JASA EDITORIAL

Introduction to the special issue on fish bioacoustics: Hearing and sound communication[a)]

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ABSTRACT:

Fish bioacoustics, or the study of fish hearing, sound production, and acoustic communication, was discussed as early as Aristotle. However, questions about how fishes hear were not really addressed until the early 20th century. Work on fish bioacoustics grew after World War II and considerably in the 21st century since investigators, regulators, and others realized that anthropogenic (human-generated sounds), which had primarily been of interest to workers on marine mammals, was likely to have a major impact on fishes (as well as on aquatic invertebrates). Moreover, passive acoustic monitoring of fishes, recording fish sounds in the field, has blossomed as a noninvasive technique for sampling abundance, distribution, and reproduction of various sonic fishes. The field is vital since fishes and aquatic invertebrates make up a major portion of the protein eaten by a signification portion of humans. To help better understand fish bioacoustics and engage it with issues of anthropogenic sound, this special issue of *The Journal of the Acoustical Society of America* (JASA) brings together papers that explore the breadth of the topic, from a historical perspective to the latest findings on the impact of anthropogenic sounds on fishes.

 https://doi.org/10.1121/10.0025553

(Received 18 March 2024; accepted 25 March 2024; published online 2 April 2024)

[Editor: James F. Lynch] Pages: 2385–2391

I. A "VERY BRIEF" HISTORY OF FISH BIOACOUSTICS

Interest in fish bioacoustics has a history tracing back at least to Aristotle, who was likely the first person known to note that fishes make sounds. Much of the history of what we now refer to as fish bioacoustics is discussed by Sand *et al.* (2023) and Moulton (1963), both of whom include references to many of the earlier articles on the subject.

While a number of early anatomists and others demonstrated that fishes have ears that share many characteristics with the ears of terrestrial vertebrates, including mammals (e.g., Weber, 1820; Retzius, 1881), it was not until the early part of the 20th century that a number of highly creative investigators demonstrated not only that fishes respond to sound, but that detection involves the otolith organs of the inner ear (e.g., Parker, 1903; Parker and Van Heusen, 1917; Westerfield, 1922; von Frisch, 1923; von Frisch and Dijkgraaf, 1935). A wide range of studies followed in the first 60 years of the 20th century, that considered hearing (e.g., von Frisch, 1938; Poggendorf, 1952), sound production (e.g., Fish, 1954; Brawn, 1961; Tavolga, 1962; Hawkins and Chapman, 1966), and communication (e.g., Tavolga, 1956; Myrberg, 1966).

Interest in what we now refer to as marine bioacoustics and particularly underwater biological sounds, arose during World War II due to "listening" for enemy ships and submarines (e.g., Fish *et al.*, 1952). Sound navigation and ranging (SONAR) operators listening for vessels would often get confused by the cacophony of sounds in the oceans, many of which were of biological origin. The U.S. Navy became concerned that submarine detection could be masked by these sounds, leading to work, primarily funded in the U.S. by the Office of Naval Research, on marine biological sounds, much of which was, for a long period, classified.

A. The influence of William N. Tavolga

While it is rare in science to be able to point to a single "event" from which future research arises, the field (and term!) known as "marine bioacoustics" can be traced to a

[a)]This paper is part of a special issue on Fish Bioacoustics: Hearing and Sound Communication.

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https://doi.org/10.1121/10.0025553

meeting in 1963 at the Bimini Marine Laboratory of the American Museum of Natural History (New York). The meeting led to a book, *Marine Bio-Acoustics*, edited by William N. Tavolga (Tavolga, 1964). This was followed in 1966 by a second conference at the American Museum, again edited by Tavolga (1967) and published as *Marine Bio-Acoustics II*. (As an aside, from what the authors of this article can determine, the first author of this article may be the only person attending that meeting still active in the field today!) Bill Tavolga not only performed some of the original descriptions of fish sounds (e.g., Tavolga, 1958), but he also did pioneering work using operant conditioning to determine behavioral hearing sensitivity (audiograms) of a number of fish species (e.g., Tavolga and Wodinsky, 1963).

