

Synthesis

Otolith research and application: current directions in innovation and implementation

Gavin A. Begg^{A,E}, Steven E. Campana^B, Anthony J. Fowler^C and Iain M. Suthers^D

^ACRC Reef Research Centre and School of Tropical Environment Studies and Geography, James Cook University, Townsville, Qld 4811, Australia.

^BMarine Fish Division, Bedford Institute of Oceanography, PO Box 1006, Dartmouth, Nova Scotia B2Y 4A2, Canada.

^CSouth Australian Research and Development Institute, PO Box 120, Henley Beach, SA 5022, Australia.

^DSchool of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia.

^ECorresponding author. Email: gavin.begg@jcu.edu.au

Abstract. The Third International Symposium on Fish Otolith Research and Application was held in Townsville, Queensland, Australia from 11 to 16 July 2004. The overall theme was ‘Innovation and Implementation’, a collection of which is published here (Volume 56, Issue 5). Although age and growth studies predominated at the Symposium, new areas of quality-control assurance, annual-increment formation in deep-sea and tropical fish, image analysis and two-dimensional feature extraction were demonstrated. New statistical approaches were also evident, particularly in the subsampling of commercial data for estimating age compositions. The chemical composition of otoliths as natural data loggers has greatly advanced since the 1998 Symposium, with the advent of micromilling machines, new instrumentation and the use of isotopes rather than elements as environmental indicators. Otoliths will continue to support modern environmental needs for fisheries, marine park assessment, metapopulation conservation and the management of stocks and biodiversity of fish.

Extra keywords: age, assessment, chemistry, climate, ecology, fisheries management, growth, otolith, symposium, validation.

Introduction

Over the past decade there have been significant developments in fisheries science, based largely on the technological advances in extracting information from the otoliths of fish (e.g. Grant 1992; Secor *et al.* 1995; Fossum *et al.* 2000; Panfili *et al.* 2002; Campana 2005). Otoliths or ‘ear bones’ are small calcified structures found in the heads of fish, which assist in detecting sound and are used for balance and orientation (Campana and Neilson 1985; Popper *et al.* 2003). More importantly for scientists and resource managers, otoliths are natural data loggers that record information in their microstructure and chemistry at different temporal scales related to their growth and environment (Kalish 1989; Campana 1999). This information, which includes age and growth, movement patterns and habitat interactions, can be interpreted at the population level in terms of the ecology, demography and life history of the species, which has become fundamental to the management of fisheries and protected species around the world. There is almost certainly no other biological structure that is more important to fishery scientists

than otoliths because of the information they contain. The challenge for scientists, however, is to continue to develop the appropriate technologies to extract information from otoliths and interpret it accurately in terms of the biology of the fish and the environments they have experienced. The motivation to establish recent developments and advances in otolith research initiated the Third International Symposium on Fish Otolith Research and Application. The Symposium was held on 11–16 July 2004 in Townsville, Queensland, Australia, the first time the Symposium has been held in the southern hemisphere. The Symposium was co-hosted by the CRC Reef Research Centre and James Cook University. Selected research from the Symposium is presented in this Special Issue and represented our state of knowledge at that time. Over 120 referees reviewed the many manuscripts that were submitted, and the editorship was coordinated by the authors under the auspices of the Managing Editor of *Marine and Freshwater Research*, Dugald McGlashan.

The Third International Symposium on Fish Otolith Research and Application brought together 280 scientists

