

H Geoffrey Moser. Larval Fishes: Taxonomy, Distribution, and Fisheries Biology

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HISTORICAL PERSPECTIVES

H Geoffrey Moser. Larval Fishes: Taxonomy, Distribution, and Fisheries Biology

Bruce C. Mundy¹ and Eric J. Hilton²

Authors' note.—H Geoffrey Moser was one of the most influential larval-fish biologists of the past century. He was perhaps best known to ASIH members as the coeditor and motivating force behind the first ASIH Special Publication, *Ontogeny and Systematics of Fishes*. His other accomplishments included an extensive body of publications on larval fishes, with descriptions of development in almost 50 families and as editor of one of the most comprehensive regional identification guides for the California Current (relevant for much of the eastern Pacific and elsewhere). He co-taught courses in larval-fish identification that trained a generation of ichthyologists in that discipline. Many of those scientists have passed that skill on to younger students, continuing his legacy to the present. In addition, he was a talented illustrator and a poet. Geoff, as he was known to his colleagues and friends, passed away unexpectedly at the age of 83 on September 30, 2021. He was interviewed for this Historical Perspective by internet during the COVID-19 pandemic at his home in Bozeman, Montana, in April, 2021 by Eric Hilton and Bruce Mundy. He also provided most of the photographs. The interview was completed through questions and answers exchanged by email. Geoff was shown all of the drafts of this account. He actively contributed to it until the day before his death and approved its content.

*Luminous fishes
In waters where solitude
Is touched by barbels*

*Swimming in the sea
Feeling the small current flows
All the while drifting*

—Two ichthyologically themed haiku by H Geoffrey Moser

H GEOFFREY (GEOFF) MOSER was born in Philadelphia, Pennsylvania on December 5, 1938, to Howard F. D. Moser, a family doctor, and Hazel M. Moser. Geoff wryly commented that his parents did him no favor when they gave him the first initial H—this was not an abbreviation for a name, but rather, it was simply the first initial of both of his parents' names. Geoff's childhood was spent first in Philadelphia and then in Ridley Park, Pennsylvania. His maternal grandfather had been a child laborer in the coal mines near Scranton, Pennsylvania, and his paternal grandfather, early in his life, taught all grades and subjects in a one-room schoolhouse in the Pennsylvania Dutch country near Reading, Pennsylvania. Geoff was proud of his Welsh and Pennsylvania Dutch (Deutsch) heritage. Geoff's paternal grandfather died when Geoff's father was a freshman at Bucknell University. Geoff's mother died of breast cancer when he was a teenager. Geoff had an older (by one year) sister, Judith ("Judy") Booth, and one brother, Kris, (younger by four years); both are deceased. Geoff's brother became a wildlife biologist and administrator, and his sister was an amateur naturalist who taught nature studies at elementary schools in Michigan. Geoff attributed his and his

siblings' interest in biology to the guidance of his father who had intended a career in biology but changed to medicine (Jefferson Medical College) when he became sole supporter of his mother. Geoff's father enjoyed fishing, which was a guiding influence for young Geoff, who began fly fishing and flytying at age 7 or 8. In reflecting on his career, Geoff said that interest in biology, once instilled, never goes away.

Biology was not the only interest that captured Geoff's imagination in his youth. Two other passions that also continued throughout his life were music and sports. Geoff recalled that "Our school system was small, so participation was kind of all-hands-on-deck for the various activities." Beginning in elementary school, Geoff played clarinet and saxophone. "In junior high, I played clarinet and tenor sax in the marching band and in senior high played in the orchestra and dance band. Orchestra played for assemblies and the dance band (Fig. 1A) played at school-sponsored dances at various nights during the year. We played mostly Glenn Miller stuff, ballads, and some up-tempo stuff for fast numbers. I mean, it was the 50s!" Geoff was also an accomplished high-school athlete who played football, basketball, and was on the track and field team as a pole vaulter and hurdler. Geoff became the football captain in 1955, his senior year, and his team was undefeated (Fig. 1B). Geoff recalled, "I think Ridley Park High may still hold the state record for number of consecutive undefeated football seasons, although it no longer exists as a high school and got incorporated by neighboring Ridley Township, a Class A school . . . Almost 70 years later, I still remember playing high school sports as if it was yesterday, and love football and watching the NFL games."

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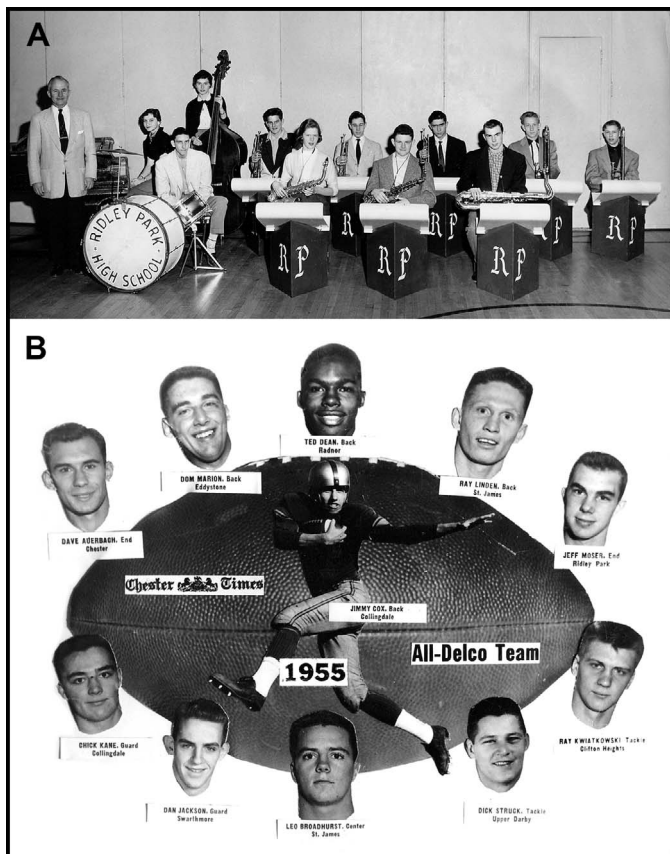


Fig. 1. (A) The Ridley Park High School Dance Band in Geoff's senior year of high school (1955–1956). Geoff, on saxophone, is in the front row, far right. (B) The Pennsylvania All-Delaware County Football Team in 1955, of which Geoff Moser was part. Geoff is in the upper right, with his first name misspelled as "Jeff."

