

Review

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The history of the *Journal of the Marine Biological Association of the United Kingdom* and the influence of the publication on marine research

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Abstract

The origin and development of the *Journal of the Marine Biological Association of the United Kingdom* is described on the occasion of the publication of the 100th volume. Papers in the Journal demonstrate how the techniques and approaches to the study of the marine environment have evolved over the 120 years of publication. The early papers provided a baseline description of the marine environment and of marine communities that allowed the effects of later perturbations of the environment to be determined. Both the early papers and the long time series of records have proved to be particularly relevant as marine scientists try to predict the long-term results of climatic and anthropogenic effects on the marine ecosystem. The Journal has now become increasingly international, with most papers coming from outside Europe.

Introduction

A brief account of the history of the *Journal of the Marine Biological Association of the United Kingdom* (JMBA) was published to coincide with 100 years since the publication of the first issue (Spooner *et al.*, 1987). The present paper updates this account and reviews the influence that articles in the JMBA have had on disseminating the results of marine research. The selection of topics covered has had to be limited and the authors regret that it has not been possible to mention all the important papers published in the JMBA.

The Marine Biological Association of the United Kingdom (MBA) was conceived following debates, at the 1883 International Fisheries Exhibition in London, as to whether the major fisheries were inexhaustible or whether catches were already declining, in some areas, due to overfishing (Southward & Roberts, 1984). Prof. E. Ray Lankester, then at University College, London, appealed for the formation of a society to study marine life, including the habits and life-histories of food fishes. He organized an initial meeting at the Linnean Society in London to consider a proposal to establish a marine laboratory for the joint purpose of encouraging the study of marine zoology and making a scientific study of questions relating to sea fisheries (Lankester, 1887a, 1887b; Bourne, 1930). The MBA was formed at a meeting held at the Royal Society in London in March 1884. Construction of a laboratory in Plymouth commenced in February 1887, with the building opening the following year (Southward & Roberts, 1984).

Development of the journal

Remit and production of the JMBA

The JMBA was established in 1887, initially to inform members of the MBA of reports on the work of the Association and also of records of observations relating to the marine biology and fisheries of the coasts of the UK: fishermen and naturalists were invited to contribute (Lankester, 1887a). The first two numbers, of what is now called the 'Old Series' (OS), were published in August 1887 and August 1888. The first number contained a list of members of the MBA, an account of the formation of the Association and a description of the Laboratory, as well as an account of the local fishing grounds and fishing industry (see Figure 1; Heape, 1887).

G.C. Bourne, the first Director appointed, wrote that the JMBA was intended 'to supply scientific information in an easily comprehensible form to those who are interested in marine fisheries' as well as accounts of animal or vegetable morphology (Bourne, 1889). Bourne wrote 'the Journal will be issued from time to time, according to the amount of work ready for publication, and will contain, besides the memoirs alluded to, abstracts of the scientific work done by the naturalists hiring tables in the Laboratory, notes and correspondence from other fishery and marine stations, abstracts of the most important results obtained by the fisheries commissioners of various Governments, and any correspondence addressed to the editor for publication'.

Since the early years, papers in the JMBA showed an appreciation of how the biota differed according to the origin of the water mass (Cleve, 1897). Papers were encouraged on 'all aspects of marine biology and oceanography'. This broad remit continued until recent years when it



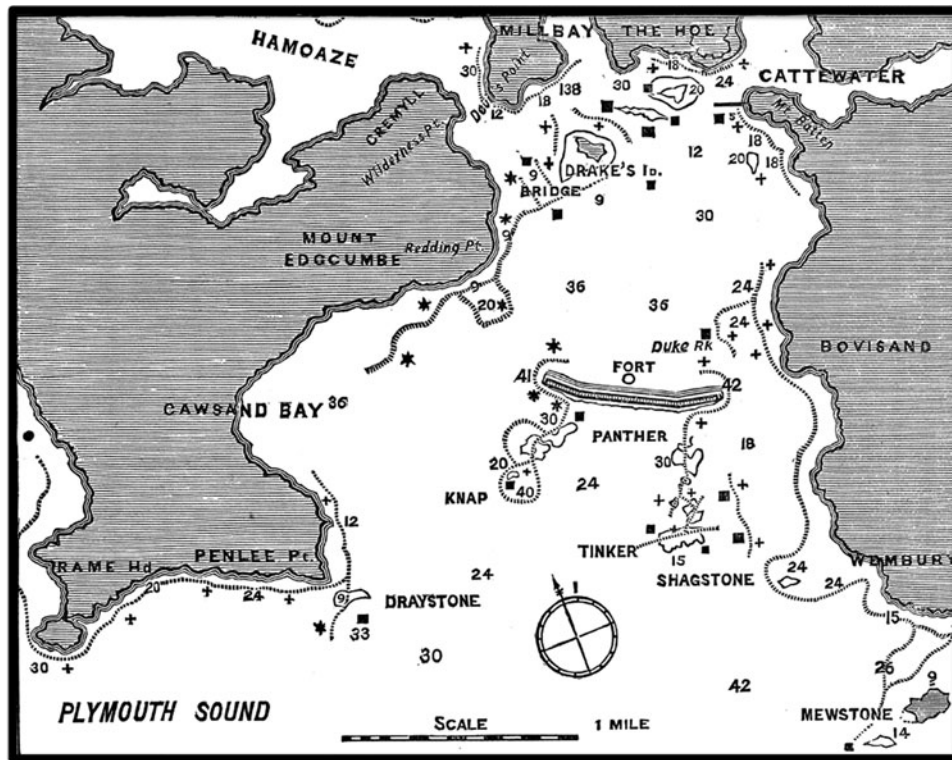


Fig. 1. From Heape (1887), original legend: 'Fishing Map of Plymouth Sound, after map published in G. and R. Books 'General Guide to Sea Fishing' No. 5. The depth is marked in feet thus 30. The best places to fish for pollock, bass and mackerel are shown by the dotted line. The crosses show places to fish in ebb tide. The stars show places to fish in flood tide.'

was stated, in 1996, that 'the primary topics covered are: (a) ecology, behaviour and fisheries; (b) physiology, ecotoxicology and biochemistry; (c) molecular, microbiology and genetics; (d) oceanography, satellite imagery and modelling'.

One of the duties of the Director under bye-law 14 was to 'prepare and edit the Journal' (Marine Biological Association, 1889). This duty was subsequently expanded in by-law 15 to 'prepare and edit the publications of the Association'. This wording was continued in the Memorandum and Articles of the Marine Biological Association of the United Kingdom from 1927 and subsequent revisions in 1945, 1971 and 1995. With the increasing number of papers published in the JMBA it became impractical for the Director to edit the JMBA along with the other required duties. The 2003 revision of the Memorandum and Articles, by the then Director and Secretary, S.J. Hawkins, therefore changed the wording to 'oversee the preparation and editing of the publications of the Association in liaison with the Editorial Board'. This wording is also used in the current Regulations and Rules of the Association, following the incorporation by Royal Charter in November 2017 (Marine Biological Association, 2017). As the editorial work increased, an Executive Editor was appointed to do a lot of the editorial work and subsequently the Director was replaced as Editor by an Editor-in-Chief who was responsible to the Director. A list of the editors, executive editors and Editors-in-Chief, with dates, is given in Table 1.

Illustrations

The early illustrations in JMBA were drawings that were engraved onto printing plates and published as plates inserted following the individual articles. For example, Cunningham (1889) made camera lucida drawings, of fish eggs and larvae, that were converted into printing plates by Glyptographie Silvestre et Cie, Paris. In this early period, commercial cameras and photographic materials

were being improved rapidly, making photography simpler and quicker for the amateur as well as the professional. Half-tone photographs and simple drawings were inserted into the text pages (Browne, 1898) while more detailed drawings and collotype plates of photographs were inserted at the end of the paper as plates (e.g. Browne, 1898, 1907), as in other scientific publications of the period; an example is shown in Figure 2. Line drawings still remained the dominant mode of illustration. Marie Lebour, for example, published 67 papers on the planktonic larvae and biology of marine fishes and invertebrates in JMBA from 1916–1954 (available from the PLYMSEA repository), all beautifully illustrated with her own line drawings (e.g. Lebour, 1917, 1923, 1933, 1944). Her 1923 paper (Lebour, 1923) contains delicate drawings, within the text, of living medusae and *Sagitta* capturing fish larvae.

D.P. Wilson had been interested in photography from childhood. He took flash photos, using magnesium powder, of cuttlefish feeding in the aquarium (Wilson, 1946) and developed his own improved lighting systems for microphotography of living larvae and post-larvae, e.g. of the starfish *Luidia* (Wilson, 1978). From the mid 1950s papers using electron microscopy to describe microplankton and sub-cellular structures appeared in the JMBA. Parke and Manton started using the technique to study dinoflagellates (Parke *et al.*, 1955). Over the following 50 years more than 130 papers in the JMBA, on a variety of topics, used electron microscopy in the studies reported.

From 1957 until 1985 the MBA employed G.A.W. Battin as a cartographer and draftsman. He standardized and improved the presentation and lettering of many of the figures published in the JMBA over this period (e.g. Newell, 1967) and drew plans of the MBA Laboratory 1963 (Russell, 1963).

Hand-coloured illustrations were occasionally used in earlier years (e.g. Parke 1949) but colour photographs or computer diagrams were introduced regularly in the online version of papers from volume 82 (2002). Authors were given the option

Table 1. Editors, Editors-in-chief* and Executive Editors of the JMBA since its formation (** Acting Editor)

Editor/(**Editor-in-chief)	Dates
E. R. Lankester	1887–June 1888
G. C. Bourne	June 1888–August 1890
W. L. Calderwood	1890–January 1893
E. J. Bles	April 1893–October 1894
E. J. Allen	January 1895–September 1936
S. W. Kemp	October 1936–May 1945
F. S. Russell	August 1945–1965
J. E. Smith	1965–1974
E. J. Denton	1974–July 1987
J. V. Howarth	1972–March 1991
M. Whitfield	August 1977–March 1991
P. E. Gibbs*	February 2002–March 2009
P. E. Gibbs* & P. R. Dando*	April 2009–December 2009
P. R. Dando*	January 2010–June 2011
M. C. Thorndyke*	January 2013–May 2017
C. L. J. Frid**	June 2017–November 2017
J. Lewis*	December 2017 to date
Executive Editors	
F. S. Russell	1936–1939
G. M. Spooner	1945–1972
J. V. Howarth	1972–July 1977
P. E. Gibbs	August 1977–December 1978
J. V. Howarth	January 1979–February 1990
L. Maddock	March 1990–April 1995
A. L. Pulsford	May 1995–December 2015

of paying for them in the printed issue, although coloured illustrations in the online versions were free. One problem was that some colour figures were converted to grey-scale for the printed version without checking that differences in the shading were clear.

