



VOL. 94, NO. 5 AUGUST 2014

JMBA

Journal of the Marine Biological
Association of the United Kingdom

CAMBRIDGE
UNIVERSITY PRESS

ISSN: 0025-3154

JMBA

JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

EDITOR IN CHIEF: PROFESSOR M.C. THORNDYKE

Sven Lovén Centre for Marine Sciences, University of Gothenburg, Sweden

EXECUTIVE EDITOR: A. PULSFORD

Marine Biological Association, Citadel Hill, Plymouth, PL1 2PB, UK

ASSOCIATE EDITORS

P. ANDERWALD, *Swiss National Park, Switzerland*
M. ARVEDLUND, *University of Copenhagen, Denmark*
J.A. BAEZA, *Smithsonian Marine Station, USA*
C.N. BIANCHI, *University of Genova, Italy*
J. CARTES, *Institut de Ciències del Mar de Barcelona, Spain*
B.K.K. CHAN, *Research Centre for Biodiversity Academia Sinica, Taiwan*
M.J. COSTELLO, *Leigh Marine Laboratory, NI, New Zealand*
M. CUNLIFFE, *Marine Biological Association of the United Kingdom, UK*
P.J.F. DAVIE, *Queensland Museum & Science Centre, Australia*
S. DUPONT, *Kristineberg University of Gothenburg, Sweden*
J. ELLIS, *Centre for Environment, Fisheries & Aquaculture Science (Cefas), UK*
M.R. ELPHICK, *Queen Mary University of London, UK*
P.G.H. EVANS, *University of Wales, Bangor, UK*
G. FAUVILLE, *Sven Lovén Centre for Marine Sciences, Sweden*
A. GEBRUK, *P.P. Shirshov Institute of Oceanology, Russia*
P.A. HENDERSON, *Piscis Conservation, Southampton, UK*
J.G. HIDDINK, *University of Wales, Bangor, UK*
D. JOLLIVET, *Station Biologique de Roscoff, France*

W.J. LANGSTON, *Marine Biological Association of the United Kingdom, UK*
V. LAPTIKHOVSKY, *Falklands Department of Fisheries, Falkland Islands*
J. LI, *University of Maryland, USA*
J. LONG, *San Diego State University, Department of Biology, USA*
F. MCGOWAN, *University of East London, UK*
D.A. MCHUGH, *Colgate University, USA*
N. MIESZKOWSKA, *Marine Biological Association of the United Kingdom, UK*
T. MOENS, *University of Ghent, Belgium*
P.D.R. MØLLER, *Natural History Museum of Denmark*
B. OKAMURA, *Natural History Museum, London, UK*
N.D. POPE, *Marine Biological Association of the United Kingdom, UK*
N. QUEIROZ, *CIBIO, Vairão, Portugal*
J.A. RAVEN, *FRS, University of Dundee, UK*
M.M. RIVADENEIRA, *Universidad Católica del Norte, Chile*
J.M. RUIZ, *Universidad de Coruña, Spain*
M. RUSSELL, *Villanova University, PA, USA*
C.D. TROWBRIDGE, *Oregon Institute of Marine Biology, University of Oregon, USA*
N.J. DE VOOGD, *Netherlands Centre for Biodiversity Naturalis, The Netherlands*
N. WHITELEY, *School of Biological Sciences, Bangor, UK*

Address all correspondence to: The Executive Editor, Journal of the Marine Biological Association, The Laboratory, Citadel Hill, Plymouth, PL1 2PB, UK. (Tel: +44 (0) 1752 633100; Fax: +44 (0) 1752 633102; e-mail: journal@mba.ac.uk)

EDITORIAL POLICY

JMBA is an international journal, publishing original research on all aspects of marine biology. Subjects covered include: ecological surveys and population studies of marine communities, physiology and experimental biology; taxonomy, morphology and life history of marine animals and plants; and chemical and physical oceanographic work. In addition we also welcome original articles and short reviews in the area of Ocean Acidification and Climate Change, Human Health and the Oceans as well as Novel Educational and Outreach tools for promoting marine biology and also marine issues related to policy and for policy makers.