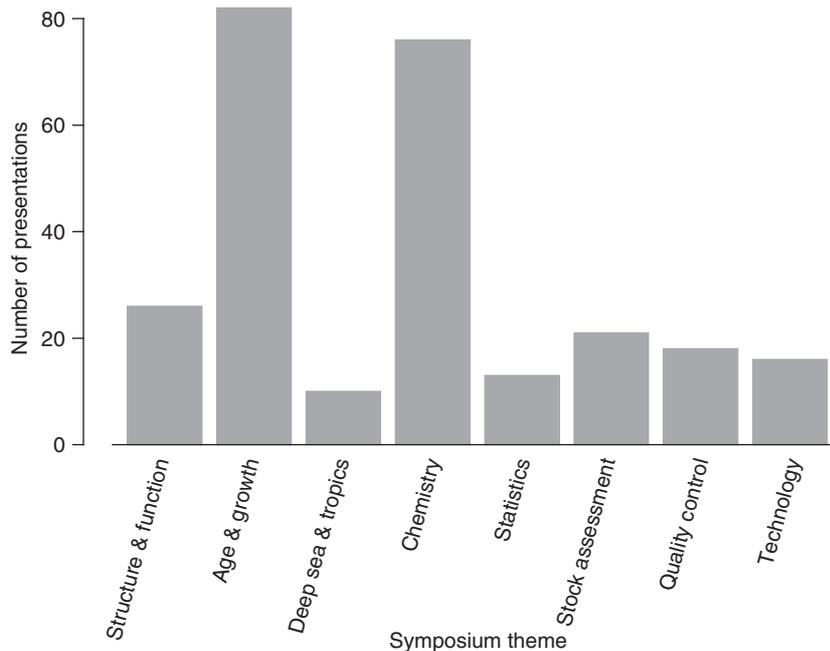


Fig. 1. Number of presentations by theme at the Third International Symposium on Fish Otolith Research and Application. A total of 262 presentations were given that addressed the following eight themes: structure and function; age and growth estimation and validation in fish, sharks and invertebrates; age determination in deep sea and tropical environments; chemical composition and applications to climate, ecology and population biology; statistics and modelling of age-based data; stock assessment and fisheries management; quality control in ageing facilities and data processing; and technological developments.

from around the world to establish the current level of understanding, state-of-the-art approaches and future directions for this increasingly important field of research and its application to fisheries assessment and management. The Symposium was the third in a series of international symposia held over the past decade to accommodate the extraordinary rate of development in otolith research. This development most likely relates to the two previous groundbreaking symposia that were held throughout this period in South Carolina, USA in 1993 (Secor *et al.* 1995) and in Bergen, Norway in 1998 (Fossum *et al.* 2000). The rate of development in otolith research, and perhaps more so its application, has continued unabated since the Second Symposium in Norway, although there has been a change in emphasis from classic age and growth studies to more applied ecological studies (Campana 2005). ‘Innovation and Implementation’ was the overall theme of the Third Symposium, reflecting the recent advancements and use of otolith-based research and encouraging the need to continue looking forwards.

The field of otolith research and its application to fisheries science has developed remarkably over the past decade as the potential for otoliths as natural data recorders has been realised and the technology for their interpretation developed. Scientific papers relating to otolith research are now being published at five times the rate that they were in the

1970s, with the annual rate approaching 200 papers per year (Campana 2005). Otolith-based research provides information on the population biology and life history of fish that is otherwise extremely difficult, if not impossible, to collect. Such information can be used to help develop management strategies to ensure the ecologically sustainable use of fisheries and the aquatic environments from which they are extracted. The most common and important applications of otolith-derived data are to provide information for stock assessments to determine the sustainability of fish stocks, but they are also being used to address a broad range of problems from fisheries management to environmental change.

The Third International Symposium on Fish Otolith Research and Application provided a forum to establish the current level of understanding in extracting otolith-derived ecological information for natural resource assessment and management. A total of 262 oral and poster presentations were delivered at the Symposium, relating to eight specific themes: (1) structure and function; (2) age and growth estimation and validation in fish, sharks and invertebrates; (3) age determination in deep-sea and tropical environments; (4) chemical composition and applications to climate, ecology and population biology; (5) statistics and modelling of age-based data; (6) stock assessment and fisheries management; (7) quality control in ageing facilities and data processing; and (8) technological developments (Fig. 1).

Each of these eight themes is represented in the papers presented in this Special Issue.