Attendees at the two meetings included some of the leading scholars in marine bioacoustics (and related fields) of the day. Some of those featured in the 1964 book include Gordon M. Wenz (of "Wenz curve" fame), Hubert and Mable Frings (invertebrate acoustic communication), Marie Poland Fish (fish sounds), Howard E. Winn (fish acoustic communication), Gerard G. Harris and Willem A. van Bergijk (lateral line and underwater acoustics), Antares Parvulescu (underwater and tank acoustics), William E. Evans (dolphin communication), and William E. Schevill (marine mammal communication). Others in attendance included such luminaries as René-Guy Busnel (from France), Sidney Galler (one of the early leaders of the U. S. Office of Naval Research - ONR), Winthrop Kellogg (dolphin sonar), and Herman Kleerekoper (fish behavior and olfaction).

Many of the same people attended the 1966 meeting, but interest in the subject had increased markedly so additional attendees included Vernon Albers (underwater acoustics), Georg von Békésy (winner of the 1960 Nobel Prize for research on human hearing), Robert Capranica (frog auditory neurophysiology), Sven Dijkgraaf (one of the true pioneers of fish bioacoustics), Åke Flock (lateral line and sensory hair cells), Lawrence Frishkopf (inner ear physiology), C. Scott Johnson (the first to study psychophysics on a marine mammal), N. B. Marshall (renowned biological oceanographer), Arthur A. Myrberg Jr. (fish ethology and bioacoustics), Kenneth Norris (dolphin acoustic behavior), Arthur N. Popper (Tavolga's graduate student!), Ronald Schusterman (pinniped hearing), James Simmons (still working today on bat echolocation), and Ernst G. Wever (comparative hearing physiology).

Both of Tavolga's volumes covered acoustics of aquatic animals from invertebrates to fishes to marine mammals and are still of great value even today. Moreover, in addition to the chapters, some of which remain true classics and are still cited (e.g., Parvulescu, 1964), Tavolga had the discussions recorded and transcribed and added at the end of each chapter in the books. These discussions remain true gems of scholarship and insight and are well worth reading (albeit, getting either volume is not easy today as they have not, to our knowledge, been digitized).

Finally, in "collusion" with her friend and colleague Bill Tavolga, Phyllis H. Cahn put together another classic meeting immediately following *Marine Bio-Acoustics II* on a related and overlapping sense, the lateral line. The book coming from this meeting, *Lateral Line Detectors* (Cahn, 1967) was as influential in the field of lateral line research as were the two volumes by Tavolga.

While it is not possible, or even likely, to say that Tavolga's two volumes spurred all subsequent research on marine bioacoustics, the proceedings were highly cited and used and clearly helped set the stage for future research. The meetings that gave rise to the volumes also were important in bringing together an international group of scholars, many of whom met for the first time, who got to know one another, and even developed collaborations. Finally, the two volumes helped biologists become aware of the physics of acoustics necessary for their research.

There have been several other meetings and books related to marine bioacoustics and, for our purposes, fish bioacoustics. These included books by Schuijf and Hawkins (1976), Tavolga *et al.* (1981), Sisneros (2016), and Webb *et al.* (2008), as well as several symposia published in journals (e.g., Fine *et al.*, 1997; Popper *et al.*, 2002).

II. THE CURRENT VOLUME

While all the cited volumes produced important and oft-cited work, few of the papers in the earlier volumes were peer-reviewed publications. In contrast, the papers in this special issue of *The Journal of the Acoustical Society of America* (JASA) have received full peer review!

One of the important points reflected by this volume of JASA is that interest in fish bioacoustics (broadly defined) continues to grow since an increasing number of questions relate not just to the basic science of the subject, but, importantly, the very substantial issue of potential effects of increased anthropogenic (human-made) sound on fishes (e.g., Popper *et al.*, 2014; Popper *et al.*, 2024).