Printing and appearance of the JMBA

The JMBA has been published in all except two years since 1887. The number of pages of scientific papers printed each year has steadily increased, with the exception of the war years, from <300 prior to 1904 to >500 in 1926 and 1927 and to >1700 since 2008 (Figure 3A). Initially, only one or two issues each year were published, with the exception of 1902 and 1905, when no issues were published and 1906 and 1930 which each had 3 issues. With the post-WWII expansion of marine research the number of issues a year was increased to 3 from 1951 and increased again to 4 from 1969 and to 6 from 1999. Eight issues a year, the current number, were printed, starting in 2008. Similarly the number of scientific papers published each year has increased from 6 in 1900 to over 170 today (Figure 3B).

As the number of submissions increased, an editorial board was introduced to help in handling the submissions. By 1988 there was an editorial board of 12, drawn from eight countries. Currently the editorial board consists of eight individuals with an additional 34 associate editors drawn from 16 countries in

total, reflecting the increased number of submissions and their broad international origin.

The journal was initially printed for the MBA by Adlard & Son, Bartholomew Close, London. This company continued printing the journal until 1897, volume 5, when the printing was transferred to William Brendon and Son, Mayflower Press, Plymouth. It was transferred again to Brook Crutchley, the printers for Cambridge University Press, in November 1937 (volume 22).

From the third number of the Journal, volume 1 of the New Series in 1889, the page size was increased to Royal Octavo to facilitate the preparation and appearance of illustrations. In November 1937 the page width was increased to allow for larger plates and figures. Following an increase in printing costs, the page margins were reduced to increase the amount of print on the page. The page width remained unchanged until February 2000, when the page size was increased to A4.

The Annual Council and Financial Reports for the MBA were published in the journal until 1992. From 1993 onwards they were issued as separate documents, freeing up more space in journal issues for scientific papers. The Annual Council Reports contained a summary of the work that scientists at the MBA had done during the year and contained advance publication of key results, as well as containing notes on observations on species and reports on scientific results that were not later published in the JMBA. For example, nearly all the neurophysiology studies conducted in the MBA Laboratory were published in the *Journal of Physiology* and elsewhere, although the key findings appeared in the Council Reports. In addition, abstracts of memoirs recording research carried out by researchers at the MBA Laboratory in Plymouth were printed in the JMBA from 1971 until 1980.

Changes in the appearance of the front cover of the journal over the years are illustrated in Figure 4. The original cover was pale blue, with an engraving of the MBA Laboratory, as seen from the sea (Figure 4A). In November 1937, with the transfer of publication to Cambridge University Press, the cover was revised and a new drawing of the MBA Laboratory was used on it. In June 1962, after enlargement of the Laboratory, a new engraving was used (Figure 4B). This continued to be used until 1989 when the cover changed to show a picture of waves breaking on a shore (Figure 4C). From 1999, volume 79, a picture of waves was inset into a black cover (Figure 4D). Coloured pictures were placed on the upper part of the front cover, first for special or themed issues, starting in February 2004 for an issue on 'Biodiversity and distribution of species' (Figure 4E) and from December 2005 onwards for every issue (Figure 4F).

Typesetting for the JMBA was carried out at the MBA from the beginning of 1990 and continued until this was taken over by Cambridge University Press.

Online publication, archiving of papers and online submission

In the 1980s the librarians of the Marine Biological Association scanned the JMBA volumes, from the first issue in August 1887 to volume 40 (1961). The papers were made freely available on the library website as pdf files and these are now available through the PLYMSEA open access repository (<http://plymsea.ac.uk/>). Subsequently, when Cambridge University Press took over as publisher of the JMBA, these issues were rescanned in early 2009, as were subsequent issues to volume 78 (1998) and made available as the JMBA Archive on the publisher's website (<https://www.cambridge.org/core/journals/journal-of-the-marine-biological-association-of-the-united-kingdom/all-issues>). The JMBA archive was launched in May 2009 and then comprised over 65,000 pages, 5900 articles and almost 100,000 linked references.

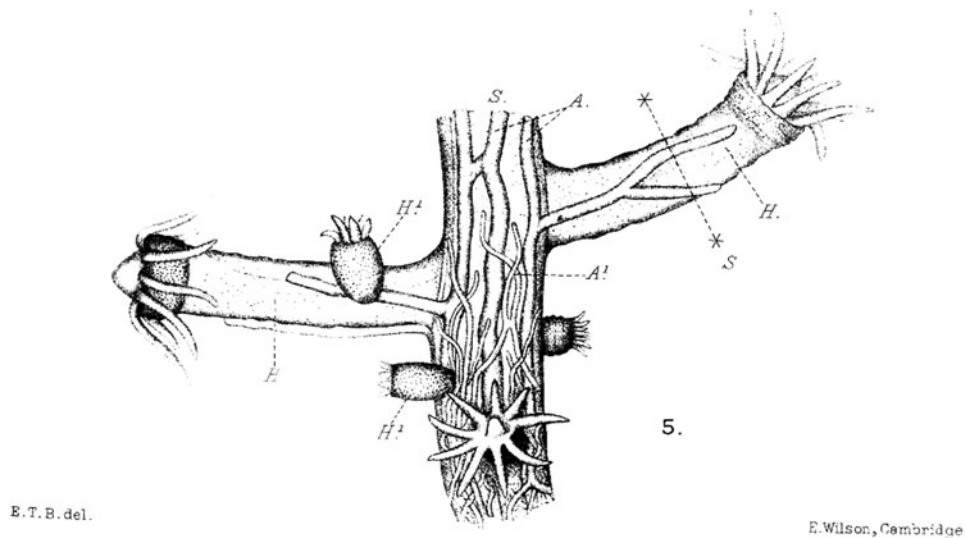


Fig. 2. Line drawing reproduced from Plate I in E.T. Browne (1907). *Bimeria biscayanana* n. sp. Portion of a branch drawn to show the arrangement of the hydranths and the auxiliary tubes. [Renamed and re-described as *Amphinema biscayanana* (Browne 1907) by Schuchert (2000).]

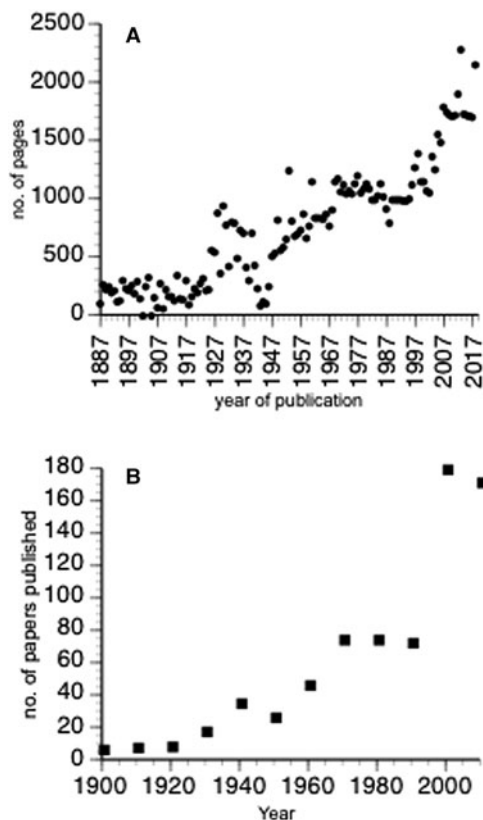


Fig. 3. (A) Number of pages printed in the JMBA in each year since 1887. (B) Number of scientific papers published in the JMBA in the first year of each decade.

In the first year over 9000 pdf files were downloaded from the archive. Whereas papers in the archive on PLYMSEA can be freely downloaded as pdf files, the papers in the Cambridge University Press archive are only freely available, without payment, as title, authors and abstracts for those published post-1990. Most papers published pre-1990 show an extract, usually the first part of the Introduction, in place of the abstract, even if there is an abstract in the full paper.

JMBA papers were made available online, in the same month that the printed publication was issued, starting in August 1999.

In 2008 papers started to be put online first, before printed publication.

In October 2005 the MBA set up a new online journal, *JMBA 2 Biodiversity Records* in response to the changing marine and coastal environment and an increasing demand for the documentation of marine organisms in locations where they had not formerly been recorded, as well as of species loss from habitats. Papers were published on the JMBA section of the MBA website. In 2008, Cambridge University Press took over this new journal, renaming it *Marine Biodiversity Records* (MBR) and hosting it on the Press website, making access free for subscribers to the JMBA. In January 2016 it was re-launched as the MBA's first online Gold Open Access Journal with Biomed Central (Springer-Nature) as the new publisher. The launch of these journals allowed more space in the JMBA for longer papers.

Online submission, using the ScholarOne system, was introduced for the JMBA (as well as for MBR) by Cambridge University Press in February 2009. The start did not go well. Manuscripts were returned to authors who had not submitted them via the new system, but had followed the, still-existing, instructions on both the MBA and Cambridge University Press websites. These stated that manuscripts should be sent as email attachments or copied onto a CD and posted.

In 2013 it was decided to make JMBA a 'hybrid journal' providing authors, upon acceptance of their article, with the option to pay an article processing charge for Gold Open Access publication. In 2018, 4.5% (10 of 222) scientific articles were open access, excluding editorials, forewords and corrigenda.