At the end of high school, a friend with whom Geoff worked at a summer camp encouraged Geoff to apply to Dartmouth College in Hanover, New Hampshire. Injuries kept him from having a college career in team sports. Instead, he pursued his lifelong enthusiasms for fishing, hiking, and skiing. While at Dartmouth, Geoff met the second major influence, after his father, for his professional development—the embryologist William Whitney Ballard (1906–1998; Martin, 1998). Ballard's research included studies of the embryology of *Lepisosteus*, *Polyodon*, *Amia*, and *Salmo*. Geoff was a teaching assistant for Ballard at Dartmouth in 1960–1961. He learned microtechnique from Hannah Croasdale (Dartmouth professor and algologist, 1905–1999), a skill that served him well later in his career. He completed an A.B. in biology at Dartmouth in 1960. His first paper, on the adrenal gland of armadillos (Moser and Benirschke, 1962), resulted from his experience working in Professor Kurt Benirschke's lab in the Pathology Department at Dartmouth Medical School. Geoff began work on a master's degree with Ballard, studying the gill-arch development of the axolotl, but did not finish that degree. Geoff met Pamela Chamberlain in Hanover and they married in 1961. Geoff and Pam (Fig. 2) had a daughter, Joscylen Moser Donnelly, born in 1962, and a son, David Moser, born in 1966. Geoff had developed an interest in marine biology, which led him to the University of Southern California



Fig. 2. Geoff and Pamela Moser in 1982 in Japan when Geoff was a visiting scientist at the Ocean Research Institute (now part of the Atmosphere and Ocean Research Institute), University of Tokyo. Photograph by Kouichi Kawaguchi.

(USC), Los Angeles, to continue his graduate studies. Geoff and Pam moved there in 1961.

The third person who became a major influence on Geoff's career was Jay Savage (Donnelly, 2013), the herpetologist well known to ASIH members who also had students in ichthyology. At the time, Savage had a grant to study the midwater fishes of the Southern California offshore basins, and Geoff joined his group working on that project. Other ichthyologists and larval-fish students in the lab's group included John Paxton, Robert Lavenberg, and William Bussing (1933–2014; Cortés and Angulo, 2015). Geoff recalled also benefiting from his interactions with the herpetology students in Savage's lab at that time, including Arnold Kluge, David Wake (1936–2021; Zamudio, 2021), Marvalee Wake, and Roy McDiarmid. In particular, Savage was a proponent of participating in ASIH and insisted that his students attend the annual meetings whenever possible. Geoff eventually gave a paper on his dissertation research at the 1966 ASIH annual meeting in Miami, Florida. In thinking back to his graduate school years, Geoff noted in particular his association with John Paxton, who had begun grad school with Savage one year prior to Geoff's arrival in California. Their time in graduate school ultimately led to a friendship that continued for the rest of Geoff's life. Another grad student at USC was Richard McGinnis, known as "Muggs" to his friends. Muggs completed a doctoral degree studying myctophid zoogeography of the Southern Ocean and later became a professor at Pacific Lutheran University. Muggs grew up in Anaconda, Montana, where his father, a former gold miner, worked at the smelter to support his family. Each summer after grad school, Geoff and his family would meet Muggs and his family at a special place on Montana's Big Hole River for a week of camping and flyfishing.

The sampling gear (Isaacs Kidd Midwater Trawl) used for the USC midwater fish studies was fitted with a plankton net for the cod end, which captured many fish larvae. The larvae piqued Geoff's interest as a project for his Ph.D. It was also



Fig. 3. Herbert Perkins (left) and Geoff Moser (right) at the California Current Resources Laboratory of the U.S. Fish and Wildlife Service in 1962. Perkins worked with Fred Berry on midwater and other pelagic fishes collected in pioneering midwater trawl surveys off southern California (Berry and Perkins, 1965).

through his friendship and interaction with Paxton that led Geoff to one of his main scientific interests, the early life history stages of the Myctophidae. He was also initially interested in larvae of Bathylagidae as well as myctophids. Savage suggested that Geoff should talk with Elbert “Ahlie” Ahlstrom (1910–1979; Radovich, 1979) at the Bureau of Fisheries Laboratory in nearby La Jolla, California. This visit not only changed the course of Geoff’s Ph.D. research, but it also shaped his research for the rest of his career. Ahlstrom already had a manuscript in preparation on bathylagid larvae, which prompted Geoff to choose a different focus for his dissertation (Moser, 1966). Geoff completed his dissertation, titled “Reproductive and developmental biology of the rockfishes (*Sebastes*) off Southern California” in 1966.

CALCOFI AND AHLIE

Ahlstrom was the fourth, and perhaps greatest, major influence on Geoff’s career. Geoff was very modest and attributed most of his successes to Ahlstrom. Ahlstrom, a fisheries biologist and ichthyologist with an international reputation, was director of the La Jolla California Current Resources Laboratory of the U.S. Fish and Wildlife Service Bureau of Commercial Fisheries (BCF) from 1959–1967 (Vlymen, 1989a). The primary focus of the Laboratory was the California Cooperative Oceanic Fisheries Investigation (CalCOFI), a multi-agency program initiated in response to the collapse of the California sardine fishery after World War II (Vlymen, 1989a; Kendall and Duker, 1998; Ohman and Venrick, 2003; Smith and Moser, 2003). The CalCOFI program was initiated in part through the efforts of Oscar Elton Sette (1900–1972; Kendall and Duker, 1998). Geoff commented that although he only met Sette once, he found him to be deeply impressive and thought that he was an exceptionally broad-thinking scientist with the unusual capability of being able to pull together federal and state fisheries agencies and academic institutions to work together. Sette organized CalCOFI to include the U.S. Bureau of Fisheries La Jolla laboratory, the California Department of Fish and Game, and

the Scripps Institution of Oceanography (SIO). With degrees from Stanford and Harvard universities, Sette directed several large fisheries programs on both coasts and is considered one of the founders of fisheries oceanography (Kendall and Duker, 1998). Sette hired Ahlstrom for the California Cooperative Sardine Research Program, which became CalCOFI. At the time of Geoff’s first visit to the lab, Ahlstrom had decided to increase his staff to process a growing backlog of samples from the extensive CalCOFI surveys. Geoff was hired in 1962 (Fig. 3), before finishing his Ph.D., and first worked for Fred Berry (1927–2001; Collette and Anderson, 2002), whose interest was in adult, pelagic fishes (Berry and Perkins, 1965). When explaining the peculiar nature of his first initial to Berry, Geoff said that it was “H, only.” Thereafter, Berry delighted in kidding Geoff about that, addressing him as Honly Moser. Geoff remembered Berry “calling over to me at the end of a day’s work, in his sonorous, sometimes booming, southern voice, ‘Honly, it’s quittin time. I’m gonna buy you a beer and wup you in a game of pool. C’mon, let’s go.’ ” In 1962, Ahlstrom asked Geoff to switch to the identification of the growing number of larval-fish specimens from CalCOFI, which changed the trajectory of Geoff’s career. Geoff considered that to be the time when he became Ahlstrom’s unofficial student (Fig. 4). He had originally intended to become a university embryology professor, but his work for Ahlstrom led him instead to a career in fisheries biology.

Ahlstrom made the prescient decision that all fish larvae, commercially important or not, in the CalCOFI samples should be sorted and identified to the lowest taxonomic level possible. Research on improving those identifications became part of the program (Vlymen, 1989a). Ahlstrom changed the scope of CalCOFI from one strictly focused on the sardine and anchovy fisheries to include the entire pelagic California Current ecosystem. This was an early example of research that enabled implementation of ecosystem-based management. Geoff was thereby given the opportunity to study larvae of many families beyond the commercially important species that were the subjects of most fisheries research. The laboratory on the SIO campus was housed in the former SIO director’s residence. Geoff benefited from the location of the laboratory on the Scripps campus. There he met and interacted with Carl L. Hubbs (1894–1979; Shor et al., 1987) and the ichthyologist and fish collection manager, Richard H. Rosenblatt (1930–2013; Montgomery, 2016), who became a close colleague and friend throughout Geoff’s career.

