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Ichthyology and Indo-Pacific Fish Conferences from the 1980s to the 2010s

Taxonomy and systematics of larval Indo-Pacific fishes: a review of progress since 1981

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Abstract This paper reviews progress in research on taxonomy and systematics of larval marine and estuarine fishes in the Indo-Pacific since the first Indo-Pacific Fish Conference in 1981. In 1981, the literature on development of fish larvae in the vast Indo-Pacific region was sparse, scattered and of very uneven quality. During the intervening 33 years, taxonomy of adult Indo-Pacific fishes has improved greatly, the proceedings of the landmark Ahlstrom Symposium were published, a large number of larval-fish atlases, or identification guides, have been produced, and the quality of descriptions of larval-fish development in journals has greatly increased. This has resulted in a great improvement in our ability to identify Indo-Pacific fish larvae, particularly oceanic taxa. However, much remains to be done, with the large majority of families having <50 % of species with described larvae, and with only a small proportion of species descriptions based on full developmental series of larvae. DNA technology has helped to establish identities of larvae, but only a small proportion of the larvae so identified have been described, so the potential for DNA to advance larval taxonomy is largely untapped. An integrative approach combining genetics and morphology is required. Online publication of descriptions of larval development and of interactive identification guides to larvae is the most efficient way to make such information available and useful to a variety of users. The great potential for larval-fish ontogeny to contribute to the study of phylogeny of marine fishes has been underrealized. The ageing of current larval-fish taxonomists, and the lack of positions for younger replacement researchers, is a major obstacle to further progress.

Keywords Ontogeny · Development · Teleostei · Larva · Identification

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Introduction

The vast majority of marine teleost fishes—regardless of their adult habitat—have a pelagic larval phase that differs greatly in morphology from the adult. The larvae of epipelagic species share the same habitat with their adults. In contrast, larvae of meso- and bathypelagic species are typically found in the epipelagic zone, much closer to the surface than their adults, and undergo an ontogenetic descent as they grow and develop (e.g. Loeb 1979). In demersal species, only a handful of taxa are known to have larvae that are not epipelagic, so the adults and larvae of most species occupy very different habitats: the larvae are in open water and faced with the challenge of finding appropriate demersal settlement habitat at the end of their pelagic phase. Typically, large morphological changes are associated with the transition between pelagic and demersal phases, although in several major clades (e.g. Tetraodontiformes), there is an extended pelagic phase that differs little morphologically from the adult. Attempts to develop clear, widely used terminology to describe these morphological and ecological ontogenetic changes and transitions have failed, largely due to wide variability among taxa in mode of development or ecology (Kendall et al. 1984). For the purposes of this paper, I will include all of the post-hatching, but pre-settlement stages of demersal species (i.e. the pelagic phase, an ecological criterion). It is common to declare the larval stage of pelagic species to end at a somewhat arbitrarily chosen morphological milestone, for example, the attainment of full fin-ray counts, or the presence of scales. But, I would prefer to be a bit flexible with pelagic species, so some of the more spectacular larval morphologies can be included.

Larvae frequently bear little resemblance to the adults for two reasons: 1) the larvae are, at least initially, incompletely developed and lack structures found in adults (e.g. scales or fins), and 2) the larvae frequently have specializations to pelagic existence that result in some of the most spectacular marine creatures known (Fig 1.), but these specializations are lost as development proceeds. Due to the great morphological differences between the adult and larval stages of many taxa, during the 19th and much of the 20th centuries, the larvae of a number of Indo-Pacific fishes were described as distinct species, or even genera (e.g. holocentrids, acanthurids, malacanthids, many eels). The last example of this sort of confusion was the description of the serranid genus *Flagelloserranus* by Kotthaus (1970), but within a year, *Flagelloserranus* was identified by Fourmanoir (1971) as the pelagic larval form of the serranid genus *Liopropoma*. In some cases, these generic names have been retained to describe the morphology of the pelagic larval stage (e.g. leptocephalus, rhynchichthys, dikellorhynchus, tholichthys, acronurus, Fig. 2). The large morphological differences between larval and adult stages make identification of the larvae challenging, and the larvae of many species and higher taxa remain undescribed.

A particular challenge for those who want to identify larval fishes results from collection methods. Many studies rely on towed nets or other relatively unselective methods to capture fish larvae. This means that larvae of species that live in a very wide variety of habitats as adults are captured in the same sample—thus, the researcher who wants, for example, to study larvae of coral-reef fishes will encounter, and must also be able to identify at least to family, larvae from oceanic and coastal, pelagic habitats, from deep, offshore waters, from soft bottoms on the continental shelf

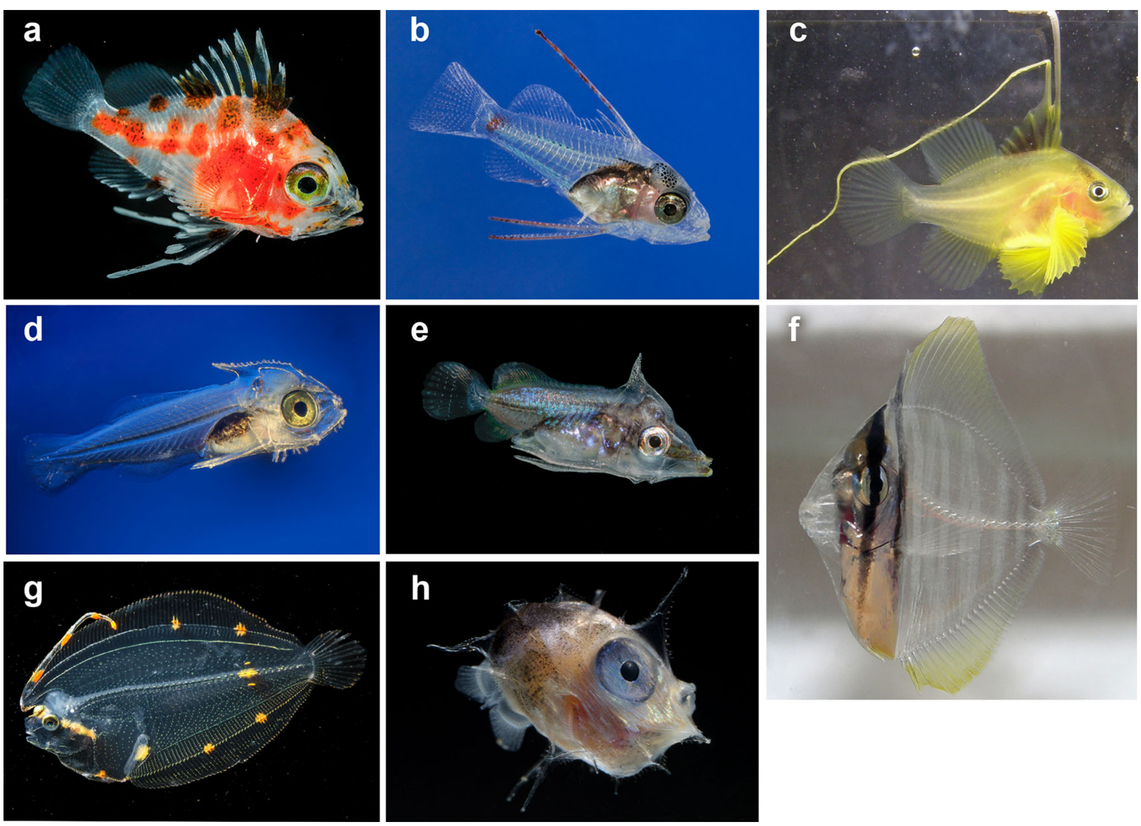

Fig. 1 Morphological diversity in larvae of Indo-Pacific fishes. Photos by Frank Baensch—http://www.bluereefphoto.org (unless noted otherwise, all are reared from pelagic eggs taken in Hawaiian waters), except **c** and **f** by Colin Wen (Great Barrier Reef, night light). Sizes are total length. **a** Serranidae, Anthiinae, *Odontanthias fucipinnis*, 20.3 mm; **b** Serranidae, Epinephelinae, *Cephalopholis argus,* ca 12 mm; **c** Serranidae, Epinephelinae, *Diploprion bifasciatum*, ca 22 mm; **d** Lethrinidae, *Monotaxis grandoculis*, 6.7 mm; **e** Chaetodontidae, *Forcipiger flavissimus*, 8.3 mm; **f** Acanthuridae, *Zebrasoma veliferum*, ca 26 mm; **g** Bothidae, *Asterorhombus* or *Engyprosopon,* 34.2 mm. Papua New Guinea, night light; **h** Molidae, *Ranzania laevis*, 5.1 mm

