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The pioneering contributions of Per Stockfleth Enger to fish bioacoustics

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I. INTRODUCTION

One of the true pioneers in the study of the bioacoustics of fishes, Professor Per Stockfleth Enger (Fig. 1), died on November 19, 2018. Per was an excellent example of a zoologist with broad interests who made contributions to a number of areas of physiology while working on a wide range of animal species. However, it was his studies on fish hearing that were especially notable. The goal of this paper is twofold. First, we mention the most significant work of an eminent biologist. Second, and more importantly, we show the context of Per's work and the significant contributions it made to fish bioacoustics, and to moving the field forward. In other words, we commemorate Per's life by providing a historical perspective on fish bioacoustics that was, very much, driven by his research.

II. PER'S EARLY LIFE

Per was born on February 24, 1929, in Oslo, Norway, where his mother, Aud, worked at the Customs Department. His father, Erling Enger, studied forestry and became a forester, but in 1927, at the age of 29, he decided to study art and moved to Oslo. Erling studied art at the State School of Handicraft and Industrial Art and later at the National Academy of the Arts, and he soon became a celebrated full-time artist. His paintings, especially of farms, cultural landscapes, and woods, are exhibited at art galleries around the world (www.artnet.com/artists/erling-enger). Per was influenced by his father's rural background and initially decided to become a forester. However, after a year of working in the forest, he changed his mind and instead started to study science at the universities of Oslo and Bergen, Norway (see Table I for an academic timeline for Enger). In 1956, Per became the first to graduate from the newly established Institute of Zoophysiology at the University of Oslo. Per later became a full professor at the institute and maintained this relationship for the rest of his life.

From 1956–1958, Per worked with the group of Haldan K. Hartline at Rockefeller Institute in New York. Hartline, winner of the 1967 Nobel Prize in Physiology or Medicine, laid the foundation for understanding how the brain processes visual information, and was the first to record the electrical activity of a single optic nerve fiber. Per learned to record single unit activity from the nervous system in Hartline's lab (e.g., Brooks and Enger, 1959). Later, Per used this technique on a fish known as the bullhead sculpin (*Cottus scorpius*) as part of his Ph.D. project. He was the first to make single unit recordings from the fish auditory system (Enger, 1963).

Per's interest in fish hearing originated from his Master's project, the aim of which was to clarify whether the Atlantic cod (*Gadus morhua*) was able to hear the high-frequency sound signals used in echo sounders in order to locate fish schools. At the time, this was an urgent issue because Norwegian fishermen claimed that such equipment scared the Atlantic cod and thus reduced catches within the very important Atlantic cod fisheries in Norway. Per's experimental approach was to investigate the effects of sound stimuli on electrical brain activity in Atlantic cod , using electroencephalogram (EEG) recordings from the Atlantic cod for the first time (Enger, 1957a). He concluded that the Atlantic cod was probably not able to detect the high frequencies used in echo sounders. Several decades later, similar recordings were reintroduced as the so-called auditory brain stem response (ABR), a technique that has been used to study hearing in many species of fish.

Per also studied energy metabolism and thermoregulation in mammals and birds (Enger 1957b), and in particular the physiological responses of pigeons exposed to cold conditions (Enger and Steen, 1957; Steen and Enger, 1957). Enger and Steen were the first to show that increased tonic muscle activity without visible shivering is important for thermoregulation below the "lower" critical temperature.

III. CONTRIBUTIONS TO FISH HEARING

Per carried out postdoctoral studies in 1963–1964 in Los Angeles, California with Thomas Szabo and he continued this collaboration for many years. During the postdoc, Per studied the sense of electroreception in fishes (Hagiwara *et al.*, 1965; Enger and Szabo, 1968). Per also spent some of this time working with Theodore Holmes (Ted) Bullock on "slothfulness in sloths" (Enger and Bullock, 1965), and he accompanied Bullock on the second cruise of the legendary National Science Foundation Alpha Helix research vessel on the Amazon River.