Reviews and special issues

Since the early years the JMBA has published occasional reviews. These were originally aimed at informing UK marine scientists of fishery practices, observations and research overseas, such as an account of the Newfoundland and Labrador fisheries (Grenfell, 1894), fishery research in the USA (Cunningham, 1894b), a report on flatfish research in Denmark (Stead, 1896) and studies on the Norwegian fisheries (Garstang, 1897). Subsequently many reviews have been aimed at an international readership, e.g. on the distribution of medusae species across the oceans (Kramp, 1961), the photon flux required for photolithotrophs (Raven *et al.*, 2000), the worldwide migration of humpback whales (Rizzo & Schulle,

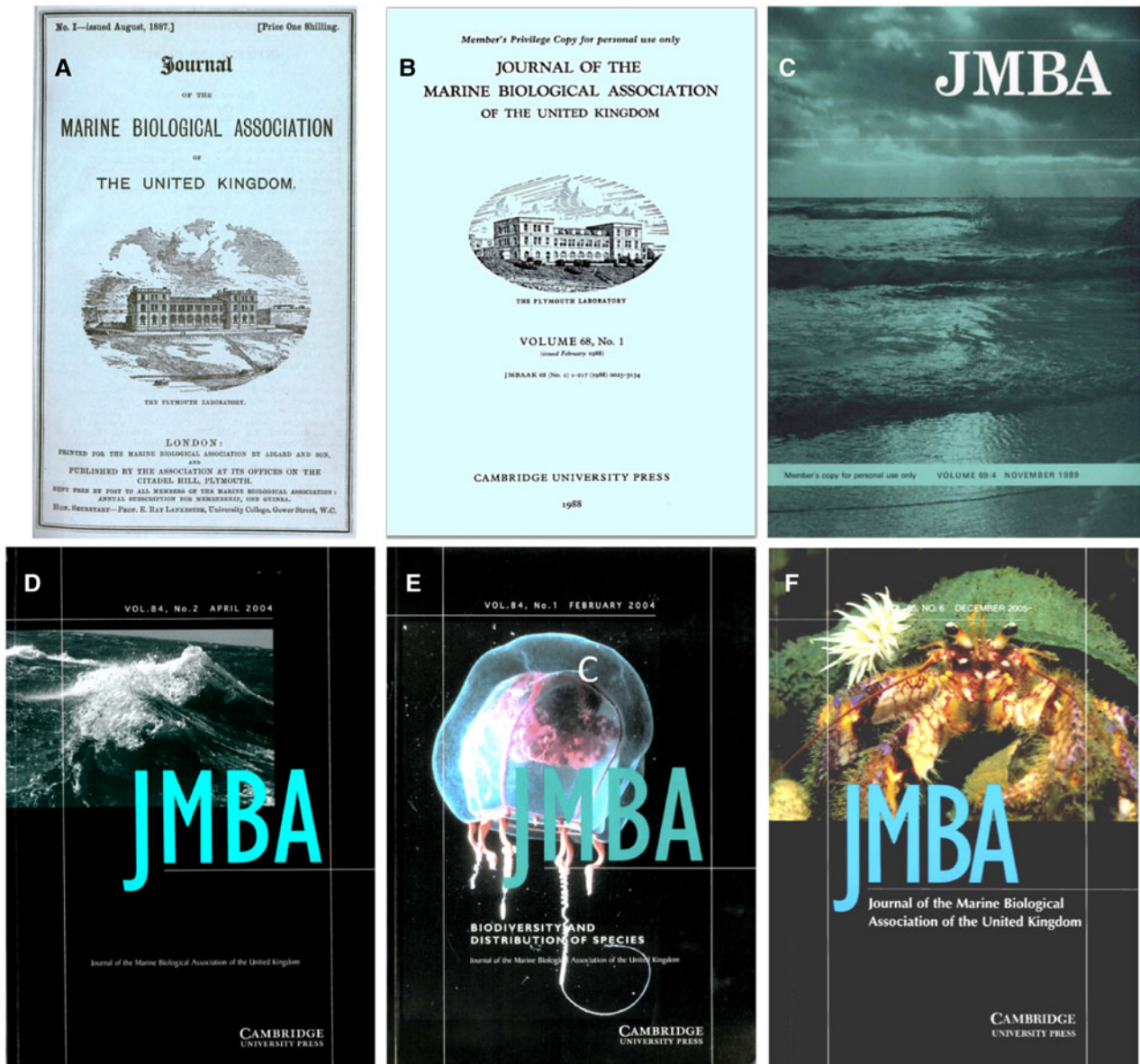


Fig. 4. JMBA covers. (A) First issue (old series) cover; (B) cover from June 1962 showing the enlarged laboratory; (C) cover from 1989; (D) cover from 1999; (E) first coloured cover (February 2004); (F) typical cover from December 2005.

2009) and the reproduction and dispersal of invertebrates at vents and cold seeps (Tyler & Young, 1999).

The JMBA has published a number of Special, or Themed issues and of issues, or issue sections, with Conference Papers (Table 2). Of particular note are the special issues, between 2007 and 2018, containing papers on cetaceans presented at annual meetings of the European Cetacean Society.

Three compilations have been published of all papers, including those in JMBA, of work that was done at the MBA. The first covered the years 1886–1913 (Anonymous, 1913), the second updated this to 1927 (Russell, 1928) and the third covered the period 1928–1950 (Russell, 1952).

The origin of published papers

Until about 1960, papers from the MBA staff and other scientists who carried out their research at the MBA, as well as members of the MBA, were prioritized for publication (Spooner *et al.*, 1987). Since the 1960s the JMBA has been open to submissions globally and this is reflected in the increased numbers of papers (Figure 3B) as well as the change in the sources of published

papers (Figure 5). Figure 5 allocates papers, published in the first year of each decade, as far as possible, to those carried out by MBA scientists, or by visiting scientists, at the MBA laboratories; those from the rest of the UK; those from Europe and those from other areas of the world. Papers were allocated to the region where most of the research was undertaken. Until the late 1960s, papers on work carried out at the MBA made up ~50% or more, of published papers. MBA scientists were then encouraged to publish in a wider range of journals and their submissions to JMBA sharply decreased. Subsequently, over 50% of papers published were from other UK laboratories until 2000 when papers from other European laboratories dominated publications in the journal. By 2010 the number of papers from South and Central America made up 30% of the total, reflecting the increase of marine laboratories and research activity in countries south of Mexico, with an increasing number also coming from Asia.

Although the JMBA has not one of the highest citation rates of marine biology journals, currently with an impact factor of 1.578, it is one of only four with a citation half-life of >10 years (Fuseler-McDowell, 1988) and has kept this long citation half-life since the Science Citation Index started in 1964. This underlines

Table 2. List of Special/Themed issues and issue sections with Conference Papers in the JMBA

Issue Title	Date(s)
Synopsis of the Medusae of the world	November 1991
R.R.S. Discovery Cruise 105	February 1992
Developmental biology of marine organisms	February 1994
The behaviour and natural history of cephalopods	May 1995
Marine biodiversity: causes and consequences	February 1996
Biodiversity and distribution of species	February 2004
Assemblages, biotopes and communities	June 2004
Feeding, breeding and distribution	August 2004
Alien and invasive species, Polychaetes	October 2004
Environment and climate change	December 2004
Xenobiotics, reproduction and development	February 2005
Gelatinous zooplankton	June 2005
Global biodiversity	August 2005
Sharks, rays and fishes	October 2005
	April 2006
Aquatic viruses	June 2006
Cetaceans	February 2007 & August 2009
Marine mammals	September 2008, December 2010, December 2012, September 2014, June 2016, August 2018
Hydrozoans	December 2008
In honour of Sir Frederick Stratten Russell, FRS	September 2010
Biodiversity and taxonomy	March 2011, August 2012
Fish ecology	September 2011
Coral reefs, the aquarium trade and the maritime industry	June 2012
Fish and fisheries	March. 2013
North Atlantic killer whale research	September 2014
Deep-sea sponges	November 2015
European Marine Biology Symposium	February 2015, December 2015, June 2016, May 2017, February 2018, December 2018
Oceans and human health	February 2016
Proceedings of the 9th World Sponge Conference	March 2016
Ascension Island	June 2017
Proceedings of the 12th International Polychaete Conference August	August 2017

the long-term value of so many of the publications in the JMBA. The 10 most cited papers in the JMBA during the first 60 years of publication are listed in Table 3 and the 10 most cited papers

subsequently are listed in Table 4. In the first period, four of the 10 papers were on macroalgae whilst in the latter period four of the 10 were pollution-related.

The JMBA has been of particular use to the MBA Library (now the National Marine Biological Library) since copies have been exchanged for periodicals and annual reports from other institutions. This journal exchange was very important in the early years of the Library, but had declined to exchanges with 119 partners in 2014 and to 59 in 2019. The decrease being due to an increasing number of journals and reports becoming available online.

The influence of JMBA papers on marine research

Sampling methods and techniques

Studies on the distribution of marine organisms require reliable and repeatable sampling methods. Key equipment originally described in the JMBA included the improved plankton indicator (Hardy *et al.*, 1936) that developed into the continuous plankton recorder (Reid *et al.*, 2003). Plankton net tows at higher speed could be improved by fitting a front cone to reduce the entry area and improve filtration (Southward, 1970). Studies on the vertical distribution of plankton (Russell, 1926) required accurate depth-related sampling and stimulated the development of opening and closing mid-water nets (Russell, 1925; Baker *et al.*, 1973). A comparison of catches, made using nets of different mesh sizes, with those using a plankton pump were reported (Pyefinch, 1949), with the pump being considered best for quantitative sampling. Other net designs described included a neuston net (David, 1965) and mid-water trawls with lights to attract fish and cephalopods (Clarke & Pascoe, 1985, 1998). Mobile deep-sea benthic carnivores can also be effectively observed using baited camera landers, with baited traps used to recover fauna in depths of >9000 m (Jamieson *et al.*, 2012).

Early attempts at enumerating bacterial numbers in seawater samples relied on culture techniques (Lloyd, 1930). From 1970 onwards, epifluorescence techniques were used for direct counts, with acridine orange or DAPI as the fluorochrome (Turley & Hughes, 1994). Latterly, flow cytometry has been used to automate counts (Zubkov *et al.*, 2007).

For sampling benthos, new grabs were described for both gravel and mud bottoms (Smith & McIntyre, 1954; Hunter & Simpson, 1976). An adaptation of the Van Veen grab to fit a video camera allowed targeted sampling of the bottom (Mortensen *et al.*, 2000). New deep-sea benthic species were described from hauls taken by a modification of the early anchor dredge (Forster, 1953). This was later developed into a heavier instrument that could dig-in, whichever side landed up (Holme, 1961). Heavy, MBA-designed, anchor dredges were first used on the continental slope in the 1950s, resulting in the discovery of many new species, including Pogonophora, i.e. gutless frenulate siboglinid tube-worms (Southward & Southward, 1958a).

Collection and observation of sub-littoral organisms by divers dates back to 1893, when Boutan (1893) employed a diver to take underwater photographs. Lyle (1929) published, in the JMBA, an account of seaweed distribution on the vertical faces of wrecks in Scapa Flow, using a professional diver to collect samples. Kitching *et al.* (1934) described a diving helmet, supplied with air pumped from the surface, that allowed a team of naturalists to survey the fauna of a sub-littoral gully with near-vertical walls. A lack of insulated suits limited dives to ~15 minutes because of low water temperatures. Bainbridge (1952) observed the behaviour of zooplankton, using a facemask and regulating valve with air fed from a compressed air cylinder on the shore or on a boat.