Employment with the Bureau of Commercial Fisheries gave Geoff access to the BCF research vessels *Black Douglas* and *David Starr Jordan*. He was able to collect adult *Sebastes* for his Ph.D. research during the slack times when the vessel was not on quarterly CalCOFI cruises. The numerous larvae of *Sebastes* in the CalCOFI samples completed the other need for his dissertation. The reproduction and early development of rockfishes and other viviparous teleosts remained a research interest throughout his career (Moser, 1967a, 1967b, 1972, 1974, 1996a; Moser et al., 1977, 1985, 2000; Moser and Ahlstrom, 1978; Moser and Butler, 1981, 1987; Sumida and Moser, 1984; Washington et al., 1984; Moser and Boehlert, 1991; Rocha-Olivares et al., 2000; Butler et al., 2003). Geoff also has a species of rockfish named for him, *Sebastes moseri* Eitner, Kimbrell, and Vetter, 1999. Geoff recalled that:

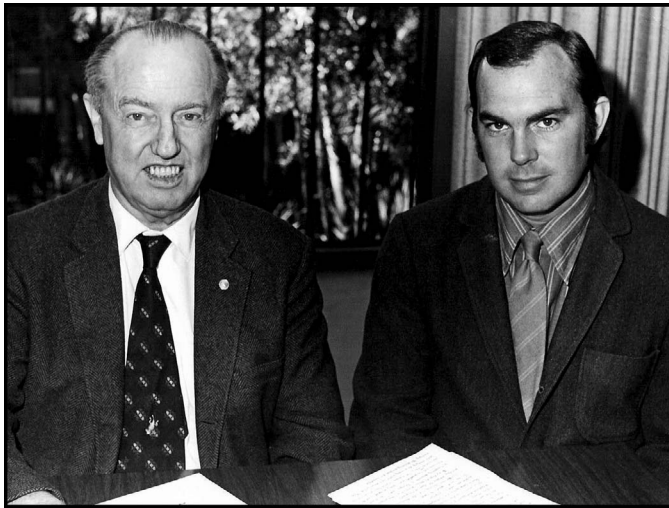


Fig. 4. Geoff Moser (right) with Elbert “Ahlie” Ahlstrom (left) in 1972, taken for a San Diego newspaper article about the Wildlife Society recognition of Moser and Ahlstrom (1970).

Blaise Eitner was a post-doc who worked in our lab for a year on rockfish genetics with Russ Vetter. I helped him with good places to catch rockfish and with identification of specimens he brought back to the lab. One day Blaise brought me a fish that I had never seen before and couldn't identify. It seemed to be a rockfish species new to science and I suggested he take it to Dick Rosenblatt for his opinion. Dick agreed that it was an undescribed species and Blaise prepared a description of the fish with Russ and Carol Kimbrell, Russ's talented lab assistant (Eitner et al., 1999). It was an honor that they wanted to name the fish after me.

In 1964, the BCF La Jolla laboratory moved from its location in the former SIO director's residence to a newly constructed, state-of-the-art fisheries research building on the SIO campus. The building also provided space for scientists from other agencies, such as the Inter-American Tropical Tuna Commission and the BCF tuna research group. The new building gave Geoff access to additional resources for his research. Aquaculture facilities let him study methods of rearing larval *Sebastes*, and the new laboratory spaces helped with continued identifications of the large backlog of CalCOFI larval-fish specimens. Geoff was able to continue attendance at scientific meetings and conferences with the support of Ahlstrom. Ahlstrom's original larval-fish identifiers were Lois Hunter, David Kramer, and Robert Counts. The increasing number of samples required more staff, and the BCF La Jolla laboratory hired more people to process samples and identify the fish larvae. With the move to the new building, Ahlstrom left his position as laboratory director to devote more of his time to research and less to administration. The research group increased in size with the addition of John Butler, Barbara McCall (née Sumida), Elizabeth Stevens, Elaine Sandknop Acuna, Susan D'Vincent, David Ambrose, and Sherri Charter. Numerous student interns (e.g., Morgan Busby, Sharon Kramer) worked with the group during summers and part-time during the school year to curate the thousands of jars and small vials in the collection.

Ahlstrom became very involved in processing and analyzing the larval fishes collected during the 1967 multi-vessel

EASTROPAC cruises in the tropical eastern Pacific Ocean (Ahlstrom, 1971, 1972). Geoff assisted, particularly with the work on the myctophids, gonostomatids, phosichthyids, and maurolucines. The EASTROPAC samples increased the taxonomic scope of specimens available to Ahlstrom and Geoff for their research. They discovered an unusual, small, slender sternopterygoid species in some of those samples, which they described as *Ariaophos eastropas* Ahlstrom and Moser 1969. This was one of two new species for which Geoff was coauthor, the other being *Bythites hollisi* Cohen, Rosenblatt, and Moser 1990 (now *Thermichthys hollisi*).

In 1970, the Bureau of Commercial Fisheries was renamed the National Marine Fisheries Service (NMFS) and transferred from the U.S. Fish and Wildlife Service, Department of Interior, to the newly constituted National Oceanic and Atmospheric Administration (NOAA) in the Department of Commerce. The La Jolla Laboratory became the Southwest Fisheries Center (SWFC; Vlymen, 1989a), now named the Southwest Fisheries Science Center.

Geoff had an unusual opportunity for a federal fishery biologist when he was awarded a Johannes Schmidt Stipendium for Oceanographers for a nine-month research fellowship at the Zoological Museum of the University of Copenhagen in 1970–1971, where he moved with his family. With Ahlstrom's support, Geoff worked with Erik Bertelsen (1912–1993; Nielsen, 1994) and Jørgen Nielsen on the fish larvae in the extensive collections of the Danish circumglobal *Dana* expeditions. The *Dana* samples included a large number of larval, juvenile, and adult myctophids that assisted Geoff in his research on that family. Nielsen recalls of his time with Geoff in Copenhagen, “I remember him as very good company both at the museum and outside. His kids got two guinea pigs from my kids . . . we taught his kids to make guinea pig sounds and they apparently did it so well that the custom officers [during a trip to Germany] were confused!” Following the fellowship in Copenhagen, Geoff had the opportunity to work at the British Museum (Natural History) in London with Norman B. “Freddy” Marshall (1915–1996; Bone and Merrett, 1998), another renowned expert on deep-sea fishes. In London, Geoff worked on larval myctophids from the Antarctic that formed the basis of his paper on *Scopelopsis* and the evolution of photophore patterns in the family (Moser and Ahlstrom, 1972). In Wormley, England, he worked at the Institute of Oceanographic Sciences on a Food and Agriculture Organization of the United Nations (FAO) contract, studying their collection of larval fishes from the Indian Ocean. Also, he went to Germany to the University of Kiel to work with Walter Nellen on his collection of larval fishes, and later to Hamburg to work briefly with Gerhard Krefft (1912–1993; Stehmann and Hulley, 1994) on specimens at the Institut für Seefischerei. The research in Europe, together with Geoff's access to the myctophid larvae in the samples of the SWFC, allowed Geoff to produce a number of papers that became standard references for the identification and distributions of larvae in that family (Moser and Ahlstrom, 1970, 1972, 1974, 1996; Ahlstrom et al., 1976; Moser et al., 1984a; Paxton et al., 1984; Olivar et al., 1999; Moser and Watson, 2001, 2006a; Sassa et al., 2002). His 1970 paper with Ahlstrom on larval Myctophinae off California won the 1971 best paper award in fish ecology and management by the Wildlife Society. Later, in the early 1980s, Geoff was able to go to Japan to work with Kouichi Kawaguchi (1940–2007) at the Ocean Research Institute (now