1. Structure and function

This theme focussed on otolith structural development and compositional characteristics, connections between and factors affecting biomineralisation processes and ultra-, micro- and macro-structure, linking growth, physiology and genetically-controlled formation of structure and stato-acoustic functionality, and applications to identification of growth structures for analysis of age, growth and physiological condition. A total of 26 presentations encompassed the fundamental aspects of this theme. Popper *et al.* (2005) provided an overview of the structure and function of otoliths, particularly with respect to hearing and balance, and how these functions change with age and growth. They also highlighted the multidisciplinary nature of otolith research and the current lack of collaborative research and information exchange among disciplines to resolve similar questions. Multidisciplinary progress may assist in understanding the underlying principles of otolith formation. Panfili *et al.* (2005) examined otolith formation from the perspective of fluctuating asymmetry; their findings failed to support the assumption that this reflects developmental instability caused by environmental and/or genetic stress. Although we have come some way in understanding the factors responsible for otolith formation, further research is needed, particularly in discerning the mechanisms that control structure and function.

2. Age and growth estimation and validation

Historically, otoliths have mainly been used in studies of age and growth. The significance of this field continues today, as reflected by the 82 related presentations at the Symposium. This theme focussed on the application of age estimation and validation techniques, analysis and interpretation of age and growth data in determining life-history characteristics and the biological and ecological significance of these data for diagnosing the potential resilience of aquatic populations. Validation of daily and annual increments in calcified structures continues to be an active area of research, although the requirement to achieve validation for every species has recently been questioned. Andrews *et al.* (2005) and Williams *et al.* (2005) demonstrated the use of radio-carbon dating and marginal increment analysis techniques for validating the periodicity of increment formation for difficult-to-age, demersal, long-lived and tropical fish species respectively. Although many now agree that annual-growth increment deposition can often be safely assumed, validation is often necessary to demonstrate the correct interpretation of the increments by researchers. With the growing numbers of age-validated otolith reference collections, the reliance on age validation for quality-control purposes may decline.

Since the observation of daily increments in fish otoliths (Pannella 1971), there has been a plethora of research that investigated the early life history of fish and the factors that influence their growth, mortality and recruitment. Baumann *et al.* (2005), Uehara *et al.* (2005) and Wilhelm *et al.* (2005) further our understanding of these investigations with studies on the short-term decoupling of otolith and somatic growth, relationships between growth rate and stable-isotope composition and impacts of upwelling zones on recruitment, where the critical period of survival may be later than that at first feeding.

A notable difference between this and the two previous symposia is an increased emphasis on structures and species other than otoliths and teleosts. Consequently, this theme also presented an opportunity to highlight the potential advantages of otoliths over other structures such as scales and fin rays, and involved age estimation for elasmobranchs and invertebrates to provide insights and new methods to otolith-based ageing techniques. An example of this change in focus was given by Arkhipkin (2005), who provided an overview of recent developments in the ageing of cephalopods, and the utility of statoliths as data loggers and ageing structures analogous to otoliths.

3. Age determination in deep sea and tropical environments

Another change in emphasis at the Symposium was reflected in the inclusion of a theme on age determination of organisms that inhabit deep-sea and tropical environments. The traditional view was that these environments lack the clear seasonal signals of temperate environments, thus preventing annual-growth increments from being deposited. However, the expansion of fisheries to deeper waters and increased expertise in tropical environments over the past decade has revealed that annual-growth increments are evident in calcified structures and can be used for ageing purposes. A total of 10 presentations discussed advances and difficulties associated with age determination for species from such environments compared to those that display more seasonality. Morales-Nin and Panfili (2005), captured the essence of these presentations by refuting the dogma attached to supposed non-seasonal growth increments in otoliths from assumed aseasonal environments, and reviewed the recent increase in studies that demonstrate seasonal increment deposition in otoliths from deep-sea and tropical environments.