Despite the breadth of his research and interests, fish hearing was Per's main scientific interest, and within this field he carried out ground-breaking research. Besides being the first to record EEG from the brains of bony fishes (Enger, 1957a), he was also the first to record single action potentials from their auditory nerves (Enger, 1963). He was also the first to detect electrical potentials (microphonics) from the ears of intact bony fishes (Enger and Andersen, 1967; Andersen and Enger, 1968) and to examine the effects of high intensity sound on the fish inner ear (Enger, 1981).

Back in the 1960s, before Per started his pioneering work, little was known of the hearing abilities of fishes. Griffin (1950) and Lowenstein (1957) had reviewed the very earliest accounts of hearing in fishes. They had concluded, based on earlier studies by Parker, von Frisch, Dijkgraaf, and others (see reviews in Moulton, 1963; Tavolga, 1971) that fishes could hear, and that sounds played an important part in their behaviour. Two sensory systems were suggested as the acoustic sensors: the paired labyrinth organs of the head (the inner ears) and the lateral line system of the head and trunk. von Frisch and his colleagues had established that the fish ear did serve as a hearing organ (e.g., von Frisch and Stetter, 1932; Dijkgraaf, 1949). It had been proposed by Dijkgraaf and others that within the fish ear

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FIG. 1. Per Stockfleth Enger (February 24, 1929–November 19, 2018).

it was the movement of the dense calcareous otoliths, relative to patches of sensory hair cells that mediated the detection of sounds. They argued that since the tissues of the head were acoustically transparent to sound in water, the dense otoliths would lag behind oscillations of the head in a sound field and the resultant relative movements would stimulate the hair cells.

Early studies of the hearing abilities of fishes also suggested that there was great variability in their sensitivity to sounds, and experiments on the same species often gave very different results. For example, comparison of hearing thresholds obtained from the goldfish (*Carassius auratus*) by various scientists showed differences of up to 60 dB (a factor of 10^3) at some frequencies (reviewed by Hawkins, 1973; Fay, 1988). It was later realized that the chief reasons for these differences lay in the different acoustic conditions under which the experiments were conducted. It had been pointed out by Griffin (1950) that more rigorous quantitative acoustic measurements were required. Indeed, Parvulescu (1964) emphasized the pitfalls in carrying out experiments in small tanks and specifying the sounds solely in terms of sound pressure (see also Rogers *et al.*, 2016). The propagated back-and-forth motion of the component particles of the medium accompanying a sound, and designated as the particle displacement, velocity, or acceleration, was also important.

In response to these observations, Per conducted experiments showing differences in the responses of goldfish exposed to sounds from loudspeakers located within a long trough, and in the air outside the trough, following the suggestions of Parvulescu. These studies were done using classical conditioning (Enger, 1966), a technique Per had learned as a student during a stay in Utrecht with Sven Dijkgraaf's group in 1953–1954. The sound pressure thresholds at frequencies below 600–700 Hz were strongly dependent upon distance to the sound source, and Per proposed that the auditory part of the ear was sensitive to particle acceleration.

Per then studied the hearing of herring (*Clupea harengus*) by recording gross multi-unit activity and single unit activity from the acoustic region of the medulla oblongata (Enger, 1967). He showed that herring can hear over a wide frequency bandwidth, extending up to a few kilohertz.

In 1967, seeking improved acoustic conditions, Per, together with Rolf Andersen from the Institute of Marine Research in Bergen, Norway, took the first step towards performing hearing experiments in the sea. Two fish species, the Atlantic cod and the bullhead sculpin, were held at different distances from an underwater loudspeaker in the sea, and microphonic potentials were recorded from their ears in response to sounds (Enger and Andersen, 1967). In the Atlantic cod, the amplitudes of these microphonic potentials, originating in the hair cells of the ear, were related to the measured sound pressures and were independent of distance. In the bullhead, potentials could be recorded only when the fish was within 1 m of the loudspeaker. It was concluded that the Atlantic cod, a fish with a swim bladder, was able to detect sound pressure, while the bullhead, without a swim bladder, could detect only the high levels of particle motion close to the source—within the acoustic near field. Enger and Andersen concluded that the swim bladder was essential for the detection of sound pressure in the far field by fishes.

