# CHAPTER 1
# Development

## 1.1 Introduction

The developmental biology of tarpons is so unusual that it seems a fitting subject for the opening chapter. I had originally intended to present the ontogeny of Atlantic and Pacific tarpons side by side, with salient features and timing emphasized at least partly in tabular form, but inconsistencies in the literature made it impossible. Specimens in the various reports were often measured at different lengths and unknown ages. Although captive rearing eliminates the age problem, it introduces confounding factors that can compromise normal rates of growth and development. Then, too, descriptions ranged in quality from detailed to superficial. Taxonomists sometimes favored particular characters, relegating others to lesser status or ignoring them. In short, I could not get comparative descriptions to line up without generalizing, which would have diluted the entire effort. What I present is therefore detailed, but in narrative form, with the two species treated separately.

Nonetheless, the pattern of their ontogeny is similar. The descriptions presented follow staging systems devised in the 1960s and 1970s by Brazilian and US scientists for Atlantic tarpons. Those for the Pacific species are less detailed and cohesive. The objective is to offer a detailed summary of tarpon ontogeny book-ended by separate sections devoted to just the leptocephalus larva.

## 1.2 The tarpon leptocephalus

There was a time when nobody knew what young tarpons looked like, but some still claimed to have seen them. Among the many tall tales is this whopper recorded in a letter from Charles H. Townsend to Mr. Grant and reproduced by Beebe (1928: 230). Townsend was traveling to the Galápagos Islands to capture

*Tarpons: Biology, Ecology, Fisheries*, First Edition. Stephen Spotte.

giant tortoises, probably for the New York Zoological Society's Bronx Zoo, when he penned this:

> "*In conversation with Mr. S. A. Venable of the Zone Police Force [Panamá Canal Zone Police], an experienced [Atlantic] tarpon fisherman, I was informed that the fish is* viviparous. *He has repeatedly observed the females seeking shallow water, generally less than 4 feet deep, where a continuous stream of young fish was poured from her vent, the young being apparently little more than ¼-inch long. The young immediately seek refuge in groups, under the large scales of the mother, each scale standing outward at an angle of probably 30°. The young clustered in these scale shelters as thickly as they could. Mr. Venable's many observations lead him to believe that the young shelter under the scales ten days or more, when they are ¾-inch long. The mother soon rids herself of the young by shaking herself and by leaping.*"

Probably because the smallest tarpons he ever saw were juveniles, taxidermist and sportsman Victor Brown of Everglades City, Florida thought they hatch fully formed. In a letter to Kaplan (1937: 91), Brown wrote: "The newly spawned tarpons, 1 to 3 inches long, immediately commence to work their way entirely out of salt water into fresh water streams, into the multitude of small creeks and canals, some going as far inland as 25 miles from the Gulf [of Mexico]."

Contrary to these kinds of statements, baby tarpons do not emerge as miniature adults. They hatch from fertilized eggs as yolk-sac larvae before morphing into leptocephali, larval forms unique to relatively few species of fishes (Hulet and Robins 1989; Inoue *et al.* 2004; Wang *et al.* 2003). Greenwood *et al.* (1966) established the superorder Elopomorpha based on representatives of all its subgroups having leptocephalus larvae (Fig. 1.1). A *leptocephalus* is a bizarre shape-shifting creature, laterally compressed, transparent with a mucinous pouch, and described variously as ribbon-, band-, or leaf-shaped. Elopomorpha is a monophyletic group, the leptocephalus an elopomorph synapomorphy. Order Elopiformes (tarpons and ladyfishes) occupies the most basal place in elopomorph phylogeny, Albuliformes and a clade consisting of Anguilliformes and Saccopharyngiformes making up a sister group (Fig. 1.2). Smith (1989: 961–962) provided an abbreviated key to elopiform leptocephali occurring in the western North Atlantic.

What constitutes a "larval fish" has been standardized to some extent (e.g. Richards 2006). The traditional definition is the interval between hatching and absorption of the yolk sac, the post-larval stage extending from termination of the larval stage to appearance of juvenile characters. In Gopinath's (1946: 8) opinion, certain groups fail to conform with this progression. He listed specifically the bonefishes, ladyfishes, tarpons, left-eye flounders, and tonguefishes, "even though they are post-larvae according to the [accepted] definition", and termed them larvae instead, "since these [fishes] undergo a complete metamorphosis before the assumption of adolescent characters." In other words, by Gopinath's definition, a tarpon leptocephalus remains a larva to the moment it commences metamorphosis. Wade (1962: 548) considered the leptocephalus to the start of its metamorphosis as a post-larva, the larval period evidently restricted to the interval between hatching

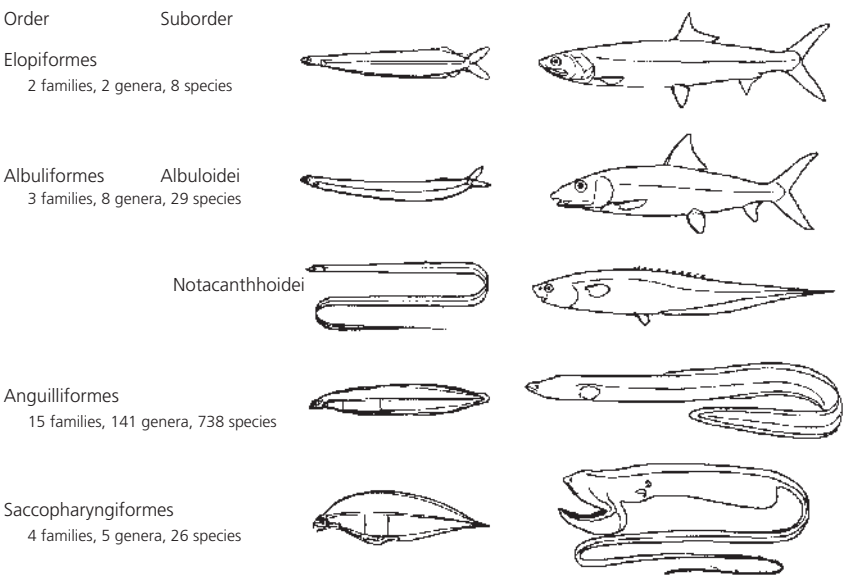


**Fig. 1.1** Higher-level classification of orders in the Elopomorpha along with numbers of taxa presently included. Representative larval and adult body forms are illustrated for each group. The Elopiformes, to which the two extant species of tarpons (*Megalops atlanticus* and *M. cyprinoides*) belong, is represented by a ladyfish, of which six species exist (*Elops* spp.). Source: Inoue *et al.* (2004: 275 Fig. 1).

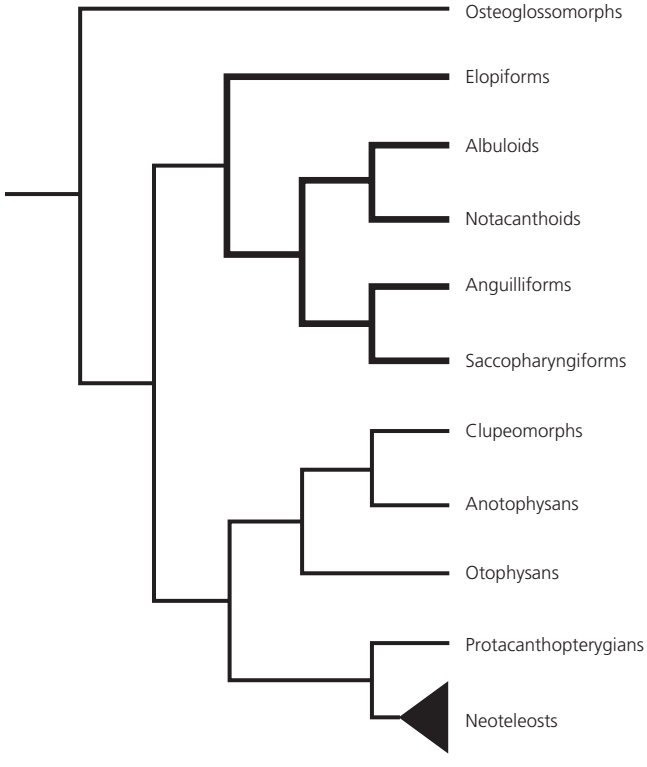


**Fig. 1.2** A modern phylogenetic hypothesis about the monophyly of Elopomorpha. See source publication for history and details. Source: Inoue *et al.* (2004: 276 Fig. 2B).

and appearance of the leptocephalus (Stage 1, see below); that is, synonymous with the yolk-sac larva. So did Alikunhi and Rao (1951), although their terminology is less clear.

A more modern treatment of how a larval fish is defined (presumably a tarpon or any other) partitions the concept into four post-hatch stages in which *flexion* refers to when the notochord becomes flexible. These are: (1) yolk-sac; (2) pre-flexion (complete yolk-sac absorption and beginning of notochord flexion); (3) flexion (start of notochord flexion to its completion); and (4) post-flexion (end of notochord flexion and start of metamorphosis).[1] The last initiates post-larval transformation, or the metamorphic stage (start of metamorphosis to completion of fin-ray development and beginning of squamation), after which juvenile traits appear and development proceeds seamlessly to the adult form with eventual attainment of sexual maturity.

## 1.3 Staging tarpon ontogeny

To my knowledge, eggs and yolk-sac larvae of either species of tarpon have not been described. Anyanwu *et al.* (2010) of the Nigerian Institute for Oceanography and Marine Research purportedly obtained fertilized eggs collected in the wild, then hatched and reared them to the fry stage in laboratory aquariums (Chapter 8.6). Surviving fry were transferred to earthen ponds and grown to juveniles. Specific information was not provided. The ultimate goal was to develop these procedures so that a reliable source of fry could be available consistently to fish farmers.

