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Introduction to the proceedings of the symposium Fish Larvae and Systematics: Ontogeny and relationships

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INTRODUCTION TO THE PROCEEDINGS OF THE SYMPOSIUM FISH LARVAE AND SYSTEMATICS: ONTOGENY AND RELATIONSHIPS

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The International Larval Fish Conference was held in Sydney, Australia (26–30 June 1995) as part of the 19th Annual Meeting of the Early Life History Section of the American Fisheries Society. At the conference, we convened a symposium ("Fish Larvae and Systematics: Ontogeny and Relationships") that was intended to stimulate the application of ontogenetic data to solve problems in fish systematics. The brief we gave the contributors to the symposium was this: "The theme of this symposium will be the use of information gained from egg and larval ontogeny in solving problems in systematics and phylogeny. Thus, we are seeking, not papers that just described larval development of various taxa (although we anticipate many papers will include this), but papers which go beyond description and use the larval characters, developmental patterns, etc. to attack problems in fish systematics. For example, we would welcome papers on how larval morphology solved problems of cryptic species amongst adults, or papers that made use of ontogenetic information to assess relationships at species, genus, family or higher level."

Twenty-one papers by authors from 10 countries were presented at this successful symposium. Twelve of those papers (including one scheduled to be presented but canceled at the last minute) are included in this volume. All the papers have had the benefit of input from expert reviewers (to whom we offer our sincere thanks), and collectively provide a good survey of recent attempts by workers around the world to apply information gained from the study of fish ontogeny to elucidate relationships among fishes. Seven countries are represented among the authors including Australia, New Zealand, South Africa, the United States, Spain and Zaire. Japanese workers are best represented, continuing their long tradition of larval fish research. Unfortunately, we were unable to persuade authors from any Asian country other than Japan to participate in the symposium.

Application of ontogenetic information to problems in systematics must be built on a foundation of sound taxonomy, anatomy and description. The papers published here provide good examples of detailed depictions of the development of a diverse assemblage of mostly marine taxa. These descriptions will be extremely valuable to those who need to identify fish larvae as part of their ecological or fisheries-related research programs. The larval stages of a number of taxa (at both generic and specific levels) are described for the first time in the included papers, and constitute important contributions by themselves. However, we convened this symposium with the goal of moving beyond simple description towards phylogenetic inference, and all the included papers meet this objective.

The ontogeny of fishes contains a wealth of information that is useful in a variety of ways beyond simple alpha-level taxonomy. This was emphasized in the landmark volume "Ontogeny and Systematics of Fishes" (Moser et al., 1984) which arose from the Ahlstrom Memorial Symposium held in La Jolla, and more recently at the Symposium on Phylogeny of Percomorpha held in Charleston (introduced by Johnson, 1993). Drawing on these contributions, we list below five broad areas where ontogenetic information can be used to augment taxonomic and systematic research.

(1) *The recognition of cryptic species, wherein differences among larvae may lead to the discovery of differences among species that were not evident in adults, or wherein identifications of larvae may precede or predict the discovery and formal recognition of adults.* The work of Moser and Ahlstrom (1974) on myctophids provides a good example of the former treatment. Olney and Markle (1979) provide an example of the latter case.

(2) *Assembly of a data set based on ontogeny that can be used as an independent test of hypothetical relationships based only on characters of adults.* Examples of this approach can be found in the Ahlstrom Symposium volume (Moser et al., 1984) where separate cladograms resulting from analysis of ontogenetic versus adult data are compared to judge the stability of existing classifications. Frequently, smaller sets of ontogenetic data or single observations on development of previously undescribed eggs or larvae become available that do not warrant full cladistic treatment by themselves, but which suggest re-examination of existing hypotheses. Ultimately, the combination of ontogenetic and adult data (see #3 below) is recommended to strengthen evolutionary hypotheses.

(3) *An additional suit of characters that can be used to extend sets of morphological data based only on adults, thereby producing more robust phylogenies.* This includes characters of eggs and embryos, larval specializations, developmental patterns, and ossification sequences. Many examples of the use of this so-called "total evidence approach" are given in the Ahlstrom volume (Moser et al., 1984). More recent examples are found in the Symposium on the Phylogeny of Percomorpha (Johnson and Anderson, 1993).

(4) *Tests of homology through the careful study of development, wherein an ontogenetic perspective can be used to identify homologous or homoplasous states in adult characters.* Johnson's (1992) work on gill arches and their implications for higher relationships of fishes demonstrated the power of this approach when applied to osteological characters. More recently, Baldwin and Johnson (1996) used the approach in their study of aulopiform fishes, and Mabee (1995) extended the approach to include other developmental (non-skeletal) features. A related use is the identification of heterochrony (Fink, 1988). In one approach, ontogenetic characters were mapped onto existing hypotheses of relationships to evaluate heterochrony as demonstrated by Winterbottom (1990) using juvenile development in gobies. In another approach, ontogenetic data were used to establish the phylogenetic relationships of the paedomorphic gobioid *Schindleria* (Johnson and Brothers, 1993).

(5) *Use of the ontogenetic criterion to polarize characters for phylogenetic analysis.* This is a controversial area, with some debate as to the validity of the approach (Kitching, 1992). There are only a few examples of the use of the so-called "direct" approach to polarity assignment pioneered by Nelson (1978) in phylogenetic studies of fishes (Leis, 1986).