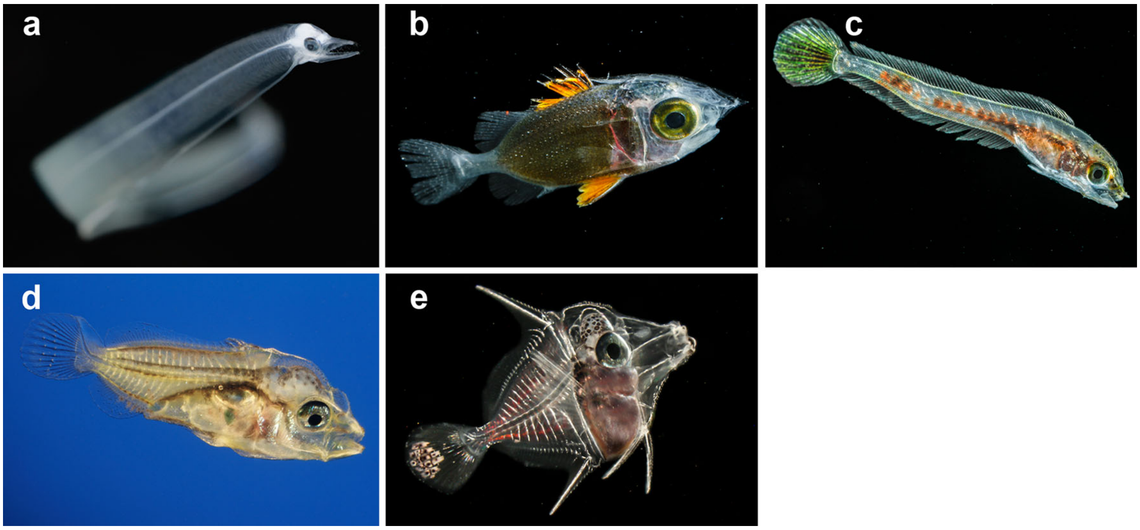

Fig. 2 Specialized larval stages originally described as new genera and the common names for their morphology derived from the generic name. Photos by Frank Baensch—http://www.bluereefphoto.org. All are reared from pelagic eggs taken in Hawaiian waters, except for **b**. Sizes are total length. **a** Anguilliformes, unidentified eel, leptocephalus stage, 15.0 mm; **b** Holocentridae, *Myripristis* sp, rhynchichthys stage, 13.4 mm, Papua New Guinea, night light; **c** Malacanthidae, *Malacanthus brevirostris*, dikellorhynchus stage, 18.3 mm; **d** Chaetodontidae, *Chaetodon* sp, tholichthys stage, 6.6 mm; **e** Acanthuridae, *Acanthurus* sp, acronurus stage, 6.9 mm

and, in many cases, from estuaries and even freshwater. As a result, the larval-fish researcher must be familiar with a much wider variety of fishes than the typical researcher who works on adult fishes. Among researchers who work on fishes—including taxonomists—the common perception is that larval-fish biology is a separate discipline, and there are relatively few researchers who have either the inclination or the ability to identify both adult and larval fishes. This perception has limited the development of larval-fish biology.

This paper is an assessment of progress through early 2014 in the taxonomy of larval fishes of the marine Indo-Pacific during the life of the Indo-Pacific Fish Conference (IPFC) series, starting in 1981. This 33 year period has been an active time for larval-fish taxonomy, not only in the Indo-Pacific, but also worldwide. During this period a need was identified and partially filled for larval-fish identification guides to document for a range of potential users, primarily fishery biologists, the hard-won ability to identify fish larvae of a generation of larval-fish biologists, primarily those working in fishery agencies and to a lesser extent at universities and museums. In addition, a number of enthusiastic workers not employed as larval-fish biologists have made major contributions to larval-fish taxonomy in their own time, either by publications in traditional journals, contributions to the identification guides mentioned above, or via the new-invented format of the world-wide web (www). During this same period, some workers have used the characters of larvae or information on homology gained from study of ontogeny of larvae to shed light on the relationships and evolution of a broad range of fish taxa. Unfortunately, the number of such researchers is small relative to the task and, in spite of the potential of this research approach, is not growing fast and may well be decreasing.

In 1981, the literature on Indo-Pacific larval-fish development and identification was scattered, uneven in quality, often in obscure journals or expedition reports, and frequently in languages that rendered much of the content inaccessible to many potential users. Larvae of many families had not been described in 1981 and few of the existing descriptions met desirable quality criteria. In 2014, we are fortunate to have hard-copy identification guides that cover a variety of Indo-Pacific regions, and from areas outside the Indo-Pacific that include Indo-Pacific taxa, and are therefore highly relevant to the Indo-Pacific researcher. Hundreds of descriptions have been published in conventional journals, and the overall quality of descriptions is much improved. Larvae in 83 % of Indo-Pacific fish families that possess a pelagic larval stage have now been described. Importantly, much of this information is freely available on the www, and we are beginning to see the development of interactive websites that assist the user to identify fish larvae.

For the purposes of this paper, the Indo-Pacific will be regarded as temperate and tropical marine and estuarine waters from the western shores of the Americas, to the eastern shores of Africa, north to the Bering Sea, but excluding the Southern Ocean. This area encompasses vast areas of oceanic habitat, coral reefs, rocky reefs and soft-bottom habitats ranging from estuaries to seagrass and *Halimeda* meadows to open sand and mud bottoms.

This paper will focus on post-hatching developmental stages, as a treatment of the identification of fish eggs is beyond my intended scope (and invitation!). Suffice to say that identification of fish eggs is more difficult than identification of larvae. Japanese authors have published the most descriptions of fish eggs, even if many of the eggs were not always fully identified at the time. Particularly prominent was S. Mito, who published, among many things from the 1950s to the 1980s, a landmark series of ten papers titled "Pelagic fish eggs from Japanese waters" that often contained coloured illustrations of eggs and early larvae, and much of whose work was summarized in Uchida et al. (1958) and Okiyama (1988). M. Okiyama's books (1988; 2014) contain a key to pelagic fish eggs (unfortunately, only in Japanese, Ikeda et al. 2014). In addition, a number of curators at Japanese public aquaria, including K. Suzuki and co-workers, published many papers containing illustrations of fish eggs. Also noteworthy are the fish-egg publications of Delsman (1972), Brownell (1979), Shao et al. (2001), Shadrin et al. (2003) and the heavily-illustrated website of Connell (2012) on western Indian Ocean fish eggs and larvae. Also, some larval-fish identification guides also included illustrations and description of fish eggs (e.g. Moser 1996, Richards 2006).

Taxonomy of larval Indo-Pacific fishes in 1981

Relatively few pre-1981 descriptions of Indo-Pacific larval fishes met what would be regarded as minimum standards today (Leis 1993), in many cases amounting to little more than illustrations with minimal text that was frequently vague or uninformative. Few publications mentioned how the identification was established, where the specimens used for the description were lodged, or how to distinguish the described larvae from others likely to be encountered in the study area. The quality of the descriptions and illustrations varied widely. The papers in and reference list of Moser et al. (1984) provide a good overview of the larval-fish taxonomic literature up to about the time of IPFC 1, at least those papers published in European languages: the pre-1981 work of authors mentioned in this section are, for the most part, included in the literature cited section of Moser et al. (1984). Several publications on the status of early-life history descriptions are also relevant to the pre-IPFC period, including Ahlstrom and Moser (1976), Ahlstrom and Moser (1981), Richards (1985) and Kendall and Matarese (1994).

The most prolific publishers of Indo-Pacific larval-fish descriptions prior to 1981 were Japanese and Indian authors. Unfortunately, many of these publications were in obscure journals that are yet to be made available on the www and are often difficult to access.

The Indian literature—primarily from before 1965—concentrated on estuarine and coastal species from soft-bottom and pelagic habitats. This body of work is highly variable in quality. Although some publications are of a high standard [e.g. the publications of S. Jones and collaborators such as Jones and Kumaran (1962; 1964)], others contain obvious misidentifications, highly imaginative or very poor illustrations and unhelpful text. Fortunately, an annotated bibliography of 1079 publications on breeding habits and development of Indian fishes is available (Jones and Bensam 1968), to assist with entry to this extensive and often ignored literature.

Japanese ichthyologists have a long tradition of research on larval marine fishes and were the first to produce a multi-author, multi-species identification guide to Indo-Pacific fish eggs and larvae—in this case, from Japanese waters (Uchida et al. 1958). This landmark volume by 9 co-authors contains descriptions of 92 species, many of which are based on complete development from the egg to juvenile stage. This sort of collaborative effort is now the norm, but our Japanese colleagues recognized long ago that, in mega-diverse areas such as the Indo-Pacific, a high degree of collaboration bringing together the expertise of as many researchers as possible is the only practical means to produce identification guides for fish eggs and larvae. At the time of the 1st IPFC, it is probably fair to say that the larvae of more Indo-Pacific fishes were described by Japanese workers than by any other nation. This was due to the efforts of not only fishery biologists employed primarily by government agencies, and university-based ichthyologists, but also by aquarists, who were often more interested in spawning behaviour than in larval development. Japanese aquaculturists were also leading contributors, although their descriptions of larvae were frequently very limited. The species covered by the aquaculture researchers included many of commercial importance, particularly scombrids, clupeiformes and to a lesser extent coastal perciform species. An important series of 13 papers titled "Manuals for the larval fish taxonomy" was published in Japanese in the journal Aquabiology between 1979 and 1986 by M. Okiyama and gives a good assessment of larval-fish taxonomy in Japan at about the time of IPFC 1. A bibliography on identification of fish eggs and larvae in Japanese waters (Mito et al. 1980) lists 777 publications, roughly 85 % of which are by Japanese authors, giving an indication of the extent of the pre-IPFC Japanese literature. Although much of this literature was summarized (in Japanese) in Okiyama (1988), it is clear that a lot of it remains inaccessible to researchers who do not read Japanese [for example, it appears that the bibliography in the landmark

"Ahlstrom volume" (Moser et al. 1984) underrepresents the contribution of Japanese early-life history authors, by citing only about a third of their publications (Leis 1985)].