4. Chemical composition and applications to climate, ecology and population biology

Providing insight into the chemical composition of calcified structures and the resulting application of this information continues to be a major motivation for otolith-based research. There has been a significant increase in such research over

the past five years (Campana 2005), attracting 76 related presentations at the Symposium. The unique chronological and chemical properties of otoliths continue to attract the attention of scientists with diverse interests ranging from fisheries science to palaeobiology. This theme focussed on organic and inorganic composition of otoliths, isotope and trace element studies, developments in analytical instrumentation, chemical mass marking and uptake and applications to stock identification, migration, life history and environmental reconstruction at daily, annual, decadal and millennial time scales.

Understanding the processes that lead to chemical uptake in calcified structures will assist in interpreting results derived from more applied studies. Morales-Nin *et al.* (2005) observed age-related trends in otolith chemistry, revealing distinct differences between the core and subsequent annuli in hake (*Merluccius merluccius*). In contrast, Elsdon and Gillanders (2005) found no influence of ontogeny on Sr : Ca or Ba : Ca concentrations in black bream (*Acanthopagrus butcheri*), and noted that tracking fish movement relies on establishing links between otolith chemistry and environmental variables. They further found that ambient and otolith Sr : Ca concentrations were similar between field-collected and laboratory-reared fish, whereas ambient Ba : Ca was inversely related to salinity, suggesting that it may be possible to reconstruct salinity regimes from otoliths.

A common application of otolith chemistry is the reconstruction of movement patterns and related stock identification. Representative case studies of Daverat *et al.* (2005), Tzeng *et al.* (2005), McCulloch *et al.* (2005), Dorval *et al.* (2005) and Hobbs *et al.* (2005) demonstrated the utility of otolith chemistry in tracking movements and/or habitat shifts throughout the life history of fish, which, in turn, can be used to infer stock structure and population connectivity (Fowler *et al.* 2005; Stransky *et al.* 2005). Similarly, Gillanders and Joyce (2005) used otolith chemistry to differentiate aquaculture and wild-harvest yellowtail kingfish (*Seriola lalandi*), whereas Niva *et al.* (2005) examined the effectiveness of alizarin-red-stained otoliths as a cost-effective mass-marking tool. The basic premise of all these studies is that otoliths, or analogous calcified structures, are metabolically inert and that elemental uptake reflects the ambient environmental conditions in which fish reside (Campana and Neilson 1985; Fowler *et al.* 1995).

5. Statistics and modelling of age-based data

Innovative approaches to data analysis and advancements in modelling of age-based life-history data are areas of research that require greater emphasis. A total of 13 presentations were given on this theme, which focussed on mathematical approaches to understanding the processes that underlie otolith structure and function, spatial and temporal analyses

of otolith structure and composition, mechanistic models at different levels of biological organisation that can be tested against physiological processes of otolith formation, growth and reproduction and ecological interactions, such as migration and competition. Sandin *et al.* (2005) used maximum-likelihood methods to explore elemental otolith signatures and dispersal trajectories of individual fish to enable detailed models of fish movement to be developed. Similarly, Cappo *et al.* (2005) developed a robust classification technique to discriminate fish residency in barramundi (*Lates calcarifer*), based on elemental ratios in scales. However, perhaps the greatest need from a pragmatic perspective for large-scale ageing operations is the need to develop alternative approaches to obtain cost-effective and representative age data for effective stock assessments. Francis *et al.* (2005) examined this need by developing a new, maximum-likelihood-based, length-mediated, mixture analysis using fish length, otolith weight and age data. Likewise, Troynikov and Robertson (2005) examined a new statistical approach for estimating age compositions using fish length and otolith weight data.

6. Stock assessment and fisheries management

The use of age-based data for stock assessment and fisheries management maintains the pragmatic requirement for otolith research. This theme focussed on the information that can be retrospectively derived from otoliths to help establish the status of a fishery resource and determine the level at which it may be exploited sustainably, including information that contributes to understanding the population dynamics, demography and life history of a species, as well as the implications associated with ageing uncertainty and the need for accurate estimates of age from representative samples of fished populations. A total of 21 presentations addressed many of these aspects. For example, Berg *et al.* (2005) explored the accuracy and precision in distinguishing two cod (*Gadus morhua*) stocks in the north-east Atlantic based on otolith growth and shape morphometrics. Similarly, Husebø *et al.* (2005) used otolith microstructure to discriminate spawning components of herring (*Clupea harengus*) and to estimate their relative contribution to overall year class strength.