The few details in this report are tantalizing and apparently unpublished formally, but if backed by adequate data would indicate that knowledge of early tarpon biology has advanced more quickly in western Africa than in the Western Hemisphere. For example, Anyanwu *et al.* (2010: 6) wrote, "The fertilized eggs are available in the coastal waters of Ondo State [Nigeria] which can be collected and hatched in the laboratory." They implied that fertilized eggs are recognized, collected, and cultured routinely by fish farmers (Chapter 8.6). The fertilized ova hatched after 24 hours, and early larvae measured 5.3–6.8 mm TL (5.0–5.7 mm SL). Plate 4 (p. 8) in their report is described as a photograph of the anterior half of a yolk-sac larva. Hatchlings experienced heavy mortality after 5 days, which Anyanwu and colleagues suggested could have resulted from a lack of appropriate food. This is doubtful, considering that evidence of feeding has been found only after metamorphosis (Section 1.6, Chapter 7.7, Appendix B).

In discussing subsequent larval stages of Atlantic tarpons, I rely mainly on descriptions of Jones *et al.* (1978: 53–62), which evidently were compiled from

[1]http://access.afsc.noaa.gov/ichthyo/StageDefPage.php. Downloaded 10 February 2015.

other sources, notably Mercado Silgado and Ciardelli (1972) and Wade (1962). Also see Mercado Silgado (1969, 1971) and Moffett and Randall (1957).

The protocol for staging tarpon leptocephali is clear through Stage 2, but Stage 3 can be confusing. To Mercado Silgado (1971) and later Cyr (1991: iv, 6), development of Atlantic tarpons comprises two larval stages. Cyr called them phases instead of stages. His Phase 1 is the equivalent of Stage 1 of other authors; his Phase 2 commences at the start of shrinkage (beginning of Stage 2) and continues until positive growth is resumed, or the beginning of Stage 3. This too conforms with the staging protocol adopted by other investigators. Wade (1962: 548), for example, wrote, "The period of initial length increase to the size at which shrinking begins is considered as *Stage I*. In *Stage II* the body gradually looses [*sic*] the 'leptocephalus' form while it is shrinking in length." To Gehringer (1958) the Atlantic tarpon larva consists of Stage 1 exclusively. However, he called Stage 2 a "metamorphic larva." Such terminology is barely useful if both are thought to be larvae, but such inconsistencies are unavoidable. Obvious interruptions in the developmental sequence are seldom clear, and at times my own descriptions of staging might seem equally vague or confusing.

Cyr cited Hardy (1978) as the source of his staging protocol, but the reference should be Jones *et al.* (1978), in which Hardy is listed as third author. They described what at first reading could be three larval stages, but of the four specimens depicted as representing Stage 3 (Jones *et al.* 1978: 60 Figure 28), the top two illustrations (Figure 28A, B) are labeled larvae, the bottom two (Figure 28C, D) juveniles. This is intentional, not an error or misprint. Under the heading "Larvae" (their p. 53), they defined Stage 3 as "a second period of length increase *which terminates with the onset of the juvenile stage* [emphasis added]." Thus they considered early Stage 3 tarpons – both Atlantic and Pacific – to still be "larvae," but the point at which the transition into juveniles happens is less exact. Wade's Stage IIIA for Pacific tarpons correlates directly with the top two Atlantic tarpons depicted by Jones *et al.* (1978: 60 Figure 28A, B), based on Harrington's (1958) work; that is, the transitional state during which body proportions switch abruptly from allometric to isometric growth (for a discussion of these terms, see Chapter 2.2).

Wade did not examine Pacific tarpons of what he called Stage IIIA (i.e. > 25 mm SL), writing (Wade 1962: 549): "Fish larger than 40 mm [SL] are without a full complement of scales, gill rakers, branchiostegal rays and the dorsal whip [the extended last dorsal ray] until they attain a length of about 130 mm [SL], but are easily distinguished as young tarpon." He considered these fish to be juveniles, designating them as Stage IIIB. Nor did he examine any Stage IIIB specimens of Pacific tarpons. As to the Atlantic tarpon, Wade (1962: 574) noted "a gradual change from allometry to isometry at the end of the Stage IIIA period." Harrington's (1958) and Wade's findings lead me to conclude that both Atlantic and Pacific tarpons commence the juvenile stage at ≈45 mm SL, the length at which growth in most body proportions (as percentage or fraction of SL) switches from allometric to isometric.

To Mercado Silgado (1969: 4; Table 1 1971: 12 and Figs. 1–4), Stage 3 represented "fry," and he cited Harrington (1958, 1966), Rickards (1968), and Wade (1962) as sources in his 1971 publication. In the 1969 report (his pp. 4–5), Mercado Silgado listed five stages, calling Stage 3 *Crecimiento Alevínivo* (i.e. Growth of Fry).[2] He termed Stage 4 *Crecimiento Juvenil* (Juvenile Growth). His Stage 5 described the adult. With few exceptions (e.g. Anyanwu and Kusemiju 2008), those writing in English have seldom applied the term "fry" to young tarpons, but its adoption might prove a useful descriptor for the stage immediately preceding the juvenile in both species if defined like this: *Tarpon fry have resumed growth at the start of Stage 3 (≈ 13.0 mm SL) and continue increasing in size until proportional morphometric growth shifts from allometric to isometric at ≈ 45.0 mm SL. A juvenile tarpon of either species is a Stage 4 fish ranging from ≈ 45.0 mm SL to onset of sexual maturity, throughout which proportional morphometric growth ceases to be allometric and becomes isometric.*

Harrington (1958: 3) investigated this division in the life history of Atlantic tarpons in detail using a large series of specimens generally classified as larvae and juveniles, noting that "The differential … growth of body parts and regions clearly reveals a transitional period …." He compared morphometric measurements of his fish with an earlier series of young Atlantic tarpons examined by Breder (1944) and found extreme allometry of body proportions in specimens of 16–19 mm SL that continued to ≈ 35–40 mm SL, "when it gradually resolves itself into what is essentially *incrementum in universum*." He continued: "The precise point at which allometry yields to isometry is not obvious, and if the latter is not complete, it is no less so than in Breder's 164 specimens, which ranged from 50 mm to 2030 mm in standard length, and in which growth was deemed only slightly heterogonic [i.e. allometric] …."

The combined series covered a large range (Harrington's from 16.0–109 mm SL). Breder had taken 18 morphometric measurements (e.g. dorsal fin origin, pelvic fin length, head length, and so forth) and presented the values as a percentage of standard length. Harrington measured the same characters. Breder's data showed negative allometry in all proportions except the last dorsal fin ray, which was conspicuously positive. Harrington's were negatively allometric only in distances from snout to origins of the dorsal and anal fins up to 35–40 mm SL.

[2] *Alevín* is sometimes translated from Spanish as the "fry" of a fish, but the term is often not specific and can simply mean "young fish." Mercado Silgado (1969: 4 and Table 1) used *alevínivo*; the term applied by Mercado Silgado and Ciardelli (1972: 157 Table 1) was *alevínico*. However, *alevin* in English ordinarily refers to yolk-sac larvae of salmonids (e.g. Hasler *et al.*, 1978, Helfman *et al.*1997: 136, Moyle and Cech, 1982: 244, Varsamos *et al.* 2005). To Bond (1979: 421), *alevin* was more general: "If yolk-bearing larvae transform directly into a juvenile [*sic*], as is the case in many salmonids and certain sculpins, these larvae are called alevins." Still other writers (e.g. Alderdice, 1988: 175) simply referred to *alevin* without a definition, evidently assuming the reader knows what it means. Tarpon larvae are excluded in any case because of their intermediate leptocephalus stages.

He wrote (Harrington 1958: 4): "Thus in the earliest growth the majority of the obvious body proportions show extreme positive allometry with reference to standard length, all these proportions then becoming isometric at about 35–40 mm. standard length, and thereafter all but one of them showing slight but unmistakable negative allometry." A Stage 3 fish and one approaching Stage 4 are shown in Fig. 1.3. How these changes became incorporated into growth is illustrated here diagrammatically (Fig. 1.4). The larger fish shown was 36.8 mm SL, and a photograph of it can be seen in the bottom figure of Harrington's Plate II. A single row of scales had formed recently, and a second row was just becoming apparent.

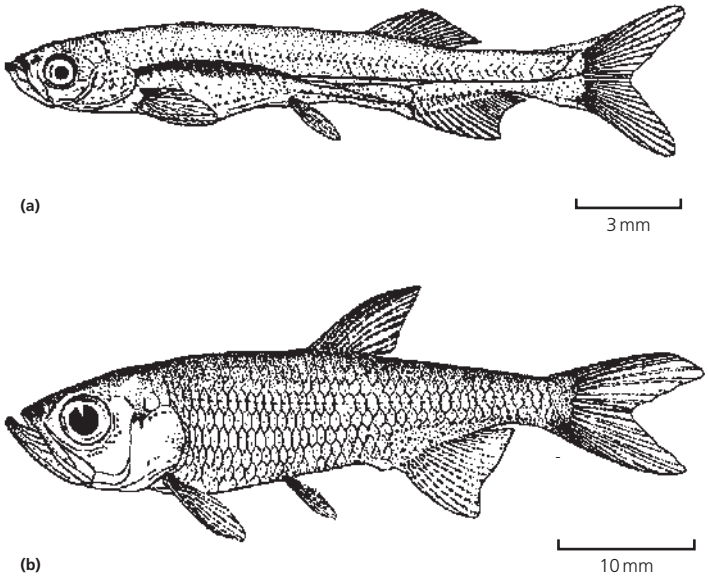


**Fig. 1.3** **(a)** Atlantic tarpon fry, Stage 3 phase X (16.9 mm SL). **(b)** Atlantic tarpon in late Stage 3 (41.0 mm SL) approaching the end of allometric growth. Source: Mercado Silgado and Ciardelli (1972: 181, Fig. 10A, B).

