

H Geoffrey Moser's contributions to fisheries biology and ichthyology

Bruce C. Mundy (contact author)^{1,2}

Jeffrey M. Leis^{3,4}

William Watson⁵

Peter Konstantinidis⁶

Email address for contact author: mundyichthyo@gmail.com

¹ Ocean Research Explorations
P.O. Box 235926
Honolulu, Hawaii 96823

² Ichthyology
Bishop Museum
1525 Bernice Street
Honolulu, Hawaii 96817

³ Ichthyology
Australian Museum Research Institute
1 William Street
Sydney, NSW 2010 Australia

⁴ Ecology and Biodiversity Centre
Institute for Marine and Antarctic Studies
University of Tasmania
Hobart, Tasmania 7001, Australia

⁵ Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
8901 La Jolla Shores Drive
La Jolla, California 92037-1508

⁶ Department of Fisheries, Wildlife, and Conservation Sciences
Oregon State University
104 Nash Hall
Corvallis, Oregon 97331

H Geoffrey Moser (1938–2021, Fig. 1), known to his colleagues as Geoff, was an influential fishery biologist and ichthyologist who worked for the National Marine Fisheries Service (NMFS) and its predecessor, the U.S. Fish and Wildlife Service Bureau of Commercial Fisheries (BCF) during his entire 40-year career. In this article for NOAA Professional Paper NMFS 24, a special volume compiled in his honor, we summarize his professional contributions and legacy. A fuller account of his life and career can be found in Mundy and Hilton (2022). Much of the following comes from that review.

Geoff was born on 5 December 1938 in Philadelphia, Pennsylvania. In 1960, he completed his undergraduate degree in biology at Dartmouth College in Hanover, New Hampshire. There he learned microtechniques for research on reproductive biology and worked as a teaching assistant to William Whitney Ballard (1906–1998) who studied fish embryology. Geoff married Pamela Chamberlain in 1961 and they had a daughter and son. Geoff entered graduate school at the University of Southern California to study under Jay Savage, a herpetologist. In addition to students in herpetology, Savage had students in ichthyology working on surveys of midwater fishes in the basins off Los Angeles. Geoff became interested in the fish larvae collected in those surveys and Savage recommended that Geoff go to the BCF in La Jolla to confer with Elbert Ahlstrom (1910–1979), a world-renowned expert on the early life history (ELH) stages of marine fishes. His meetings with Ahlstrom resulted in Geoff being hired in 1962 by the BCF La Jolla Laboratory while he completed his Ph.D. His first supervi-

sor, Frederick Berry (1927–2001), worked with midwater fishes. Soon thereafter, Geoff switched to work under Ahlstrom on the identification of the numerous fish eggs and larvae collected in samples of the California Cooperative Oceanic Fisheries Investigations (CalCOFI), in which the BCF La Jolla Laboratory had a major role. His entire 40-year scientific career was at the BCF La Jolla Laboratory, which eventually became the NMFS Southwest Fisheries Science Center (SWFSC). During his career, he published over 200 papers on the ELH stages of over 40 fish families and edited 2 major books. In 1996 he was awarded a NOAA Bronze Medal for “superior federal service for a career of scientific excellence of lasting benefit to the nation.” Geoff retired to Montana in 2002 to enjoy trout fishing, hunting, hiking, and other outdoor activities. He continued his hobby of writing poetry and essays, as well as volunteering for Trout Unlimited and the Red Cross. H Geoffrey Moser passed away on 30 September 2021 in Bozeman, Montana, at the age of 83 years.

CalCOFI is an extensive multi-decade cooperative research program, engaging collaboration between the BCF La Jolla Laboratory (later called the NMFS SWFSC), the California Department of Fish and Wildlife, and the Scripps Institution of Oceanography (McClatchie, 2014). Initially established to investigate the causes of the collapse of the Pacific sardine population in the California Current region, CalCOFI became one of the longest oceanographic and fisheries time series (Ohman and Venrick, 2003). It was also an early leader in the approach of ecosystem-wide research in support of ecosystem-based