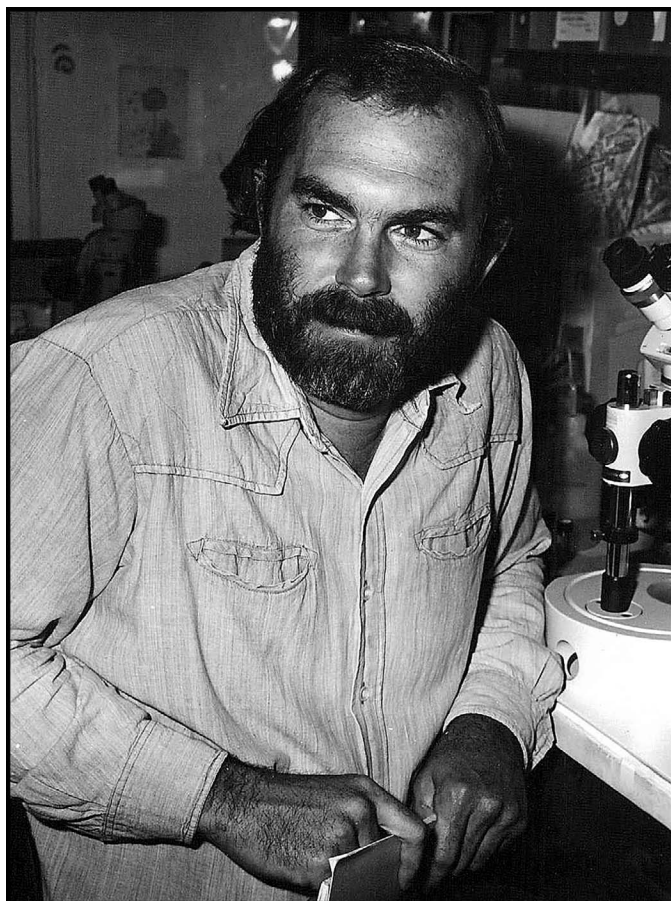


Fig. 5. Geoff Moser in 1977 while co-teaching the larval-fish identification class with Elbert Ahlstrom at the NMFS SWFC, La Jolla.

part of the Atmosphere and Ocean Research Institute), University of Tokyo. He also went to Hokkaido to work with Kunio Amaoka, and then on to Osaka. The research with Kawaguchi and others resulted in papers on stomiiform larvae (Ahlstrom and Moser, 1969; Weihs and Moser, 1981; Kawaguchi and Moser, 1984, 1993; seven chapters in Moser, 1996b), continuing Ahlstrom's studies with which Geoff had collaborated. Work with collections of oceanic fish larvae also enabled Geoff to continue Ahlstrom's studies on the Argentiniformes, the group that initially caught Geoff's interest when he was in graduate school (Ahlstrom et al., 1984; Olivar et al., 1993; four chapters in Moser, 1996b).

Geoff published many of his observations and hypotheses about larval-fish morphology in a book chapter on the biology of marine fish larvae (Moser, 1981) that was edited by Reuben Lasker (1929–1989; Vlymen, 1989b). The book resulted from a series of lectures presented by Lasker and his research team leaders (John Hunter, Paul Smith, and Geoff) at the College of Ocean and Fisheries Sciences, University of Washington. This paper may be underappreciated because it is not generally available. However, Geoff's chapter summarizes numerous ideas about the adaptive significance of morphological characters of marine fish larvae, including mimicry of cnidarians by those larvae having elongate, ornate fin rays and intestines, and the flicker-fusion hypothesis of predator distraction for the ubiquity of rows of serial melanophores in fish larvae.

THE AHLSTROM AND MOSER LARVAL-FISH COURSES

Ahlstrom taught a course on the identification of larval fishes in 1971 while Geoff was in Europe. The course was initially intended primarily for biologists working with ichthyoplankton at the NMFS fisheries centers, but also included scientists from universities. The course was taught for seven years in a row and expanded to include scientists from a number of other countries. Geoff co-taught the six courses from 1972–1977 with Ahlstrom (Fig. 5). Each day of the course consisted of a morning lecture and afternoon laboratory, reviewing taxa based on the understanding of phylogeny at that time. Many of the researchers who later came to the forefront of the study of the early life history of marine fishes took these courses, and many of those passed on the knowledge from the Ahlstrom-Moser courses to students of their own, such as the authors of this Historical Perspective. A series of similar courses were later co-taught by John E. Olney (1947–2010; Hilton et al., 2011), who had been a student in the last SWFC course (Fig. 6), and Ed Houde. Current courses, such as those being offered by Peter Konstantinidis, Nalani K. Schnell, and others, can be seen as direct descendants of the Ahlstrom-Moser courses. Ahlstrom also taught a graduate course on larval-fish biology at SIO in which Geoff, who at the time was a research associate in the Marine Biology Research Division of SIO, gave a guest lecture. Although Geoff was not on the faculty at SIO, he assisted ichthyology graduate students with their work, adding to his training legacy. For example, he served on the graduate committee for Lo-Chai Chen's Ph.D. work on *Sebastes* (Chen, 1971).

After the courses at SWFC ended, Ahlstrom and Geoff co-taught a larval-fish identification course at the Universidad Autónoma de Baja California School of Marine Science, Ensenada, Mexico, shortly before Ahlie died. After Ahlie passed away, Geoff continued teaching in Mexico with two courses on larval-fish identification at the Centro Interdisciplinario de Ciencias Marinas in La Paz. The second of these was taught by all members of Geoff's research group. Geoff also taught courses at Mazatlan and at the Instituto Nacional de Pesca in Mexico City. In 1997, Mexico had developed its own version of CalCOFI, Investigaciones Mexicanas de la Corriente de California (IMECOCAL), to study the changes in anchovy and sardine populations off its Pacific coast (Gaxiola-Castrol and Najera-Martinez, 2002; Baumgartner et al., 2008). The courses at SWFC and in Mexico took a lot of energy and preparation for both Ahlstrom and staff, occupying about three months of each year in which they were taught. Eventually, Geoff's other obligations prohibited spending that much time on them and he could not continue the classes. The courses are undoubtedly one of the greatest legacies that Ahlie and Geoff gave to ichthyology.