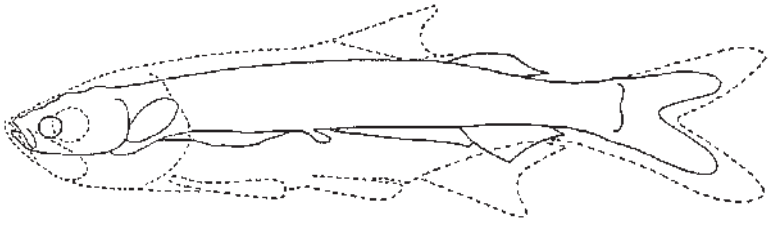

**Fig. 1.4** Profiles of an Atlantic tarpon 36.8 mm SL (broken lines) and an earlier specimen of 16.0 mm SL (solid lines), the second superimposed onto the first and enlarged proportionately so that standard lengths of the two illustrations coincide. Source: Harrington (1958: 5 Fig. 2). 

In discussing Stage 4, Mercado Silgado (1969: 4) wrote: "*Se observa en este Estado, el nuevo crecimiento y la verdadera morfología de un sábalo adulto. Es aquí donde se empieza a notar las escamas y la prolongación del último radio de la aleta dorsal, llegándose a observar la aparición de este radio claramente cuando el animal alcanza una longitude aproximada de 71 mm de longitud standard en el laboratorio.*" [This stage reveals the true morphology of an adult tarpon. It is here where you start to notice the scales and begin to clearly see the extension of the last ray of the dorsal fin, this ray becoming clearly evident when the animal reaches ≈71 mm SL in the laboratory.]

His description of Stage 4: "*Este Estado abarca los juveniles de sábalos en el momento en que aparece la prolongación del último radio de la aleta dorsal hasta una longitud aproximada a los 1000 mm de longitud standard que es cuando el sábalo pasa a ser adulto por llevarse acabo a esta longitud aproximadamente su primer desove.*" [This stage encompasses juvenile tarpons from the moment when prolongation of the last dorsal fin ray is apparent to ≈1000 mm SL; that is, when the tarpon becomes an adult, approximately the length at its first spawning.]

The last ray of the dorsal fin is diagnostic of adult tarpons of both species (e.g. Fig. 1.5). Mercado Silgado's Stages 3 and 4 are identified mainly by development of the last dorsal fin ray, and a fish in Stage 3, although still a juvenile, begins to resemble the adult. Keep in mind that for Stage 3 this conclusion is correct by his definition because Stage 3 is extended to 71 mm SL and based essentially on a single character (appearance and elongation of the last ray of the dorsal fin). These observations scarcely compare with Harrington's important finding that a tarpon longer than ≈45 mm SL ceases to grow allometrically. Consequently I would define Stage 3 as encompassing 13.0–45.0 mm SL instead of the range 13.0–71.0 mm SL recommended by Mercado Silgado and Ciardelli (1972), as reflected here in Table 1.1. An Atlantic tarpon between ~45 and ~1000 mm SL therefore can be considered a juvenile, unless evidence can be found that specimens within any part of this range are sexually mature. Length at maturity is much less for Pacific tarpons, perhaps as short as 300 mm FL (Chapter 3.6).

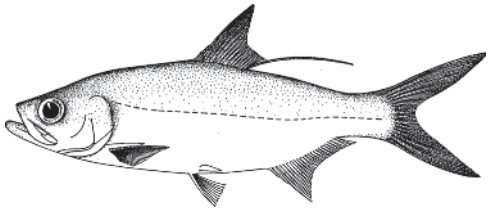

**Fig. 1.5** Illustration of an adult Pacific tarpon showing the elongated last ray of the dorsal fin. Source: Food and Agriculture Organization of the United Nations. 1984. Bianchi (1984: 3). *Field Guide: Commercial Marine and Brackish Water Species of Pakistan* by G. Bianchi. FAO Species Identification Sheets for Fishery Purposes, Project UNDP/FAO Pak/77/033. Rome, Italy. Reproduced with permission.

**Table 1.1** Growth stages and phases partitioned by length of Atlantic tarpon leptocephali (Stages 1 and 2) and fry (Stage 3). Stage 3 has been modified to 13.0–45.0 mm SL based on Harrington's (1958) finding that allometric growth ceases at ≈45 mm SL. See text for an explanation of phases. Source: Mercado Silgado and Ciardelli (1972: 157 Table 1).

| Stage | Phase | Length (mm SL) |
|---|---|---|
| Stage 1 | I and II | 1.7–11.0 |
| | III | 11.0–17.5 |
| | IV | 17.5–24.0 |
| | V | 24.0–28.0 |
| Stage 2 | VI | 28.0–25.0 |
| | VII | 25.0–20.0 |
| | VIII | 20.0–15.0 |
| | IX | 15.0–13.0 |
| Stage 3 | X | 13.0–71.0 [13.0–45.0] |

Mercado Silgado (1971) and Mercado Silgado and Ciardelli (1972) further partitioned the first three developmental stages into 10 phases identified by Roman numerals (Table 1.1): Stage 1 (phases I–V), Stage 2 (phases VI–IX), and Stage 3 (phase X). The second report, published in Spanish, is careful, detailed, and unavailable in English. I translated their descriptions of Atlantic tarpon developmental stages (see Appendix B). Their effort adds depth to the original staging systems of others.

Mercado Silgado (1971) did not mention a tenth phase or describe fry development. However, Mercado Silgado (1969: unnumbered page Table 1) listed Stage 4 (juvenile) as consisting of phase XI and the adult (Stage 5) as encompassing phase XII. These last two were eliminated by Mercado Silgado and Ciardelli (1972) in their final staging system.

Changes in morphology in the following sections are described as occurring at approximate body lengths. I emphasize that length alone is an unreliable predictor of the age of a leptocephalus and therefore not representative of its true ontogenetic status. Growth varies by individual, and so does the timing of metamorphosis. Increments formed on the *otoliths*, or "ear stones," are sometimes used to estimate the age of fishes (e.g. Chapters 2.6, 7.2). These are hard structures in the vestibular labyrinth consisting mainly of calcium carbonate and lesser concentrations of other elements embedded in a matrix of minor organic components.

Shenker *et al.* (2002), for example, examined otoliths of 41 Atlantic tarpon leptocephali caught at Sebastian Inlet, Florida as they entered Indian River Lagoon from the Atlantic Ocean during summer 1995, finding no correlation between length (15.5–22.1 mm SL) and age (15–26 days, $\bar{x}$ = 20.2 days). The oldest larvae (24–26 days) included both the shortest specimen and some of the longest (>20 mm SL). Thus the time when metamorphosis commences seems not to follow a particular pattern.

Findings of Tzeng *et al.* (1998: 182) for Pacific tarpon leptocephali were similar. Based on otolith counts, leptocephali entering Gongshytyan Brook estuary, northern Taiwan between 15 and 24 September 1995 were 20–39 days old ($\bar{x}$ = 28.5 days) and had already begun metamorphosis, meaning that some were twice as old as others. The authors noted that length on arrival was independent of age and that age related inversely to growth rate, implying differential rates of growth offshore through Stage 1 to onset of metamorphosis. The conclusion: "Slower-growing fish apparently metamorphosed later, and faster-growing fish arrived in the estuary earlier, than did [*sic*] slower-growing ones." If subsequent growth at inshore "nurseries" indeed offers survival advantages (Chapter 4.6), early penetration of lagoons and estuaries would appear to enhance fitness.

As touched on above, larval tarpons of both species undergo sequential growth stages (also called stanzas) during which organs and structures develop as metamorphosis proceeds. When experiencing metamorphosis, an organism advances to the next developmental stage through changes in shape and size. As mentioned, an Atlantic tarpon's early development encompasses three such stages encompassing radical changes. Because these occur along a continuum rather than abruptly, metamorphosis is like a time-lapse film as the animal shape-shifts, its appearance blending smoothly through one stage and into the next as certain features arise and others fade from view. Partitioning metamorphosis into stages is inevitably artificial and misleading. The depiction of leptocephali caught in a plankton tow (Fig. 1.6) or by some other means are snapshots in time, single frames extracted from a running film.

Hildebrand (1934) caught what he believed was a larval Atlantic tarpon – a leptocephalus – in transition to becoming a juvenile. The specimen, obtained at the mouth of Core Creek, Beaufort, North Carolina might have been the first found in the Western Hemisphere, but it was inadvertently destroyed before a drawing could be made. Only Hildebrand's cursory description remains.

## 1.4 Development of Atlantic tarpons

Some areas of the body where morphometric measurements of young Atlantic tarpons have been described are illustrated diagrammatically in Fig. 1.7.

### Stage 1 – Growing leptocephalus

Stage 1 is a period of growth taking place offshore and characterized by transparency, a ribbon-like body, and large fang-shaped teeth. It encompasses specimens of 1.7–28.0 mm SL (Table 1.1). Cyr's (1991: 11) Stage 1 specimens (Phase 1 in his terminology), which included data from two Gulf of Mexico cruises, were 6.3–23.8 mm SL and 5.2–30 days old. Wade (1962: 555) reported fish of 11.0 and 11.7 mm SL. Spawning and early development into Stage 1 take place entirely offshore in full-strength saline waters (e.g. Cyr 1991: 17; Jones *et al.* 1978: 53; Smith 1980) and culminates in a completely formed leptocephalus.

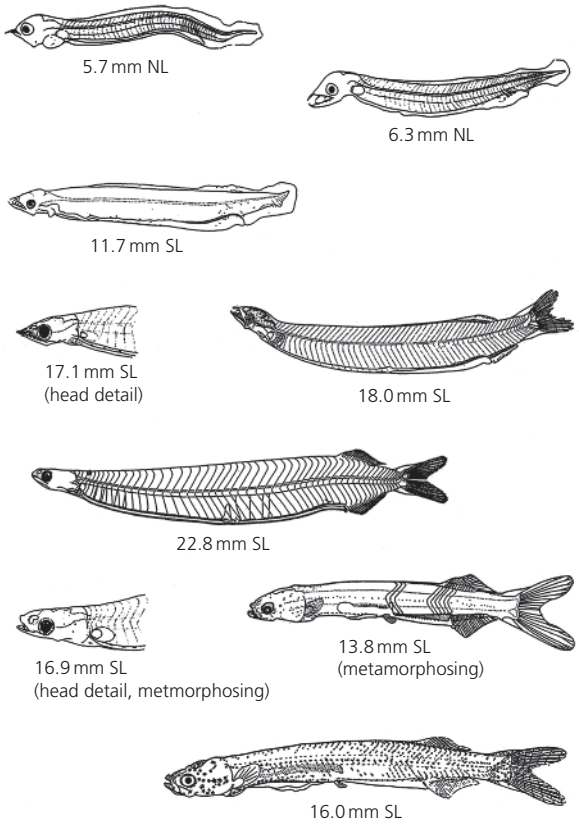


**Fig. 1.6** Stages 1 and 2 Atlantic tarpon larvae. Source: Fahay (2007: 13). © Northwest Atlantic Fisheries Organization. Reproduced with permission.