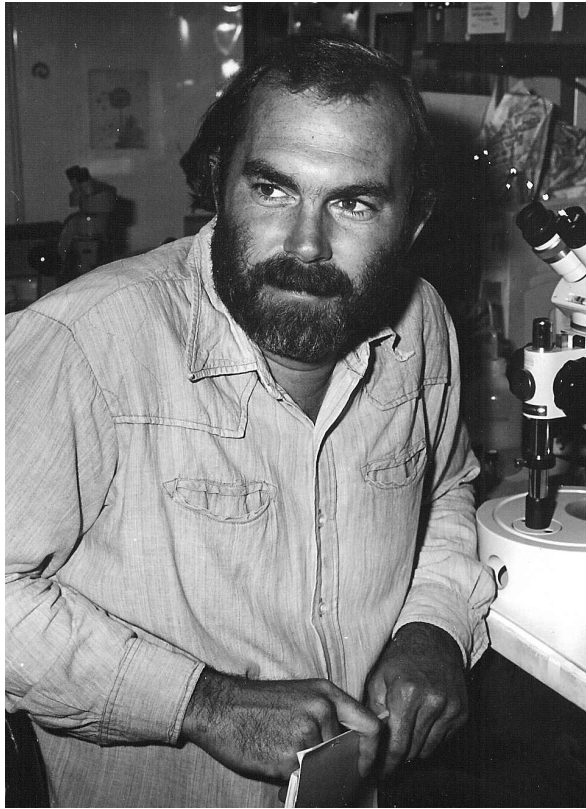


Figure 1

H Geoffrey Moser (1938–2022) in 1977 co-teaching the larval-fish identification class (with Elbert Ahlstrom, not pictured) at the NOAA Southwest Fisheries Center in La Jolla, California. Photograph provided by H G. Moser, photographer unknown. Reprinted from Mundy and Hilton (2022).

fisheries management. The accurate identification of the ELH stages of fishes collected by CalCOFI was an essential basis for its subsequent analyses of long-term (>70 years) trends in ichthyoplankton and fisheries.

Ahlstrom moved away from his administrative responsibilities as laboratory director beginning in 1964 and Geoff became the head of the SWFSC ELH identification team (Vlymen, 1989; McClatchie, 2014; Fig. 2). His success in this role was one of his chief professional accomplishments, providing data for the numerous publications he and others authored about the fish populations, ecosystem changes, and fishery management activities in the CalCOFI region (Smith and Moser, 1988; Ohman and Venrick, 2003; McClatchie, 2014). Geoff enjoyed work at sea and led or otherwise participated in many of the cruises that collected specimens and data for the CalCOFI program. His leadership style for the identification team is described by Elaine Sandknop Acuña, a long-time member of that team, thus—“those of us who

worked with Geoff were the beneficiaries of intelligent and generous assistance. His often critical comments were not only helpful, but were leavened with encouragement and enthusiasm. I will always be deeply grateful to Geoff for his friendship of more than 56 years. We should all have such leaders and friends.”

Geoff’s second major professional contribution was the transfer of knowledge about the identification of fish eggs and larvae to others. As with his CalCOFI contributions, this began when he worked for Ahlstrom and continued through his own efforts after Ahlstrom’s death in 1979. Geoff and Ahlstrom taught 6 courses on fish egg and larval identification to students and other colleagues in 1972–1977. Geoff also taught 3 similar courses in Mexico, the first jointly with Ahlstrom and the last 2 with others from his staff. The participants in these courses were from many countries. Many became leaders in the field in their own right, and some taught similar courses in later years, continuing Geoff’s legacy of mentorship (Mundy and Hilton, 2022).

The other part of Geoff’s transfer of knowledge about the identification of fish ELH stages consists of his numerous publications on that topic. He described the developmental stages of many species, edited 2 large books, and produced influential papers on the best methods of describing fish eggs and larvae. Geoff’s many papers on individual taxa are given in his bibliography at the end of this article.