EARLY LIFE HISTORY SECTION AND THE ONTOGENY AND SYSTEMATICS OF FISHES

In addition to the ASIH, Geoff was a member of the American Fisheries Society (AFS). The AFS members who worked with fish larvae decided that an Early Life History (ELH) section of the society was needed, following an early life history symposium in 1977. Although the section initially had a freshwater emphasis, Geoff participated in its planning group along with Darryl Snyder, Lee Fuiman, and others. The AFS ELH section was authorized by the general AFS membership at the society's 1979 annual meeting in West Yellowstone,



Fig. 6. (A) The participants in the 1972 class on the identification of marine fish larvae that was taught by Geoff Moser and Elbert Ahlstrom in La Jolla (in the back row, left side). The students, not named in the order shown, included: Anne Naplin, Karl Niggol, and Kenneth Waldron (NMFS Seattle Laboratory); Thomas Kazama (NMFS Honolulu Laboratory); Thomas Potthoff and Edmond Metzger (NMFS Miami Laboratory); John Finucane (NMFS St. Petersburg Laboratory); Ruth Stoddard (NMFS Narragansett Laboratory); Sally Richardson and R. Gregory Lough (Oregon State University); Sara Guzman and Thalia Castro (Instituto Nacional de Pesca, Mexico); Richard Haight and Chester Mattson (NMFS Auke Bay Laboratory); Barbara Sumida (University of Hawaii); Elaine Sandknop, Mary Kalin, John Butler, and Elizabeth Stevens (NMFS La Jolla Laboratory). This was the first class that Geoff co-taught. (B) The international participants in the 1977 class on the identification of marine fish larvae that was taught by and Elbert Ahlstrom and Geoff Moser in La Jolla (in the back row, right side). The students, not named in the order shown, included: Olayinka Babalola (Nigerian Institute for Oceanography and Marine Research); Robert Behrstock (Humboldt State University); M. Elizabeth Clark and Pat Wagner (University of Alaska); Francois Conand (Centre ORSTOM, New Caledonia); César F. Coto (Centra de Ciencias del Mar y Limnología, Mexico); C. B. Lalithambika Devi (National Institute of Oceanography, Kerala, India); T. Saunders English, Leanne Legacie, and Bruce Miller (University of Washington); Doris Finan (NMFS Sandy Hook, New Jersey, Laboratory); Marta Gerritón (Departamento de Oceanología, Chile); F. Douglas Martin (University of Maryland); John Olney (Virginia Institute of Marine Science); Allyn Powell (NMFS Beaufort, North Carolina, Laboratory); D. A. Robertson (New Zealand Ministry of Agriculture and Fisheries); Bruce Stewart (Moss Landing Marine Laboratory, California); and John Tucker (North Carolina State University). This was the last class that Geoff co-taught with Elbert Ahlstrom.

Montana and officially created at the 1980 annual AFS meeting in Louisville, Kentucky. The section remains strong today, and many of its annual meetings have been held in conjunction with the annual ASIH meetings. A career achievement award

named in honor of Ahlstrom was created by the AFS ELH section; Geoff Moser was its first recipient in 2006.

Change came for the SWFC and Geoff's career with Ahlstrom's death in August, 1979. As John Paxton recalls, Ahlstrom's "unexpected passing must have been a shock to Geoff, who lost a mentor, coauthor, friend, and icon. While Geoff was not alone in this regard, as Ahlie had many coauthors and coworkers, he must have gone through a particularly hard time." Ahlstrom's passing also led to Geoff's contribution that may be the one for which he is best known to ASIH members as lead editor of the first special publication of the ASIH. Reuben Lasker, then head of the SWFC Coastal Resources Division, which included Geoff's group, asked Geoff to organize a symposium to be held in Ahlstrom's honor. Ahlstrom, with Geoff, had discussed a book about the contribution of larval-fish research to systematic ichthyology (Moser et al., 1984b). They had created an outline and drafts of some of the chapters, but did not have time to complete the project. Geoff assembled the outline, drafts, and Ahlstrom's data and notes, and discussed the project first with SWFC colleagues. His goal was to bring ichthyoplankton and systematic experts together in a symposium and publication that would unite the two disciplines and demonstrate the utility of early life history characters for systematics. The steering committee for the symposium included Daniel Cohen (1930–2016; Collette, 2019), Sally Richardson (1944–1986; Collette, 1986), Michael Fahay, Geoff Moser, Arthur Kendall, Jr., and William Richards (Fig. 7). The group first met in 1982 at a NOAA facility in Boulder, Colorado, because of its central location. Later committee meetings were at the Gulf Coast Research Laboratory, again at Boulder, and in Miami. The committee recruited prominent larval-fish researchers from universities, museums, and NMFS laboratories across the United States and from many other countries to contribute symposium talks and chapters for a resultant book. Initially conceived as including only marine teleosts, the project was expanded to include extant freshwater groups except for the Osteoglossomorpha. The symposium, which was held in August 1983 at the University of California, San Diego, was the first global review of the early life history stages of teleosts. The publication remains the only one on that subject today.

Geoff had fond memories of working on the production of the Ahlstrom symposium volume. The five editors took on oversight of different chapters. Geoff, with Bill Richards as managing editor, worked together in Miami on the task on overseeing the project and putting all of the chapters together; Geoff himself was a coauthor on eight of the chapters. Richards, who was then editor of the *Bulletin of Marine Science*, which was published by Allen Press, suggested Allen Press as a prospective publisher for the Ahlstrom symposium. Allen Press did not have the funds to publish it and at first doubted the sales potential for the volume. Richards suggested that the ASIH could serve as a possible sponsor for the publication, and C. Richard Robins (1928–2020; Smith, 2016) at the University of Miami, then ASIH President, supported the project. The ASIH agreed to publish it through Allen Press, but also did not have the funds to do so. The steering committee put out a call for prepublication subscriptions and successfully raised the funds to support publication. Geoff and Bill Richards took the completed manuscript to Allen Press in Lawrence, Kansas. They mistrusted bringing the original artwork for the 364 figures



Fig. 7. (A) The first meeting of the steering committee for the symposium on The Ontogeny and Systematics of Fishes, in honor of Elbert Ahlstrom, at Boulder, Colorado in 1982. From left to right: Sally Richardson, Michael Fahay, Arthur Kendall, Jr., William Richards, and Geoff Moser (Daniel Cohen, not in photo). (B) The steering committee for the symposium on The Ontogeny and Systematics of Fishes, in Miami, Florida in 1983. From left to right: Daniel Cohen, Sally Richardson, Michael Fahay, Geoff Moser, Arthur Kendall, Jr., and William Richards.

of the volume (most of them new and with several illustrations each) in checked baggage and purchased an extra airline seat for the package containing them. The symposium volume was published as ASIH Special Publication Number 1 (Moser et al., 1984b). The editorial team was awarded the U.S. Department of Commerce Silver Medal for Distinguished Achievement in 1985 for publishing the book. It, and its chapters, are still among the most cited works on larval-fish identification.