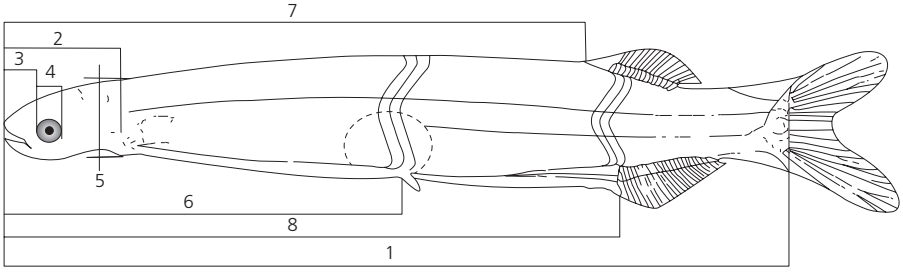


**Fig. 1.7** Atlantic or Pacific tarpon larva, depicting where some (but not all) measurements are typically taken. Numbers indicate the following measurements (mm) or counts (9–15 not illustrated): 1 – *standard length* (SL); 2 – *head length* (HL) tip of snout to posterior fleshy margin of operculum; 3 – *snout length*, tip of snout to anterior edge of bony orbit; 4 – *eye diameter*, anterior inner edge of bony orbit to posterior inner edge of orbit; 5 – *depth*, angle of base of pelvic fin vertically to dorsal outline of body; 6 – *prepelvic length*, tip of snout to origin of pelvic fin; 7 – *predorsal length*, tip of snout to origin of dorsal fin (or dorsal fin fold); 8 – *preanal length*, tip of snout to origin of anal fin (or posterior edge of anus); 9 – *fin-ray counts*; 10 – *total myomere counts*, from anterior-most to last myomere in caudal area, these last becoming indistinct when hypural plate forms; 11 – *prepelvic myomere counts*, from anterior-most myomere to myomere the ventral extremity of which approximates origin of pelvic fin; 12 – *predorsal and preanal myomere counts*, same as 11 above; 13 – *lateral line scales*, counted from opercular flap to posterior scale of caudal fin; 14 – *teeth*, number on each side of upper and lower jaws; 15 – *gill rakers*, number (including rudiments) on upper and lower limbs of first gill arch on one side. Source: Wade (1962: 551 Fig. 1, 552, 615–616 Table 3, 619–622 Table 5).

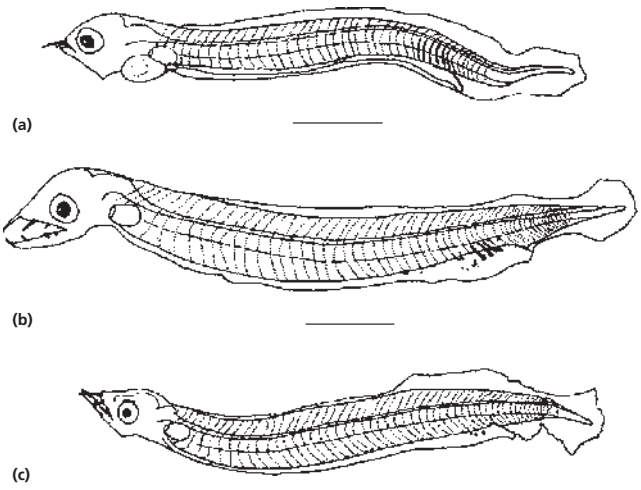


**Fig. 1.8** Early Stage 1 Atlantic tarpons from the Yucatán Channel, Mexican Caribbean, and Gulf of Mexico (exact collection locations unclear). **(a)** 5.7 mm NL, **(b)** 6.3 mm NL, **(c)** 8.1 mm NL). Scale bars = 1 mm. Source: Smith (1980: 138 Fig. 2).

As mentioned, eggs and yolk-sac larvae (pre-Stage 1) have not been identified, but this statement might be true only for Atlantic tarpons in the Western Hemisphere. Floating masses of fertilized eggs have reportedly been collected and photographed off western Nigeria (Anyanwu and Kusemiju 2008: 120 Figure 9.4). Among the shortest tarpons so far recovered in the western Atlantic was a recently hatched specimen from the Gulf of Mexico (Smith 1980). It measured 5.7 mm NL and retained remnants of a yolk sac (Fig. 1.8a). The yolk sac evidently disappears by ≈6.0 mm NL (Smith 1980). Cyr (1991: 11) reported specimens of 8.1–23.2 mm SL (age 9.5–30 d, $n$ = 29) and 6.3–23.8 mm SL (5.19–22.25 d, $n$ = 103) for Stage 1 leptocephali caught during his cruises. Stage 1 is variable and lasts ≈30–40 d (Cyr 1991: iv), and growth is linear over days 7–24 post-hatch (Cyr 1991: 13). Cyr (1991: 15) speculated that if growth is asymptotic before subsequent metamorphosis, Stage 1 could be prolonged substantially.

*Principal sources used in descriptions*: Jones *et al.* (1978: 53–57) for leptocephali of 9.4–27.9 mm SL and the original descriptions of Harrington (1958, 1966); Mercado Silgado and Ciardelli (1972: 159–166); and Wade (1962: 555–559). Also see Chacón Chaverri and McLarney (1992, Appendix C); Gehringer (1958); Mercado Silgado (1969: 4, 1971: 9–10); and Smith (1980).

*Meristic description*: Fin rays: dorsal 12–13, anal 20–22, caudal 17 (at 11.7 mm SL, 19 at ≥17.5 mm SL). Myomeres (at 22.0–27.9 mm SL): total 54–57, predorsal fin 37–42, preanal fin 40–43, prepelvic fin 22–24, at swim bladder 21–25. Teeth (at 9.4–22.0 mm SL): upper 1 + 7 to 0 + 3, lower 1 + 6 to 1 + 3. Vertebrae (at 17.5 mm SL): 7 hypural plates.

*Body proportions as percentage of SL*: At 9.4–22.0 mm SL, height at pectoral fins 5.1–8.5, snout length 2.9–4.9, horizontal eye diameter 2.0–3.2; at 9.4–27.9 mm

SL, head length (HL) 8.2–14.5, preanal fin length 77.6–88.0; at 21.3–27.9 mm SL, preventral fin length 49.2–55.9.

*Body proportions as percentage of HL*: At 11.0–21.3 mm HL, snout length 24.4–31.3, horizontal eye diameter 17.7–23.5.

*Narrative description*: Body ribbon-like early in Stage 1, elongated, thin laterally, deep; head small, triangular, eel-like, wider than body in dorsal aspect; brain clearly visible; eye nearly round; snout sloping gently from top to tip; upper body height reduced at pectoral region by 17.5 mm SL; body compressed laterally at 23.0 mm SL, thicker along whole length and not ribbon-like; at 24.0–27.9 mm SL height greatest at pelvic fins and has decreased at caudal peduncle and pectoral fin region. Head still triangular when viewed dorsally and wider than body to at least 17.5 mm SL, shifting at 23.0 mm SL from eel-like to bullet-shaped, losing triangularity and now slightly wider than body when viewed in dorsal perspective; width nearly uniform except for bulge at eyes; snout rounded. Snout more pointed by 27.9 mm SL, cartilaginous structures evident in posterior operculum. Nostrils visible as shallow depressions at 17.5 mm SL, evidently still not bifurcate. Mouth large early in Stage 1, oblique and extending to pupil, lower jaw protruding at 11.7 mm SL, jaws equal at 17.5 mm SL. Mouth smaller by 23.0 mm SL, gape much shorter. First tooth in upper jaw fang-like; posterior teeth needle-like, uniform in diameter, in a single row extending to angle of gape; teeth of lower jaw thicker, anterior pair evidently not set in jaw; teeth absent by 23.0 mm SL, and cartilage developing in maxillary and mandible. Eye nearly round at 11.7 mm SL, oval at 17.7 mm SL. Gill filaments well-formed at 23.0 mm SL, but gill rakers absent. Dorsal finfold originating ≈66% of body length behind head; caudal finfold truncated, margin invaginated dorsally and ventrally anterior to urostyle at 11.7 mm SL. Finfold reduced to remnants anterior to caudal fin at 21.3 mm SL. At 11.7 mm SL, 8 probable ray bases in dorsal finfold visible opposite myomeres 41–44. At 13.4–14.0 mm SL, 8 incipient dorsal fin-ray buds appear, the fin rays first seen at 20.3 mm SL. By 23.0 mm SL, 12th dorsal fin ray splits, posterior half slightly elongated. At 24.0 mm SL, origin of dorsal fin apparent at myomere 42. At 11.7 mm SL, an opaque area is visible in the postanal area of the median finfold, perhaps indicating a developing anal fin; at 13.4–14.0 mm SL, 14–15 incipient anal fin-ray buds can be seen, and rays are obvious at 20.3 mm SL. At 27.9 mm SL, an incipient anal fin is visible underneath myomere 44. At 17.5 mm SL, caudal fin forked with unbranched rays, but start of branching apparent by 23.0 mm SL. Pectoral fin a convex bud at 11.7 mm SL, a little larger by 21.3 mm SL. Pelvic fin buds visible at 20.0 mm SL and present at myomere 24 by 23.0 mm SL. Developing vertebrae visible at 11.7 mm SL, and urostyle prominent and tipped slightly upward, the angle becoming steeper by 17.5 mm SL. Tubular gut extending ≈75% length of body at 11.7 mm SL, terminating at anus opposite myomeres 44–47; at 17.2 mm SL, gut is slightly looped, or indented, at ventral surface just anterior of vent. By 24.0 mm SL,

heart located posteroventrally to pectoral fin in the shape of a figure eight, but nonfunctional. The swim bladder, which develops as an out-pocket of the esophagus, is apparent by 11.7 mm SL at myomeres 22–23, expanding slowly, and at 21.3 mm SL resembling a short cylindrical sac arising from the digestive tract at myomeres 23–24. Swim bladder extends dorso-caudally ≈ 33% of the distance to the central nerve cord, extending ≈66% of the distance by 23.0 mm SL and now stretched between myomeres 23 and 25. At 17.5 mm SL, kidney located dorsally to gut between myomeres 35 and 41, appearing larger by 23.0–27.9 mm SL, extending from myomeres 35–45 and now separated from posterior end of digestive tract.