Thai researchers have described numerous larvae, but most of their work appeared in grey literature reports or in-house publications of limited distribution, and sadly this body of work is relatively unknown outside Thailand. A group of illustrations of Indo-Pacific larval fishes by Thai author S-N Vatanachai (1974) are probably the best known larval taxonomy output from Thailand, primarily because they have appeared in intergovernmental publications and have been reproduced by a number of western authors (e.g. Thresher 1984). Unfortunately, the very nice illustrations by Vatanachai were identified only to family in these international publications and were not accompanied by written descriptions. Like the Indian publications, the Thai research concentrated on local, inshore waters and the larvae found there, but unlike the Indian publications, only a minority of the Thai publications are in English and many are in difficult to access grey literature agency reports. Fortunately, the recent identification atlas of Southeast Asia larval fishes had many Thai contributors (Konishi et al. 2012).

The former USSR had a large fleet of oceanographic research vessels and, consequently, a large research effort on pelagic ecosystems, including fish larvae. Major contributions were made by numerous authors, including T. N. Belyanina, S. A. Evseenko, N. N. Gorbunova, N. V. Parin and T. A. Pertseva-Ostroumova [see citations in Moser et al. (1984)]. Most of this research, which concerned primarily larvae of oceanic fishes, was published in Russian, but much of it was translated into English. Sadly, the breakup of the USSR resulted in a large decline in publication of early life history research on marine fishes.

European workers also contributed to pre-1981 taxonomy of Indo-Pacific fish larvae. Some reports on expeditions by European research vessels in the Indo-Pacific contained illustrations of fish larvae (e.g. Nellen 1973), and a series of taxonomic monographs (the Carlsberg Foundation's "Dana Reports") based on the cruises of the Danish RV *Dana* contained descriptions of larval stages, primarily of mesopelagic species with wide distributions. The Dana Reports were authored between 1937 and 1991 by workers from a range of nationalities. A Dutch researcher in the second fifth of the 20th century, H. C. Delsman, published a series of 24 papers describing fish larvae mostly based on reared eggs captured in the Java Sea [reprinted under one cover in Delsman (1972)]. These were of a very high standard for the period. In the 1970s, a series of five publications (Notes Ichthyologiques I-V) containing illustrations and short descriptions of both adult and larval fishes from the southwest Pacific were published by French ichthyologist P. Fourmanoir. These were followed by a long paper in a similar format on larvae and juveniles of 86 species of coastal fishes (Fourmanoir 1976). Larvae of many Indo-Pacific species were illustrated for the first time in these publications.

Workers in Australia had described the larvae of a few mostly temperate, coastal perciform fishes before 1981 [see review in Neira et al. (1998)]. In New Zealand, fisheries biologists D. A. Robertson and J. Crossland produced a series of papers on the eggs and larvae of New Zealand coastal fishes between 1973 and 1981 and New Zealand university worker, P. J. H. Castle, produced many publications describing the leptocephalus larvae of marine eels from various regions of the Indo-Pacific. Kingsford (1988) reviewed the early life history of coastal fishes in northern New Zealand, including some taxonomic work.

Hawaiian researchers, led by fishery workers in the 1950s and 60s, in particular W. M. Matsumoto, concentrated on larvae of scombrid and istiophorid species, and late-stage acanthuroid larvae of several species were described or illustrated in the 1960s by university researchers such as J. E. Randall and D. E. Strasburg. An identification/distribution atlas of Hawaiian fish larvae commonly taken in near-shore, surface, daytime plankton tows included partial developmental series of 46 oceanic and shorefishes (Miller et al. 1979).

The California Cooperative Oceanic Fisheries Investigation (CalCOFI) program off the west coast of Mexico and USA began in 1949, and during the 1970s the CalCOFI research team headed by E. H. Ahlstrom and H. G. Moser produced a series of major, high-quality descriptions of larval development in oceanic fishes that occur widely in the Indo-Pacific, in particular myctophids and stromateoid fishes, but also some shorefish families such as scorpaenids and pleuronectids [citations in Moser (1996)]. These publications were highly influential, and many other workers followed the formats established by Ahlstrom and Moser. These descriptions were incorporated into a larval-fish identification guide published in 1996 (Moser 1996). Ahlstrom and Moser also led the way in applying characteristics of marine fish larvae to questions of relationships (e.g. Moser and Ahlstrom 1970, 1973; Ahlstrom and Moser 1976), a research agenda that has also been very influential.

In the northern East Pacific, S. L. Richardson and co-workers and J. B. Marliave described a number of fish larvae in the 1970s and early 1980s. Most of this work was incorporated into a larval-fish identification guide published in 1989 (Matarese et al. 1989).

Although it is nominally about the early life-history stages of fishes from the mid-Atlantic Bight (east coast of the USA), the six-volume American atlas (Jones et al. 1978) was an early milestone and very useful in the Indo-Pacific, particularly at the family and genus levels.

After IPFC 1 (1981)

The 1980s saw the appearance of a number of larval-fish identification guides by American, Australian, Japanese and other researchers (Table 1) that greatly expanded the available information on identification of Indo-Pacific larval fishes. All had the goal of illustrating and describing full series of larvae and focused on providing illustrations and diagnoses rather than attempting full descriptions. The production of these identification guides has continued to the present.

The first Australian books (Leis and Rennis 1983; Leis and Trnski 1989) aimed at identification of tropical larval shorefishes to the family level, particularly those from coral reefs. In 2000, a combination of the two earlier publications, updated to include additional taxa, was published (Leis and Carson-Ewart 2000), and soon after a soft-cover edition appeared with a few errors corrected (Leis and Carson-Ewart 2004). In contrast, the other books (Table 1) were aimed at the species level and included larvae from oceanic fishes as well as shorefishes. A guide to larvae of Australian temperate fishes set a high standard (Neira et al. 1998). This publication described larvae of 124 species (115 are marine or estuarine), estimated to be 17 % of the temperate Australian fauna.

The first major post-1981 American larval-fish atlas of relevance to the Indo-Pacific (Fahay 1983) concerned the NW Atlantic, of which the oceanic taxa were most relevant to the Indo-Pacific. It appeared in a greatly expanded second edition (Fahay 2007), which is available on the www thanks to the North Atlantic Fishery Organization (http://www.nafo.int/publications/fahay/pdfs.html). The 1981 publication was the first of several high-quality larval-fish identification guides produced by fishery biologists from the US National Marine Fisheries Service. The order of appearance of the other three such guides was roughly in order of the diversity of the regional faunas that they covered. The northern East Pacific between 38° and 66°N was covered by Matarese et al. (1989) and included illustrations of many full developmental series: a very high proportion of them were original. The species most relevant to the warmer waters of the Indo-Pacific were from meso- and bathypelagic habitats as adults. Moser (1996) covered the CalCOFI area of the eastern Pacific from the California/Oregon border to Baja Calfornia in Mexico, and again it was the oceanic taxa that were most relevant to the rest of the Indo-Pacific, although also covered were a number of shorefish genera and even species that also occur in the Indo-West Pacific. Richards (2006) covered the region from the Mid-Atlantic Bight to Mexico. A high proportion of the shorefish families and genera included in Richards (2006) also occur in the Indo-Pacific, as do many of the oceanic species.

Chinese and Taiwanese authors produced a number of larval-fish identification guides in the 1980s and 1990s (Zhang et al. 1985; Anonymous-Editor 1985; Chiu 1999), but probably because they were in Chinese, they did not receive wide attention in other countries. Further, some of the earlier content was uneven in quality.

Larval-fish identification guides for South Asian waters helped make the earlier work by Indian and Thai workers more readily available. Some of the Thai larval-fish work was summarized by Chayakul (1990), and a more recent guide to larvae of fishery species of the SE Asian region by Thai and Japanese authors (Konishi et al. 2012) was a valuable contribution to this region. Importantly, both are in English, making their content widely available, although the earlier publication was a Fishery Department Technical Paper and thus of limited availability. A guide to the early stages of mangrove habitat fishes summarized in English some of the earlier Indian research (Jeyaseelan 1998) and was published by UNESCO, thus making it readily available to workers of the region. Finally, a well-illustrated publication by Russian authors on the eggs and newly hatched larvae of marine fishes of Vietnam presents its relatively limited text in both English and Russian (Shadrin et al. 2003).