ICHTHYOPLANKTON DATA MANAGEMENT AND DISTRIBUTION, AND FISHERIES MANAGEMENT

As a federal fishery biologist, Geoff considered his first responsibility to be the provision of scientific information for the conservation and management of fisheries resources. As part of that, he felt that publication of raw data of the

CalCOFI time series was important. In that regard, he anticipated the current NOAA Public Access to Research Results mandate for agency scientists (NOAA Research Council, 2015). SIO published summary reports on the oceanographic data from CalCOFI cruises, and Geoff decided that would also be appropriate for the NMFS SWFC ichthyoplankton work from those cruises. To accomplish this, he teamed with the SWFC data manager Richard Charter. This effort led to a series of 40 reports coauthored by their staff that provided the ichthyoplankton data from the CalCOFI cruises and other surveys, thereby establishing one of the most extensive sets of publicly available data for a long-term time series (e.g., Ambrose et al., 1987; Pommeranz and Moser, 1987; Watson et al., 2002); the publication of these data reports under the direction of William Watson has continued since Geoff's retirement. Many of the larvae from the cruises, particularly the earlier ones, were re-identified to ensure data quality based on increased knowledge about the identification of larvae over the years. This was possible because all of the CalCOFI and other samples were carefully preserved and curated under Geoff's and Watson's management. Sherri Charter has played a key role in the management of the collection. Geoff considered that the publication of these data reports in conjunction with Rich Charter's computer time series adds to their public accessibility and value.

Another of Geoff's contributions to fishery biology came when scientists at the SWFC developed a new stock assessment method for commercial species having pelagic eggs and well-defined spawning areas and seasons—the egg production method (Lasker, 1985). Geoff's contribution to this was explained by Lasker (1985, p. 1):

This egg production method is based on an original finding by Moser (1967b) that postovulatory follicles can be seen and used to determine time of spawning in rockfish. Hunter and Goldberg (1980) and Hunter and Macewicz (1980), following upon this suggestion, developed criteria for aging postovulatory follicles in anchovy and hence the frequency of spawning of natural populations . . . Parker's (1980) model, in which all parameters can be estimated, uses an estimate of egg production divided by the product of batch fecundity and the proportion of females in the mature stock, and accounts for the fact that spawning in anchovies is relatively continuous. Estimates of egg production are derived from direct plankton net sampling . . . Moser and Ahlstrom (1985) developed the criteria for staging the eggs.

Geoff participated in the SWFC planning meeting for development of this method, introducing the analysis and importance of postovulatory follicles to the group. The egg production method is now a standard stock assessment tool for clupeiforms and other species that meet its criteria, and it continues to be used for CalCOFI stock assessments. For this, the SWFC team that developed and implemented the method, including Geoff, was awarded a NOAA Bronze Medal for superior federal service.

THE ATLAS OF EARLY STAGES OF FISHES IN THE CALIFORNIA CURRENT REGION

From early in their association, Ahlstrom and Geoff had discussed producing a small handbook for the identification of the fish larvae of the CalCOFI region. They did not find

the time to do that while Ahlstrom was alive. Geoff's work was later occupied by numerous papers on the development of a variety of taxa and on the symposium volume. Impetus to publish the guide for the California Current region came when larval-fish biologists at the other NMFS science centers began work on guides for their regions. First, Michael Fahay of the NMFS Northeast Fisheries Center published a guide to the identification of the fish larvae from the western North Atlantic (Fahay, 1983, 2007). Mike commented that "I couldn't have prepared my monograph on NW Atlantic fish development without Geoff's help early on." A guide to the identification of larval fishes from Alaska, Oregon, and Washington followed, produced by scientists at the NMFS Alaska Fisheries Science Center (Matarese et al., 1989). Geoff decided that the time had come for the SWFC to produce its guide. He enlisted William Watson in this effort, along with others of his group, and assigned chapters on the various families to them. Scientists from other institutions were also asked to help with chapters in their areas of expertise.

Numerous illustrations were available from previous publications of the SWFC ichthyoplankton group, including those by George Mattson, Henry Orr, Barbara Sumida McCall (who also produced many new illustrations for the volume), Bill Watson, Geoff, and others. However, Geoff noted that

Starting our ID guide required a slew of new illustrations. Through Gary Brewer, a former USC colleague who had worked at the Natural History Museum of Los Angeles County on nearshore ichthyoplankton and was then with Marine Minerals Management, I was able to attain a 50K grant to hire illustrators. Nancy Arthur, Mary Vona, and Rob Walker were talented fine artists who became expert larval-fish illustrators under the guidance of Bill Watson. As my group worked away on their chapters for the guide, they continued to work on their assigned duties building the CalCOFI ichthyoplankton time series. I was very proud of their efforts . . . the guide continues to be a valuable resource for larval-fish researchers around the world and I will be forever grateful for, and in awe of, what my group was able to accomplish. I know I'm guilty of oversharing with all of this but I feel that quality illustrations are a vital part of our work and wanted to emphasize how our group contributed to this important element in larval-fish research.

The project grew in size and how to publish the volume became a question, as it did for the symposium book. John Hunter, Geoff's colleague and then head of the group in which Geoff worked, suggested that CalCOFI Atlas series might be a good outlet. The CalCOFI atlases were large monographs usually devoted to maps of oceanographic observations. Allen Press agreed to publish the book as they had for the symposium volume, but funding was once again requested up front. That was less of a problem for the identification guide because of the success of the previous book. Geoff obtained financial support from the director of the SWFC, Izadore Barrett, as well as from other NMFS center directors, and also sold prepublication subscriptions as was done for the 1984 book. George Hemingway, CalCOFI Coordinator at SIO, played a major role in obtaining prepublication funding. Allen Press this time wanted a camera-ready manuscript, which Geoff said "gave him gray hairs," as a new requirement. As before, Geoff and George

Hemingway took the manuscript to Allen Press in Lawrence, Kansas. The guide was published in 1996 and is one of the most complete and useful works of its type (more information about its history is given in Geoff's preface to the book; Moser, 1996b: p. iii-iv). Its utility is enhanced because it is now available as a pdf on the internet. William Watson played a central role in the production of the guide. As sole author or in collaboration, he wrote more than half the chapters, produced many of the illustrations, trained and oversaw the contracted illustrators, pasted-up the final plates, and helped authors with his writing skills. Geoff was the sole author of 22 chapters (primarily those on the Stomiiformes and Myctophiformes) and coauthor of 24 others. With the publications by Fahay (1983, 2007), Matarese et al. (1989), Moser (1996b), and Richards (2006), all NMFS regions, except for the Pacific Islands region, have ichthyoplankton identification guides. The sizes of these guides increased consecutively, as did the expense of their publication. At this point, it seems unlikely that a guide for the Pacific Islands region could be produced in printed form. In the future, such guides may be best published as internet resources, such as that of the NMFS Alaska Fisheries Science Center's Ichthyoplankton Information System (<https://access.afsc.noaa.gov/ichthyo/>).