Stage 1 larvae are lightly pigmented, possessing a few scattered melanophores on the posterior area of the gut dorsally to the central nerve cord at 11.7 mm SL. Also at this length, three chromatophores are evident on the ventral surface of the opercula, six on the dorsal border of the gut anterior to the swim bladder, and one on the swim bladder itself. From ≈13.4 mm SL to the end of Stage 1, dense, dark brown chromatophores show up as a fringed patch curving over the eyeball when viewed from a dorsal perspective, and small patches of chromatophores are occasionally evident on the fleshy margin below the eye. By 17.1 mm SL, a series of elongated chromatophores is visible along the dorsal edge of the intestine; a few others are scattered over the posterior part of the intestine and above the anus, and a series of elongated chromatophores can be seen on the myosepta below the midline. The caudal fin has a few chromatophores, and one exists below the pectoral fin. By 22.8 mm SL, about five lines of pigment are apparent below the lateral line on the caudal peduncle. By 24.0 mm SL, there is one stellate chromatophore on the lower head anterior to the heart, one on the heart, and 3–4 behind the heart. A row of elongated chromatophores extends along the dorsal surface of the gut to where the intestine and kidney separate; about four chromatophores can be seen above the kidney. A series of melanophores is visible at the base of the anal fin rays, as are four lines of melanin in dorsoventral alignment below the lateral line on the caudal peduncle. By 27.9 mm SL, dorsoventral lines are apparent on a minimum of five myomeres in a J-shaped pattern on the caudal peduncle.

*Duration*: Based on back-calculated hatch dates, Cyr (1991: 12, 26 Figure I-7) gave the estimated duration of Stage 1 as 33–51 days (95% CIs, $\bar{x}$ = 38 days, $n$ = 29, 1981 cruise) and 27–29 days ($\bar{x}$ = 28 days, $n$ = 103, 1989 cruise). Estimates based on counts of otolith increments: 15–32 days ($\bar{x}$ = 23.5 days ± 3.77 SD, $n$ = 23). Smith (1980) had earlier proposed 60–90 days, but his sample size was small ($n$ ≈25), and collections had been made at far-flung locations.

## Stage 2 – Shrinking leptocephalus

Often called the "metamorphic stage," although changes that are obviously metamorphic continue through Stage 3 and early Stage 4. Growth stops drastically during the second larval stage, and tarpon larvae shrink, a startling example

of what some have called "negative growth," an oxymoronic term. Stage 2 demonstrates that length alone is an unreliable diagnostic feature of tarpon ontogenesis. Wade (1962: 548) justified defining growth as change in morphology with age, not necessarily accompanied by increased size. To me, this stretches the definition beyond usefulness and its original descriptive intent (Chapter 2). I consider Stage 2 strictly a period of shrinkage accompanied by morphological change, but not "negative growth" or growth in any sense.

Stage 2 ordinarily involves specimens of 28.0–13.0 SL (Table 1.1). *Note in the descriptions below that when leptocephali shrink during Stage 2, length ranges are reversed and instead of increasing they diminish.* Stage 2 is thus notable for dramatic reduction in overall size and characterized by diminishing length, gradual loss of the ribbon-like form, and anterior shifting of the fins. Stage 2 occurs almost exclusively inshore (Cyr 1991: 17; Jones *et al.*, 1978: 53; Mercado Silgado 1971; Mercado Silgado and Ciardelli 1972; Smith 1980; Wade 1962; Zerbi *et al.* 2001). Exactly when the larval stage terminates and the next stage begins, as assessed from otolith increments, is often not obvious. Stage 2 is accompanied by a loss in length of > 14 mm SL (>40%) over two weeks. Richards (1969) described and illustrated the first Stage 2 Atlantic tarpon larva recovered from west Africa in the eastern Atlantic.

*Principal sources used in the descriptions*: Jones *et al.* (1978: 58–61) for leptocephali of 27.3–13.0 mm SL. Also see Mercado Silgado and Ciardelli (1972: 167–182) and Wade (1962: 559–561).

*Meristic description:* Fin rays: dorsal 12–13, anal 20–22, caudal 17. Myomeres: total 55–57, predorsal 42–36, preanal 43–38, prepelvic 24–21, at coelom 14–24. Vertebrae (at 17.0 mm SL): ≈6 hypurals.

*Body proportions as percentage of SL*: at 23.7–16.9 mm SL, height at pectoral fins 6.8–9.5, snout length 3.8–4.7, horizontal eye diameter 1.7–2.5; at 27.3–13.0 mm SL, head length 9.2–26.9, prepelvic fin length 53.0–48.4, preanal fin length 83.7–71.5, predorsal fin length 79.3–69.2.

*Narrative description*: Body height decreases from 27.3 to 25.0 mm SL. At 17.0 mm SL, height at pectoral fins increases markedly, and bottleneck-like appearance disappears. At 27.3 mm SL, snout's dorsal concavity is almost gone; the cranial bones are visible. At 20 mm SL, mouth has shifted dorsally, and jaws are longer. By 17 mm SL the lower jaw is a little longer than the upper, head larger in relative size, and a swelling is visible between developing mandibles in area of the future gular plate. By 15 mm SL, nostrils well developed, gular plate forming; teeth present. At 15–13 mm SL, eyes have become more rounded, upper and lower jaws well formed. By 17.0 mm SL, dorsal and anal fins have become longer and higher; some rays of caudal fin are branched; pectoral fins are larger and more pointed, their fleshy bases reduced. At 15 mm SL, lobes of the caudal fin are symmetrical. At 15.0 mm SL, gut has formed completely; scales still absent. At 16.9 mm SL, a slight loop, or indentation, still evident in ventral surface of the gut just anterior to vent.

At 27.3 mm SL, heart clearly visible; by 20 mm SL, circulatory system has become functional. The swim bladder, oval in shape, is apparent by 27.3 mm SL above myomeres 23–24, extending from myomeres 24–27 at 21.1 mm SL. At 17.0 mm SL, swim bladder has become more inflated and extends forward to myomeres 20–21.

Pigmentation at 27.3 mm SL similar to that of 27.9 mm SL specimens of Stage 1; two melanophores apparent above dorsal area of swim bladder. At 25 mm SL, dorsal part of caudal peduncle has two stellate chromatophores, ventral part with dorsoventral lines that in some specimens have lost the J-shape. Pigment has become denser on the head and extremes of upper and lower caudal lobes and is now visible over hypurals, on pectoral fins and central nerve cord, and ≈75% of kidney; pigment has merged over swim bladder forming a single patch. By 23.7–16.9 mm SL, a series of elongated chromatophores visible following dorsal edge of intestine. A series of small chromatophores is present on intestine above anus and another on myosepta at midline. A few chromatophores visible on myosepta above kidney and on anal fin, and small chromatophores apparent on dorsal surface of swim bladder. A few others have appeared on the anal, dorsal, and caudal fins, and one below the pectoral fin. Pigment can be seen above and on the eyeball and its fleshy margin below. One specimen had four subsurface and one surface chromatophores on or below the lower part of the brain. By 15 mm SL, body has become more opaque, its dorsal and lateral portions silvery. Pigment is concentrated along top of head and extends along dorsal surface of body; coelom densely pigmented. At 13 mm SL, eye is black.

*Duration*: Cyr (1991: 16) estimated Stage 2 to last ≈14 d, but it often has no discernible endpoint. Based solely on counts of otolith increments, Cyr (1991: 12–13) estimated 5–24 days ($\bar{x}$ = 14.2 ± 4.25 SD days, $n$ = 23). However, note the extensive range and large standard deviation. He mentioned that in estimating ages of both Stage 1 and 2 larvae, checks (i.e. discontinuities; see Casselman 1983: 2) in otolith microstructures were difficult to interpret and therefore subject to error (Cyr 1991: 15).

## Stage 3 – Fry

*Principal sources used in the descriptions*: Jones *et al.* (1978: 61–62) for leptocephali of 12.6 to ≈25 mm SL. Also see Mercado Silgado and Ciardelli (1972: 182–183); Wade (1962: 561–566).

Stage 3 is defined by renewed growth and characterized by increasing length and dramatic alteration of body form. To Mercado Silgado and Ciardelli (1972) it encompasses specimens of 13.0–71.0 mm SL (Table 1.1). I restrict it to the resumption of growth at ≤ 13.0 mm SL and ending at ≤ 45 mm SL, the point at which proportional changes in body features become isometric with growth in length (Section 1.3). Notable changes include increased body height at the pectoral fins, increased snout and head length, increased height of the

dorsal and anal fins, and enlargement of the pectoral fins. Near the end of Stage 3 the body loses some of its transparency, becoming gradually opaque and often silvery.

*Meristic description*: Fins spineless, dorsal 12–17, anal 19–25 (including fin rays that merge with continued growth). Myomeres of predorsal fin 37–39, those of preanal fin 38–41. Upper teeth 0–6, lower teeth 0–8. Gill rakers 1 + 7 (at 13.1 mm SL), 2 + 13 (at 13.8 mm SL), 5 + 14 (at 15.9 mm SL), 8 + 21 (at 20.2 mm SL). Branchiostegal rays 7–15 (at 13.1–15.9 mm SL).