The authors of the symposium contributions that follow in this volume have used a wide variety of approaches and methods in their efforts to meet our established theme. We regard this diversity of approaches as a healthy sign. Those familiar with the field will note that a number of the authors are presenting in this volume their first attempt in this field of research. The backgrounds of these authors are primarily in marine ecology, biological oceanography and fisheries research, but also included are important contributors to the taxonomic literature on larvae who have contented themselves with stopping at the descriptive level in the past. Several contributors are "old hands" in this field (but not as many as we had hoped), but most encouraging are the papers derived from recently-completed masters theses or doctoral dissertations, providing a sure sign that there will be more to come in the future. We were most disappointed that we could include no papers by established systematists who had not previously applied developmental information to their systematic problems: no "old dogs" decided to learn new tricks for the symposium. Perhaps this collection of papers will encourage them by the new insights into fish relationships that it offers.

None of the papers in these symposium proceedings used larval development as a means of discovering new taxa or solving problems in alpha taxonomy—the first area that we note above. Such contributions often result from fortuitous collections and are relatively rare. Most of the authors used ontogenetic information in the third way noted above—as additional characters to be combined with other adult features. The use of ontogenetic data in this total evidence approach is becoming more common among ichthyologists, although there is certainly room for improvement. This is not to say that use of developmental information will always be helpful, as Cavalluzzi (this volume) demonstrates.

The second most common use of ontogenetic data in this symposium was in the comparative sense of the second area—phylogenetic inference was derived from developmental data, and then compared to previous conclusions arising from examination of adults. This was most often done informally; that is, cladograms were not constructed but the author pointed out that the new ontogenetic data seemed to agree (or disagree) with the adult information. Use of ontogeny in this way could benefit by being more formalized, as done by Gago in his work on trichiurid fishes (this volume). As a result of his contribution to our symposium, Gago was named co-recipient of the Sally Richardson Award for the best paper at the Sydney meetings in an encouraging recognition of this approach.

None of the included papers attempted to use ontogenetic information in either the fourth or fifth ways—to investigate homology and heterochrony, or to assign polarity using the direct method. Unfortunately, there are only a few examples of the first approach in the ichthyological literature, and it is likely that use of Nelson's (1978) method has been discouraged by its controversial nature.

Where does this leave the field of ontogeny and systematics of fishes? Ten years ago, following the publication of the "Ahlstrom" volume, an increase in the use of developmental information in fish systematics was anticipated. Yet, this has not taken place. As noted by Johnson (1993: 22) in his introduction to the Symposium on Percomorph Phylogeny "Most comparative osteological and phylogenetic studies of fishes do not incorporate development . . . " By far the most common use of developmental information in fish phylogeny since the Ahlstrom Symposium has been with groups of fishes where highly specialized larval stages provide a wealth of "new" characters for analysis (Johnson, 1993). However, the numbers of such groups are limited, and investigators are "skimming the cream" of this opportunity, especially among marine fishes (e.g., acanthurids, Tyler et al., 1989; carapids, Markle and Olney, 1990; serranids, Baldwin and Johnson, 1993).

So, what is the future of the use of ontogeny in groups of fishes that have unspecialized larvae? Our colleagues G. D. Johnson and C. Baldwin (Division of Fishes, Smithsonian Institution) believe that the future of this field lies in the use of ontogeny to evaluate structural homology, yet this is an area where there has been little work. This type of research is laborious and requires specialized training, especially in the dissection and identification of minute nubbins of developing cartilage and bone that are usually overlooked by reasonable people. Furthermore, the process often requires extensive series of specimens arranged in closely-spaced age intervals along the developmental trajectory. As a result, the limitations of qualified investigators and available material may be factors that negatively influence progress in this field.

How could material be scarce considering the establishment of large larval fish collections at several museums in the USA and Australia, the existence of the extensive DANA collections, and the literally millions of larvae in the collections of universities, fishery laboratories, and oceanographic institutions around the globe? Our experience is that availability of suitable study material is a problem in many groups of fishes, especially those of shallow, tropical waters (<200 m, or over the continental shelves). In spite of the establishment of well curated and catalogued collections of larvae, the vast majority of material is in "mixed-station or mixed-taxa collections," making it effectively unavailable to all but the investigator able to visit the institution, and spend considerable time sorting through these mixed collections on site. This material must be made more accessible if the field is to flourish. Further collecting is also necessary in shallow and near-reef waters, and unconventional collecting methods (Brogan, 1994) must be applied to extend our knowledge of cryptic or previously unavailable taxa. Rearing in the laboratory is sometimes a viable means of obtaining good-quality developmental series, but it is time-consuming, often expensive, may result in developmental anomolies, and can hardly be expected to supply the bulk of material in most groups.

Much of the argument against the use of the ontogenetic criterion for direct assessment of polarity seems to boil down to the view that it may not work in all cases, and that if this approach is used, one may make mistakes in polarization of characters [e.g., see the re-evaluation of Leis' (1986) study of *Plectropomus* by Johnson (1988) or Mabee's (1993) analysis of character ontogeny in centrarchids]. However, few systematists would argue that the indirect methods of outgroup polarization are fault-proof. The theoretical considerations of both sides are well presented by Kitching (1992). What is required are empirical tests—character sets could be polarized in both ways, and the resulting information used to construct separate phylogenies that would then be tested for congruence. Areas of cladogram congruence pose no problem, indeed, they offer increased confidence in the resulting hypotheses of relationships. The question is what to do about the inevitable areas of non-congruence. We see no alternative to an initial return to the lab bench—to a detailed re-examination of the morphological and ontogenetic evidence—in an attempt to better understand the morphologies which form the basis of the conflicting cladograms. If this fails to resolve the issue, the assumptions of the two methods need to be carefully examined, and rejected if appropriate. In the end, a parsimony-based decision may be necessary: the method that makes the fewest assumptions should be used. Ultimately, it must be recognized that both the direct and indirect methods are applications of parsimony (Weston, 1988).

The symposium in Sydney was stimulating. We hope the papers presented there and contained herein will give a hint of the potential of developmental information to make substantial contributions to fish systematics, and will stimulate others to attempt to use it.

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