7. Quality control in ageing facilities and data processing

A major shift in otolith research and the use of age-based data has been in the fundamental requirement to ensure quality control in ageing facilities and data processing. This shift represents a move from basic research to one of consolidation and acceptance of standardised applications and protocols. With guidelines for ageing fish becoming available for an increasing number of species, so too will the adoption of quality-control procedures for the improvement of stock

assessment and fisheries management. A total of 18 presentations represented this shift, with this theme focussed on the development of a framework for the application of quality assurance and quality-control mechanisms to protocols for the determination of fish age, including the levels of precision and accuracy to be used as qualifiers in statistical terms and evaluation of individual methods of age determination to provide data for stock assessments.

Morison *et al.* (2005) reviewed quality assurance and quality-control practices that are currently used in ageing facilities around the world. No clear consensus on desirable standards for quality issues such as staff training, use of reference sets or reading protocols were found, although this needs to be rectified. However, Kimura and Anderl (2005) provided an example of a large-scale ageing facility, which implements quality-control mechanisms. Coupled with quality-control practices is the desire to implement automated ageing protocols that remove the subjectivity associated with individual reader bias, while increasing accuracy and cost effectiveness. Palmer *et al.* (2005) introduced some of these issues and detailed a new method for two-dimensional feature extraction of otolith increments that provides robust numerical descriptors of growth structures.

8. Technological developments

Considering the progress in otolith research and the acceptance of standardised methods for application of age-based data, it is imperative that we continue to develop technologies that will assist in the extraction and interpretation of these data. This theme focused on the broad range of technological developments that have occurred in otolith-based research in recent years including image analysis techniques, publication media, micromilling instrumentation, elemental and isotopic analysis techniques, new computer software and protocols for age estimation. A total of 16 presentations demonstrated our current progress and future directions in these developments. A significant area of technological development involves the use of image analysis techniques. Parisi-Baradad *et al.* (2005) and Piera *et al.* (2005) demonstrated the use of image analysis and classification techniques to characterise otolith shape, which, in turn, can be used for a range of purposes including pattern recognition, ageing, and species and stock identification.

Conclusion

The Third International Symposium on Fish Otolith Research and Application provided an important forum where scientists from around the world established the current level of understanding in extracting and interpreting otolith-derived information. Knowledge gained from the Symposium should lead to the refinement or development of new technologies for accessing and interpreting this information. This may involve the development of new equipment or software, as well as the

development of collaborative and multidisciplinary research aimed at resolving outstanding problems. Recent developments in otolith microstructure and chemistry, for example, have only been possible because of the advances in analytical technologies, an area of research that is continually evolving.

Outcomes from the Symposium, through improved technologies and approaches, will lead to the improved assessment and management of exploited and protected aquatic species. The papers that form this Special Issue detail some of these approaches and present current ideas in developing techniques, protocols and interpretations of otolith-derived data. Over the next five years, the true success of the Symposium will be judged through developing technologies, changing practices and increased collaborations in this field, at the next Symposium in California.

Acknowledgments

We would like to thank all the authors of the 69 manuscripts that were submitted for consideration for the Special Issue. Competition for limited space was intense and many difficult decisions were made. We also mark the large contribution of more than 120 referees who contributed insightful and cogent manuscript reviews. The efforts of all parties ensured the timely publication of this Special Issue. We also thank the Scientific Steering Committee and all the delegates who attended the Symposium as well as our numerous sponsors, who made the Symposium possible, including the CRC Reef Research Centre, James Cook University, Bureau of Rural Sciences, Department of Agriculture, Fisheries and Forestry, Department of Environment and Heritage, Fisheries Research and Development Corporation, Primary Industries Research Victoria, Queensland Department of Primary Industries and Fisheries, South Australian Research and Development Institute, Western Australia Department of Fisheries, Australian Institute of Marine Science, Australian Society of Fish Biology, CSIRO Marine Research and Northern Territory Department of Business, Industry and Resource Development. The Symposium was proudly supported by *International Science Linkages* established under the Australian Government's innovation statement, '*Backing Australia's Ability*'.