In many ways, Moser (1996b) was the culmination of Geoff's years of dedication and expertise on larval fishes, and his direction of the post-Ahlstrom CalCOFI ichthyoplankton group. Geoff was awarded the NOAA Bronze Medal in 1996 for "superior federal service for a career of scientific excellence of lasting benefit to the nation." Geoff's research continued after the publication of the guide, with several other papers, but much of his time was occupied with the production of the numerous data reports from the first 38 years of the CalCOFI surveys. He decided to retire from SWFC and federal service in 2002. After retiring, he authored or coauthored six more peer-reviewed papers, including a book chapter that reviewed the ecology of ichthyoplankton in the California Current (Moser and Watson, 2006b). Geoff returned full-circle to anatomical/histological studies of reproduction, with which his scientific career began at Dartmouth, in his most recent ichthyological publication, a sole-authored paper on a South African clinid (Moser, 2007). Geoff received an Outstanding Career Achievement Award from the American Institute of Fishery Research Biologists in 2006, in addition to the AFS ELHS's Elbert H. Ahlstrom Career Achievement Award and awards from NOAA mentioned above. With characteristic modesty, Geoff said that most of his career was the result of pure good luck. He attributed his success to the wonderful people with whom he worked and collaborated, particularly Elbert Ahlstrom and all the members of his research group. Reuben Lasker's research team leaders (John Hunter, Paul Smith, Nancy Lo, Rich Charter, Gail Theilacker, Daniel Huppert, Michael Laurs, Ron Lynn, and Russ Vetter) were valuable partners and friends during the years Geoff worked at the SWFSC. He said that you meet the greatest people while working in ichthyology and oceanography and considered those friends to have been the best reward of his career.

INFLUENCES, FRIENDS, AND THE JOYS OF LIFE

Geoff mentioned several other professors at USC who influenced his career in biology: John Mohr, a protozoologist; Andrew Starrett (1930–2008), a mammologist; and Russell

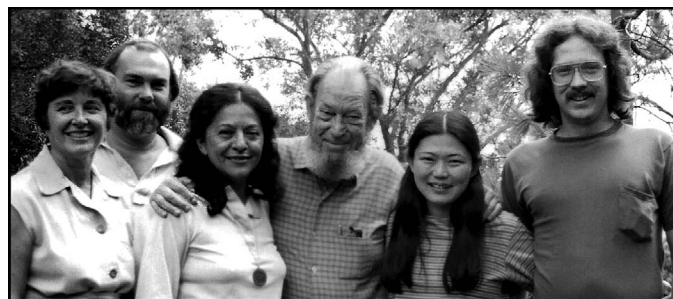


Fig. 8. The ichthyoplankton group at the SWFSC, c. 1983. From left to right: Elizabeth (Betsy) Stevens, Geoff Moser, Elaine Sandknop Acuna, Eric Bertelsen (Visiting Scientist), Barbara Sumida, and Morgan Busby. Photo courtesy of Morgan Busby.

Zimmer, an invertebrate zoologist. Erik Bertelsen (1912–1993) at the Dana Collection (Fig. 8) was a close friend and mentor. Several ichthyologists who were George Myers' students at Stanford University were important influences. Of those, Geoff particularly mentioned Dan Cohen (Fig. 9A), one of the other editors of *Ontogeny and Systematics of Fishes*, as being like an uncle. Another good lifelong friend, as well as coauthor, was Bill Richards (Fig. 9B). Bill was born and raised in Scranton, Pennsylvania, and he and Geoff became colleagues and close friends early in their federal careers, sharing the bond of Welsh heritage.

By the time Geoff went to Europe, he had developed a condition that affects some other ichthyologists—a sensitivity to formalin. Jørgen Nielsen and Niels Christensen kindly transferred all of the Dana Expedition collections that Geoff worked on to alcohol. At the British Museum of Natural History (now the Natural History Museum, London), he had to tentatively estimate geographic distribution of an Antarctic myctophids by laboriously swirling unopened collection jars, because of the highly concentrated formalin.

When in Japan, Kouichi “Koh” Kawaguchi and others would go to a working-man's pub after work. It was during the evenings at the pub when Koh introduced Geoff to the haiku of the famous master Matsuo Bashō (1644–1694), which inspired Geoff to take up that art form (see epigraph).

Geoff mentioned other colleagues as well. In particular, there was sadness when he spoke of Sally Richardson, also a coeditor of the Ahlstrom symposium volume. Sally moved to the Museum of Comparative Zoology at Harvard University in 1985, and she and Geoff had made plans to work together on pleuronectiform larvae following the 1986 meeting of the Early Life History Section (ELHS) in Miami. Unfortunately, this was not to be, as Sally died unexpectedly just prior to the conference (Collette, 1986). Geoff went to the Museum of Comparative Zoology (MCZ) soon after to help Karsten Hartel organize her specimens, which was one of the saddest times for him. He remembered Sally as a very special person.

Other ichthyologists that he mentioned were also fishing buddies. Geoff stayed with John Olney (Fig. 9C) at the Virginia Institute of Marine Science (VIMS) for one week in 1986, during which John took him fishing for Black Drum—they didn't catch any but the memories and comradery they shared made up for the lack of success. George Boehlert (1950–2018) was first a graduate student at Scripps who studied rockfishes. With the obvious connection to Geoff for that interest, the two became friends, colleagues, coauthors (Moser and Boehlert, 1991), and eventually, as Geoff put it,