Indeed, while much of the early interest in anthropogenic sound was (and continues) to be with marine mammals, there is a growing appreciation that fishes and aquatic invertebrates make up over 99% of all marine animal species. Critically, "…fish and other seafood products provide vital nutrients for more than three billion people around the globe and supply an income for 10 to 12% of the world's population" (https://bit.ly/3RKtjHS), though the actual percent of the population depends on regions of the world (https://bit.ly/47NJdpJ)! Also, see Tidwell and Allan (2001). Thus, concern about the potential effects of anthropogenic sound on fishes is a critical and growing issue since detrimental effects on fish and invertebrates will have a substantial impact on human populations!

The intent of this special issue of JASA is to bring together a broad spectrum of research on fish bioacoustics. We also want to help raise awareness of the subject and provide an overview of what is known and, more importantly perhaps, what is not known, particularly as it relates to how anthropogenic sounds can impact fishes.

We realized that many of the more senior workers in the field have rarely, if ever, had an opportunity to share some of their "backstory" as to how they entered the field, nor have they had the opportunity to share their personal thoughts about their major career contributions. (Indeed, not many senior investigators in any field are given the opportunity to "look back" and "look forward" in the fields to which they devoted their careers.) Moreover, recognizing that many of the more senior investigators have a broad and deep perspective on the field that only comes from the "wisdom of age" and experience, we asked several of our authors to share their thoughts about how the field has progressed, and what they see as some of the most important research questions that they will not likely be able to study themselves. Our hope is that such papers will encourage pursuit by the next generation(s) of fish bioacoustics researchers.

In addition to these insights from senior scholars, the issue contains articles by slightly less "senior" colleagues who are still very active as researchers, and they too provide unique perspectives that may well shape the next several years of research. Finally, we have more "traditional" papers on a diverse array of fish bioacoustics topics that are "cutting edge" in moving our field forward, and shaping what we know.

A. "Problem" with this special issue!

This volume of over 50 papers covers a plethora of topics on fish bioacoustics. We made attempts to "classify" articles based on topics but quickly discovered that this was impossible since many papers overlap with several topics. To get around this problem, we broke the papers into three broad topics (Personal Histories, Sensory Reception, and Sounds and Sound Production) and then divided them into sub-sections. However, the critical thing to note is that many of the papers can be cited in multiple groupings emphasizing the interdisciplinary nature of bioacoustics.

Indeed, we also realize that various readers may see different organizations for the papers, and that is perfectly fine. Thus, our goal in the groupings is to provoke ideas and encourage readers to explore other papers and find those of greatest interest and value to them. Indeed, think about libraries of old (perhaps pre-2000) and how, as we looked for journal volumes or books on shelves, we would perhaps browse the table of contents of the whole volume of the journal or books and of journals that were nearby—and often serendipitously find unexpected material that shed new light on issues or took us in new directions. We are hoping that browsing the contents of this special JASA issue, and not just looking at one paper of interest, might provide new ideas and new light on the thinking of our readers. So, browse the table of contents of this special issue and discover many ideas and new lines of thought!

III. TOPIC 1: PERSONAL HISTORIES OF FISH BIOACOUSTICS RESEARCH

Sadly, many of the great pioneers of fish bioacoustics of the mid to late 20th century, including Per Enger (Enger, 1963, 1976) (note, a few representative citations are provided here for those deceased colleagues not cited elsewhere in this paper), Sven Dijkgraaf (Dijkgraaf and Verheijen, 1950; Dijkgraaf, 1960), Richard R. Fay, Taro Furukawa (Furukawa and Ishii, 1967; Furukawa, 1981), James Moulton, Arthur A. Myrberg Jr., Marie Poland Fish (Fish, 1954), William N. Tavolga, and Howard Winn (Winn, 1964), are deceased, but each made amazing contributions to our field. Of course, there are many other "pioneers," but for the most part, those people did not spend most of their career as fish bioacousticians (e.g., the bee communication pioneer and Nobel Prize recipient, Karl von Frisch).