References

- Andrews, A. H., Burton, E. J., Kerr, L. A., Cailliet, G. M., Coale, K. H., Lundstrom, C. C., and Brown, T. A. (2005). Bomb radiocarbon and lead-radium disequilibria in otoliths of bocaccio rockfish (*Sebastes paucispinis*): a determination of age and longevity for a difficult-to-age fish. *Marine and Freshwater Research* **56**, 517–528. doi:10.1071/MF04224
- Arkhipkin, A. I. (2005). Statoliths as 'black boxes' (life recorders) in squid. *Marine and Freshwater Research* **56**, 573–583. doi:10.1071/MF04158
- Baumann, H., Peck, M. A., and Herrmann, J.-P. (2005). Short-term decoupling of otolith and somatic growth induced by food level changes in postlarval Baltic sprat, *Sprattus sprattus*. *Marine and Freshwater Research* **56**, 539–547. doi:10.1071/MF04140

- Berg, E., Sarvas, T. H., Harbitz, A., Fevolden, S. E., and Salberg, A. B. (2005). Accuracy and precision in stock separation of north-east Arctic and Norwegian coastal cod by otoliths – comparing readings, image analyses and a genetic method. *Marine and Freshwater Research* **56**, 753–762. doi:10.1071/MF04172
- Campana, S. E. (1999). Chemistry and composition of fish otoliths: pathways, mechanisms and applications. *Marine Ecology Progress Series* **188**, 263–297.
- Campana, S. E. (2005). Otolith science entering the 21st century. *Marine and Freshwater Research* **56**, 485–495. doi:10.1071/MF04147
- Campana, S. E., and Neilson, J. D. (1985). Microstructure of fish otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 1014–1032.
- Cappo, M., De'ath, G., Boyle, S., Aumend, J., Olbrich, R., Hoedt, F., Perna, C., and Brunskill, G. (2005). Development of a robust classifier of freshwater residence in barramundi (*Lates calcarifer*) life histories using elemental ratios in scales and boosted regression trees. *Marine and Freshwater Research* **56**, 713–723. doi:10.1071/MF04218
- Daverat, F., Tomas, J., Lahaye, M., Palmer, M., and Elie, P. (2005). Tracking continental habitat shifts of eels using otolith Sr/Ca ratios: validation and application to the coastal, estuarine and riverine eels of the Gironde–Garonne–Dordogne watershed. *Marine and Freshwater Research* **56**, 619–627. doi:10.1071/MF04175
- Dorval, E., Jones, C. M., Hannigan, R., and van Montfrans, J. (2005). Can otolith chemistry be used for identifying essential seagrass habitats for juvenile spotted seatrout, *Cynoscion nebulosus*, in Chesapeake Bay? *Marine and Freshwater Research* **56**, 645–653. doi:10.1071/MF04179
- Elsdon, T. S., and Gillanders, B. M. (2005). Consistency of patterns between laboratory experiments and field collected fish in otolith chemistry: an example and applications for salinity reconstructions. *Marine and Freshwater Research* **56**, 609–617. doi:10.1071/MF04146
- Fossum, P., Kalish, J., and Moksness, E. (2000). Editorial foreword. In 'Special Issue: 2nd International Symposium on Fish Otolith Research and Application, Bergen, Norway, 20–25 June 1998'. *Fisheries Research* **46**, 1–2. doi:10.1016/S0165-7836(00)00126-0
- Fowler, A. J., Campana, S. E., Jones, C. M., and Thorrold, S. R. (1995). Experimental assessment of the effect of temperature and salinity on elemental composition of otoliths using solution-based ICPMS. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 1421–1430.
- Fowler, A. J., Gillanders, B. M., and Hall, K. C. (2005). Relationship between elemental concentration and age from otoliths of adult snapper (*Pagrus auratus*, Sparidae): implications for movement and stock structure. *Marine and Freshwater Research* **56**, 661–676. doi:10.1071/MF04157
- Francis, R. I. C. C., Harley, S. J., Campana, S. E., and Doering-Arjes, P. (2005). Use of otolith weight in length-mediated estimation of proportions at age. *Marine and Freshwater Research* **56**, 735–743. doi:10.1071/MF04127
- Gillanders, B. M., and Joyce, T. C. (2005). Distinguishing aquaculture and wild yellowtail kingfish via natural elemental signatures in otoliths. *Marine and Freshwater Research* **56**, 693–704. doi:10.1071/MF04133
- Grant, A. (Ed.) (1992). 'Age Determination and Growth in Fish and Other Aquatic Animals.' Special Issue of *Australian Journal of Marine and Freshwater Research* **43**, pp. 879–1330.