The use of the swim bladder essentially involves a single sound detector, and it was thought that this would prevent such fishes from determining the direction to a sound source. Per and his Norwegian colleagues encouraged a group of Dutch scientists to visit Norway to perform experiments in the sea on directional hearing by fishes. Arie Schuif, the leader of the Dutch group, was a student of Sven Dijkgraaf at the University of Utrecht. An experiment was set up beneath a raft in a Norwegian fjord at the island of Sotra, and sounds were presented from different directions. The experiments confirmed that the Ballan wrasse (*Labrus bergylta*), a species with a swim bladder, was able to detect changes in the direction from which sounds were coming (Schuijf *et al.*, 1972). This was to be the first of several key results from the Dutch group working in Norwegian waters.

Similar experiments on fish hearing were also carried out in a Scottish fjord, using sound exposure techniques based on the original experiments carried out by Per in the sea (reviewed by Hawkins, 2014). The pioneering work done by Per encouraged further hearing experiments to be carried out under free field conditions, where the ratio of particle motion to sound pressure could be varied by changing the distance between the sound source and the fish.

TABLE I. Timeline in career of Per S. Enger.

1953–1954	Nine month stay in Utrecht during his master study, with Sven Dijkgraaf's group. Learned conditioning techniques.
1955–1956 (winter)	Expedition with Per F. Scholander to Panama. Metabolism and thermoregulation in tropical animals.
1956 (autumn)	Candidatus realium degree at Institute of Zoophysiology, University of Oslo. Thesis: The electroencephalogram of the codfish.
1956 (autumn)	Assistant professor at Institute of Zoophysiology.
December 1956–August 1958	Research stay with Haldan K. Hartline at Rockefeller institute in New York. Learned micro electrode techniques.
1963	Doctoral degree at the University of Oslo. Thesis: *Single unit activity in the fish auditory system.*
1963–1964	Postdoc in LA in Susumu Hagiwara's group. Worked with him, Thomas Szabo and Ted Bullock (electric fish and sloth).
1965	Associate professor at the Medical Faculty, University of Oslo.
1967	Member of the second Alpha Helix expedition together with Ted Bullock.
1970	Professor at the Institute of Zoophysiology.
1971–1972	Visit for some weeks to Aberdeen to work with Tony Hawkins, Colin Chapman, and Olav Sand on directional hearing.
1975–1976	Sabbatical in Paris with Szabo.
1981	Elected member of the Norwegian Academy of Science and Letters.
1981–1983	Dean of the Faculty of Mathematics and Science at the University of Oslo.
1984–1985	Sabbatical (6 months) at Scripps, La Jolla, with Ad Kalmijn.
1996–2018	Professor Emeritus at the University of Oslo.

Olav Sand, a graduate student of Per, who had previously been working with Per in Oslo, moved to Scotland and joined Colin Chapman in investigating the hearing abilities of two species of flatfish, the plaice (*Pleuronectes platessa*) and the dab (*Limanda limanda*), both lacking a gas-filled swim bladder. It was demonstrated that the unaided otolith organs in the absence of a swim bladder were sensitive to particle motion rather than sound pressure (Chapman and Sand, 1974). Later, Sand re-joined Per in Oslo and they provided direct evidence of an auditory function of the swim bladder in the Atlantic cod (Sand and Enger, 1973). Microphonic potentials were recorded from the ears of Atlantic cod during exposure to sounds in a Norwegian fjord, while the swim bladder was inflated and deflated.

On a short visit to Scotland by Per, Enger, and Sand, a debate began with Scottish scientists Colin Chapman and Tony Hawkins over the possible mechanisms of directional hearing in fishes. It was decided that the directional properties of the ear could be investigated by vibrating a fish in different directions. An experiment was carried out with microphonic potentials being recorded from the ear of the haddock (*Melanogrammus aeglefinus*). The fish was mounted in air and clamped to a vibration table, consisting of a rotatable metal slab resting upon a foam-rubber bed. The fish was artificially respirated by passing water across its gills, and the slab was driven back and forth by an electromagnetic vibrator. The amplitude of the potentials proved to be a function both of the stimulus strength and of the direction of vibration (Enger *et al.*, 1973). It was concluded that different groups of hair cells within the otolith organs showed different patterns of directional sensitivity when stimulated by vibration.