One of the 2 books he edited is the only global review of the ontogeny of fishes (Moser et al., 1984a) and has been cited about 300 times. The other is a comprehensive 1505-page guide to the identification of the early stages of fishes in the California Current region (Moser, 1996a); it has been cited about 500 times (note that these citation counts do not include citations of the individual chapters). Both are landmark publications that continue to be used frequently and stand as the best resources for their topics. Geoff initiated both and took the lead in editing them (Figs. 2 and 3), in addition to contributing a number of chapters in each. For the first book, *Ontogeny and systematics of fishes*, William Richards, formerly of the NMFS Southeast Fisheries Science Center, a larval-fish biologist and co-editor of the volume, commented “All of the committee members [Fig. 3] worked very hard writing their own contributions and reviewing other manuscripts. It all came together, and Geoff and I spent a week at my office with final reviews and marking copy for the printer which we took to Allen Press. Geoff was tireless and carefully read every contribution at least once.” Geoff and his 5 co-editors were awarded a Department of Commerce Silver Medal for Distinguished Achievement in 1985 for the book.

Geoff’s papers on myctophid larvae (Fig. 4) remain the basis for their identification (e.g., Moser and Ahlstrom, 1970, 1974, 1996; Moser et al., 1984b; Moser



Figure 2

Part of the NOAA Southwest Fisheries Center ichthyoplankton group managed by Geoff Moser at the time of the production of *The early stages of fishes in the California Current region* (Moser, 1996a). From left to right: H Geoffrey Moser, William Watson, Sharon Charter, Elaine Sandknop Acuña, Richard Charter (who supervised and was the data manager for the NMFS California Cooperative Oceanic Fisheries Investigations that worked closely with Geoff's group), Barbara Sumida MacCall, and David Ambrose. Most of this group are contributing authors of many chapters in the volume. Moser, Watson, and MacCall also drew many of the high-quality illustrations for the volume. Photo courtesy of William Watson, NOAA Southwest Fisheries Science Center.

and Watson, 2006). Geoff and Ahlstrom won the Wildlife Society's 1971 best paper award in fish ecology and management for their 1970 paper on myctophid larvae of the California Current region. William Richards says "H Geoffrey Moser was the expert, bar none, on the identification of early life history stages of lanternfishes (Myctophidae) worldwide. His work was impeccable and set the standard for everyone. Besides his myctophid work he was an expert on all the fishes of the west coast of the United States especially the California coast." Moser's myctophid larvae publications have been cited over 600 times. Geoff's papers on West Coast rockfish (Sebastinae) larvae (Fig. 5), beginning with his Ph.D. dissertation (Moser, 1966) and the publication that resulted from it (Moser, 1967), are also the basis for the identification of that diverse and difficult group (e.g., Moser et al., 1977; Moser, 1996b). His rockfish publications have been cited 866 times. He eventually was author or coauthor of descriptions of the early stages of

over 40 families of fishes, as exemplified by the chapters that he authored or coauthored in the comprehensive guide to early stages of fishes in the California Current region (Moser, 1996a).

Ahlstrom pioneered the use of ontogenetic characters in fish systematics and recruited Geoff into that research. Geoff's interest in the application of larval characteristics to fish systematics is evidenced by numerous publications (Moser and Ahlstrom, 1972; Ahlstrom and Moser, 1976; Ahlstrom et al., 1976; Moser et al., 1984a; Ahlstrom et al., 1984; Paxton et al., 1984), including 2 general reviews of the topic (Moser and Ahlstrom, 1974; Ahlstrom and Moser, 1981) prior to the publication of the global review *Ontogeny and systematics of fishes* (Moser et al., 1984a). Seventy-one chapters by many authors in that review applied larval characteristics to research on fish systematics. This research has since been carried forward by others (e.g., Tyler et al., 1989; Leis et al., 2002; Johnson et al., 2009; Baldwin, 2013; Gill and Leis, 2019), in-



Figure 3

The steering and editorial committee for the symposium *The ontogeny and systematics of fishes* held at the University of California, San Diego, California, in 1983 and the resultant book (Moser et al., 1984). From left to right, with their affiliations at the time of the project: Daniel Cohen (1930–2016; Los Angeles County Museum of Natural History, previously at the NMFS Systematics Laboratory, Washington, D.C.), Sally Richardson (1944–1986; Gulf Coast Research Laboratory, Ocean Springs, Mississippi), Michael Fahay (NOAA Northeast Fisheries Center, Highlands, New Jersey), Geoff Moser (1938–2021; NOAA Southwest Fisheries Center, La Jolla, California), Arthur Kendall, Jr. (NOAA Northwest and Alaska Fisheries Center, Seattle, Washington), and William Richards (NOAA Southeast Fisheries Center, Miami, Florida). Reprinted from Mundy and Hilton (2022).

cluding papers in this volume (Girard et al., 2024; Smith et al., 2024).