- Hobbs, J. A., Yin, Q.-z., Burton, J., and Bennett, W. A. (2005). Retrospective determination of natal habitats for an estuarine fish with otolith strontium isotope ratios. *Marine and Freshwater Research* **56**, 655–660. doi:10.1071/MF04136
- Husebø, Å., Slotte, A., Clausen, L. A. W., and Mosegaard, H. (2005). Mixing of populations or year class twinning in Norwegian spring spawning herring? *Marine and Freshwater Research* **56**, 763–772. doi:10.1071/MF04170
- Kalish, J. M. (1989). Otolith microchemistry: validation of the effects of physiology, age and environment on otolith composition. *Journal of Experimental Marine Biology and Ecology* **132**, 151–178. doi:10.1016/0022-0981(89)90126-3
- Kimura, D. K., and Anderl, D. M. (2005). Quality control of age data at the Alaska Fisheries Science Center. *Marine and Freshwater Research* **56**, 783–789. doi:10.1071/MF04141
- McCulloch, M., Cappo, M., Aumend, J., and Müller, W. (2005). Tracing the life history of individual barramundi using laser ablation MC-ICP-MS Sr-isotopic and Sr/Ba ratios in otoliths. *Marine and Freshwater Research* **56**, 637–644. doi:10.1071/MF04184
- Morales-Nin, B., and Panfili, J. (2005). Seasonality in the deep sea and tropics revisited: what can otoliths tell us? *Marine and Freshwater Research* **56**, 585–598. doi:10.1071/MF04150
- Morales-Nin, B., Swan, S. C., Gordon, J. D. M., Palmer, M., Geffen, A. J., Shimmield, T., and Sawyer, T. (2005). Age-related trends in otolith chemistry of *Merluccius merluccius* from the north-eastern Atlantic Ocean and the western Mediterranean Sea. *Marine and Freshwater Research* **56**, 599–607. doi:10.1071/MF04151
- Morison, A. K., Burnett, J., McCurdy, W. J., and Moksness, E. (2005). Quality issues in the use of otoliths for fish age estimation. *Marine and Freshwater Research* **56**, 773–782. doi:10.1071/MF04217
- Niva, T., Keränen, P., Raitaniemi, J., and Berger, H. M. (2005). Improved interpretation of labelled fish otoliths: cost-effective tool in sustainable fisheries management. *Marine and Freshwater Research* **56**, 705–711. doi:10.1071/MF04143
- Palmer, M., Álvarez, A., Tomás, J., and Morales-Nin, B. (2005). A new method for robust feature extraction of otolith growth marks using fingerprint recognition methods. *Marine and Freshwater Research* **56**, 790–793. doi:10.1071/MF04207
- Panfili, J., de Pontual, H., Troadec, H., and Wright, P. J. (2002). 'Manual of Fish Sclerochronology.' (IFREMER-IRD coedition: Brest, France.)
- Panfili, J., Durand, J.-D., Diop, K., Gourène, B., and Simier, M. (2005). Fluctuating asymmetry in fish otoliths and heterozygosity in stressful estuarine environments (West Africa). *Marine and Freshwater Research* **56**, 505–516. doi:10.1071/MF04138
- Pannella, G. (1971). Fish otoliths: daily growth layers and periodical patterns. *Science* **173**, 1124–1127.
- Parisi-Baradad, V., Lombarte, A., Garcia-Ladona, E., Cabestany, J., Piera, J., and Chic, O. (2005). Otolith shape contour analysis using affine transformation invariant wavelet transforms and curvature scale space representation. *Marine and Freshwater Research* **56**, 795–804. doi:10.1071/MF04162
- Piera, J., Parisi-Baradad, V., Garcia-Ladona, E., Lombarte, A., Recasens, L., and Cabestany, J. (2005). Otolith shape feature extraction oriented to automatic classification with open distributed data. *Marine and Freshwater Research* **56**, 805–814. doi:10.1071/MF04163
- Popper, A. N., Fay, R. R., Platt, C., and Sand, O. (2003). Sound detection mechanisms and capabilities of teleost fishes. In 'Sensory Processing in Aquatic Environments'. (Eds S. P. Collin and N. J. Marshall.) pp. 3–38. (Springer-Verlag: New York.)
- Popper, A. N., Ramcharitar, J., and Campana, S. E. (2005). Why otoliths? Insights from inner ear physiology and fisheries biology. *Marine and Freshwater Research* **56**, 497–504. doi:10.1071/MF04267
- Sandin, S. A., Regetz, J., and Hamilton, S. L. (2005). Testing larval fish dispersal hypotheses using maximum likelihood analysis of otolith chemistry data. *Marine and Freshwater Research* **56**, 725–734. doi:10.1071/MF04144