*Body proportions as percentage of SL*: at < 17.2 mm SL, height at pectoral fins 9.9–17.0, head length 20.7–28.6, predorsal fin length 61.8–76.0, preanal fin length 70.2–78.6.

*Body proportions as percentage of HL*: at < 17.2 mm SL, snout length 17.3–26.2, eye diameter 21.4–29.3.

*Narrative description*: At 13.8 mm SL, body height at pectoral fins has increased relative to SL, but decreased posteriorly. By 15.9 mm SL, shape of head irregular, mandible oblique and extending to a point in vertical alignment with pupil; posterior end of mandible distinctly flared. Teeth present on lower jaw throughout Stage 3 and at 13.9–14.1 mm SL are developing on upper jaw. The eye at 12.6 mm SL has become compressed dorsoventrally; the nares are bifurcating. At 13.8 mm SL, swim bladder is enlarged anteriorly, now extending to myomere 12 and characterized by a dorsal finger-like projection from the posterior region to halfway up lateral line. Origin of dorsal fin now at myomere 37, that of anal fin at myomere 39. Height of anal fin exceeds that of dorsal fin; last ray of anal fin has split. Fleshy bases of pectoral fins have been reduced, incipient rays evident on pelvic fins.

By 13.8 mm SL, chromatophores present on head and body and densely populate snout, opercula, regions above brain and below midline. Pigment apparent on bases of dorsal fin rays and anterior and posterior rays of dorsal and anal fins, respectively. Surface of swim bladder pigmented, as is the gut and area separating the gut and kidney. By 15.9 mm SL, chromatophores outline the myomeres and are developed on the body above the midline.

## Stage 4 – Juvenile

*Principal sources used in descriptions*: Harrington (1966); Jones *et al.* (1978: 62); Pinto Paiva and Ferreira de Menezes (1963); and Wade (1962: 566–567) for specimens ≥25.2 mm SL; and Mercado Silgado (1969 Table 1) for specimens of 71.0–1000 mm SL. Also see Moffett and Randall (1957). I have allowed some overlap in lengths of early juveniles with larger Stage 3 specimens starting at ≈25 mm SL.

*Meristic description*: Fins spineless, dorsal fin 14–18, anal fin 24–28 (up to 59.9 mm SL). With growth, counts of rudimentary fin rays have become reduced by consolidation. Gill rakers 9 + 24 (at 25.2 mm SL), 16 + 34 (at 35.0 mm SL), 17 + 34–22 + 40 (at 51–271 mm SL). Branchiostegals 22–25 (at 51–271 mm SL).

*Narrative description*: Body torpedo-shaped at 25.2 mm SL, but has deepened considerably by 51.0 mm SL. At 25.2 mm SL, mouth is large, lower jaw projected, maxillary wide and reaching to posterior margin of eye. Full appearance of the adult has been attained by 194.1 mm SL, at which point the maxillary extends past the eye, the snout is obtusely conical; bands of villiform teeth are apparent on the jaws, tongue, vomer, palatines, pterygoids, and sphenoid. Incipient scales first appear along lateral line at ≈ 30–34 mm SL (Harrington 1966: 868 stated 32 mm SL at first scale formation), and actual scales by 36.8 mm SL, 1 above and 2 below lateral line. Pores in lateral line can be seen at 51.0 mm SL. Axial scales form by at least 78 mm SL. At 25.2 mm SL, fourth dorsal and fifth anal fin rays are the longest; anal fin is falcate, its origin slightly posterior to insertion of dorsal fin; pectoral fins have broadened, their central rays almost to the origin of pelvic fins, which are now about halfway between the snout and hypural plate. By 140 mm SL, two specialized scales cover the uppermost and lowest caudal fin rays. At 194.1 mm SL the dorsal fin's filamentous ray has a visible groove on its underside; anal-fin sheath is scaly, and its last ray appears; caudal fin scaly. At 25.2 mm SL, body is opaque, the internal organs now hidden.

Pigmentation mostly above lateral line. Gular plate heavily pigmented; opercula silvery. Pigment present on tip of mandible, snout, and occiput. Juveniles continue to darken dorsally with age. Moffett and Randall (1957: 5) described a juvenile of 33 mm (FL?) seined from an isolated pond in the Florida Keys, declaring it recently metamorphosed: "The body is translucent except for the region over the abdomen and a less marked band the length of the body at the level of the vertebral column which are silvery. There is a dusky area mid-anteriorly in the dorsal fin. *The caudal fin is emarginated, not forked* (emphasis added). The last dorsal ray is not longer than the preceding rays."

They also examined a specimen of 42.5 mm FL from the same location. It was "more silvery, the dusky spot on the dorsal is still distinct, the caudal is now forked, and the last dorsal ray has elongated slightly." Still another specimen, this one measuring 63 mm FL, "is almost completely silvery (only a region along the back and another at the base of the anal fin do not show metallic reflection), the spot on the dorsal is faint, and the last dorsal ray is relatively longer (it does not exceed the length of the long anterior rays of the dorsal fin until a fork length of about 130 mm. is attained)." The length at which the tail becomes obviously forked – a clearly visible character – seems to have been largely overlooked in other descriptions I read.

## Stage 5 – Adult Atlantic tarpon

*Principal sources used in descriptions*: Jones *et al.* (1978: 53 and references); Mercado Silgado (1969: 5–6).

*Meristic description*: Fin rays: dorsal fin 13–16, anal fin 22–25, caudal fin 7 + 10 + 9 + 6–7, pectoral fin 13–14; pectoral and pelvic fins with axillary processes.

Vertebrae: precaudal 53–57, caudal 33–34. In their original description, Cuvier and Valenciennes (1846: 398)[3] gave counts of dorsal 13, anal 22, caudal 30, pectoral 13, branchiostegal 22–23, ventral 9. Gill rakers 19–22 + 36–40. Lateral line scales: 41–48 (counts based partly on some juvenile specimens).

*Body proportions* (as percentage of SL and based partly on some juveniles): body height 23.5–29.0, head length 25.0–31.0, snout length 4.5–6.2, eye diameter 5.3–9.5.

Fin-ray enumeration in adult Atlantic tarpons depends on whether fused rays are counted as joined or separate. Counts of rays in dorsal and anal fins given above, which are cited widely and uncritically in species descriptions, might be low by three or four. As Breder (1944: 224) pointed out, "In large fish the first four or five [rays] are consolidated into a solid leading edge, which have generally been counted as one ray. In the smallest sizes the separation of these rays is evident and doubtless, if small fish instead of large were generally available to taxonomists, the usage would have developed differently."

This raises the dorsal and anal ray counts to, respectively, minimums of 16 and 25. Table V of Breder (1944: 225) displays ray counts of these two fins from the literature, indicating that only Fowler (1936) gave "full" counts; that is, by including in lower-case Roman numerals the number of rays prior to their fusion. The counts then become iv–v + 10–11 (dorsal fin) and iv–v + 18–19 (anal fin).

The older literature contains some peculiar speculation about possible function of the extended last dorsal ray. Southworth (1888: unpaginated) referred to it as "an osseous bayonet, about nine inches long ….Whether this weapon – for such it surely must be – is for attack or defense, no one, as yet, seems able to determine." Breder (1929: 59) wrote: "The produced last dorsal ray functions in the tremendous leaps that the tarpon is famed for. It is concave below and adheres to the side of the fish, bending and securing the dorsal to the right or left, so determining the direction of the fall."

Babcock (1936: 61) did not believe him, and rightly so, writing: "There is nothing in the anatomical or muscular structure of the tarpon that lends color to the theory that the fish controls its jumps by manipulating its dorsal fin by the use of the ray and after observing hundreds of fish I am satisfied that this is not the case."

Depending on how rays of the dorsal and anal fins of the Pacific tarpon are counted, numbers for the two species potentially overlap, in which case the

[3]According to Bailey (1951), Valenciennes alone should be credited. *Histoire Naturelle des Poissons* comprises 22 volumes. The description of the Atlantic tarpon appeared in Vol. 19. Cuvier died 13 May 1832, and Valenciennes prepared the material for all volumes, starting with Vol. 10 published in 1835. Bailey's assessment might be correct in the sense that Valenciennes did the work alone, but when read in the original French it seems his intent was to sustain their collaboration even after Cuvier's death (see my text comments). Even today, a colleague who has died can still be listed as a coauthor.

characters would fail to be diagnostic. The original description of *M. cyprinoides* (Broussonet 1782: 62–65) omitted any mention of counting method, and perhaps this feature should be revisited for both *M. atlanticus* and *M. cyprinoides* using samples consisting of a range of body lengths.

*Narrative description*: Fins spineless, pectoral and pelvic fins with axillary processes. Body deep, compressed, eyelids adipose. Mouth large, oblique, maxillary extending far past eye in large specimens; gular plate elongated between rami of lower jaw; mandible projecting prominently, tail deeply forked. Scales cycloid, exceptionally large, firmly attached, borders crenulated and membranous. Lateral line complete, decurved anteriorly. Single high dorsal fin with last ray elongated and easily distinguished. Coloration silvery, darker above.

The habitat seems to temporarily influence color. Atlantic tarpons both large and small reportedly acquire a "golden," or "brassy," tint while spending time in freshwater or waters of low ionic strength, a phenomenon apparently confirmed by Breder (1944: 233–234) in aquarium experiments. Ferreira de Menezes and Pinto Paiva (1966: 85) wrote that Atlantic tarpons appearing along coastal Ceará State, Brazil during the last quarter of the year are brassy, but those arriving in June, July, and August (austral winter) in smaller aggregations are "fatty individuals, silvery-white colored, suggesting that they come from waters of high salinity … ." However, Moffett and Randall (1957: 5) captured juveniles in an isolated tidal pond in the Florida Keys, where the *practical salinity*, $S_p$, (explained in Chapter 6.1) ranged from ≈ 19–33, reporting they "had a definite bronze cast." They also noted, "Juvenile tarpon from ponds with dark brown water were colored distinctly darker on the back."