An example of Geoff's influence on the production of high-quality descriptions is the "dynamic" approach to describing larval development that Geoff and Ahlstrom advocated (Ahlstrom, 1962). It is highly desirable to use the dynamic approach in descriptions and it has become a major influence on the way the ontogeny of fishes is described. The approach takes structures through their development (e.g., the spines on the preopercle first appear at 2 mm, increase in number to 7 by 5 mm and begin to decrease in number from 9 mm, finally disappearing by 11 mm) rather than saying "a 5-mm larva looks

like this, a 7-mm larva looks like that, etc." Geoff also included meristic and morphometric data in tabular or graphical form in his descriptions of larvae, and promoted their similar inclusion in the descriptions published by others. Michael Fahay, formerly of the NMFS Northeast Fisheries Science Center, writes that "I have also been strongly influenced by Geoff's many publications on the question of how to present ontogenetic data. We have all been told many times over that we can't construct dichotomous keys because of the dynamic nature of larval development. I credit Geoff (and Ahlie) with developing the use of comparative tables into which one can insert a vast amount of useful information at levels ranging from

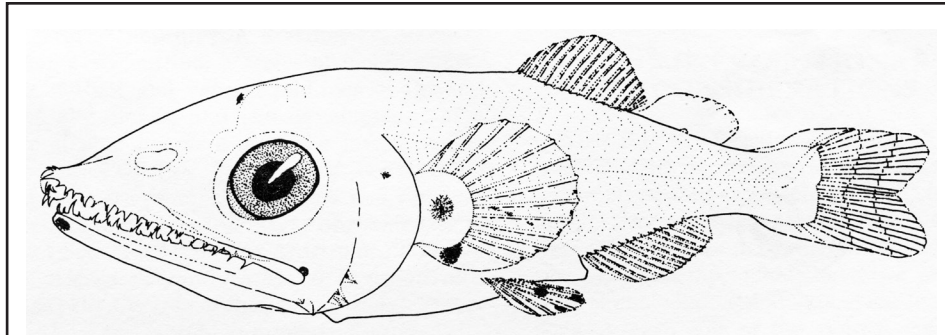


Figure 4

Illustration by Geoff Moser of an 8.7-mm-standard length lanternfish larva, *Lampanyctus* (*Nannobranchium*) *bristori*, from Moser and Ahlstrom (1974, identified therein as *Lampanyctus niger*). Geoff was a talented, expert illustrator in addition to being a world authority on the identification of myctophid larvae.

Order, all the way down to Species. I have used this tool many times.”