After WWII, self-contained underwater breathing apparatus (scuba) became more available and studies made with their aid

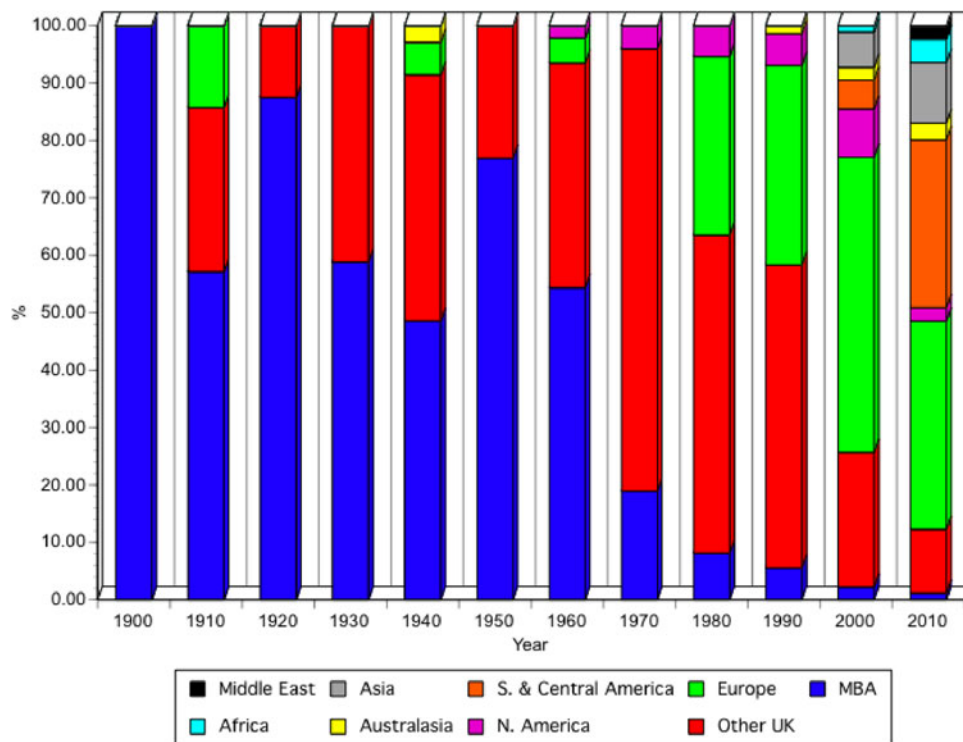


Fig. 5. Percentage of papers published in the JMBA, from the MBA, the rest of the UK or different regions of the world, in the first year of every decade, starting from 1900. North America includes Mexico.

started to be published in the JMBA in the 1950s. Forster (1954, 1959) used scuba to descend to 24 m to observe the biota of rock faces and to study grazing by *Echinus esculentus*. Papers, recording specimens observed and collected by scuba diving, were also published on the distribution of sub-littoral algae around the Isle of Man (Kain, 1960) and on the geology of the English Channel (Phillips, 1964).

Diver-operated equipment described include plankton nets (Potts, 1976) and a diver controlled epibenthic dredge (Kritzler & Eidemiller, 1972). The use of a still-camera lander to take pictures along a transect for estimating overall epifaunal density was described (Vevers, 1951) and a stereo-camera system for close-up photographs of the seabed on the continental slope was also developed (Southward *et al.*, 1976). McIntyre (1956) compared the efficiencies of the Agassiz trawl, Van Veen grab and still camera for estimating faunal densities on the same grounds. The use of towed video and still camera sleds (Holme & Barrett, 1977) allowed larger areas to be surveyed for epibenthos as well as by fitting a camera to the headline of a trawl (Dyer *et al.*, 1982). For surveys at higher speed, an off-bottom towed camera was described (Blacker & Woodhead, 2009). Cameras and data loggers have also been fitted to large marine organisms to observe feeding behaviour, e.g. turtles (Heithaus *et al.*, 2002).

In recent years, remotely operated vehicles (ROVs) have been used for both sampling (Ramirez-Llodra & Segonzac, 2006; Oliver *et al.*, 2015) and observations of organism behaviour e.g. in squid (Hunt *et al.*, 2000) and leptomedusae (Hidaka-Umetsu & Lindsay, 2018).

Biotope mapping on larger scales is now carried out acoustically, combined with ground-truthing by grabs, underwater video and/or still cameras and trawls (Brown *et al.*, 2004; Foster-Smith *et al.*, 2004). The development of this activity has become increasingly important with the establishment of networks of marine protected areas (MPAs) to ensure that they cover as much biodiversity as possible (Howell *et al.*, 2010). A comparison of modern mapping techniques in the English

Channel with previous methods described in the JMBA showed good correspondence (Coggan & Diesing, 2008). For plankton blooms both airborne and satellite mapping techniques have been described (Garcia-Soto *et al.*, 1996).

Many of these sampling methods and survey techniques, first published in the JMBA, are recorded in manuals on benthic sampling (Eleftheriou, 2013), habitat mapping (Coggan *et al.*, 2007) and marine monitoring (Davies *et al.*, 2001).

Molecular approaches to determine genetically discrete populations and cryptic species started with the use of electrophoretic techniques to study protein differences from the 1970s onwards, e.g. in barnacles (Dando & Southward, 1980) and hydroids (Thorpe *et al.*, 1992). From the 1990s PCR techniques allowed nucleic acid differences to be studied alone (Karageorgopoulos & Lewis, 2008) or together with protein differences (Wilding *et al.*, 1999).

Papers in the JMBA suggest that we can improve our knowledge of the past distribution of many species by DNA analysis of historical samples. Methods are now available to identify species in formalin-preserved Continuous Plankton Recorder samples, using PCR of extracted DNA (Kirby & Reid, 2001). This approach has been used to identify the main species responsible for the rise in echinoderm larval numbers in the North Sea from the late 1980s onwards, following a rise in sea temperatures, when larvae of *Echinocardium cordatum* dominated the plankton (Kirby & Lindley, 2005).

Marking and tracking movements of marine fauna

Papers in the JMBA show the evolution of methods of marking marine animals to follow their movements. External tags, secured by ties through the muscle or skin of fish, or the epimeral suture of crabs (e.g. Hartley, 1947; Bennett & Brown, 1983), can be lost or loose tags can be placed on different specimens by fishermen wanting to claim the reward. Described methods to overcome this problem in fish include tattooing numbers on their opercula

Table 3. Top 10 citations in the *Journal of the Marine Biological Association of the United Kingdom* from 1887 to 1956

Year	Author(s)	Title	Citations
1949	Harding	The use of probability paper for the graphical analysis of polymodal frequency distributions.	392
1920	Orton	Sea-temperature, breeding and distribution in marine animals.	228
1929	Poole and Atkins	Photo-electric measurements of submarine illumination throughout the year.	217
1942	Mare	A study of a marine benthic community with special reference to the micro-organisms.	160
1926	Yonge	Structure and physiology of the organs of feeding and digestion in <i>Ostrea edulis</i> .	158
1948	Parke	Studies on British Laminariaceae. I. Growth in <i>Laminaria saccharina</i> (L.) Lamour.	144
1952	Black and Mitchell	Trace elements in the common brown algae and in seawater.	138
1950	Black	The seasonal variation in weight and chemical composition of the common British Laminariaceae.	138
1951	Gauld	The grazing rate of planktonic copepods.	137
1950	Knight and Parke	A biological study of <i>Fucus vesiculosus</i> L. and <i>F. serratus</i> L.	127

(Stevens, 1976) or by freeze-branding marks on their skin (Dando & Ling, 1980). Branding has also been used to mark starfish (Kurihara, 1998). Marking shelled molluscs by painting numbers or engraving marks on the shells has long been used. The technique has been applied to small juveniles using a code system of coloured dots (Gosselin, 1993). A comparison of methods for marking scallops, *Pecten maximus*, concluded that flexible plastic tags fixed with cyanoacrylate gel was the preferred method (Ross *et al.*, 2001).

The problem with all the above methods is that the animal has to be recaptured to gain information. An advance came with the use of ultrasonic pingers that allowed the tagged individual to be detected underwater using either a directional hydrophone or a fixed array of omnidirectional hydrophones (Green & Wroblewski, 2000; Giacalone *et al.*, 2006). Ultrasonic pingers were used with pressure-sensitive transmitters to study the depth of eels in the water column during migration (Parker & McCleave, 1997). External data storage tags, recording time, temperature and pressure, allowed movements to be calculated after recovery of the tag and showed that movements of thornback rays were much greater than determined from the use of conventional tags alone (Hunter *et al.*, 2005). An improvement was made by inserting the tags in the peritoneal cavity to prevent tag loss (Righton *et al.*, 2007).

Livestock ear tags have been used for marking blue sharks in mark-recapture studies (Stevens, 1976) but this method has now given way to geolocation tags for satellite tracking (Southall *et al.*, 2003), with the advantage that boats are not needed to recover or track the fish. Satellite tracking has also

Table 4. Top 10 citations in the *Journal of the Marine Biological Association of the United Kingdom* from 1957 to present

Year	Author(s)	Title	Citations
1967	Wood <i>et al.</i>	Determination of nitrate in seawater by cadmium-copper reduction to nitrite.	689
1986	Bryan <i>et al.</i>	The decline of the gastropod <i>Nucella lapillus</i> around South-West England: evidence for the effect of tributyltin from antifouling paints.	521
1968	Droop	Vitamin B12 and marine ecology. IV. Kinetics of uptake, growth and inhibition in <i>Monochrysis lutheri</i> .	492
1974	Droop	The nutrient status of algal cells in continuous cultures.	398
1987	Gibbs <i>et al.</i>	The use of the dog-whelk, <i>Nucella lapillus</i> , as an indicator of tributyltin (TBT) contamination.	357
1981	Langdon and Waldock	The effect of algal and artificial diets on the growth and fatty acid composition of <i>Crassostrea gigas</i> spat.	287
1976	Parke and Dixon	Check-list of British marine algae – third revision.	254
1977	Boyden	Effect of size upon metal content of shellfish.	228
2005	Purcell	Climate effects on formation of jellyfish and ctenophore blooms: a review.	226
1988	Gibbs <i>et al.</i>	Sex change in the female dog-whelk, <i>Nucella lapillus</i> , induced by tributyltin from antifouling paints.	224

been used successfully for turtles (Hays *et al.*, 1991) and for following migrations and diving behaviour of cetaceans (Corkeron & Martin, 2004; Eskesen *et al.*, 2009).