Then, there are many others who are still with us and who have equally long careers, but who can contribute and share important insights not only into their topics but some of the history of how they became interested in the topic and their thoughts about the value of their contributions. Several authors, including Sheryl Coombs (Coombs, 2023), Jacqueline F. Webb (Webb, 2023), and Horst Bleckmann (Bleckmann, 2023) discuss their formative work on the lateral line. Olav Sand (Sand, 2023), Richard R. Fay (Fay *et al.*, 2023), Friedrich Ladich (Ladich, 2024), and Arthur N. Popper (Popper, 2023) share insights on how fishes detect sound. Anthony D. Hawkins (Hawkins, 2022) shares thoughts about bioacoustics in general, but with a focus on Atlantic cod (*Gadus morhua*), while Allen F. Mensinger (Mensinger, 2024) provides insights into bioacoustics of oyster toadfish (*Opsanus tau*) and Clara Amorim (Amorim, 2023) discusses acoustics in reproductive behavior. Moreover, Michael L. Fine (Fine, 2023) discusses his work on anatomy and mechanisms of sound production. while John C. Montgomery (Montgomery, 2023) shares thoughts on hearing and sound production Finally, Catherine A. McCormick (McCormick, 2023) and Bernd Fritzsch (Fritzsch and Elliott, 2023) explore the anatomy of the auditory central nervous system.

IV. TOPIC 2: SENSORY RECEPTION, INCLUDING HEARING, LATERAL LINE, MORPHOLOGY, AND NERVOUS SYSTEM

Some of the earliest work on fish bioacoustics focused on sound detection capabilities and mechanisms, reviewed by Fay *et al.* (2023), Sand (2023), Ladich (2024), Mensinger (2024), and Popper (2023). More specific studies on hearing include those of Bendig *et al.* (2023) who examine hearing and its relationship to otolith morphology, and Nissen and Mensinger (2023) examine hearing in several species of invasive carp. Lugli (2023) provides a model for auditory sensitivity in the presence of ambient noise. The effects of environmental noise on hearing is addressed by Maurer *et al.* (2023). Popper and Calfee (2023) review hearing in sturgeon, a group of fishes for which we know little about bioacoustics, but many of which are endangered.

The anatomy of the ears of very deep sea fishes is the subject of the paper by Deng *et al.* (2023) while Bendig *et al.* (2023) discuss the ear and hearing in centrarchid fishes (sunfish) and also consider the otolith and how it might affect audition. Another comparative story is told by Chapuis *et al.* (2023) who focus primarily on elasmobranchs while otolith movements in response to sound are discussed by Wei and McCauley (2022).

The lateral line is a critically important sensory system of fishes, and it is considered in both form and function in papers by Coombs (2023), Bleckmann (2023), and Webb (2023).

V. TOPIC 3: SOUNDS AND SOUND PRODUCTION, INCLUDING PASSIVE ACOUSTIC MONITORING, SONIC MECHANISMS, AND ANTHROPOGENIC SOUNDS

A. Sounds and sound production

As stated previously, at least since the days of Aristotle we have known that fishes produce sounds (e.g., Moulton, 1963). Interest in sounds, sound production, and acoustic communications continues today, with a focus not only on sound communication but also on the use of fish sounds to locate animals and passive acoustics monitoring (PAM), to protect sites where animals congregate for feeding and reproduction and from human encroachment.

The sounds themselves are discussed by Amorim (2023) in an article on the role of sounds in fish reproduction, by Banse *et al.* (2023) who discuss sounds in open waters, Bittencourt *et al.* (2023) who consider fish choruses and their variation, and Colbert *et al.* (2023) who examined sounds of oyster toadfish in response to ship and other anthropogenic sounds. Hawkins (2022) shares insights into the sounds of Atlantic cod and haddock (*Melanogrammus aeglefinus*), Hawkins *et al.* (2023) share insight into Australian fish chorus diversity, while Iafrate *et al.* (2023) discuss calling of Atlantic midshipman (*Porichthys plectrodon*) using an unmanned vehicle.