These observations indicate to me that tannic and humic acids might actually be the agents staining the fish brownish, although they do not explain Breder's aquarium experiments. Nor do they eliminate the possibility of selective dorsal darkening in pigmented waters as camouflage from aerial and terrestrial predators. Breder (1944) and Ferreira de Menezes and Pinto Paiva (1966) had suggested that the bright, silvery appearance of a tarpon indicated it had recently been living in high-salinity waters, as did Victor Brown, taxidermist and angler, in a letter to Kaplan (1937: 92): "Within 3 days, after they [adult females] run into the brackish water rivers from the open Gulf [of Mexico] waters, their scales change from turquoise blue to bronze." Another possibility? Inshore waters are commonly tinted yellow by refractory organic pigments (*gelbstoff*). A reflective silvery appearance has camouflage value in transparent offshore waters (Brady *et al*. 2015), but turning brassy might be advantageous inshore.

Gudger (1937) described a rare albino Atlantic tarpon. It weighed 12.2 kg (27 lb) when alive; the mounted form measured 114.3 cm TL (≈45 in.).

Cuvier and Valenciennes (1846: 398–399) wrote of the tarpon's color in more detail based on a drawing sent by one of his correspondents, presumably in contact with Valenciennes and not Cuvier, who had died almost exactly 15 years before publication of Volume 19. Note, however, that the drawing was

sent to *nous*, not *je* (to *us*, not to *me*), indicating that Valenciennes perhaps still considered Cuvier his collaborator when describing the Atlantic tarpon. The description reads:

> *"La couleur, bleu plombé sur le dos, est d'un bel argenté sous le ventre, sur les joues et sur les opercules. Le bord membraneux de cet os n'a pas cette tache noire si caractéristique dans l'espèce précédente. Les nageoires dorsale et caudale sont plus ou moins grises; les ventrales sont jaunâtres. D'après un dessin qui nous a été transmis par M. L'Herminier, il y aurait, quelques teints jaunes dorés sur les écailles de la nuque et des taches rougeàtres sur le bord du préopercule et à l'angle de l'opercule. La dorsale, lisérée de bleu, serait verdâtre comme l'anale; la caudale et les ventrales plombées."*

I translate this as:

"The color, leaden blue on the back, a beautiful silver on the belly, cheeks, and gill covers. The membranous edge of this bone [the operculum] does not have the characteristic black spot of the other species. The dorsal and caudal fins are more or less gray; ventral [fin] yellowish. From a drawing that was sent to us by Monsieur L'Herminier, there would be some tints of golden yellow on the scales of the neck and reddish spots on the edge of the preopercle and the angle of the operculum. The dorsal [fin], edged with blue, and being green like [the] anal [fin]; caudal and ventral [fins] leaden."

How much these subtle hues were influenced by light reflected and refracted through guanine crystals in the scales, shifting wavelengths caused by time of day and sky conditions, and status of the fish (alive or dead) is impossible to know. The black spot on the operculum is not evident in Broussonet's illustration of the Pacific tarpon, *Megalops* (= *Clupea*) *cyprinoides*, nor did I find it mentioned specifically in his original description of the fish's head or notice it in modern photographs and illustrations (e.g. Fig. 1.5). Perhaps this character, if it exists, is restricted to certain regional populations. The specimen depicted in a color photograph by Bagnis *et al.* (1987: 272), for example, has a black patch on the body visible at the posterior edge of the operculum.

Jordan and Evermann (1896: 409) removed the Atlantic tarpon from *Megalops* and placed it in a new genus, *Tarpon*, based solely on one perceived character difference: "The posterior insertion of the dorsal fin distinguishes the single species of *Tarpon* from the East Indian *Megalops cyprinoides*, a fish of similar habit, in which the dorsal is inserted above the ventrals." After examining a series of both fishes in collections of the US National Museum, Hollister (1939: 450–451) declared this character not valid and questioned whether Jordan and Evermann actually made the requisite measurements. She wrote:

> "It is apparent that the dorsal fin is in the same position in the two species, that is, in the same relative distance from the snout. But the ventral fins in *Tarpon* are nearer the snout than in *Megalops*, giving the illusion of the dorsal being more posterior in position in *Tarpon* than in *Megalops*."

She showed this in an illustration; whether the drawings were to scale was not mentioned (Fig. 1.9).

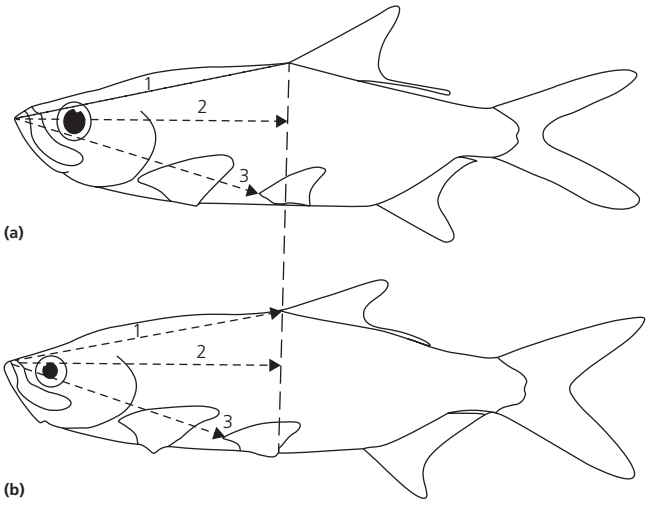


**Fig. 1.9** **(a)** Pacific tarpon, **(b)** Atlantic tarpon. The distance in **(a)** represented by the line 3 is longer than that represented line 3 in **(b)**. The position of the ventrals is farther form the tip of the snout in **(a)** than the **(b)**. Lines 1 and 2 are equal in both, showing that position of the dorsal fins is identical in the two species. Source: Hollister (1939: 451 Text-fig. 1). Reproduced from G. Hollister: Young *Megalops cyprinoides* from Batavia, Dutch East Indies, including a study of the caudal skeleton and a comparison with the Atlantic species *Tarpon atlanticus*, with permission from the Wildlife Conservation Society Archives.

In addition to differences in placement of the ventral fins, Hollister noted variation in numbers of vertebrae (57 in the Atlantic tarpon, 68 in the Pacific species) and also in fin-ray counts, but whether she counted the rays as fused or separated is not stated (see meristic description above). The Atlantic tarpon supposedly has 12–15 rays in its dorsal fin compared with 19–21 in the Pacific tarpon. Counts of anal fin rays are 19–22 vs. 24–27. Details of the scales (Fig. 1.10) and caudal skeleton also seemed to Hollister to provide distinguishing features (see Hollister 1939: 460–467 and her accompanying Text-figs. 14–21).

In general appearance, the Atlantic tarpon is more slender (Gill 1907: 39) and has a smaller eye than its Pacific counterpart, which conflicts in one character with its original description. Cuvier and Valenciennes (1846: 398) wrote of the Atlantic species: "*Ce poisson la tête plus courte; le corps plus haut, plus trapu. L'oeil sensiblement plus petit*." [This fish has a shorter head; the upper body, stockier. The eye significantly smaller.] Based simply on looking at photographs and illustrations, the Pacific tarpon appears to me the stockier species as an adult, which was also Hollister's conclusion, and seems evident in Fig. 1.9.

*Maximum size and longevity*: The current angling record is 130 kg (length unstated).

According to Heilner (1953: 220), "On August 6, 1912 … native [commercial] fishermen at Hillsboro Inlet on the east coast of Florida caught a tarpon in their nets 8 feet, 2 inches long [≈249 cm] and estimated to weigh 360 pounds [≈163 kg]." Kaplan (1937: 93) gave its estimated weight as 352 lb [~157 kg].

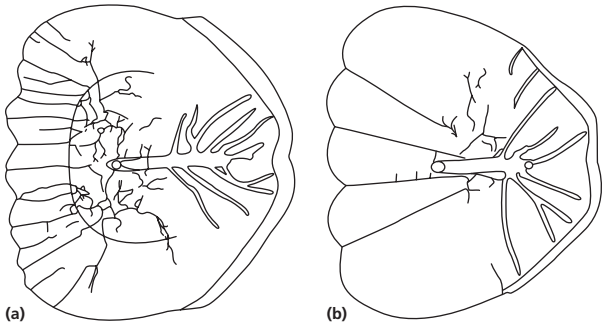


**Fig. 1.10** Tarpon scales. **(a)** Pacific tarpon of 300 mm SL, 15th scale in the lateral line from below the anterior margin of the dorsal fin (see Text-fig. 9 of source publication). **(b)** Atlantic tarpon of 238 mm SL, 18th scale in the lateral line from below the anterior margin of the dorsal fin (see Text-fig. 11 of source publication). Source: Hollister (1939: 460 Text-fig. 12 and Text-fig. 13). Reproduced from G. Hollister: Young *Megalops cyprinoides* from Batavia, Dutch East Indies, including a study of the caudal skeleton and a comparison with the Atlantic species *Tarpon atlanticus*, with permission from the Wildlife Conservation Society Archives.

Norman and Fraser (1938: 97) also mentioned this fish, and in an example of how hearsay can eventually become fact, Beebe and Tee-Van (1928: 34), stated authoritatively: "The world's record for size, at this date, is 8 feet 2 inches long with an estimated weight of 350 pounds." According to Jordan and Evermann (1904: 85), "the largest taken with a harpoon weighed 383 pounds, if we may believe the record …." Breder (1929: 60) wrote: "They reach a large size and records run as high as 8 feet 2 inches with an estimated weight of 350 pounds." Earlier, a fish like this might be considered medium-sized. Cuvier and Valenciennes (1846: 399), in describing the Atlantic tarpon, told us: "*M. L'Herminier nous en a envoyé un de quatre pieds un pouce, mais je trouve dans ses notes qu'on en pêche à la Guadeloupe qui ont jusqu'à seize pieds de longueur.*" [Monsieur L'Herminier sent us one [a specimen] four feet long, but I [presumably Valenciennes] find in his notes that [these] fish in Guadeloupe [presently part of the French West Indies] reach up to sixteen feet in length.] On the next page (p. 400): "*Marcgrave*[4] *en a déjà vu de onze à douze pieds de long et de la grosseur d'un homme* …." [Marcgrave had already seen [specimens of] eleven to twelve feet in length and the size of a man ….] No doubt both reports are early fish tales.[5]

[4]Georg Marcgrave (1610–1644), German naturalist, astronomer, and cartographer whose writings on natural history impressed Cuvier. I assume Marcgrave's observations of tarpons were made during his explorations at the Dutch colony in Brazil, starting in 1638.