Microchemical analysis of otoliths is being increasingly used to show the habitats occupied by individuals at different stages during their lives, particularly with anadromous species. A recent example demonstrates that the majority of European eels, *Anguilla anguilla*, spend most of their adult lives in a particular salinity environment, without migrations away from this home range (Arai *et al.*, 2019).

Describing the marine ecosystem

A first task for the MBA, on establishment, was to record the species of marine animals and plants present locally, although much had been done by local naturalists prior to this (Boalch, 1996). In the first issue of the JMBA, the laboratory superintendent described the local fishing industry and the species caught (Heape, 1887). Subsequently the fisheries for the main pelagic species, herring, pilchard and mackerel, were described (Ridge, 1889; Roach, 1890; Calderwood, 1891; Roach, 1891) and research into the spawning and nursery areas, growth rates and fecundity of these species was reported (Ford, 1933; Corbin, 1947; Steven, 1949).

An initial fauna list for Plymouth Sound and the nearby off-shore area was produced (Heape, 1888). This formed the basis for assessing subsequent changes in the distribution of species.

Additional lists for species groups, including sublittoral algae (Johnson, 1890), tunicates (Garstang, 1891), oligochaetes (Beddard, 1889), turbellaria (Gamble, 1893) and nemertines (Riches, 1893) were published. A later publication described the meio- and micro-benthos and the methods of sampling these (Mare, 1925). Seasonal changes in micro-plankton (organisms passing through fine nets) were described by Lebour (1917). Baseline data on fish catches in South Devon bays (Garstang, 1903), a major study on the benthos and bottom deposits between Start Bay and the Eddystone (Allen, 1899) and descriptions of the fauna of local estuaries (Allen & Todd, 1900, 1902; Percival, 1929) were published. A detailed study of the distribution of the benthic fauna in the English Channel was undertaken by Holme (1966). Check-lists of British marine algae were published (Parke & Dixon, 1964, 1976) and a check-list of British marine diatoms was published in 1954 and updated in 1974 (Hendey, 1954, 1974). The latter list was later expanded to include freshwater and brackish water species (Hendey *et al.*, 1986). As information on the local fauna accumulated separate fauna lists for the area were published in 1904, 1931 and 1957 (Marine Biological Association, 1904, 1931, 1957).

The breeding seasons, in the Plymouth area, of invertebrate species with planktonic larvae, were studied by identifying the larvae of species and recording their seasonal distribution in the plankton. Similarly, the breeding seasons of fish were established by examining the seasonal distributions of fish eggs and larvae in plankton hauls (Russell, 1973). The papers in the JMBA on the identification of plankton have led to guides on the identification of species, e.g. Russell (1976) and Conway (2015).

Faunal studies on deep-sea species were first published on specimens collected in the Celtic Sea at depths down to 730 m (Bell, 1890; Bourne, 1890) and in northern Biscay at depths down to 810 m (Browne, 1907; Hickson, 1907; De Morgan, 1913). More frequent collections were made in these areas from the 1950s onwards, with the increasing availability of suitable vessels, leading to the discovery of several new species, including sponges and bryozoans (Hayward & Ryland, 1978), corals (Zibrowius, 1974), brachiopods (Atkins, 1959), polychaetes (Southward, 1963) and fish (Forster, 1967). In 2015 the JMBA published a special issue on the results of the International Workshop on Taxonomy of Atlanto-Mediterranean Deep-Sea Sponges (Xavier *et al.*, 2015).

Since the 1990s there has been an increasing number of papers in the JMBA on the distribution, ecology and nutrition of deep-sea hydrothermal vent and cold seep fauna from sites worldwide, including the Atlantic (Gebruk *et al.*, 2000a; Stöhr & Segonzac, 2005; Sitjà *et al.*, 2019), the Caribbean (Gracia *et al.*, 2012), the Gulf of Mexico (Maldonado & Young, 1998), the Indian Ocean (Herring, 2006), the South Pacific (Short & Metaxas, 2011), Japan (Yamaguchi *et al.*, 2004) and the North Pacific (Southward *et al.*, 1994).

Nutritional studies and the food web

Important early JMBA papers were on the results of studies on the food web. Lebour published papers on the diet of post-larval fish (Lebour, 1918, 1919a, 1919b) and on the food of planktonic invertebrates, both from the stomach contents of freshly collected organisms and from observations on those given mixed plankton in plunger jars (Lebour, 1922, 1923). Food selection by juvenile fish was observed in aquaria (Lebour, 1919a). Much later, integrated studies on the plankton communities revealed the complex temporal relationships between viruses, bacteria, phytoplankton and zooplankton (Rodríguez *et al.*, 2000). Viruses were found to be a major controlling factor on the structure of both bacterio-plankton (Hewson & Fuhrman, 2006; Hewson *et al.*, 2006) and

phytoplankton (Wilson *et al.*, 2002; Nagasaki *et al.*, 2006) communities.

Early studies off Plymouth were reported on the food of benthic invertebrates from local fishing grounds (Hunt, 1925) as well as on the selection of benthic species as food items by different species of fish in relation to the quantitative abundance of their prey (Steven, 1930). The latter study recognized the problems of organism avoidance of sampling gear and related the behaviour of both the bottom fauna and the fish to explain the observed species differences in diet. Both these publications used aquarium observations of the animals to help explain feeding differences between species. Observations on the behaviour of animals in aquaria were published both as collected notes, e.g. Wilson (1949b) and as separate papers on individual species, including angler fish (Wilson, 1937), brachyurans (Lebour, 1944) and holothurians (Fankboner, 1981).

The diets of the main pelagic fish in the area, herring, pilchard and mackerel, were described in JMBA papers. Bullen (1912) found the diet of mackerel changed from the filtration of plankton to sight hunting of larger zooplankton and small fish during the season. Euphausiids were a major component of the diet of herrings offshore (Lebour, 1924). In the estuaries herring mainly fed on mysids (Ford, 1928b).

The identification of cephalopod species, using 'beaks' (Clarke, 1963) allowed the diets of apex predators to be described from stomach contents. The diets of large marine animals, described in JMBA papers, included those of giant squid (Lordan *et al.*, 1998), albatross species (Seco *et al.*, 2016), blue sharks (Stevens, 1973), otters (Heggberget, 1993), monk seals (Salman *et al.*, 2001) and whales (Lick & Piatkowski, 1998; Santos *et al.*, 2001). Some whales were found to eat a mixture of cephalopod prey or cephalopods and fish while others ate mainly a single cephalopod species (Clarke & Young, 1998). These studies led to a review of niche separation in beaked whale species (MacLeod *et al.*, 2003).

Since the beginning of this century there have been a number of papers in the JMBA on the use of stable isotope data to assess the trophic relationships of organisms including nematodes (Moens *et al.*, 2005), polychaetes (Nithart, 2000), gastropods (Korb, 2003), vent shrimps (Gebruk *et al.*, 2000b) and crabs (Tsuchida *et al.*, 2011), ophiuroids (Fourgon *et al.*, 2006), sharks (Estrada *et al.*, 2003), sea lions (Páez-Rosas & Auriolles-Gamboa, 2014) and whales (Mendes *et al.*, 2007). These food web studies also demonstrate the wide geographic coverage of marine biology studies published in the JMBA, covering all the oceans.

Culture of marine organisms

Many papers in the JMBA describe attempts to culture marine phytoplankton, zooplankton, invertebrates and fish larvae. Early attempts were made to rear the larvae of food fishes in order to describe their developmental stages (Cunningham, 1889, 1894a, 1894b; Garstang, 1900b; Jones, 1972), although for the more common species it was possible to follow development stages from observations of the ichthyofauna in the plankton (e.g. Lebour, 1919c; Ford, 1922; Demir, 1972; Demir *et al.*, 1985).

These papers, as well as many others, contributed to Russell's identification guide to the eggs and planktonic stages of British marine fishes (Russell, 1976).

A major advance was the development of the plunger jar system by E.T. Browne and the then MBA director, E.J. Allen (Browne, 1898). A glass disc was moved up and down in an inverted bell jar full of seawater, by means of a water-filled bucket, that emptied via a siphon when full. The gentle movement of the water in the bell jar prevented the plankton sinking to the bottom of the vessel. This system allowed medusae and planktonic crustaceans to be kept alive and their behaviour, feeding, food

preferences and development studied (Lebour, 1922, 1923). Similar observations were made on echinoderm (MacBride, 1900), fish (Lebour, 1925) and gastropod larvae (Lebour, 1933). The use of plunger jars also allowed planktonic larvae to be reared through metamorphosis so that their species could be identified, e.g. Lebour (1934). These studies and others contributed to texts on embryology (MacBride, 1914; Young, 1990).

From the early issues, the JMBA has published papers on oyster cultivation, from accounts of it in Roman times (Günther, 1897) and descriptions of oyster fisheries (Fowler, 1890) to experiments on rearing larvae to settlement on different algal cultures (Bruce *et al.*, 1940). Feeding adult oysters on algal cultures before spawning was found to increase larval numbers and their survival (Helm *et al.*, 1973).

It was soon noted that phytoplankton required trace nutrients, such that artificial seawater media produced poor growth (Allen & Nelson, 1910; Allen, 1914). Several species were found to require organic compounds for growth, reviewed by Johnston (1955), including the haptophyte *Isochrysis galbana* Parke (Figure 6). Parke (1949) isolated the latter species from a fish pond. Subsequently high density culture techniques were developed for the species (Kain & Fogg, 1958), which required vitamin B12, as did the diatom *Skeletonema costatum* (Droop, 1955). *Isochrysis galbana* is now the most widely cultured species for rearing bivalve larvae in aquaculture (Helm *et al.*, 2004) and *S. costatum* cultures are a good food for several bivalves and crustaceans including juvenile rock oysters (O'Connor *et al.*, 1992) and shrimp post-larvae (Gleason & Wellington, 1988). Cultures have been fed to adult *Crassostea gigas* infected by *Alexandrium minutum*, to speed up detoxification (Gueguen *et al.*, 2008).