Sounds and sound production are considered by Vasconcelos *et al.* (2024) who discuss the acoustic repertoire of a potential model cyprinid species (*Danionella cerebrum*) for understanding the role of the brain in controlling sound production. Tellechea *et al.* (2022) share insights into sound and sound production mechanisms of southern black drum (*Pogonias courbina*), and Fine (2023) considers similar topics in oyster toadfish. Chang *et al.* (2022) discuss the sounds produced by the variegated cardinalfish (*Fowleria variagata*). We note that the Chang *et al.* paper is the first to describe newly discovered sounds in a well-known family of fish, indicating there is still much to discover.

Somogyi and Rountree (2023) examine sound production in the presence of boat noise while Looby *et al.* (2023) conduct a broad database examination of the context of fish behavior and acoustic communication in subtropical fishes. The sounds of migrating Pacific salmon (*Oncorhynchus* spp.) are considered by Murchy *et al.* (2023). Sounds can also be used for species identification, as demonstrated by Raick *et al.* (2023) with several species of piranhas. Finally, Mosharo and Lobel (2023) explore the best speakers to use in sound playback studies for fishes.

Mechanisms of sound production are considered by Han *et al.* (2023) who examine the role of the swim bladder in three-spined toadfish, (*Batrachomoeus trispinosus*), while Su *et al.* (2023) look at call properties of *yellow croaker (Larimichthys crocea)* during reproductive behavior. Webb McAdams and Smith (2023) consider the relationship between sounds and body size in loricariid catfishes as do Matsubara *et al.* (2023) in the white-edged rockfish *(Sebastes taczanowskii)*. Millot *et al.* (2023) describe mating sounds in the two-spotted goby (*Pomatoschistus flavescens*) and the effect of water temperature on the acoustic features of the sounds.

B. Soundscape and anthropogenic sound

A major reason for the increased interest in fish bioacoustics is the growing concern about the effects of anthropogenic sounds on aquatic life. Potential impacts of anthropogenic sound were rarely considered until the late 1990s, and interest has increased substantially since the publication of the first set of interim criteria for fishes (Popper *et al.*, 2014), which included participants in this special JASA issue including Coombs, Hawkins, Fay, and Popper.

The soundscape involves all the sounds in an environment, many of which may be relevant for fishes since sound provides them with a three-dimensional and long-distance "view" of their world, even in the absence of light. Understanding this soundscape, and how it can be impacted by anthropogenic sound, is critical if we are to ultimately ensure the well-being of fishes. Banse *et al.* (2023) discuss the characterization of the soundscape and fishes, while Luczkovich *et al.* (2024) share findings that show the impacts of hypoxia on fishes and their calling. Colbert *et al.* (2023) specifically examine how shipping and other anthropogenic sources impact the calling of oyster toadfish during the breeding season in the Chesapeake Bay, while Hom *et al.* (2024) consider oyster toadfish and anthropogenic sound in urban environments. Waddell and Širović (2023) examine the effects of both anthropogenic noise and the soundscape on four estuarine species while Hubert *et al.* (2024) discuss experiments looking at the effects of anthropogenic sound on free-ranging pelagic fishes. One of the critical issues in soundscapes and fishes is that most fishes only hear the particle motion component of the sound field. Therefore, the soundscape must be examined from this perspective, as done by Jones *et al.* (2022), who also consider anthropogenic sound and invertebrates.

Interactions between fishes and the soundscape are discussed by Roberts and Rice (2023), who also consider an important new issue which they refer to as the vibroscape. They describe the vibroscape as sounds from the substrate which are likely to be important for both fishes and invertebrates (e.g., Hawkins *et al.*, 2021; Roberts and Wickings, 2022). Finally, Kim *et al.* (2023) describe an automated method to separate different species in fish choruses that make up a complex soundscape.

Anthropogenic sounds and their (potential) impact on fishes were considered in several papers. The impact of explosions located at different distances from (caged) fishes was explored by Jenkins *et al*. (2022). In a companion study, Smith *et al*. (2022) used the same animals and described the effects of exposure on the sensory hair cells of the ear. Response of the ear to anthropogenic sounds is also considered from the perspective of modeling by Wei and McCauley (2022).