During this period, Japanese authors continued their tradition of producing high-quality, multi-author larval-fish atlases. Ozawa (1986) is a collection of papers on larvae from oceanic waters of the Kuroshio region, including species that are oceanic as adults as well as some that are demersal, but have oceanic larvae. Significantly, this publication is in English and also includes distributional information, which distinguishes it from most of the other major Japanese larval-fish guides. The landmark publication on the early stages of fishes from Japanese waters edited by Okiyama (1988) including both marine and freshwater species has recently appeared in a greatly expanded second edition Okiyama (2014). Sadly, M. Okiyama passed away only a short time before the publication of this magnificent second edition, which includes separate keys to pelagic fish eggs (Ikeda et al. 2014) and to fish larvae (Kinoshita 2014). Such keys are rare in publications on larval-fish identification, probably because they are so difficult to construct due to the major morphological changes that the larvae undergo. The excellent introduction to the leptocephalus larvae of eels by Miller and Tsukamoto (2004) includes much information on the biology of eel larvae in addition to an identification guide, primarily to family and subfamily level. In contrast to most other larval-fish publications, which rely on drawings, it makes extensive use of good-quality colour digital photos of the leptocephalus larvae.

French researchers have produced three identification guides to the settlement-stage larvae of coral reef fishes

Table 1 Identification guides to larvae of Indo-Pacific marine and estuarine fishes published since IPFC 1 (1981). Text in English, unless noted otherwise

Publication	Taxa Described	Taxonomic Coverage	Region	Remarks
Leis and Rennis (1983)	10 orders, 49 families	Coral-reef fishes (not eels)	Indo-Pacific	Some illustrations poorly reproduced
Fahay (1983)	13 orders, 92 families	Marine fishes	NW Atlantic	
Zhang et al. (1985)	44 families	Marine fishes	Chinese waters	In Chinese
Anonymous-Editor (1985)	unstated	Marine and estuarine fishes	Taiwanese waters	6 papers in Chinese: many illustrations, including colour photos. Several misidentifications
Ozawa (1986)	9 orders, 15 families	Larvae found in oceanic waters	Western North Pacific	Primarily oceanic families
Houde et al. (1986)	12 orders, 53 families	Coastal fishes	Western Arabian Gulf	
Okiyama (1988)	26 orders, 216 families	Marine and freshwater fishes	Japanese waters	In Japanese; key to eggs included
Leis and Trnski (1989)	11 orders, 53 families	Shore fishes (not eels)	Indo-Pacific	Companion to Leis and Rennis (1983)
Matarese et al. (1989)	22 orders, 96 families	Marine fishes	Northern East Pacific	
Chayakul (1990)	13 orders, 33 families	Marine, coastal fishes	Gulf of Thailand	Primarily identification to family, but many to genus or species
Olivar and Fortuno (1991)	17 orders, 53 families	Marine fishes	Eastern South Atlantic	Benguela Current region
Moser (1996)	25 orders, 141 families	Marine fishes	Eastern North Pacific	CalCOFI region
Neira et al. (1998)	11 orders, 57 families	Marine and freshwater fishes	temperate Australian waters	
Jeyaseelan (1998)	9 orders, 38 families	Mangrove habitat fishes	South Asian waters	Many taxa described from juveniles only
Chiu (1999)	18 orders, 75 families	Marine fishes	Taiwanese waters	In Chinese
Leis and Carson-Ewart (2000)	17 orders, 124 families	Coastal fishes (not eels)	IndoPacific	All contents from Leis and Rennis (1983) and Leis and Trnski (1989), updated and expanded
Beltran-Leon and Herrera (2000)	21 orders, 89 families	Marine fishes	Pacific waters of Columbia	In Spanish
Shadrin et al. (2003)	11 orders, 31 families + Incertae sedis	Coastal fishes	Vietnamese waters	Eggs and newly hatched larvae. In Russian and English
Miller and Tsukamoto (2004)	3 orders, 20 families	Eels and other fishes with leptocephalus larvae	World	Many colour photos
Leis and Carson-Ewart (2004)	17 orders, 124 families	Coastal fishes (not eels)	Indo-Pacific	Soft cover edition of 2000 book with a few corrections
Richards (2006)	24 orders, 214 families	Marine fishes	Western Central Atlantic (FAO fishing area 31)	Some chapters published as NOAA Technical Memoranda from 1994
Maamaatuaiahutapu et al. (2006)	10 orders, 36 families	Settlement-stage coral reef fishes	French Polynesian waters	Colour photos of settlement-stage and metamorphic larvae. In French
Fahay (2007)	30 orders, 203 families	Marine fishes	Northwest Atlantic	Revision and expansion of Fahay (1983)
Juncker (2007)	7 orders, 25 families	Settlement-stage coral-reef fishes	Wallis and Futuna (western Pacific)	Colour photos of settlement-stage and metamorphic larvae. French and English text
Richards (2008)	17 orders, 103 families	Marine fishes	Kuwaiti waters, Arabian Gulf	Incorporated Houde et al. (1986)
Kendall (2011)	22 orders, 98 families	Marine fishes	World oceans	

Table 1 continued

Publication	Taxa Described	Taxonomic Coverage	Region	Remarks
Konishi et al. (2012)	18 orders, 92 families	Species from “marine capture fisheries”	Southeast Asian waters	
Collet et al. (2013)	8 orders, 28 families	Settlement-stage coral-reef fishes	La Reunion, Indian Ocean	Colour photos of settlement-stage larvae and settled juveniles. In French
Okiyama (2014)	30 orders, 277 families	Marine and freshwater fishes	Japanese waters	Expanded 2nd edition of Okiyama (1988). Includes separate keys to eggs and larvae. In Japanese

from locations in the Pacific and Indian Oceans (Maamaatuaiahutapu et al. 2006; Juncker 2007; Collet et al. 2013). These three publications are in a similar format and rely on colour photographs of live larvae and settled juveniles.

Two identification guides to the larvae of the “Gulf” (Persian Gulf to some, and Arabian Gulf to others) produced by teams led by American authors were published by the Kuwait Institute for Marine Science. The first (Houde et al. 1986) was based on a one-year survey of fish eggs and larvae in the western Gulf and included information on distribution of larvae in this shallow area. It described and illustrated many of the species, although many taxa were not identified beyond family level and a few were misidentified. However, the taxonomic work was original and groundbreaking for the Indian Ocean. In contrast, the second Kuwaiti publication (Richards 2008) is purely an identification guide, benefiting from over 20 years of progress in larval-fish taxonomy. All the illustrations were previously published, many in Houde et al. (1986), and some are from other regions as examples.

Two larval fish guides by Spanish-speaking researchers are also available. Larvae and eggs of the temperate, southeast Atlantic were addressed by Olivar and Fortuno (1991), a publication in English that is most useful in the Indo-Pacific region for pelagic species. A publication on the fish larvae off the Pacific coast of Columbia (Beltran-Leon and Herrera 2000) complements the CalCOFI Atlas of Moser 1996 by covering larvae found south of the CalCOFI area. The text is in Spanish and includes distributional information on the larvae.

Finally, the book edited by Kendall (2011) was derived from two larval-fish identification courses taught by the book’s contributors in the 21st century that were modelled on courses presented by E. H. Ahlstrom in the 1970s. This book attempts to summarize the essential characteristics of the larvae of a broad range of marine fishes and is probably better viewed as an entry into the science of identification of marine larval fishes than as an identification guide. It does, however, cover a large portion of families of fishes in the Indo-Pacific region.

These identification guides by design present what are essentially diagnoses to species rather than full descriptions of larval development. The illustrations do not always show, nor does the text always mention, what may be important characteristics from the point of view of systematics or phylogeny if these are not important for distinguishing species. This means that systematists need to be cautious when using these guides for character data. It also reinforces the need for the specimens used for descriptive purposes to be deposited in archival institutions where they will be available for study.

A large number of descriptions of larval development of Indo-Pacific species have been published in journals since 1981, and a major challenge is keeping track of and obtaining access to this body of literature. There have been too many such publications since 1981 to review them here, but some general statements about them are worthwhile. There is no journal dedicated to larval-fish biology or taxonomy. Although some journals have at times contained a high proportion of larval-fish taxonomic papers, this has usually been due to the interests of the editor of the day, and the emphasis largely disappeared when the editorship changed. A high proportion of the published descriptions of larval-fish development appear in journals of limited distribution that are not typically captured by the major indexing services or search engines, and a fair number of them are in languages other than English which makes their content hard for many researchers to access.

Descriptions of fish larvae development are contained in journals that focus on a variety of non-taxonomic subjects ranging from aquarium-based studies of spawning behaviour to studies on aquaculture methods (Table 2). Many of these publications contain little more than images of larvae (often photos that show few diagnostic features) and contain little, if any, meaningful descriptive text, because their purpose is not taxonomic. However, these non-taxonomic papers are often the only information available on the eggs

Table 2 Sources of larval-fish descriptions and their characteristics

Source: subject/venue	Illustrations	Descriptive text and tables	Diagnosis to distinguish from larvae of related taxa	Stated identification rationale	Specimens lodged in archival collection	Examples
Aquaculture/journal	Photos or drawings, variable in quality	Minimal	Seldom	Spawned in captivity from known adults	Seldom	Leu et al. (2009)
Spawning behaviour in aquarium/journal	Photos or drawings, variable in quality	Minimal	Seldom	Spawned in captivity from known adults	Seldom	Tanaka et al. (2007)
Taxonomic description/journal	Usually drawings & good	Extensive	Usually	Usually	Usually	Stevens et al. (1989)
Identification atlas	Usually drawings & good	Minimal to extensive	Usually	Varies	Varies	Table 1
Larval ecology/journal	Often absent	Minimal	Very seldom	Seldom	Seldom	McCormick et al. (2002)
Private photo website	Photos, usually good	Absent to minimal	Absent to minimal	Usually absent	Seldom	Baensch (2014)
Semi-professional identification website	Photos, usually good	Moderate	Varies	Varies	Seldom	Connell (2012), Victor (2014)
Professional taxonomic website	Drawings, or photographs usually good	Minimal to extensive	Yes	Usually	Usually	Matarese et al. (2012)

or larvae of the species involved. Therefore, although the standards of taxonomic descriptions of larval development of Indo-Pacific fishes have improved in the past 34 years, the amount of useful taxonomic information in the primary literature has not increased as much as a perusal of titles might suggest.