Others subsequently took up the technique of whole-body vibration and polar diagrams were prepared (Sand, 1974; Fay and Olsho, 1979; Hawkins and Horner, 1981), which demonstrated the directional sensitivity of primary auditory afferent nerve fibers in fishes. This provided the basis for understanding the determination of sound source localization in fishes (reviewed in Sand and Bleckmann, 2008; Hawkins and Popper, 2018). It became evident that discrimination of direction was based on the directional sensitivity to particle motion by the sensory hair cells, even in fishes with a swim bladder. The physiological evidence that the fish ear was sensitive to the direction of the source stimulated further research by a number of scientists on the mapping of the orientation of sensory hair cells along the different otoconial epithelia using scanning electron microscopy (SEM) (e.g., Dale, 1976; Enger, 1976; Popper, 1976).

Binaural interaction may improve the acuity of auditory directional discrimination in fish. In 1979–1980, Kathleen Horner, a graduate student working in Scotland, visited Enger and Sand in Oslo in order to explore whether such interaction occurs. By recording single unit activity in the acoustical lobes and the torus semicircularis of the Atlantic cod, during various patterns of blocking of the posterior saccular nerves, the central processing of binaural information was demonstrated (Horner *et al.*, 1980).

Armed with proof that fish were sensitive to particle motion, Per set about testing the effects of very loud sounds on the hearing of fish. By employing high intensity pure tones, presented at over 180 dB re 1uPa for several hours to Atlantic cod, Per was the first to demonstrate, using SEM, that damage could be done by excessive sound stimulation of the sensory hair cells of the inner ear (Enger, 1981).

Later, in a study with his students of the effects of intense sounds upon juvenile Atlantic salmon, *Salmo salar*, it was shown that very low frequency sounds (5–10 Hz), termed infrasound, were most effective in eliciting responses from the fish (Knudsen *et al.*, 1992). In the last scientific paper involving Per, the behavioral effects of infrasound on cyprinids were tested. In Lake Borrevann, Norway, acute avoidance responses, at a distance up to 10 m from a 16 Hz infrasound projector were revealed by utilizing an echo sounder (Sonny *et al.*, 2006).

IV. OTHER CONTRIBUTIONS

Per Stockfleth Enger, as a true zoophysiologist, had very broad research interests, from hearing to energy metabolism and thermoregulation in animals. Abroad, he worked in the Netherlands, Panama, Brazil, Scotland, France, and the United States, and performed research on 35 different animal species, including the aforementioned sloth as well as the reindeer (Flydal *et al.*, 2001) and the zebra finch (Aulie and Enger, 1969). Moreover, Per also had interests in the lateral line, and this culminated in his spending some months at Scripps Institute at the University of California, San Diego, working with Ad Kalmijn on the role of the lateral line in fishes (Enger *et al.*, 1989).

Per was an international authority on hearing in fishes. In 2001, at an international symposium on Fish Bioacoustics in Evanston Illinois, Per was honored, along with three other fish bioacoustic pioneers, Arthur A. Myrberg, Jr., Taro Furukawa, and William N. Tavolga, for his research in this field (Popper *et al.*, 2002), and he later published a paper that summarized some of his work (Enger, 2002).

As a teacher, Per had great ability to inspire his students. He was very knowledgeable, but at the same time humble and empathetic. He was always optimistic and in a good mood, and an expert in transferring energy and intrepidity to his students, many of whom became close friends until the very end. Per's optimism, friendliness and ability to improvise also made him an excellent conflict solver and administrator. He had several managing positions at the Institute of Zoophysiology in Oslo, and later the Institute of Biology, and in 1981–1983 he was dean of the Faculty of Mathematics and Science at the University of Oslo. In 1981 he was elected as Fellow of the Norwegian Academy of Science and Letters. From 1996 until his death, November 19, 2018, Per was a Professor Emeritus at the University of Oslo.

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The authors of this article were all colleagues and/or friends of Per Stockfleth Enger. We all knew Per, and deeply respected him as colleague, friend, and, to several of us, a mentor. We honor Per's memory by writing this paper, and we dedicate it to Per's children, Astrid and Audhild, and to his grandchildren, Ellen and Gunnar.

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