- Secor, D. H., Dean, J. M., and Campana, S. E. (1995). 'Recent Developments in Fish Otolith Research.' (University of South Carolina Press: Columbia, SC.)
- Stransky, C., Garbe-Schönberg, C.-D., and Günther, D. (2005). Geographic variation and juvenile migration in Atlantic redfish inferred from otolith microchemistry. *Marine and Freshwater Research* **56**, 677–691. doi:10.1071/MF04153
- Troynikov, V. S., and Robertson, S. G. (2005). Estimating age composition using the Fredholm first-kind equation. *Marine and Freshwater Research* **56**, 745–751. doi:10.1071/MF04152
- Tzeng, W. N., Severin, K. P., Wang, C. H., and Wickström, H. (2005). Elemental composition of otoliths as a discriminator of life stage and growth habitat of the European eel, *Anguilla anguilla*. *Marine and Freshwater Research* **56**, 629–635. doi:10.1071/MF04167
- Uehara, S., Syahailatua, A., and Suthers, I. M. (2005). Recent growth rate of larval pilchards *Sardinops sagax* in relation to their stable isotope composition, in an upwelling zone of the East Australian Current. *Marine and Freshwater Research* **56**, 549–560. doi:10.1071/MF04221
- Wilhelm, M. R., Painting, S. J., Field, J. G., Kerstan, M., and Durholtz, M. D. (2005). Impact of environmental factors on survival of larval and juvenile Cape anchovy *Engraulis encrasicolus* (G.) in the southern Benguela upwelling region, determined from hatchdate distributions: implications for recruitment. *Marine and Freshwater Research* **56**, 561–572. doi:10.1071/MF04145
- Williams, A. J., Davies, C. R., and Mapstone, B. D. (2005). Variation in the periodicity and timing of increment formation in red throat emperor (*Lethrinus miniatus*) otoliths. *Marine and Freshwater Research* **56**, 529–538. doi:10.1071/MF04129