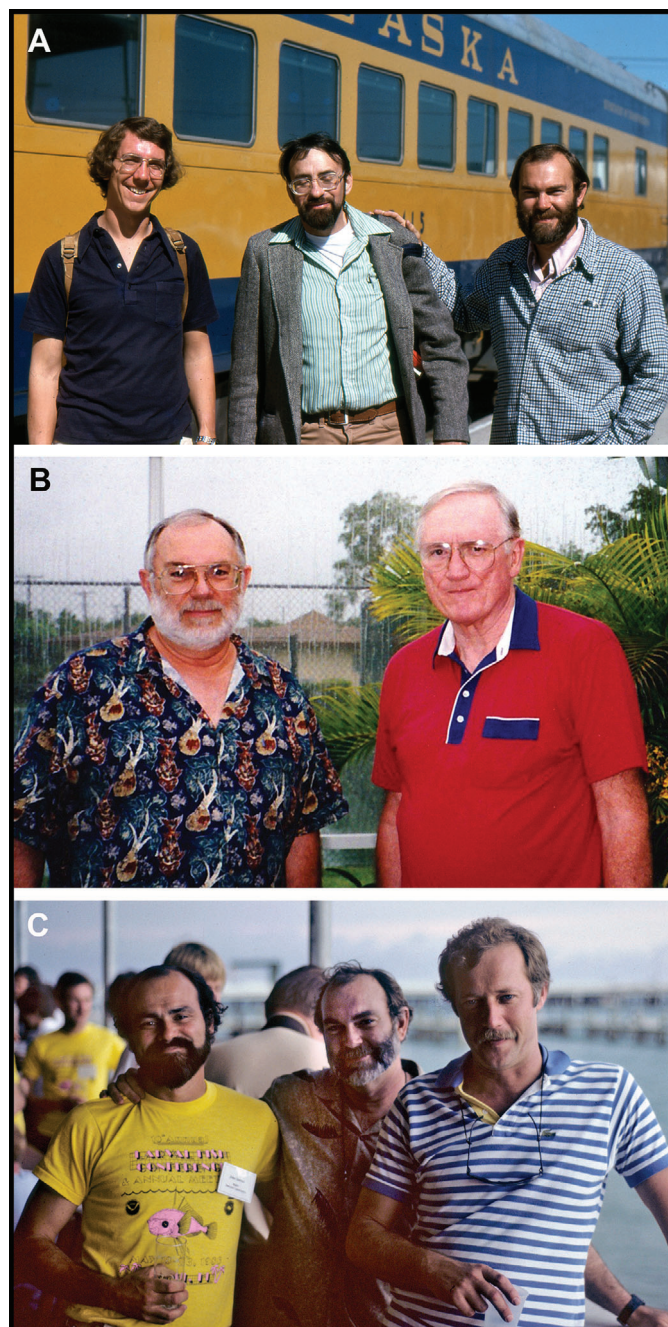


Fig. 9. (A) Jeff Leis, Dan Cohen, and Geoff Moser boarding a train for the field trip following the 1976 ASIH meeting in Fairbanks, Alaska. Photo courtesy Jeffrey Leis. (B) Geoff Moser and Bill Richards in Miami, Florida, 1997. (C) Larval-Fish Conference in Miami, 1986. Right to left: Jeff Govoni, Geoff Moser, and John Olney. Photo: George Boehlert.

like brothers. Geoff and George went fishing together for bonefish and tarpon. Geoff added, with a glint in his eye, that there are additional favorite stories of his about adventures with colleagues, but that he couldn't tell for publication.

At retirement, Geoff moved to Bozeman, Montana where he and Pamela could enjoy a life away from urban Southern California. The trout streams, hunting, hiking, and skiing were major enticements. Geoff had always been a fisherman (Fig. 10), and he enjoyed fly fishing in Montana's streams. In retirement, he served as a volunteer hydrographer for Trout



Fig. 10. Geoff Moser in 1989 with a rainbow trout on the bank of the Ahuriri River, New Zealand, just before dark, and just before releasing the fish. Photograph by his son, David Moser.

Unlimited's Montana Water Project. He was also, briefly, a volunteer member of the Disaster Action Team for the Five Rivers Red Cross Chapter in Bozeman.

Geoff's talents went beyond ichthyological research and management of government programs. During his career, Geoff worked with many artists who provided illustrations for his papers and the books that he edited, and considers the illustrations to be among the most important parts of his publications. He most admired the work of George M. Mattson (1913–1991), a professional artist who was originally hired by Ahlstrom when the proto-CalCOFI lab was on the campus of Stanford University, and who worked at the SWFC for 23 years since the 1950s (e.g., his half-tone illustrations in Ahlstrom, 1957). Geoff never felt that his own illustration approached the quality of Mattson's illustrations, but in fact, he was an accomplished artist who did illustrations in his papers (Fig. 11). He described the beginnings of his work as a scientific illustrator thus:

I was very interested in reproductive biology and as result chose to do a study of reproduction and development of the viviparous rockfishes of the northern Pacific for my dissertation. My anatomical illustrations of ovarian larvae were also my favorites and luckily George Mattson was available to do the planktonic larvae and juveniles. George's technique was to take Kodachrome photos of the eggs and larvae with a macro-photo setup and then project the images on illustration board in the darkroom and work with them in pencil and, ultimately, with split-point pen and India ink. I did all my illustrations using the drawing attachment to the Wild M5 scope. Photomicrographs of histological material were done with the camera attachment of my Wild M20. The paper was published in 1967 in *Copeia* [Moser, 1967a] and I presented it at ASIH in Miami. Fittingly the last fish drawings I did after retirement were for a paper on viviparous South African clinids published in the *African Journal of Marine Science* [Moser, 2007]. These included a brood of larvae in the ovary of a pregnant clinid. No planktonic larvae in that study.

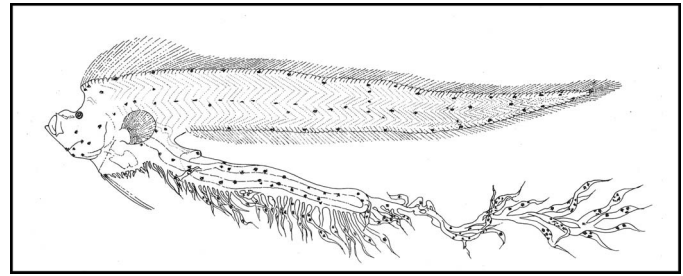


Fig. 11. Illustration of a larval *Lamprogrammus* from Moser (1981).

When asked about his favorite drawing, Geoff replied,

Probably the most memorable drawing I made was the *Lamprogrammus* larva I published in my 1981 book chapter [Fig. 11]. I included the illustration as an example of an exterilium larva . . . How could I forget executing that illustration with the aid of my Wild M5 Camera lucida . . . every organ, myomere, and pigmentation dotted in with my handy Rapidograph pen, with the specimen carefully pinned on the wax-bottomed petri dish. I think I got it all down correctly as I haven't heard otherwise!

The specimen was later identified as *Lamprogrammus brunswigi* by Mike Fahay and Jørgen Nielsen and the illustration was included in their paper in *Ichthyological Research* (2003).

He also remembered that

Carl Hubbs asked me if would do him a favor and provide an illustration of a 23mm *Mesobius berryi* to be included in a paper he was writing with Dr. Iwamoto on macrourids. I did the illustration for which he thanked me. That illustration has particular meaning because I was able to do something for Carl after all the kindness and encouragement that he and Laura extended to me when I was getting started in ichthyology. Also, Carl named that species after Fred Berry who was my first supervisor at the lab and a dear friend. . . . After George retired, I did my own illustrations and eventually Ahlie hired Barb Sumida McCall on a Smithsonian Grant. Barb was a superb illustrator and larval-fish biologist. Also, Henry Orr was added to the lab graphics shop and he also began to do larval-fish illustrations for Ahlie. Years later, following Ahlie's passing, I was able to hire Bill Watson to replace a vacancy in our group. With Bill, we then had an expert ichthyoplankton biologist and a master illustrator.

Geoff was also a poet. One of us [BCM] remembers that Sally Richardson treasured a copy of one of his books of poems that Geoff had given her in the late 1970s or early 1980s. Haiku became Geoff's preferred style for many years after his trip to Japan. Writing poetry became Geoff's primary hobby during retirement; he said that was "something to do in the long winters of Montana." Geoff's books of poems were self-published, and he described them as "not a retirement fund, just retirement fun." His early poetry books were small handmade chapbooks, published by himself. In recent years, he used Amazon's self-publishing service to publish books of humorous poems about every-day life, along with poems about birds, trees, and other aspects of nature.

Geoff said that he never met anyone in ichthyology that he did not like. For many, that might seem fulsome, but those who knew Geoff can believe it. His enthusiasm, modesty, and generosity toward others contributed to his success and influence as a mentor, program manager, and highly productive scientist.

ACKNOWLEDGMENTS

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