Most of the larval-fish taxonomic papers published in peer-reviewed journals describe larval development of one or a small number of species. All too often, the authors make little attempt to summarize or even fully cite the literature on the family involved, or to provide sufficient information for readers to distinguish larvae of the described species from related or similar taxa. Such diagnoses are important if descriptions of larval development are to be truly useful to researchers who want to identify larvae for ecological or fishery studies, for example. Journal publications describing larvae of multiple species of related genera or families by the Ahlstrom and Moser research group set the standard by providing not only sound descriptions of larval development in the dynamic style, but also information on how to distinguish the related larvae from each other and from similar larvae of more distantly related taxa. This includes papers on gonostomatids, myctophids, stromateoids, scorpaenids and pleuronectids in the 1970s and perciform fishes, including blenniids, kyphosids, sciaenids and serranids in the 1980s [see Moser (1996) for citations].

Books that address the life history of fishes may include taxonomic information and illustrations of the eggs or larvae. A good example is Able and Fahay (1998) for estuarine fishes on the Atlantic coast of the USA, whereas Whitfield (1998) covers South African estuarine fishes. Some Japanese books for a general audience provide good colour photos of late fish larvae or recently settled juveniles, and these can be very useful for ichthyologists. Examples are Masuda and Kobayashi (1994) and Senou and Yoshino (2002).

Ironically, in the Indo-Pacific, larvae of oceanic fishes, including meso- and bathypelagic species, are probably better known and described than are larvae of coastal fishes. This is primarily because these oceanic species typically have very widespread distributions, often including the Atlantic, thus making descriptions of larvae from other regions applicable to the Indo-Pacific. Shorefish species, in general, have much more restricted distributions, so taxonomic work on shorefish larvae from outside the Indo-Pacific is not as transferrable at the species level, although it may be at the generic level.

Fahay (2007) [based largely on Kendall and Matarese (1994)] estimates that in the Indo-Pacific, only 10 to 34 % of marine fish species have described larvae (Indo-Pacific regions mentioned by Fahay are: Japanese waters, 34 % of 3500 spp.; tropical Indo-Pacific, 10 % of 3921 spp.; temperate Australia, 18 % of 645 spp.; NE Pacific, 44 % of 592 spp.; Eastern Pacific, 73 % of 800 spp.). This compares with as many as 82 % of 131 spp. in UK waters of the NE Atlantic (but, perhaps oddly, only 37 % of 260 spp. in the North Sea).

Table 3 contains estimates for each family of Indo-Pacific fishes of the percentage of species with described

Table 3 Estimated percent of species with described larvae in 324 Indo-Pacific fish families expected to have pelagic larvae. Values are the author's subjective estimate based on various sources, in particular Kendall (2011) and the publications in Table 1. All descriptions of larvae are included, regardless of their completeness, but excluding descriptions based only on yolk-sac larvae. Family composition and order in the table follow Eschmeyer (2014), with a few exceptions, and include only described species. Note that the new edition of Okiyama (2014) was received too late to be incorporated into this table: so, some families will now have higher percentages than estimated here

Percent of species with described larvae	Indo-Pacific fish families expected to have pelagic larvae
≥ 90	Elopidae, Megalopidae, Anguillidae, Derichthyidae, Cyematidae, Eurypharyngidae Chanidae, Giganturidae, Bathysauroididae, Radiicephalidae Stylephoridae, Lophotidae, Scomberesocidae, Gibberichthyidae, Anoplogastridae, Barbourisiidae, Rondeletiidae, Hypoptychidae, Aulorhynchidae, Neoceratiidae, Aulostomidae, Fistulariidae, Anoplopomatidae, Hexagrammidae, Normanichthyidae, Rhamphocottidae, Percichthyidae, Lateolabracidae, Centrogenyidae, Dinolestidae, Lactariidae, Pomatomidae, Rachycentridae, Nematistiidae, Coryphaenidae, Menidae, Lobotidae, Leptobramidae, Dichistiidae, Ostracoberycidae, Enoplosidae, Cryptacanthodidae, Ptilichthyidae, Zaproridae, Pseudaphritidae, Trichodontidae, Icosteidae, Luvaridae, Zanclidae, Scombrolabracidae, Xiphiidae, Amarsipidae, Tetragonuridae, Psettodidae, Triodontidae ***n* = 55**
≥ 50 to < 90	Clupeidae, Gonorynchidae, Chirocentridae, Bathylagidae, Osmeridae, Scopelarchidae, Evermannellidae, Myctophidae, Neoscopelidae, Veliferidae, Lampridae, Regalecidae, Lophiidae, Monocentridae, Diretmidae, Berycidae, Stephanoberycidae, Grammicolepididae, Ceratiidae, Melanonidae, Phycidae, Sebastidae, Anoplopomatidae, Hemitripteridae, Agonidae, Moringuidae, Dinopercidae, Scombropidae, Echeneidae, Lutjanidae, Drepaneidae, Oplegnathidae, Pholidae, Anarhichadidae, Bovichtidae, Pholidichthyidae, Schindleriidae, Kurtidae, Scatophagidae, Scombridae, Istiophoridae, Nomeidae, Pleuronectidae, Molidae ***n* = 44**
> 10 to < 50	Albulidae, Chlopsidae, Nemichthidae, Serrivomeridae, Nettastomatidae, Saccopharyngidae, Engraulidae, Argentinidae, Microstomatidae, Opisthoproctidae, Alepocephalidae, Bathylaconidae, Salangidae, Diplophidae, Gonostomatidae, Sternoptychidae, Phosichthyidae, Ateleopodidae, Aulopidae, Synodontidae, Notosudidae, Ipnopidae, Alepisauridae, Paralepididae, Trachipteridae, Polymixiidae, Carapidae, Ophidiidae, Atherinidae, Isonidae, Atherinopsidae, Belonidae, Hemiramphidae, Exocoetidae, Melamphaidae, Trachichthyidae, Anomalopidae, Cetomimidae, Zeidae, Pegasidae, Caulophrynidae, Melanocetidae, Himantolophidae, Oneirodidae, Linophrynidae, Bregmacerotidae, Gadidae, Centriscidae, Solenostomidae, Syngnathidae, Setarchidae, Neosebastidae, Scorpaenidae, Caracanthidae, Apistidae, Tetrarogidae, Synanceiidae, Aploactinidae, Congiopodidae, Dactylopteridae, Triglidae, Hoplichthyidae, Platycephalidae, Cottidae, Psychrolutidae, Ereuniidae, Stichaeidae, Howellidae, Latidae, Acropomatidae, Polyprionidae, Serranidae, Symphysanodontidae, Callanthiidae, Plesiopidae, Terapontidae, Priacanthidae, Sillaginidae, Malacanthidae, Carangidae, Bramidae, Arripidae, Emmelichthyidae, Datnioididae, Hapalogenyidae, Gerreidae, Haemulidae, Sparidae, Lethrinidae, Pempheridae, Glaucosomatidae, Kyphosidae, Monodactylidae, Chaetodontidae, Pomacanthidae, Pentacerotidae, Cirrhitidae, Chironemidae, Aplodactylidae, Cheilodactylidae, Latridae, Cepolidae, Mugilidae, Pomacentridae, Labridae, Odacidae, Bathymasteridae, Chiasmodontidae, Champsodontidae, Ammodytidae, Trichonotidae, Creediidae, Leptoscopidae, Labrisomidae, Chaenopsidae, Draconettidae, Clinidae, Dactyloscopidae, Blenniidae, Rhyacichthyidae, Kraemeriidae, Ephippidae, Siganidae, Sphyraenidae, Gempylidae, Trichiuridae, Centrolophidae, Ariommatidae, Stromateidae, Caproidae, Citharidae, Paralichthyidae, Bothidae, Poecilopsettidae, Rhombosoleidae, Achiridae, Samaridae, Triacanthidae, Ostraciidae, Monacanthidae, Tetraodontidae, Diodontidae ***n* = 143**
≤ 10	Muraenidae, Synaphorancihdae, Muraenesocidae, Ophichthidae, Congridae, Monognathidae, Pristigasteridae, Platytroctidae, Stomiidae, Paraulopidae, Chlorophthalmidae, Bythitidae, Aphyonidae, Antennariidae, Chaunacidae, Ogcocephalidae, Gobiesocidae, Holocentridae, Oreosomatidae, Zenionidae, Thaumatichthyidae, Gigantactinidae, Macrouridae, Moridae, Peristediidae, Cyclopteridae, Liparidae, Zoarcidae, Ambassidae Pseudochromidae, Opistognathidae, Kuhliidae, Apogonidae, Epigonidae, Leiognathidae, Caristiidae, Nemipteridae, Sciaenidae, Polynemidae, Mullidae, Toxotidae, Scaridae, Uranoscopidae, Percophidae, Pinguipedidae, Tripterygiidae, Callionymidae, Odontobutidae, Eleotridae, Gobiidae, Microdesmidae, Xenisthmidae, Acanthuridae, Soleidae, Cynoglossidae, Triacanthodidae ***n* = 56**
Larvae unknown	Protanguillidae, Myrocongridae, Bathysauropsidae, Pseudotrichonotidae, Parabrotulidae, Tetrabrachiidae, Lophichthyidae, Dentatherinidae, Hispidoberycidae, Cyttidae, Parazenidae, Euclichthyidae, Pataecidae, Gnathanacanthidae, Eschmeyeridae, Bembridae, Banjosidae, Bathyclupeidae, Parascorpididae, Scytalinidae, Thalasseleotrididae, Paralichthodidae, Aracanidae ***n* = 23**
Larvae of family known, but no Indo- Pacific larvae identified to species	Halosauridae, Notacanthidae, Colocongridae ***n* = 3**