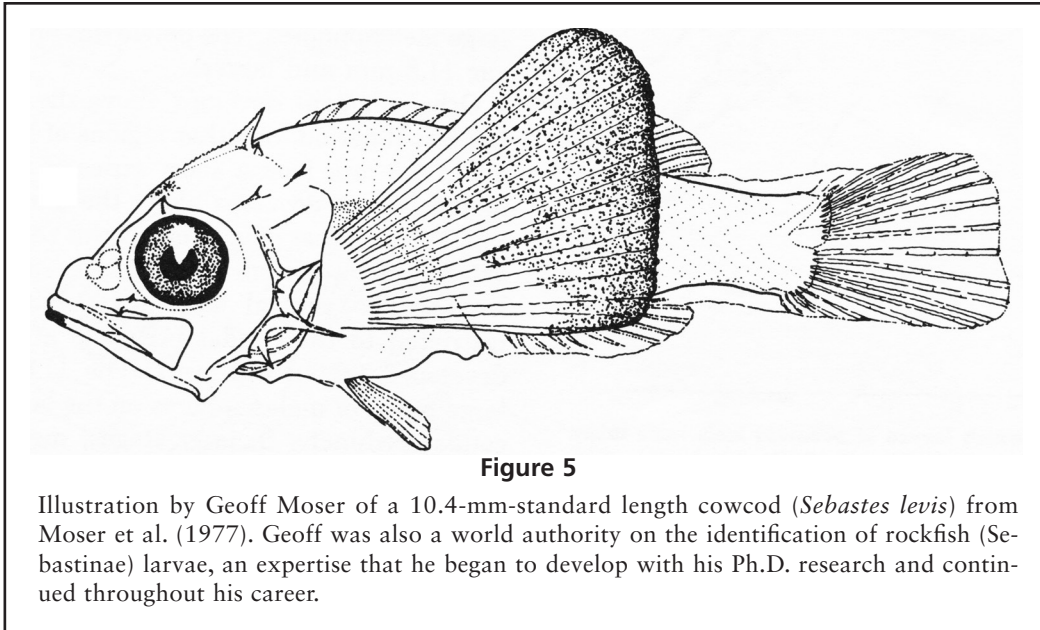
High quality accurate drawings are perhaps the single most important part of a good ELH description. Geoff was a superb scientific artist (Figs. 4 and 5) and promoted the techniques of producing clean, informative illustrations of ELH stages. Michael Fahay writes that “The Larval Illustration ‘style’ developed by Geoff Moser and colleagues Barbara Sumida, George Mattson, Henry Orr, Bill Watson, and a few others from the La Jolla Lab has been adopted by almost all other biologists and illustrators involved with ontogenetic development of marine fishes. I dedicated my monograph on development of fishes from the western North Atlantic Ocean [Fahay, 1983, 2007] to these illustrators, (and listed them by name) including those from the La Jolla ‘school.’” Helpful papers on the identification of fish eggs and larvae, their curation, illustration, and other topics can be found in Moser et al. (1984a), a reference that is strongly recommended for those seeking an introduction to the study of the ELH stages of marine fishes.

Geoff’s activities to disseminate knowledge about the ELH stages of fishes included his participation in the planning group that established the ELH Section of the American Fisheries Society (Margulies, 2005). He had long recognized the need for such a group to further research on the topic and hold conferences where scientists with similar interests could meet to exchange ideas. The Section was formally established in 1980, but the first ELH conference was held in 1977 and they have been held in almost every year since. The Section established the Elbert H. Ahlstrom Lifetime Achievement Award for outstanding career contributions to ELH research. Geoff was the first recipient in 2006.

The study of larval fish assemblages was another area of research in which Geoff had a major influence.

Geoff’s definition of assemblages was “groups of taxa that occur together relatively frequently and are consistently part of each other’s environment” (Moser et al., 1987:98). For his assemblage analyses, he used techniques developed by his colleagues at the Scripps Institution of Oceanography (Fager, 1957; Fager and McGowan, 1963). He was an early advocate for their use outside of the CalCOFI area. A good example is the symposium he, Paul Smith, and Lee Fuiman convened that was published as the first part of a volume of *Bulletin of Marine Science*, titled “Advances in the early life history of fishes. Part 1. Larval fish assemblages and ocean boundaries” (Moser et al., 1993). The introduction to that symposium stated “The need to focus on ichthyoplankton assemblages as an integral part of their environment is central to this understanding [of the ecology and evolution of fish faunas and their constituent populations] and is the basis for this symposium” (Moser and Smith, 1993:283). Geoff and Paul Smith made sure that more junior scientists, including 2 of the co-authors of this paper, were involved in that symposium.

Geoff was more willing than some contemporaries to accept that behavior by larval fishes could have a major influence on their distribution and dispersal. It has now been realized that fish larvae are not simply passive particles that drift in the ocean, as once thought. Instead, they quickly transition from plankton to nekton as they develop their skeletal elements and musculature (Leis, 2006). Michael Fahay notes that interest in the behavioral role of characteristics that appear during larval development of marine fishes and are then lost in juveniles “can be traced directly to Geoff’s paper on the functional value of what came to be known as Transitory Characters (Moser, 1981). Geoff did a great job explaining the functional values of these characters.” It was long thought that rates of mortality of fish eggs and



