2010)
Tom Curtis (2010)
Rolf Daniel (2012)
Steven L. Daniel (2011)
Michelle Danyluk (2010)
Atin R. Datta (2010)
Frank B. Dazzo (2010)
Angelo DePaola, Jr. (2012)
Ronald P. de Vries (2011)
Thomas DiChristina (2012)
Alan DiSpirito (2011)
Jan Dolting (2010)
Daniel P. Dougherty (2012)
Irina S. Druzhina (2011)
Doris d'Souza (2011)
Nicole Dubilier (2010)
Siobain Duffy (2010)
Nancy DuTeau (2011)
Richard Eaton (2010)
Leo Eberl (2011)
T. S. Edrington (2010)
Henry L. Ehrlich (2010)
Christopher Elkins (2011)
Marie Elliot (2011)
K.-D. Entian (2010)
Slava Epstein (2010)
Danilo Ercolini (2012)
David Faguy (2011)
Joseph O. Falkinham III (2010)
Matthew W. Fields (2011)
Martin Fillion (2012)
Turlough Finan (2010)
Steven E. Finkel (2010)
Madilyn Fletcher (2011)
Steven Foley (2011)
Christopher Francis (2010)

Herbert L. Fredrickson
(2010)
Michael Friedrich (2012)
Masao Fukuda (2012)
Rebecca Gast (2011)
Elke Genersch (2012)
Manuela Giovannetti (2012)
Mark Gomelsky (2011)
Heidi Goodrich-Blair (2012)
Lawrence Goodridge (2012)
Joerg Graf (2011)
Irene R. Grant (2010)
Leslie Gregg-Jolly (2011)
Jean Guard-Bouldin (2010)
Mary Lou Gueriot (2011)
John Gustafson (2012)
Martin W. Hahn (2010)
Ken Hammel (2012)
Theo A. Hansen (2010)
Hauke Harms (2010)
Steven Harris (2011)
Valerie J. (Jody) Harwood (2012)
Terry C. Hazen (2010)
Qiang He (2010)
Zhili He (2010)
Brian Hedlund (2011)
Hermann J. Heipieper (2011)
Ute Hentschel (2012)
Alfredo Herrera-Estrella (2011)
David Hibbett (2011)
Russell T. Hill (2011)
Dallas G. Hoover (2012)
David J. Hopper (2010)
Hor-Gil Hur (2012)
Fumio Inagaki (2010)
Douglas Inglis (2012)
Ralph Jack (2012)
Janet K. Jansson (2010)
Lee-Ann Jaykus (2012)
Tom Jeffries (2011)
Kristen Jellison (2012)
Paul R. Jensen (2011)
Carlos A. Jerez (2011)
Mike Jetten (2010)
D. Barrie Johnson (2011)
Yves Jouanneau (2012)
Juan Luis Jurat-Fuentes (2012)

David Kaplan (2010)
Levente Karaffa (2012)
Boran Kartal (2011)
Charles W. Kaspar (2010)
James E. Keen (2010)
John J. Kelly (2012)
Robert M. Kelly (2011)
William Kenealy (2012)
Angela Kent (2010)
Philip J. Kersten (2010)
Mary Jo Kirisits (2010)
Maia Kivisaar (2010)
Staffan Kjelleberg (2011)
Martin G. Klotz (2011)
Allan Konopka (2011)
Konstantinos Konstantinidis
(2012)
Joel E. Kostka (2010)
George Kowalchuk (2012)
Lee Krumholz (2012)
Indira Kudva (2010)
Kirsten Kuesel (2010)
Timothy M. LaPara (2012)
Laurie LaPat-Polasko (2012)
Gisèle LaPointe (2010)
Luis Larrondo (2011)
Yin-Won Lee (2010)
Mary Beth Leigh (2010)
Jeffrey T. LeJeune (2012)
Michael Lemke (2011)
Johan Leveau (2012)
Tine Rask Licht (2011)
Celeste Linde (2011)
Markus Linder (2011)
Nic D. Lindley (2010)
John T. Lisle (2012)
Shuang-Jiang Liu (2011)
Wen-Tso Liu (2010)
Jon Lloyd (2010)
Tillman Lueders (2012)
G. T. Macfarlane (2011)
Sandra Macfarlane (2011)
Robert Mach (2012)
Eugene Madsen (2012)
Walter F. Mahaffee (2011)
Antonio Maldonado (2011)
Mike Manefield (2011)