Maurer *et al*. (2023) examined the effects of amplitude and duration of anthropogenic sounds on fish behavior. Somogyi and Rountree (2023) examined fish sound production in the presence of boat noise, while Pieniazek *et al.* (2023) reviewed a number of field studies that examined the effects of anthropogenic sound on the behavior of wild fishes. Popper *et al*. (2023) raise the issue of the potential impact on fishes and aquatic invertebrates of sounds produced by a wide range of new offshore energy devices called Marine Energy Converters (MECs) and they detail the research questions needed to determine the potential effects on fishes. A similar approach was taken for potential impacts by offshore windfarms (Popper *et al*., 2022).

VI. CONCLUSIONS

Fish bioacoustics, with a particular focus on the potential impacts of anthropogenic sound, is becoming more important as humans increasingly rely on fishes and aquatic invertebrates for food. Indeed, an informal and simple search on Google Scholar for fish plus words related to fish bioacoustics (e.g., hearing, sound, sound production, soundscape) yielded few papers before the year 2000. The number increased to 40 in 2010 and 250 in 2020, while in 2023 there were 363 papers (including many from this special issue of JASA). These (albeit crude) results help make the case for the increasing importance of fish bioacoustics as underwater anthropogenic sounds are becoming more ubiquitous. It is also evident that there is a need for additional research.

Indeed, one "problem" in fish bioacoustics (and most other aspects of fish biology) is that there are over 34 000 extant species of fishes, a greater number of species than for all other vertebrate groups combined. Moreover, fishes inhabit an immense range of ecological niches from the intertidal to deep-sea trenches (e.g., Helfman *et al*., 2009). From the perspective of fish bioacoustics, investigators have a wealth of species with amazing diversity in their engagement with sound. Therefore, it is relatively "easy" to find a species that will allow one to ask interesting and important questions.

However, the "downside" of fish diversity and lifestyles is that by choosing species that interest the investigators or are easy to access and maintain (etc.), we wind up with a breadth of data. However, the results provide relatively little "in depth" understanding details about hearing capabilities, acoustic behavior, and potential impacts of anthropogenic sounds. Thus, for most species studied we know about ear responses to sound (which is not hearing—see definition of "hearing" in Popper and Hawkins, 2021) in somewhat over 100 fish species and about behavioral responses to sound (hearing) in far fewer species (e.g., Ladich and Fay, 2013). However, we know much more about fundamental aspects of hearing, such as masking, sound discrimination, sound localization, and processing in the Central Nervous System in only a few species such as goldfish, toadfishes (family Batrachoididae), and Atlantic cod (e.g., Popper *et al*., 2019). Yet, only by knowing more about these fundamental aspects of hearing in select species will we start to understand the sounds fishes detect and respond to and be able to design tools to allow us to protect fishes from anthropogenic sounds.

Finally, one of the significant questions for future fish bioacousticians is how species should be selected for study: Should investigators place emphasis on selecting species that may interest them for some reason (e.g., they produce sounds in interesting ways), and/or species that are easy to work with or "popular," such as zebrafish (*Danio rerio*) (Popper and Sisneros, 2022) and *Daniella cerebrum* (Vasconcelos *et al*., 2024)? Alternatively, should we focus on species of greater relevance to human food supplies or perhaps those most impacted by human activities such as development of offshore energy sources, shipping, etc. (e.g., Popper *et al*., 2022; Pieniazek *et al*., 2023; Popper *et al*., 2023)?

Clearly, there are no easy answers to these questions, and the actual answers are likely to be complex. However, in thinking about questions of most relevance to both ensure food for humans and protect species, perhaps these questions should attract greater consideration in terms of research and research funding!

ACKNOWLEDGEMENTS

This paper is dedicated to Professor Anthony D. Hawkins. Tony is one of the truly great pioneers in fish bioacoustics in the 20th and 21st centuries, starting with his earlier papers in the 1960s and continuing to the paper he has in this special issue of JASA. Most of the authors of this introductory article have had the honor of working with Tony over the years, and he has always been the most amazing collaborator, scholar, colleague, and, perhaps most importantly, friend.

AUTHOR DECLARATIONS

Conflict of Interest

The authors declare they have no conflict of interest.

DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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