larvae are especially high in the earliest stages, particularly at first feeding, during what was called the critical period. But Michael noted “That mortality is not necessarily punctuated by ‘critical periods’ but is a continuous feature of ontogeny (or maybe the entire life span) [see Houde, 2008; McClatchie, 2014]. That the development of Transitory Characters is highest in the stages subsequent to those earliest stages, suggests that survival is somehow more ‘critical’ in those later stages.” Geoff’s thoughts on the role of behavior and transitory larval characteristics have become the basis of a newly-emerged field of research based on the observations of live fish larvae in situ by towed plankton-imaging systems (Greer et al., 2016), in chambers deployed in the sea (Paris et al., 2008), by divers following them in open water (Leis et al., 1996), and by divers who go into open water at night to observe and photograph live plankton and micronekton (Nonaka et al., 2021). This is also true of laboratory-based research on larval-fish swimming (e.g., Stobutzki and Bellwood, 1997; Fisher et al., 2000; Leis, 2010) and sensory ontogeny (Leis et al., 2011; Mouritsen et al., 2013; Bottesch et al., 2016).

Geoff’s knowledge about postovulatory follicles as indicators of spawning in fishes and the histological techniques to identify them formed the impetus for the development of the egg production method for stock assessment (Lasker, 1985). He also contributed the technique for classifying the developmental stages of eggs necessary for that method (Moser and Ahlstrom, 1985). The egg production method has since become a widely used, standard technique in stock assessment for those commercial species that meet its assumptions, especially temperate stocks of clupeiform and gadiform fishes. Numer-

ous examples can be found in the set of papers from the second part of the symposium published in the volume of *Bulletin of Marine Science*, titled “Advances in the early life history of fishes. Part 2. Ichthyoplankton methods for estimating fish biomass” (Hunter et al., 1993) and in the article “Egg production methods in marine fisheries: an introduction” from the journal *Fisheries Research* (Bernal et al., 2012).

Another critically important professional contribution was Geoff’s recognition of the value of collections of ELH stages of fishes. When Geoff began work at the La Jolla Laboratory and for the next several years, ichthyoplankton samples were stored in whatever space was available after completion of processing and they were largely ignored after that. Geoff became increasingly alarmed at the prospect that the samples could be lost through neglect and arranged for them to be retrieved and organized as a survey time-series collection, curated vial-by-vial to assure that they were in good condition, adjusting the pH in each vial as needed, re-filling vials where preservative evaporation had become a problem, and attempting (with mixed results) to salvage samples where evaporation had passed the point of no return. That process continues to this day under the leadership of Sharon Charter, and the SWFSC ELH sample archive has advanced from an assortment of whatever spaces were available to a current climate-controlled, sample archive room rated for storage of highly combustible materials. The ELH sample archive currently houses survey samples from the mid-1930s to present from the California Current vicinity, as well as from surveys from the eastern tropical Pacific and central Pacific during the past 50+ years. The intact state

and good condition of these collections have facilitated a wide variety of retrospective analyses; for example, SWFSC staff are working through the CalCOFI time series to bring all larval fish identifications (beginning in 1951) to current standards in order to have a taxonomically well-resolved time series of 70+ years. Examples of the use of the archived samples include immunohistochemical studies (Kwan et al., 2022), and larval taxonomic studies aimed at providing population dynamics information to inform fishery management (Mason et al., 2022). None of this would have been possible without Geoff's foresight.

Following the encouragement of Geoff and others, larval fish collections have been added to the archives of several major museums including, among others, the U.S. National Museum of Natural History, the Natural History Museum Los Angeles County, the Museum of Comparative Zoology at Harvard University, the Australian Museum, and the Burke Museum at the University of Washington which houses the ichthyoplankton collections of the NMFS Alaska Fisheries Science Center.

The legacy of Geoff's contributions in all of these areas endures and will remain influential for many years to come. We take great pleasure in presenting the papers in this volume to honor his contributions.

Acknowledgments

Foremost, H Geoffrey Moser gave information on his career and accomplishments during interviews prior to his death in September 2021 and provided the bibliography of his publications. Eric Hilton (Virginia Institute of Marine Science) facilitated those interviews and conducted them along with Bruce Mundy. Elaine Sandknop Acuña (NMFS SWFSC, retired), William Richards (NMFS SEFSC, retired), and Michael Fahay (NMFS NEFSC, retired) contributed text to this retrospective. This is Ocean Research Explorations contribution no. ORE-16.

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