The rotifer *Brachionus plicatilis* Müller was also shown to require vitamin B12 for growth (Scott, 1981). *Brachionus plicatilis* is a good first food for the post-larvae of the flatfish turbot and brill (Jones, 1972). Studies on the diet of post-larval and young juvenile marine fish were reported (Lebour, 1918, 1919b, 1920) and have been widely cited, since they provided a basis for deciding the size and type of food organisms that were suitable for different fish species and at different stages of development, e.g. brill and turbot (Jones, 1972) and pilchard (Blaxter, 1969).

Allen & Nelson (1910) described in detail methods for isolating single phytoplankton cells and keeping them in single species cultures. They listed 18 species of diatoms that they had in culture. Parke (1949) maintained six dinoflagellate species in culture at Plymouth, although two were lost as a result of wartime damage to the laboratory. These cultures formed the basis of the MBA Culture Collection, that now has ~400 strains (Marine Biological Association, 2018). Much of the MBA collection formed the basis of the Culture Collection of Algae and Protozoa when it was originally established in Cambridge, before being transferred to the Culture Collection of Algae and Protozoa at the Dunstaffnage Marine Laboratory. The MBA Culture Collection still holds strains of phytoplankton not in culture elsewhere and cultures, used for research and for larval food, are both supplied to, and deposited from, laboratories worldwide, e.g. Williams *et al.* (2016), Taylor & Cunliffe (2017) and Xu *et al.* (2018).

Recording anthropogenic and environmental change

Overfishing

The 130 years since the JMBA was first published have seen many changes in the marine environment and in the distribution of species. Even by 1887 sewage pollution had depleted the number of fish species within Plymouth Sound (Bourne, 1889) and shellfish fisheries in the local estuaries had been badly affected by mine and china clay wastes (Anonymous, 1856; Heape, 1887). One of

the early papers considered the statistical evidence that overfishing had reduced stocks (Garstang, 1900a). The catch rates, of bottom fish, by vessels were compared, between 1875 and 1898, by converting the fishing power of steam trawlers to 'smack units', i.e. to the daily catch of a deep-sea sailing smack. Garstang concluded, 'that the rate at which sea fishes multiply and grow, even in favourable seasons, is exceeded by the rate of capture'. Unfortunately these words were not heeded and the same unit-effort approach to fisheries statistics has shown a still continuing decline of North Sea fish stocks (Thurstan *et al.*, 2010).

Changes in temperature and other climate variables

The early JMBA publications, as well as many others, provided the initial basis from which the effects of both anthropogenic and climate change on the marine ecosystems in UK waters were subsequently detected. Both short-term changes, such as the effect on the benthos of the cold 1928–29 (Orton & Lewis, 1931) and 1962–63 winters (Holme, 1967), and longer-term climatic changes (Southward, 1960; Southward *et al.*, 1995; Hawkins *et al.*, 2003; Capasso *et al.*, 2010; McHugh *et al.*, 2010; Mieszkowska *et al.*, 2014) have been described, based to a greater or lesser degree on earlier studies published in the JMBA.

It was Cunningham (1906), appointed in July 1887 as the first fisheries naturalist to the MBA, who first noted an alternation between warm-water species and cold-water species in the seas off south-west England, writing 'As the Cornish coasts form the northern limit of the range of the pilchard, it seems possible that in certain periods the drift of warm water from the south extends further to the north, and that the pilchard then extends its wandering – while in other periods the drift of warm water is weaker or takes another direction, and that for this reason the north coast is deserted by the pilchard and visited by the herring' (Cunningham, 1906). Orton (1920) noted that a minimum breeding temperature appeared to be a physiological constant for marine species and that this was one of the ways in which temperature controlled their distribution. Changes in mean seawater temperatures were shown to correlate well with an alternation between pilchard and herring fisheries (Southward *et al.*, 1988). Related changes between water temperatures and the distribution of other fish species in the region were reported (Stebbing *et al.*, 2002). In the late 1920s the local herring fishery supported 300 vessels working out of Plymouth (Ford, 1928a). This fishery collapsed shortly afterwards, during the 1930s (Southward *et al.*, 1988), due to a regime shift in the ecosystem in the northern North Atlantic resulting in warmer sea temperatures, leading to colder water species migrating northwards (Drinkwater, 2006).

Similar changes in the distribution of fish post-larvae, a series started by Russell (1930) and followed for almost 50 years (Russell, 1973), showed long-term changes in species and species abundance that correlated with changing climate and water temperatures. Purcell (2005) reviewed the literature on the distribution and abundance of jellyfish and ctenophore species and concluded that ocean warming was a cause of changes in their distributions.

Changes in zooplankton composition, as well as in phytoplankton and zooplankton abundance (Russell, 1973; Robinson & Hunt, 1986) correlated with environmental variables and climatic changes. The observed inter-annual variations in sea surface and seabed temperatures were considered to be due to changes in the atmospheric circulation patterns brought about by changes in the amount of heat received by the Earth from the sun (Maddock & Swann, 1970). Movements of water masses could be tracked by 'indicator' species of zooplankton, such as species of *Parasagitta* and *Calanus* (Russell, 1935; Southward, 1962a). Changes in sea surface temperatures in a 150-year time series from the Bay of Biscay and adjacent areas, were correlated

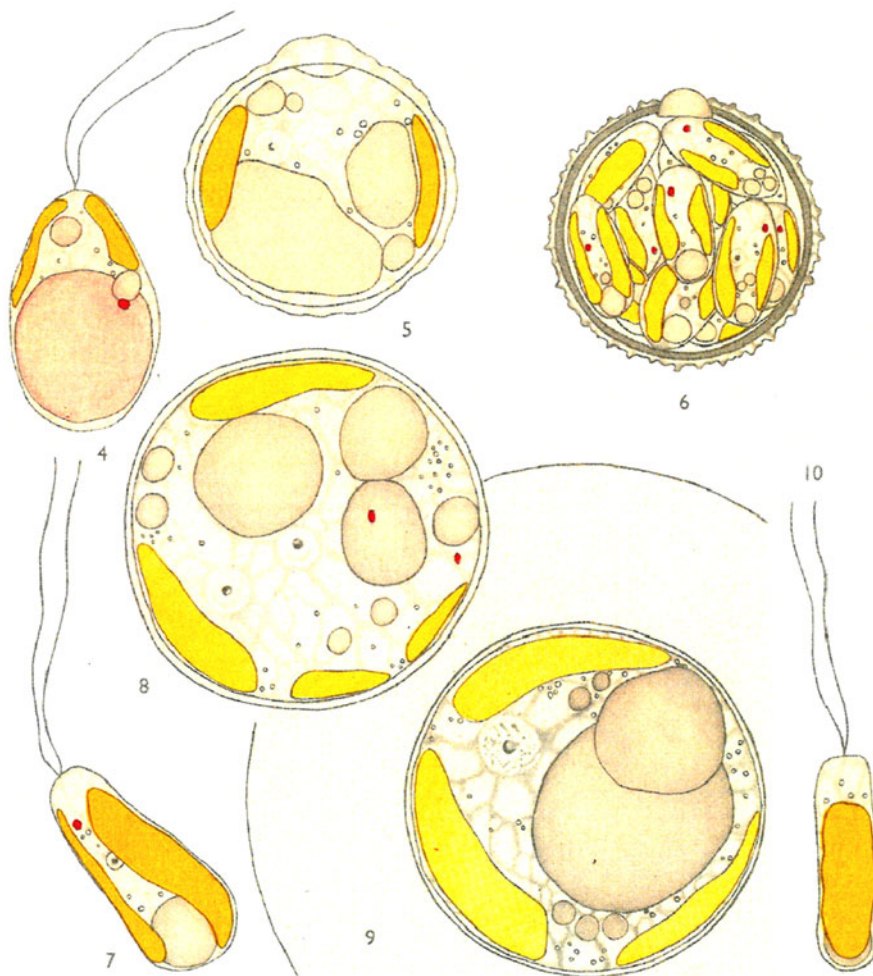


Fig. 6. *Isochrysis galbana* n.g. n.sp., reproduced from Plate 1 of Parke (1949), Figures 4–10, an example of an early hand-coloured illustration. 4, older motile stage; 5, immature cyst; 6, mature cyst; 7, young motile stage with lateral chromatophores; 8, reproduction in the palmelloid phase binucleate stage; 9, reproduction in the palmelloid phase uninucleate stage; 10, young motile stage.

with the Atlantic Multidecadal Oscillation indices and to changes in the zooplankton in the western English Channel (Garcia-Soto & Pingree, 2012). Patterns in phytoplankton distribution were related to changes in weather patterns (Maddock *et al.*, 1989).

Examinations of the distribution of plankton, benthic invertebrates and fish species require boats, nets and corers, grabs, or cameras, to assess species' occurrence and abundance. A less costly approach to study the effects of physical and chemical environmental changes on the distribution of marine species is to study the distribution of intertidal rocky shore organisms.

A classic, much-cited, early paper describing intertidal zonation at Wembury details the zonation of barnacles and macroalgae on rocks (Colman, 1933). Moore (1936) subsequently examined the zonation distribution of the northern barnacle species *Semibalanus balanoides* and the southern barnacle *Chthamalus stellatus* around Plymouth, in relation to food supply and suspended matter in the water. This distribution study was extended to the British Isles and northern France (Moore & Kitching, 1939). Subsequently, Crisp & Southward (1958) showed that changes in the relative distributions of the two species were correlated with their temperature tolerances (Southward, 1958) and the environmental temperatures that influenced the beat rate of their cirri (Southward, 1957, 1962b). A longer-term, 40-year study showed that fluctuations in the relative numbers of *Chthamalus* and *Semibalanus* followed sea temperatures, with a 2-year lag, in a cyclical manner that was close to the 10–11 year sunspot cycle (Southward, 1991). This pattern diverged from the solar cycle after 1975, probably related to major climatic changes (Southward, 1991).

Distribution studies considering other intertidal species were reported by Crisp & Southward (1958). The southern barnacle species *Balanus perforatus* was displaced from many sites by the exceptionally cold winter of 1962–63 but subsequently recovered and colonized sites as much as 100 km east of previous records for the English Channel (Herbert *et al.*, 2003). Studies of these distributional changes in the density and range of intertidal organisms were later expanded to cover the south-west peninsula and subsequently the whole British Isles and nearby Continental European shores. Fifty years of observations on the distribution and densities of intertidal fauna enabled links to be established between faunal changes in the eastern Atlantic intertidal zone and changes in the Atlantic Multidecadal Oscillation (AMO) (Mieszkowska *et al.*, 2014). Historical datasets are proving vital for attempts to predict future changes in littoral ecosystems (Hawkins *et al.*, 2015).