Papers describing work involving experimental procedures on living animals will be published only if they comply with the legal requirements of the UK Home Office. In the case of species not covered by the current law, papers will be published only if it is judged that the experiments have been conducted in a humane manner and adequate precautions taken to minimize stress.

Authors may like to know that papers published in the *JMBA* are covered by the following abstracting or indexing services: *Animal Breeding Abstracts, ASFA, Biological Abstracts, Biological and Agricultural Index, Chemical Abstracts, Current Advances in Ecological Sciences, Current Contents, Current Titles in Oceanography, FISHLIT, Geological Abstracts, GeoRef, Helminthological Abstracts, Lead Abstracts, Nutrition Abstracts, Oceanic Abstracts, Selected Water Resources Abstracts, ZINCscan.*

SUBSCRIPTIONS

The *JMBA-Journal of the Marine Biological Association of the United Kingdom* (print ISSN 0025-3154; electronic ISSN 1469-7769) is published eightfold in February, March, May, June, August, September, November and December. The 2014 subscription price (excluding VAT) of a volume, which includes print only is £1173 (US \$1879 in USA, Canada and Mexico), print and online access, is £1354 (US \$2166 in USA, Canada and Mexico). The online-only price available to institutional subscribers is £1045 (US \$1670 in USA, Canada and Mexico).

Orders, which must be accompanied by payment, may be sent to a bookseller, subscription agent or direct to the publisher: Cambridge University Press, The Edinburgh Building, Shaftesbury Road, Cambridge, CB2 2RU, UK, or in the USA, Canada and Mexico, to Cambridge University Press, Journal Fulfillment Department, 100 Brook Hill Drive, West Nyack, New York 10994-2133, USA. EU subscribers (outside the UK) who are not registered for VAT should add VAT at their country's rate. VAT registered subscribers should provide their VAT registration number. Japanese prices for institutions are available from: Kinokuniya Company Ltd, PO Box 55, Chitose, Tokyo 156, Japan.

Periodical postage paid at New York, NY, and at additional mailing offices. **Postmaster:** send address changes in USA, Canada and Mexico

to *Journal of the Marine Biological Association*, Cambridge University Press, 100 Brook Hill Drive, West Nyack, New York 10994-2133, USA.

Claims for missing issues should be made immediately on receipt of the subsequent issue.

COPYRIGHT/PHOTOCOPYING

The journal is registered with the Copyright Clearance Center, 222 Rosewood Drive, Danvers, MA 01923, USA. Organizations in the USA which are also registered with CCC may therefore photocopy material (beyond the limits permitted by sections 107 and 108 of US copyright law) subject to payment to CCC of the per-copy fee of \$16.00. This consent does not extend to multiple copying for promotional or commercial purposes. Code 0025-3154/2014.

ISI Tear Sheet Service, 3501 Market Street, Philadelphia, PA 19104, USA, is authorized to supply single photocopies of separate articles for private use only. Organizations authorized by the UK Copyright Licensing Agency may also photocopy material subject to the usual conditions. For all other use, permission should be sought from Cambridge or the American branch of Cambridge University Press. *Microfilm copies* of back numbers are available from University Microfilms International, 300 North Zeeb Road, MI 48106-1346, USA.

No part of this publication may otherwise be reproduced, stored or distributed by any means without permission in writing from Cambridge University Press, acting for the copyright holder.

Cover illustration: emperor angelfish, *Pomacanthus imperator*, from a reef near Manado, Sulawesi, Indonesia, 20 m depth. Image by Michael Arvedlund.

©2014 Marine Biological Association of the United Kingdom
(Registered Charity no. 226063)

Information on the JMBA

ELECTRONIC ACCESS

JMBA: *Journal of the Marine Biological Association of the United Kingdom* is one of the titles included in the Cambridge Journals Online service which can be found at: <http://journals.cambridge.org>
Further information on this and on other Press titles can be found at <http://journals.cambridge.org/> or <http://www.cambridge.org/>