Helene Marquis (2012)	Mark Osborn (2010)	Verena Seidl (2012)	Kumar Venkitanarayanan (2011)
Terence L. Marsh (2011)	Joerg Overmann (2010)	Gordon Shephard (2010)	Alain Vertes (2010)
Andrew P. Martin (2011)	Hans Paerl (2011)	Stefan Sievert (2012)	Anne K. Vidaver (2011)
Maria Esperanza Martínez-Romero (2010)	Rebecca Ehrlich Parales (2011)	Mark Silby (2012)	Adrián A. Vojnov (2010)
Jan Martinussen (2011)	Jakob Pernthaler (2012)	Simon D. Silver (2011)	Gerrit Voordouw (2011)
Juergen Marxsen (2011)	M. Julia Pettinari (2011)	Pascal Simonet (2012)	Carmen Wachter (2010)
Emma Master (2012)	Gregg Pettis (2011)	Mitch Singer (2011)	Michael Wagner (2010)
Harold D. May (2010)	Laurent Philippot (2011)	Randall S. Singer (2012)	Irene Wagner-Döbler (2011)
J. Vaun McArthur (2011)	Flynn Picardal (2010)	Brajesh Singh (2010)	Aljoscha Wahl (2012)
Robert McLean (2012)	Roger W. Pickup (2010)	Kaarina Sivonen (2011)	Judy D. Wall (2012)
Katherine McMahon (2012)	Carmen Pin (2012)	Evan Skowronski (2012)	Peng G. Wang (2012)
Brian McSpadden-Gardener (2010)	James L. Pinckney (2011)	Joan L. Slonczewski (2011)	Todd Ward (2010)
Rainer Meckenstock (2012)	Anton F. Post (2010)	Hauke Smidt (2011)	Bart Weimer (2010)
Rick Meinersmann (2012)	Rolf Prade (2012)	Patricia A. Sobecky (2010)	Helge Weingart (2012)
William Metcalf (2011)	Maria Prieto (2012)	John Spear (2010)	Alan Welman (2012)
Patricia D. Millner (2012)	Jim I. Prosser (2011)	Andrew Spiers (2010)	Irene Wesley (2012)
Donald K. Milton (2012)	Cheryl L. Quinn (2012)	Eric Stabb (2010)	Marvin Whiteley (2010)
Kiwamu Minamisawa (2011)	John P. Quinn (2012)	Alfons J. M. Stams (2010)	Martin Wiedmann (2011)
Jamal Mohamed (2012)	Jos M. Raaijmakers (2011)	Robert J. Steffan (2010)	Steve Wilhelm (2012)
William W. Mohn (2011)	Michael Rappé (2012)	Alexander Steinbüchel (2011)	Rolf-M. Wittich (2011)
Sylvain Moineau (2011)	Gerald R. Reeck (2010)	John Stolz (2010)	Mark J. Wolcott (2010)
Istvan Molnar (2011)	Bernd Rehm (2012)	Wolfgang Streit (2012)	K. Eric Wommack (2012)
Melanie Mormile (2010)	Gregor Reid (2012)	Marc Strous (2011)	Thomas K. Wood (2011)
Jochen Mueller (2012)	Walter Reineke (2010)	Joseph Sturino (2010)	Randy Worobo (2010)
Peter Muriana (2011)	Geoffrey D. Robson (2011)	Marcelino Suzuki (2010)	Hong-sheng Wu (2012)
Yuji Nagata (2012)	Margie Romine (2011)	Zuzana Sýkorová (2011)	Lihua Xiao (2012)
István Nagy (2010)	Neil Rowan (2011)	Cristina Takacs-Vesbach (2012)	Dong Xu (2011)
Cindy H. Nakatsu (2010)	Edward G. Ruby (2010)	Ken Takai (2010)	Jian Xu (2010)
Diane G. Newell (2010)	Michael J. Sadowsky (2010)	Ralph Tanner (2011)	Jagjit Yadav (2011)
Walter G. Niehaus, Jr. (2010)	Daád A. Saffarini (2011)	Gerald W. Tannock (2011)	Ching-Hong Yang (2011)
Brendan A. Niemira (2012)	Badal C. Saha (2010)	Ron Teather (2010)	Suleyman Yildirim (2011)
Hideaki Nojiri (2012)	Andrew D. Sails (2010)	Andreas Teske (2012)	Jill Zeilstra-Ryalls (2011)
Kenneth M. Noll (2011)	Maria Sandkvist (2012)	Michael G. Thomas (2012)	Chuanlun Zhang (2012)
Norbert Nowotny (2012)	Robert Sanford (2012)	Ian P. Thompson (2011)	Qijing Zhang (2011)
George-John Nychas (2012)	Sima Sariaslani (2012)	Effie Tsakalidou (2010)	Erwin G. Zoetendal (2012)
Kevin P. O'Connell (2011)	Brian Saunders (2010)	Masataka Tsuda (2012)	Angeles Zorreguieta (2010)
Julie Olson (2012)	Patrick D. Schloss (2012)	Jos Vanderleyden (2010)	
Ronald S. Oremland (2012)	Andreas Schmid (2011)	Wouter van der Star (2011)	
	Andreas Schramm (2010)	Paul van der Wielen (2011)	
	Bernhard Seiboth (2011)		

Thomas E. Shenk, *Chairman, Publications Board*

Barbara M. Goldman, *Director, Journals*

Barbara S. Slinker, *Production Editor*

Stephanie L. D'Agostino, *Assistant Production Editor*

Michael E. Lerman, *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: \$1,361, U.S.; \$1,455, Canada (plus 5% GST, or 13% HST where applicable); \$1,471, Europe; \$1,508, Latin America; \$1,512, rest of world. Member print subscription prices (per year) are: \$173, U.S.; \$288, Canada (plus 5% GST, or 13% HST where applicable); \$283, Europe; \$320, Latin America; \$324, rest of world. Single copies are: \$100, nonmember; \$50, member (Canadians add 5% GST, or 13% 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.76.3.2010 CODEN: AEMIDF

Copyright © 2010, 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.