larvae. The families are not randomly distributed in terms of the percentage of larvae described. Seventeen percent ($n = 55$) of families have ≥90 % of larvae described—most of these families are small, with only a handful of species, the exceptions primarily being families of major commercial importance such as Anguillidae. The families for which ≥50 to ≤90 % of larvae are identified constitute 14 % ($n = 44$) of the total and are either oceanic fishes of wide distribution (e.g. Bathylagidae, Myctophidae), commercially important (e.g. Clupeidae, Sebastidae, Lutjanidae, Scombridae, Pleuronectidae) or small, with few described species. It is noteworthy that the only scombrid genus for which larvae are unknown is *Gasterochisma*, a highly distinctive monotypic taxon that is considered the basal scombrid by most authors. This is in spite of a long-standing effort by several larval-fish taxonomists to locate and identify the larvae of *Gasterochisma*. The majority (70 %, $n = 225$) of families have <50 % of described larvae, with a bias toward lower percentages. Many of these are large families, with a predominance of shorefish families, but also including many oceanic, pelagic and deep benthic families. Of these 226 families, 56 have <10 % of larvae described: 26 are perciform families, including some of the most speciose families of Indo-Pacific shorefishes (e.g. Gobiidae, Apogonidae) and many of commercial importance (e.g. Leiognathidae, Nemipteridae, Sciaenidae). Also, poorly known are several speciose families of eels, bythidids, soleids and cynoglossids. A total of 23 families (7 %) have unknown larvae and a further three (1 %) are known at the family level, but no Indo-Pacific species have described larvae. These last two categories include a range of relatively small families, mostly from deep water, but also including some shorefish families (e.g. Protanguillidae, Dentatherinidae, Pataecidae, Gnathanacanthidae and Aracanidae).

These numbers must be treated with caution and can, in fact, be misleading. For example, the paedomorphic Schindleriidae contains only three described species, two of which have described larvae, but a large number of undescribed, cryptic schindleriid species are known (Kon et al. 2007, 2011), none of which have known larvae. Further application of genetic tools will almost certainly result in the discovery of cryptic species in other families. In some families, the rate of description of new Indo-Pacific species since 1981 has far outpaced the description of larvae. In large part, this is a result of the immature taxonomy of the family involved: it is difficult to determine the identity of larvae when the adult taxonomy is uncertain. Families in which more than 20 new species were described in the past 10 years all would be likely to have a lower percentage of described larvae today than they did in 2004: these include Gobiidae, Bythitidae, Liparidae, Serranidae, Soleidae, Labridae, Zoarcidae, Apogonidae, Ophichthidae, Pinguipedidae, Pomacentridae, Cottidae and Tripterygiidae (see Eschmeyer 2014), with the addition of Stomiidae, Macrouridae, Pseudochromidae and Scorpaenidae, if the period 2000–09 is included (Eschmeyer et al. 2010). In addition, another 20 families had 10 or more new species described in the past 10 years. Clearly, the era of discovery of Indo-Pacific fishes is not over, and this just makes the job of larval-fish taxonomists all the more difficult. On the other hand, progress in the taxonomy of adult Indo-Pacific fishes since 1981 by a large number of workers makes it more likely that taxonomy of larval fishes can progress. The Indo-Pacific, especially the tropical areas, will always lag other regions in terms of percentage of larvae described due to the vast areas and the high species diversity involved compared to the north Atlantic and northeast Pacific.

On the other hand, larvae of some taxa are known, but descriptions have not yet been published (G. D. Johnson, personal communication, 2014). A few families of Indo-Pacific fishes will be considered next to highlight some of the issues involved.

One of the Indo-Pacific shorefish families with the most species described as larvae is the Pomacentridae, with >50 species (ca. 40 Indo-Pacific) described (about 15 % of the species worldwide are described; see Murphy et al. 2007). Many of the pomacentrid larvae were described in a series of 12 papers containing illustrations, including colour photos, by Y Tanaka and co-workers, published between 1998 and 2008 primarily in the Bulletin of the Institute for Oceanic Research and Development, Tokai University (see Murphy et al. 2007 for citations). Unfortunately, this Tokai University publication now has no website (A. Fukui, personal communication, 2014), which makes these publications very difficult to access, because it seems that this journal had a limited circulation in hard copy. This shows one of the real problems in taxonomy of Indo-Pacific fish larvae—access to important literature from small circulation journals. The fact that none of the illustrations or information from Tanaka's pomacentrid papers was included or even cited in the new edition of Okiyama (2014) means that these important contributions will remain largely hidden from future researchers.

The family Lutjanidae, which contains more than 80 Indo-Pacific species, has received much attention due to its importance to fisheries. Just over 50 % of Indo-Pacific lutjanid species have described larvae (Table 4), but fewer than half of the descriptions are based on series that include preflexion-, postflexion- and settlement-stage larvae. So, even in one of the more studied shorefish families, there is much to do. Among the 18 Indo-Pacific lutjanid genera, only *Lutjanus* contains more than 10 species, and only four additional lutjanid genera contain more than three species (Table 4). Among these five large genera, 32 % of

Table 4 Family Lutjanidae, showing the number of species in each Indo-Pacific genus, and the number that have described larvae (descriptions may not be based on a full series of larvae, but exclude those based only on yolk-sac larvae). Indo-West Pacific (*IWP*) and East Pacific (*EP*) treated separately. Only one lutjanid species occurs in both areas: *Aphareus furca*

Genus	IWP species	IWP larvae described	EP species	EP larvae described	Source*
Aphareus	2	1 (1)	1	(1)	2
Aprion	1	1	0	NA	2
Caesio	8	4 (1)	0	NA	1, 4
Dipterygonotus	1	1	0	NA	4
Etelis	3	2 (3)	0	NA	2
Gymnocaesio	1	1	0	NA	4
Hoplopagrus	0	NA	1	1	10
Lipocheilus	1	0	0	NA	NA
Lutjanus	40	13	9	4 (3)	5, 10
Macolor	2	2	0	NA	8
Paracaesio	8	(8)	0	NA	6
Parapristipomoides	1	(1)	0	NA	6
Pinjalo	2	2	0	NA	9
Pristipomoides	8	4 (1)	0	NA	2
Pterocaesio	10	3	0	NA	4
Randallichthys	1	1	0	NA	6
Symphorichthys	1	1	0	NA	3
Symphorus	1	1	0	NA	3
Total	91	37 (15)	11	5 (4)	

Numbers in brackets refer to tentative identifications to species or in the case of *Parapristipomoides* and *Aphareus* to genus

NA indicates not applicable

* Source codes: *1* Kojima (1988); *2* Leis and Lee (1994); *3* Leis and Bray (1995); *4* Yokoyama et al. (1994), Reader and Leis (1996); *5* Doi et al. (1994), Shimose and Tachihara (2005), Leu and Liou (2013), Leis (unpublished); *6* Leis et al. (1997a); *7* Leis (2005); *8* Leis (2007), Hay and Leis (2011); *9* Leis (2008); *10* Moser (1996)

included species have described larvae. Among the 13 genera with three or fewer species, 77.8 % of the species are described, strongly indicating that the larvae of the smaller genera are as characterized by specializations that allow them to be identified and diagnosed as are the adults.

An economically important shorefish family with a similar diversity to the Lutjanidae is the Sparidae, with about 100 species. About 45 % of worldwide sparid species recognized at the time of the 6th IPFC in 2001 had described larvae (Leis et al. 2002). However, it is likely that this percentage has decreased, as 13 new sparid species have been recognized in the past decade, particularly in the genus *Acanthopagrus* (e.g. Iwatsuki and Heemstra 2010; Iwatsuki 2013), whereas a similar effort has not been put into description of sparid larvae over the same period.

The mesopelagic family Myctophidae has received much attention by the Ahlstrom/Moser group (see Moser 1996) and more recently by M. P. Olivar [Olivar et al. (1999), and citations therein]. This has resulted in a relatively high proportion of species with described larvae, estimated to be 58 % (M. P. Olivar, personal communication, 2014), but within the speciose genus *Diaphus* the percentage of species with described larvae drops to 28 %. This points out clearly where more work is required. Another factor contributing to the high percentage of myctophid with described larvae is the wide distribution of many of the species.