Changes in other environmental conditions

Papers in the JMBA describe the effects of a wide range of natural and anthropogenic effects on the marine ecosystem, including the effects of increased footfall over a rocky shore (Boalch *et al.*, 1974), changes in the benthos resulting from the discharge of china clay wastes (Probert, 1975, 1981) and the effects of eutrophication on infauna and fish (Quillien *et al.*, 2017). Both pre-effect and post-effect surveys have been used to study sites and comparisons of fauna changes along effect gradients used to evaluate impacts. One particularly interesting case was the impact of the infection of seagrasses, *Zostera* species, by a slime mould (Muehlstein *et al.*, 1991).

The fauna of the Salcombe estuary were first described by Allen & Todd (1900), including the species inhabiting the *Zostera* beds inside the harbour entrance. In the early 1930s *Zostera* beds started dying on both sides of the Atlantic (Graham & Atkins, 1938). Wilson (1949a) examined the dead and dying *Zostera marina* beds near Salcombe that had been surveyed 50 years previously and found a marked decline in both the number of individuals and the numbers of macroinfaunal species, as well as marked changes in sand deposition due to the death of the *Zostera*. In the Tamar estuary, at Plymouth, Hartley (1940), who studied the estuarine fish population in 1936 and 1937, wrote 'in days gone by some of the Saltash men made a living all the year round by catching 'smelts' (*Atherina presbyter*). Now this fish has become so rare that its capture excites comment: I have myself seen only nine specimens in two years' work.' This species spawns in *Zostera* beds (Kennedy & FitzMaurice, 1969), attaching its eggs with long filaments to vegetation and its loss occurred at the time the *Zostera* beds died out. These studies have contributed to our knowledge of the role of *Zostera* beds in the marine ecosystem (Fonseca & Fisher, 1986).

Other major factors affecting the distribution of marine fauna include earthquakes. Although the 2016 Kaikoura quake is perhaps best known for its effects on marine life, no studies on the marine effects of this have been published to date in the JMBA, although changes in the zonation of intertidal biota following the 2011, Mw 9.0, earthquake in east Japan have been described (Noda *et al.*, 2016).

Marine chemistry

It was early appreciated that different water masses contained different plankton communities (Cleve, 1897). The chemical composition of seawater, not just the salinity, was related to the species composition, particularly of the phytoplankton (Atkins, 1923a, 1923b). Harvey (1926), who devised a more accurate method for determining nitrate in seawater, by reduction to nitrite and colorimetric measurement of the nitrite after diazotization, using a Duboscq colorimeter, showed that uptake by phytoplankton removed all nitrate from the upper layers of the sea in summer. Nitrate was thought to be regenerated by vertical mixing with deeper water in winter but Pingree & Pennycuik (1975) showed that significant transfer also occurred through the thermocline. The analytical method for nitrate was refined by several authors but was always difficult to undertake at sea. Finally a more sensitive method was developed, passing water through copperized cadmium filings to convert the nitrate to nitrite (Wood *et al.*, 1967). This technique was subsequently adapted for automation, using AutoAnalyzer and submersible FIA systems (Oudot & Montel, 1988; Daniel *et al.*, 1995; Zhang, 2000).

Papers in the JMBA also show developments in the measurement of dissolved phosphate in seawater. Early methods required large volumes of water and concentration of phosphate by precipitation, before colorimetric determination as phosphomolybdate (Matthew, 1916). The method was later refined and made more sensitive with a newly designed colorimeter (Harvey, 1948) and a single solution reagent for phosphate determination was subsequently introduced (Murphy & Riley, 1958). A comparative study of the methods of seawater inorganic phosphate analyses was made (Jones & Spencer, 1963). Atkins (1923a) used the loss of phosphate from the water column during the year and the phosphate content of phytoplankton, to estimate the annual primary production of the English Channel as 1.4 kg phytoplankton m^{-2} over a water depth of 70 m. A similar production figure was obtained from the change in alkalinity of seawater due to photosynthesis (Atkins, 1922).

The complexity of seawater nutrient studies was revealed by the development of a method for determining total dissolved nitrogen and phosphorus by irradiating seawater with UV from a mercury arc lamp before analysis (Armstrong & Tibbitts, 1968). Analysis over an 11-year period showed that, unlike inorganic nitrogen and phosphate, total N and P changed little over the year (Butler *et al.*, 1979). Thus the lost inorganic nutrients were replaced by equivalent organic nutrients that could be utilized by phytoplankton (Harvey, 1940; Antia *et al.*, 1975).

Other significant analytical methods published in the JMBA include those for ammonia (Newell, 1967), amino acids (Riley & Segar, 1970), iron (Armstrong, 1957) and silicate (Liss & Spencer, 1969). All the above, as well as other JMBA publications, helped to develop the methods described in later manuals of seawater analysis (e.g. Strickland & Parsons, 1972; Grasshoff *et al.*, 1999).

Physical oceanography

In order to understand the movement of pelagic fish eggs it was necessary to understand the drift of surface water. Drift bottles, described by Nelson (1922), that were weighted to make them almost completely submerged just below the surface or to float close to the bottom, were used to follow water movements throughout the year. Surface drift was measured in the English Channel, North Sea and Irish Sea (Garstang, 1898; Carruthers, 1925). In subsequent studies surface and bottom drift bottles were deployed together (Carruthers, 1927). Studies on water temperatures and salinities showed that episodic movements of surface water from the Atlantic into the English Channel occurred (Harvey, 1925). Carruthers *et al.* (1951) examined continuous current meter data from the Seven Stones Light Vessel, situated between Land's End and the Isles of Scilly, for 1939–1941 and found an ESE residual flow of 2.5 miles day^{-1} . Deployment of a satellite-tracked ARGOS float, drogued at 10 m, south of the Isle of Scilly, revealed a residual clockwise current around the islands with a mean speed of 1 $m s^{-1}$ in one circumnavigation (Pingree & Maddock, 1985). Cooper (1952a, 1952b) studied the effect of winds causing mixing of deep and surface water on the continental slope and the effect of canyons in channelling nutrient-enriched water into the English Channel by means of internal oceanic waves. He explained how similar conditions carried shoals of boar fish, *Capros aper*, well into the English Channel (Cooper, 1952a). In 1888 this deep-sea fish was filling the nets of trawlers working off Plymouth (Cunningham, 1888).

Drogued ARGOS floats and neutrally buoyant ALACE floats, that rose to the surface at intervals to allow a satellite fix, were used to follow the path of a 'meddy' (an eddy with a core of high salinity Mediterranean outflow water) starting off the continental slope west of Lisbon (Pingree, 1995). The meddy was followed for 204 days with a mean westward track and had a rotational time of 2.5 days.

A compilation of oceanographic data from the above, and other, studies of the NE Atlantic (Pingree, 2002) revealed the complexities of the circulation system. A number of eddy systems were identified and followed, some of which had wave-like properties. The ARGOS and ALACE floats, together with current meter and shipboard measurements, allowed a correlation with satellite altimeter data of sea level anomalies, such that the altimeter data interpretation of eddies, internal wave and current systems could be verified. Long-term changes from 1992 to 2002 in the North Atlantic Current and the Subtropical Gyre transport were correlated with the winter NAO Index.

On a smaller scale, a study of wave-induced water circulation in sands (Webb & Theodor, 1972) described how dissolved and finely particulate organic matter would be supplied to interstitial

microbiota (Meadows & Anderson, 1968) and affect the small-scale distribution of epibenthic organisms.

Physiology and biochemistry

Although studies on the giant nerve axon of cephalopods are the best known of the physiological studies undertaken at the MBA (Sims, 2014), the results were not published in the JMBA, but in journals including *Nature* and the *Journal of Physiology*. A summary of the history of this research was published in the JMBA (Hill, 1950).

A theme of many physiology papers in the JMBA is how marine organisms can sense and respond to changes in the environment, such as temperature, pressure/sound/vibrations, salinity and light. A number of early papers describe the use of conditioned responses of fish to determine their ability to detect changes in temperature, to as little as 0.03°C (Bull, 1936), salinity, vibrations (Bull, 1928) and light wavelengths (Bull, 1935). A mesopelagic deep-sea fish was shown to have different pigments in the part of the retina receiving light from above to the part receiving light from below (Denton & Lockett, 1989). Pioneering studies on bioluminescence and fish eyes were published in JMBA by J.A.C. Nicol in the 1950s. He first investigated the light-producing glands of the polychaete *Chaetopterus* (Nicol, 1952) and then luminescence in other marine species, with a much-cited joint paper with G.L. Clarke, on comparative studies on luminous pelagic animals, in JMBA (Clarke *et al.*, 1962).

In a series of papers on clupeids, the linked swimbladder-inner ear-lateral line system was described as the set of organs that could respond to vibrational pressures and allow the fish to estimate the direction and distance of the source (Allen *et al.*, 1976). The frequency responses of this system were described (Denton *et al.*, 1979; Gray & Denton, 1979) as were the startle response of herring shoals (Blaxter & Hoss, 1981). The response was most sensitive in smaller fish with a threshold of 2–18 Pa (Blaxter & Hoss, 1981). Herring larvae only responded when the otic bulla contained gas, but showed a tactile response soon after hatching (Blaxter & Batty, 1985).

Papers also describe how many marine organisms achieve neutral buoyancy in seawater. Many phytoplankton cells reduce their density, after sinking into dark nutrient-rich waters, so that they can ascend again into the photic zone for photosynthesis after acquiring more nutrients (Steele & Yentsch, 1960). Pelagic eggs of teleostean fish achieve buoyancy by having a water content with a reduced salinity (Craik & Harvey, 1987). Lipid contributes only a minor component to the buoyancy.

Sodium and potassium ions were replaced by lighter ammonium ions in some squids to increase buoyancy (Clarke, 1979) and also in the chaetognath *Sagitta elegans* (Bone *et al.*, 1987). In some mesopelagic fish, neutral buoyancy was achieved by reducing skeletal density and protein mass (Denton & Marshall, 1958) and such fish are probably only capable of short burst swimming (Blaxter *et al.*, 1971). In contrast, most elasmobranchs reduce their density by depositing large amounts of oil in their livers (Bone & Roberts, 1969). The cephalopod *Nautilus* achieves buoyancy by replacing seawater in the shell chambers by gas and by water with a lower density (Denton & Gilpin-Brown, 1966). Similarly *Sepia* achieves neutral buoyancy by displacing water with gas in the chambers of the cuttle bone (Denton & Gilpin-Brown, 1961).