In morphologically conservative families, especially those of little commercial importance, far fewer Indo-Pacific species have described larvae. This includes the Labridae and Scaridae, and Bythitidae [which, in spite of being viviparous, has pelagic larvae—note that some of the recent revisions of reef bythidid taxa (e.g. Schwarzhans et al. 2005) do contain illustrations of advanced pre-parturition embryos that would be helpful in taxonomic studies of the larvae]. However, even the commercially important Lethrinidae has only a few species with described larvae, even though some species are in culture, so the acquisition of identified larvae of some species should not be difficult. In families that have small and cryptic adults, such as Gobiidae and Tripterygiidae, even fewer species have described larvae, and this is compounded by a relative lack of morphological diversity among larvae of different species or genera and the high rate of newly described species mentioned above.

Online resources

A factor that could not have been foreseen in 1981 is the development of the Internet and its ability to convey up-to-date information everywhere at low cost. There are now a variety of online larval-fish resources ranging from out-of-print reference books, such as the Ahlstrom Symposium Proceedings [Moser et al. (1984) - http://www.biodiversitylibrary.org/item/23343#page/5/mode/1up] to an interactive "Ichthyoplankton Information System" for the NE Pacific (Matarese et al. 2012).

Many older larval-fish publications are now available online, usually free of charge, and can be found using simple search engines. In particular, much of the early Indian literature is available on the websites of the relevant Indian government agencies, and the Biodiversity Library has much relevant content.

A number of independent and aquarium researchers who specialize in rearing fish eggs and larvae have established personal or institutional websites where they provide illustrations of the eggs and larvae, frequently photos in colour of live larvae and often notes on occurrence in the field or on rearing techniques. These are seldom descriptions of larval development in the taxonomic sense, but the information on what the larvae look like is seldom, if ever, available elsewhere and is very valuable. Two such websites that specialize on larvae of Indo-Pacific fishes are Connell (2012) for the Indian Ocean coast of South Africa and Baensch (2014) for Hawaii. Rather than using conventional publishing venues, aquarium researchers frequently post photos of reared larvae on blogs such as the following illustrating larvae of *Heniochus diphreutes*: http://risingtideconservation.blogspot.com.au/2011/11/schooling-bannerfishso-close.html. Unfortunately, these websites may not be permanent and keeping track of them or even finding them can be a challenge.

A high-quality semi-professional website (http://www.coralreeffish.com/) is run by B. C. Victor (2014). It contains an under-construction photographic guide to larvae of coral reef fishes based on images of preserved settlement-stage larvae. It is currently restricted to Caribbean species, with the goal of expanding to the East Pacific and Indo-West Pacific.

As divers become more adventurous, *in situ* photos of rare fish larvae are appearing in various popular publications and on personal websites. Some examples are D'Avella (2014), who includes photos of larval flatfish and a deep-sea ophidid, and the FishPix site of the National Science Museum, Tokyo (http://fishpix.kahaku.go.jp/fishimage-e/), which includes photos of many larvae and also the pelagic juveniles of demersal fishes.

In a more conventional mode, taxonomic descriptions of fish larvae are now starting to appear first on institutional websites, rather than in journals. LarvalBase (www.larvalbase.org) contains illustrations and descriptions of fish larvae, but when accessed in April 2014, it had not been updated since September 2006, and the website was not functioning properly. The Australian Museum website contains illustrated descriptions of larval development of seven species from the families Aulopidae, Aploactinidae, Percichthyidae, Monodactylidae and Labridae, three of which have not appeared in conventional publications (http://australianmuseum.net.au/larval-Fishes). The Division of Fishes at the Smithsonian Institution National Museum of Natural History maintains a website (Smith 2014) containing high-quality photos of settlement-stage live larval fishes from Belize, some of which are congeners of Indo-Pacific species. The Ichthyoplankton Information System [IIS—Matarese et al. (2012), http://access.afsc.noaa.gov/ichthyo/index.php] contains descriptions of fish larvae from the NE Pacific not available elsewhere and, for all species included therein, comparative information to enable the user to distinguish larvae of these species from others in the region. The IIS is the premier online larval-fish identification site and is a development of Matarese et al. (1989). The IIS is updated regularly and contains both a character search (interactive identification key) and a taxon search function. A total of 21 orders, 73 families and 290 taxa are covered from waters from Northern California to the Bearing Sea. "For each taxon, a description of the eggs and larvae is provided along with pigment and/or morphological diagnostic characters for distinguishing them from similar-looking species. If available, data for the following ELH features are presented: Egg (diameter, number and size of oil globules, yolk, chorion, and pigment on yolk and embryo) and Larvae (hatch size, preanal length, flexion length, length at transformation, sequence of fin development, and larval pigment pattern)" (Matarese et al. 2012). Other than worldwide, free access, the clear advantages of such online resources are the ability to update regularly, almost in real time, and to use interactive software to aid the identification process. The future of larval-fish taxonomy lies in such online developments, and maintenance of peer review is critical to their credibility. This can be accommodated by establishing an editorial board that handles peer review, just as with conventional journals.

Ontogeny and systematics

Attempts have been made to use morphological characteristics of fish larvae and their ontogeny to assess relationships among teleost fishes. The publication of the monograph "Ontogeny and Systematics of Fishes" (Moser et al. 1984) with 87 papers by 76 authors covering all major bony fish groups (this volume was produced in honour of E. H. Ahlstrom, who passed away a short time before) was a milestone in this research field and continues to provide source material for researchers as well as providing many influential hypotheses of relationships. Many of the relationship trees in this volume were produced with a cladistic approach, although "varying degrees of sophistication are apparent" (Winterbottom 1986). A subsequent symposium on ontogeny and systematics of fishes resulted in a group of 13 publications mostly using a cladistic approach (Leis et al. 1997b), but covering only Anguilliformes, Argentinidae, Myctophidae, Beryciformes, Pleuronectiformes and 10 perciform families. Although sessions on this research theme are a regular feature of the IPFC series, only a small proportion of the oral presentations have been published. Sadly, only a small group of researchers continue to exploit the potential of fish ontogeny to assess relationships and determine homologies. Amongst them, G. D. Johnson, R. Britz and their co-workers are especially active. Today, attempts to assess relationships of fishes are dominated by the use of DNA technology, typically with little or no use of morphological characters or ontogeny (see Mooi and Gill 2010).

Two important studies published since IPFC 1 revealed that two kinds of highly specialized epipelagic larvae, originally described as belonging to distinct families, were, in fact, the larvae of fishes that live as adults at meso- or bathypelagic depths. *Rosaura* (new genus) *rotunda* (new species) was described in the new family Rosauridae in 1954 by D. W. Tucker (Tucker 1954). By the mid-1960s, E. H. Ahlstrom and F. H. Berry recognized that the rotund *Rosaura*, in fact, constituted the larval stage of the enigmatic, rather elongate mesopelagic family Giganturidae, in spite of the major morphological differences between the two. But, they did not publish their findings before Ahlstrom's death in 1979 ended their research project (Johnson and Bertelsen 1991). Not until 1991 did R. K. Johnson and E. Bertelsen publish the definitive morphological evidence documenting the remarkable ontogenetic changes that remodel the 'rosaura' larva into the highly specialized giganturid adult form. In 2009, G. D. Johnson and co-workers (Johnson et al. 2009) documented the "most extreme example of ontogenetic metamorphoses and sexual dimorphism in vertebrates" when they showed that fishes then assigned to three families with very different morphologies—Mirapinnidae, Megalomycteridae and Cetomimidae—were larvae, males and females, respectively, of one family. The Mirapinnidae, described as a new order in 1956 (Bertelsen and Marshall 1956), lacks scales and lateral lines, but has a large mouth with almost vertically oriented jaws and, in most individuals, a long ribbon-like streamer formed from the skin of the caudal fin. Amazingly, Mirapinnidae was shown to be the larval stage of a revised family Cetomimidae, with the Cetomimidae as originally conceived constituting adult females, and the former Megalomycteridae constituting adult males, neither of which bore any real resemblance to the larvae or each other. This conclusion was based on both detailed morphological work and genetic evidence, and shows the power of integrative systematics.

In addition to many of the chapters in the Ahlstrom symposium volume (Moser et al. 1984), studies that are of particular relevance to the Indo-Pacific that use ontogeny to assess relationships include: Leis (1986); Johnson (1988); Tyler et al. (1989); Baldwin and Johnson (1993); Leis et al. (2002); Leis (2005); Hilton and Johnson (2007); Hilton et al.(2010); Schnell et al. (2010); Britz and Johnson (2012); Konstantinidis and Johnson (2012a, b).

This 33-year IPFC period has seen many of the major contributors to the field of taxonomy and systematics of marine fish larvae cease publishing due either to passing or retirement. This includes E. H. Ahlstrom, A. W. Kendall Jr., S. Mito, H. G. Moser, M. Okiyama, and W. J. Richards. Many of these pioneers worked for fishery agencies, which supported taxonomic work on larval fishes because of the utility of larval-fish surveys in providing data essential to the goals of fishery conservation and management. With the production of the identification atlases listed in Table 1, the perception amongst many fishery scientists is that there is little need to support taxonomic research on larval fishes. With this source of support for larval-fish taxonomy decreased, and no corresponding move from universities or museums to fill the gap, it seems that we may have already seen the golden age of larval-fish taxonomy.