Clarke (1978a, 1978b, 1978c), in three substantial papers in JMBA, provided evidence for the hypothesis that, because of the physical properties of spermaceti oil, sperm whales are able to achieve neutral buoyancy over their geographic range, when they dive below 200 m, by lowering the temperature of the oil in the spermaceti organ in their head by about 3°C. Clarke

proposed that this was mainly done by cooling the blood, passing it through the skin in the head, before circulating around the organ.

A number of papers have reported mechanisms of camouflage in marine organisms, including the ways in which pelagic fish, such as silvery teleosts and hatchet fish, reduce their visibility to predators (Denton & Nicol, 1966; Janssen *et al.*, 1986). The processes that create the silvery appearance during smoltification of salmon were also described (Denton & Saunders, 1972). An unusual elongated eye in the octopus *Vitreledonella richardi* was considered to minimize the silhouette and reduce predation (Land, 1992). Some sponges use an external sediment crust as camouflage (Schönberg, 2016).

These adaptations of marine organisms to their environment now form part of the text of books on marine biology, marine ecology and the physiology of marine organisms (Newell, 1976; Barnes & Hughes, 1999; Kaiser *et al.*, 2011).

The discovery of species of small, gutless, frenalate tubeworms (Southward & Southward, 1958b; Southward, 1978) led to investigations on their uptake of dissolved organic compounds from the sediment as a nutritional source (Southward & Southward, 1980). Following the discovery of symbiotic, chemoautotrophic bacteria in their larger vestimentiferan relatives from hydrothermal vents (Cavanaugh *et al.*, 1981), it was discovered that similar bacteria also occurred in frenalates (Southward, 1982; Southward *et al.*, 1986). Further investigations showed that some thyasirid and lucinid bivalves (Dando & Southward, 1986; Southward, 1986) and nematodes (Austen *et al.*, 1993) also obtained nutrition from endosymbiotic chemosynthetic bacteria. Stable isotope studies revealed different nutritional sources for three chemosynthetic bivalve species at the Logatchev hydrothermal site (Southward *et al.*, 2001). Other species at vents can harvest chemosynthetic epibiotic bacteria from their surfaces (Suzuki *et al.*, 2009; Tsuchida *et al.*, 2011).

These papers on bacterial symbionts in nematodes, siboglinid tubeworms, bivalves, crustaceans and other species have been cited in reviews of these fields (Kiel, 2010; Hilário *et al.*, 2011; Duperron *et al.*, 2013).

Pollution studies

Oil spills

The massive oil spill resulting from the grounding of the Torrey Canyon oil tanker on the Seven Stones Reef, between Cornwall and the Isles of Scilly in 1967 led to a major investigation by the MBA into the effects of crude oil and of the oil dispersants used at that time on marine life. Publications showing the effects of oil and dispersants on organisms started appearing in the JMBA the following year (Corner *et al.*, 1968; Wilson, 1968; Bryan, 1969). These and other studies by scientists at the MBA resulted in the rapid publication of the book ‘Torrey Canyon’ Pollution and Marine Life: A Report by the Plymouth Laboratory of the Marine Biological Association of the United Kingdom’ (Smith, 1968) that concluded that the oil dispersants used at the time were more damaging than the oil itself. This led to the JMBA becoming a popular journal for publishing studies on observations on the results of oil spills elsewhere, including the Amoco Cadiz spill off Brittany (Brule, 1987), the Erika spill off Pays de la Loire (Pavillon *et al.*, 2002), the Sea Empress spill off Wales (Reynolds *et al.*, 2003), the Prestige oil spill off Spain (Bustamante *et al.*, 2010) and the Volgoneft-248 spill off Turkey (Tas *et al.*, 2011).

Follow-up studies, on the recovery of the intertidal fauna in particular, were published, e.g. Southward & Southward (1978). Fifty years after the Torrey-Canyon spill the Industry Technical Advisory Committee (ITAC) annual meeting, organized by Oil

Spill Response Ltd, was held in Plymouth, at which the problems of defining the long-term changes resulting from oil spills and dispersant use were summarized. A session was also included on the ecological and sociological long-term effects of the Torrey Canyon oil spill citing the early studies published in JMBA (Hawkins *et al.*, 2017b). The inter-tidal and low sub-tidal flora and fauna on some sheltered shores had taken 15 years to return to their pre-spill conditions and the value of long-term monitoring was emphasized. Oil spill dispersants have continued to be used in the marine environment, but the dispersant industry has modified the ingredients and now gives more attention to the 'net environmental benefit' of their use (Lessard & Demarco, 2000).

Heavy metal pollution

Metal mining for lead, silver, tin and copper has an ancient history in Devon and Cornwall. Tin smelting dates back to the early Bronze Age (Miles, 1975; Hausten *et al.*, 2010), although large-scale mining did not become established until Roman times (Mehang *et al.*, 2012). Effluent from these mines and the leachates from the mine spoil heaps entered rivers and estuaries and affected marine life (Garnacho *et al.*, 2001; Daka & Hawkins, 2004). Seasonal variation in the copper content of coastal seawater was measured (Atkins, 1953) and probably reflected periods of increased river flow. Drainage waters from coal mines were also shown to have adverse effects on estuarine fauna (Woolsey & Wilkinson, 2007).

Several papers describe the adaptation of invertebrates to living in sediments containing high concentrations of heavy metals, including lead (Daka & Hawkins, 2004), manganese (Bryan & Hummerstone, 1973a), mercury (Clark & Topping, 1989) and zinc (Daka & Hawkins, 2004). Common estuarine organisms were studied as indicator species to be analysed for metal contamination in estuaries. These included the brown seaweed *Fucus vesiculosus* (Bryan & Hummerstone, 1973b), the barnacle *Balanus improvisus* (Rainbow *et al.*, 2002), the bivalve *Scrobicularia plana* (Bryan & Hummerstone, 1978) and the gastropod *Littorina littorea* (Bryan *et al.*, 1983; Mason & Simkiss, 1983).

Papers have described the physiological and behavioural effects of copper (Blaxter, 1977; Manley, 1983; Garnacho *et al.*, 2001) and its effects on larval development (Ruiz *et al.*, 1996). Concentrations of copper and zinc, just above the respective maxima of 25 and 138 nM, found in seawater from the English Channel, were shown to inhibit carbon fixation rates in phytoplankton (Davies & Sleep, 1979, 1980) and low concentrations of mercury (5 µM) inhibited algal cell division (Davies, 1976).

Some of the above studies led to separate MBA publications on biological indicator species for heavy metal contamination in estuaries (Bryan *et al.*, 1980) and on the history of heavy metal pollution of the Fal estuary due to mining activity (Bryan & Gibbs, 1980). The papers published in the JMBA made an important contribution to a review of the effect of trace metals on organisms in the British Isles (Rainbow, 2018).

Tributyl tin (TBT)

Following the introduction of marine anti-fouling paints containing tributyl tin (TBT) compounds, populations of the dogwhelk, *Nucella lapillus*, showed marked declines in numbers in the vicinity of harbours and marinas (Bryan *et al.*, 1986, 1987, 1993). The cause of the decline was found to be the development of a penis and vas deferens on the female, in response to TBT exposure. The vas deferens overgrowing the vulva prevented the release of egg capsules and thus rendered the female sterile (Bryan *et al.*, 1986, 1987). Other gastropods were similarly affected (Gibbs *et al.*, 1991; Kohn & Almasi, 1993; Averbuj & Penchaszadeh, 2010). The accumulating evidence of the damage caused by

these antifouling paints led to the UK banning the use of the anti-fouling agent on vessels <25 m length overall in 1986, although larger vessels could still use it. An EU ban on the presence of TBT-based antifouling coatings on ship hulls in EU ports was introduced in January 2008 and a global ban on both the application and presence on ship hulls of TBT-based antifoulants the following September. The recovery of gastropod populations in affected areas in Watermouth Cove, an area affected by leaching from the hulls of pleasure craft, was described (Crothers, 2003); even outside the cove, it took 13 years for the population of *Nucella lapillus* to recover. In areas where there were no nearby unaffected populations and scarce natural habitat, artificial hard substrata provided stepping-stones that facilitated the migration of *Nucella* (Bray *et al.*, 2012).

The early reports regarding the effects of TBT pollution formed the basis for longer-term recovery studies. At a site near a shipyard in Falmouth, Cornwall, the population of the gastropod *Ocenebra erinacea* was still severely affected 20 years after initial exposure (Gibbs, 2009). The TBT concentration in sediments off Southampton had only halved after 33 years (Langston *et al.*, 2015). Reviews in other recent papers on stress in intertidal communities and the global impacts of TBT also cite early studies published in the JMBA (Crowe *et al.*, 2000; Sousa *et al.*, 2014).

Discussion

Papers published in the JMBA, since 1887, reveal the development of collection, measurement and survey techniques, as well as our understanding of the marine ecosystem and the inter-relationships of different organisms from viruses to cetaceans. These papers are now cited in modern texts on marine ecology (Barnes & Hughes, 1999; Kaiser *et al.*, 2011) and fisheries ecology (Jennings *et al.*, 2001) as well as in manuals on sampling methods in the marine environment, e.g. Eleftheriou (2013).

The long series of records of changes in the distributions and densities of species, together with corresponding data on the physical and chemical environment, has allowed the development of models to forecast future ecosystem changes in different areas of the oceans (Zacharias *et al.*, 1999; Huang & Brooke, 2011; Hattab *et al.*, 2013).

Since the earliest records, marine organisms have been affected by both cyclical climatic changes and anthropogenic discharges and pollutants. Disentangling the causes of ecosystem changes resulting from multiple stressors is complicated. A recent analysis (Hawkins *et al.*, 2017a) stresses the need for continued long-term observations and reveals the value of the early ecosystem studies published in the JMBA. The records published in the JMBA have been especially useful in describing the changes in the English Channel ecosystem through periods of warming and cooling, as well as describing the effects of and the recovery from pollution events (Southward *et al.*, 2005).

The JMBA started as a 'house journal' for the members of the Marine Biological Association of the United Kingdom, publishing work carried out at the Plymouth Laboratory by members, staff and visiting scientists. It has evolved, by the 100th volume, to become a truly international journal for marine science, publishing papers from around the world dealing with the marine environment and marine biota, from the intertidal to the hadal zone. The JMBA continues to contribute to our knowledge on how changing climates may affect our oceans in future. One uncertainty, at the time of writing, is how the proposals, by major funding agencies, that all future scientific publications resulting from their grants must be in fully open access journals (McNutt, 2019), will affect the JMBA.

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