The past 30 years have seen major developments in genetic methods that have made it relatively easy and inexpensive to use both mitochondrial and nuclear DNA in taxonomy and systematics. The use of DNA to establish or confirm identities of fish larvae is now common, particularly in difficult groups, where morphological development is conservative, and there are few morphological differences among taxa (e.g. Leis et al. 2007; Soars and Leis 2010; Leis et al. 2011). Once this is done, it is frequently possible to identify the morphological characteristics in the larvae that enable identification [e.g. Baldwin et al. (2008); Victor et al. (2009); Marancik et al. (2010), studies on Atlantic cardinalfishes, snappers and groupers, respectively, and Rocha-Olivares et al. (2000) on Pacific rockfishes]. A number of papers have used DNA barcoding to identify a range of larvae more or less as a proof of concept (e.g. Zhang et al. 2004; Pegg et al. 2006; Hubert et al. 2010; Ko et al. 2013), but, unfortunately, have not taken the next step and provided descriptions or diagnoses of the larvae thus identified and, in some cases, have neglected to deposit their study specimens in an archival collection.

Hubert et al. (2014) provided digital photographs of the larvae they barcoded as part of their BOLD entries. This is a useful first step, but it is usually not possible to identify larvae based on such images, as they fail to show important diagnostic characters. It is now possible to obtain sufficient DNA for such analyses from a single eye of a larval specimen, so there is no reason to damage the larva beyond that, leaving the specimen for deposition in a collection. We are a long way from being able to mass analyze mixed samples of larval fishes (e.g. from plankton tows) and garner anything other than qualitative indications of the species present. Attempts to quantify the outputs in such studies have yet to overcome a fundamental problem: do the DNA amounts detected come from one large individual or many small individuals or even many eggs, or some combination of these? Today, it seems that the lure of DNA methodology (e.g. DNA barcoding) that promises quick, easy and cheap identification has led some to conclude that there is little need for more morphology-based taxonomic research on larval fishes. In this context, it is important to point out that DNA-based identifications are not infallible: among other issues, typically, some specimens cannot be sequenced, and incorrect or ambiguous identifications occur (e.g. Rocha-Olivares 1998; Hubert et al. 2014). Further, although barcoding-based methods are decreasing in cost, morphology-based visual pre-sorting prior to applying barcoding techniques is still more cost-effective for processing more than a small number of specimens, even if the goal is relatively uninformative bulk processing for presence/absence determinations (W. Watson, personal communication, 2014).

Clearly, genetic techniques can offer a lot to the task of initial identification of fish larvae, but an obstacle to their use is the relatively high error rate in the major sources of sequence data (GenBank and BOLD). Apparently, the problem is particularly acute with important commercial Indo-Pacific fishes such as epinepheline serranids (B. C. Victor, personal communication, 2014). In fact, Victor (in press) states that a major problem is “the proliferation of misidentifications on the barcode database (BOLD), sometimes making the database useless by inexperienced users who cannot apply their own ad hoc quality control or collect their own voucher specimens (note that GenBank is far worse, with no revisions or third-party comment after submissions)”. It is unclear if a very high error rate is the norm for most fish taxa, but it does indicate the need for caution when using these databases for identification of larval fishes.

Collection building

Taxonomic work on larval fishes requires good series of specimens, which usually means large numbers of specimens and specimens in good condition. Museums are the traditional source for specimens used in taxonomic studies. Unfortunately, relatively few museums maintain significant larval-fish collections, and although some marine

Table 5 Some major collections of larval fishes with important Indo-Pacific content. Specimens from the listed collections are available for study by bona fide researchers. A lot constitutes the specimens of a particular taxon from a single collection event, typically a net tow

Institution	Acronym	Lots	Specimens	Collection emphasis	Remarks
Australian Museum	AMS	45,842	ca 1,000,000	Tropical reef and Australian coastal	M. McGrouther, personal communication, 2014
Burke Museum of Natural History & Culture, University of Washington	UW	48,000	7,252,455	Northern Pacific	UW website (specimens = eggs + larvae), 2008
CSIRO National Fish Collection	CSIRO	8,955	58,162	Australia	A. Graham, personal communication, 2014
Museum of Comparative Zoology, Harvard	MCZ	28,000	141,000	Atlantic	MCZ website, 2008
Museum Victoria	NMV	4,000	> 60,000	Southeast Australia	D. Bray, personal communication, 2014
National Marine Fisheries Service, La Jolla	NMFSLJ	800,000	>> 1,000,000	CalCOFI region	W. Watson, personal communication, 2014
National Museum of Science and Nature, Tokyo	NSMT	ca 30,000	ca1,000,000	Western Pacific	K. Matsuura, personal communication, 2014
Natural History Museum of Los Angeles County	LACM	57,000	> 1,000,000	Southern California inshore	R. Feeney, personal communication, 2008
Scripps Institution of Oceanography	SIO	5,500		Eastern Pacific	H. J. Walker, personal communication, 2014
Zoological Museum, University of Copenhagen	ZMUC	200,000	> 1,000,000	Dana collections	J. Nielsen, personal communication, 2008

laboratories house large collections of fish larvae from ecological or fishery studies, these larvae are not often accessible for loan or study. Fortunately, some institutions do house collections of Indo-Pacific fish larvae that are accessible for study and the major ones are listed in Table 5.

The future

The future of larval-fish taxonomy lies in putting descriptions and identification guides on the www, where they can take full advantage of interactive software and the ability to update the content as new information becomes available. As noted above, conventional dichotomous keys for fish larvae are difficult to produce due to the large morphological changes associated with growth and development, but interactive software can largely circumvent this problem, to the benefit of authors and users. Efforts to produce regional larval-fish guides can benefit by the ability to make available chapters or species accounts as they are submitted by contributors, rather than waiting until the last section by the slowest author is complete before publication. Another factor in favour of online publication is that hard-copy larval fish identification guide books have become so expensive that many potential users are unable to afford them. For example, the list price for Okiyama (2014) is ¥42,000 and that of Leis and Carson-Ewart (2000) is €375, or about US$410 and US$520, respectively at the time of writing. Publishers perceive that there is a small market for such publications and this plus the large size of the books results in high prices. This is not an issue for online content.

Increasingly, genetic approaches will be used to confirm or establish identities of larvae, but for this to be of general benefit, such research must be combined with good taxonomic descriptions and deposition of the identified specimens in archival collections. Museums that maintain fish collections are encouraged to accept larval specimens, or, alternatively, networks of museums must work together and designate a subset of their number as specialist centres for larval-fish collections, as has been done in Australia, the USA and Japan. Once established, these specialist centres should encourage fishery agencies and universities to deposit their larval-fish collections in the centre and pay the relatively small costs involved to access the collections and their associated data. This will not only benefit taxonomic research, but also fishery and ecological research by providing the ability to delve into these collections in the future to obtain data on fish larvae and fish populations.

The usefulness of larval-fish data, not only for fishery-related work, but also for answering questions about long-term trends, including climate change, is demonstrated by the CalCOFI program. The CalCOFI program was initiated in 1949 to address fishery-related questions, but the founders of this program had the foresight to archive the larval-fish and zooplankton samples. As taxonomic advances were made, it was possible to return to the collections of fish larvae and identify them, and the data were then made available—initially in hard-copy atlases, but later via an online database (http://www.calcofi.org/). The CalCOFI database, of which the larval-fish data play a key part, has become so useful that it was identified as a national science treasure in 1997. This was only possible because the collections were archived and taxonomic research on them was supported.

With the decrease of the larval-fish taxonomic effort within US fishery agencies following the publication of the four regional larval-fish atlases (Fahay 1983; Matarese et al. 1989; Moser 1996; Richards 2006), and the failure of natural history museums to consider larval-fish taxonomy, or the use of ontogeny in studies of phylogeny, as priority areas for hiring or research, it appears that the past 33 years may well have been the apogee of larval-fish taxonomy. Indo-Pacific countries with high-diversity marine fish faunas may offer the best hope for future progress in larval-fish taxonomy, if they want to use larval-fish surveys to assess and manage their living marine resources. But at present, few of these countries have the resources to support either the basic taxonomy or the surveys themselves. Much of the larval-fish taxonomy research is currently being done by either retired researchers or enthusiastic volunteer researchers neither of whom are paid for their work (see the section on online resources), and this is clearly unsustainable. Like taxonomists in general, the cohort of larval-fish taxonomists are ageing rapidly, and there are few jobs for potential young replacements. Several things are required for any taxonomic research to progress: perceived need, collections, trained researchers and allocated resources. Today, the need for more research is perceived by larval-fish researchers, but by few others. Larval-fish collections are adequate, albeit smaller and less accessible than optimal. Trained, young researchers are available, but institutional commitment to provide them with the positions and resources to do the job is largely absent. Yet, there is much taxonomic work to do, and DNA-based approaches alone will not achieve what is required—only an integrative approach, combining genetic and morphological aspects will do the job.

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