[5]Measurements in the old literature must be considered in historical context. In the mid-nineteenth century, one *pouce* (French inch) equaled 1.066 English inches, meaning that a 12-foot fish of 144 English inches examined by an Englishman would be ≈ 3657.6 mm, but longer (≈3899 mm) if a Frenchman measured it. The difference in this case (only 241.4 mm, or ≈ 6.6%) still leaves Marcgrave's reports looking fishy.

In a survey by Crabtree *et al.* (1995) of southern Florida tarpons, the oldest female was 55 years, the oldest male 43 years. Female Atlantic tarpons can live at least 64 years. A specimen captured in the Florida Keys in August 1935 died at Chicago's John G. Shedd Aquarium in October 1998 (Tim Binder, personal communication 5 January 2015). The husbandry record is incomplete. The fish was neither weighed nor measured when received, nor were any data recorded after its death. Apparently it was a juvenile when captured. Costa Rican Atlantic tarpons are also long-lived, some surviving to at least 48 years (Crabtree *et al.* 1997).

## 1.5 Development of Pacific tarpons

The Pacific tarpon's development has not been described in as much detail (e.g. Blanco 1955: 97–98; Hollister 1939; van Kampen 1909), and duplicating the above format of subsections is impossible. Species differences are slight (Wade 1962: 555) with exception of size at late juvenile and adult stages. According to Ellis (1956: 6), "Incubation lasts for about 20 hours, the young hatching out as prolarvae and quickly developing into small leptocephali." Neither a citation nor evidence to back this claim was presented. To my knowledge, initial development of the Pacific tarpon has not been reported.

Tsukamoto and Okiyama (1993: 379) considered the Pacific tarpon larva to have four early developmental stages, adding a "sluggish growth phase" between Stages 2 and 3, and noting that it seems unique to the Pacific tarpon in not having not been included in descriptions of the developmental stages of other Elopomorpha. I doubt its validity as a stand-alone feature and exclude it from the staging system used here, but incorporate the ontogenetic changes listed by Tsukamoto and Okiyama (1997) as occurring in early Stage 3 (here termed fry). The "sluggish growth phase" is probably an artifact of captivity. For example, captive Pacific tarpons reared by Chidambaram and Menon (1947) and maintained four weeks shrank progressively but never completed metamorphosis. Holstvoogd (1936: 4) claimed metamorphosis to take seven weeks in the laboratory prior to resumption of growth (i.e. initiation of Stage 3). Ellis (1956: 6) also gave seven weeks, but did not provide a citation. Others have reported metamorphosis as happening much faster (see Stage 2 description below). Alikunhi and Rao (1951:108), writing of grow-out of Pacific tarpons in aquaculture, said, "while marketable size was attained in the natural pond in the course of less than ten months, during the same period only less than half that size was attained in the aquaria [*sic*] and nursery tanks."

That captive conditions likely affect growth and development is illustrated by two examples. First is Holstvoogd's (1936: 4) description. Larvae captured when arriving at estuaries in the vicinity of Batavia (now Jakarta), Java, Indonesia were ≈23 mm SL (26 mm TL), and starting metamorphosis, when they shrank

to 17 mm SL. During this process the usual shifting of structures occurred. Postanal myomeres increased from 17–20, for instance, and the anus shifted forward six myomeres. By completion of Stage 2 the anus had shifted forward a total of 13 myomeres. Growth in length (Stage 3) then commenced. At ≈24 mm SL the number of caudal vertebrae equaled the adult number, and except for shape of the dorsal fin, metamorphosis was considered finished.

In the second example, Alikunhi and Rao (1951: 105–109) described leptocephali captured in backwaters of the Adyar River near Madras (now Chennai), India on 6 October 1947. They measured 23.0–28.0 mm (presumably SL)[6] when acclimated to freshwater over ≤ 24 hours in the laboratory. Most had completed Stage 2 after 9 days (by 15 October), the shortest shrinking to 16.5 mm SL, and structures shifted as expected (i.e. at minimum standard length the dorsal fin was at myomere 36, the anal fin at myomere 42, the anus at myomere 41). Growth then resumed (Stage 3), reaching ≈20.5 mm SL over two weeks. During this time the dorsal and anal fins shifted forward, the dorsal beginning at myomere 27, the anus to myomere 38 (its adult position). Vertebrae numbered 38 (preanal) and 30 (postanal), and shifting of all structures was complete. *However, growth over the next four weeks reached 49 mm SL, more than twice that of Holstvoogd's fish in the same amount of time*.

The first tarpon leptocephalus described was identified as belonging to the Pacific species (Fig. 1.11). [van Kampen 1909: 10 unnumbered figure]. Beebe (1928: 228–229) provided an English translation of van Kampen's original article published in German (see below), along with a better inked reproduction of his illustration (Beebe 1928: 228–229, unnumbered figure following p. 228). Although van Kampen did not know the age of his specimen or note its length specifically, he seemed to be discussing a fish of ≈25 mm TL (≈22 mm SL) mentioned in his text. If so, larval development differs little from that of the Atlantic species. Because the leptocephalus came from an inshore location it was probably in Stage 2. Beebe's translation:

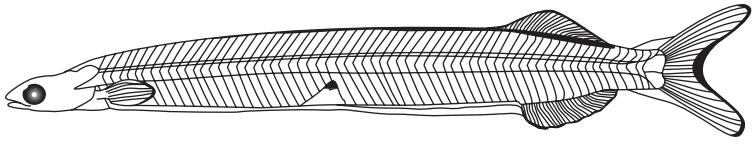

**Fig. 1.11** First illustration of a Pacific tarpon leptocephalus (≈25 mm TL or ≈ 22 mm SL). The specimen is probably Stage 2 based on the presence of pelvic fins and pigment, dorsal and anal fins placed far back, and advanced development of median fins and swim bladder (Wade 1962: 594). The inshore capture site is also diagnostic. Source: (van Kampen 1909: 10 unnumbered figure).

[6] Alikunhi and Rao (1951) did not state whether their length measurements were FL, SL, or TL. I assume SL here.

In the month of January, fish larvae appear in the brackish water of the harbor canals of Batavia (see illustration) which are very similar to that of *Albula*, nevertheless it can not belong to this genus, but must be related to the *Megalops cyprinoides*, on later elucidated grounds. The total length of the larvae collected by me varies from 23 to 30 mm. yet all appear to be in the same stage of development. Older stages I have not yet found, and the development of the larvae is unknown.

The body is band-like. One animal of 25 mm total length (22 without the caudal) has a depth [height] of 3 mm. It is quite transparent; in life only the eyes and swim bladder are distinct.

The fins, with the exception of the ventrals, are already well developed, and much larger than in the youngest of Gill's stages (*Albula*), which otherwise correspond most closely with the Batavia larvae. Dorsal and anal fins lie far back, the first somewhat in front of, but for the most part over the latter. The dorsal has eighteen rays, and in front of these are plain evidences of one or more undeveloped rays; the last ray is somewhat larger than the others and this gives a hint of the filament of the adult *Megalops*. The anal fin possess [*sic*] twenty-seven rays, the caudal twenty, from each of which ten hypurals are formed. The small rim-rays of the tail fin are only visible in the first stage. The ventrals are the smallest of all, and lie in the middle of the body.

Of the inner organs the swim bladder is developed ahead of the rest. In life it appears as a small shimmering point. It lies above the ventrals.

There are about sixty-nine muscle bands evident, of which forty-eight or nine compose the body (between the ventrals and anus, 22), and twenty or twenty-one the tail.

On the ventral aspect of most of the myomeres is a chromatophore. Besides these, small chromatophores lie along the upper and lower caudal rays, and along the posterior edge of this fin. Above the swim bladder lies a pigmented cap.

A methylene blue preparation of [a] 30 mm larva, reveals the osseus beginnings of the cranium, the basal part of the pectorals and the fin-ray supports of all unpaired fins, but not yet the vertebral column. The ray supports of the dorsal and anal fin rest upon two pieces of which the distal (basiostegal) is small and round.

The great number of rays of the anal fin makes it unlikely that the larvae under consideration belongs to *Albula conorhynchus*, which possess only 9–10. In comparison the number agrees well with allied *Megalops cyprinoides* (anal rays 23–28), while in *Elops saurus* these are also much [*sic*] fewer (15–17). Other near related forms do not occur in the Archipelago. I dare assert with considerable assurance that this larva is that of some specimen of *Megalops*, especially as this genus is the only one which occurs commonly in the harbor canals of Batavia.

## Stage 1 – Growing leptocephalus

*Principal sources used in descriptions*: Alikunhi and Rao (1951); Chen and Tzeng (2006); Chen *et al.* (2008); Chidambaram and Menon (1947); Delsman (1926); Gopinath (1946: 9); Tsukamoto and Okiyama (1997); Tzeng *et al.* (1998); and Wade (1962: 567–569).

At 16.1 mm SL, slope of snout flatter, eye diameter relatively larger than Atlantic tarpon, but still very similar in form and structure; eight teeth per side in both jaws, an increase of two in the upper and three in the lower, and two more teeth in each jaw than Atlantic tarpon of similar length, although arrangement, size, and shape of the teeth are the same. At 20–27 mm TL (Chidambaram and Menon 1947), head depressed, mouth with pointed teeth, alimentary

canal straight, muscle fibers in myomeres arranged in parallel rows, caudal fin forked; HL 10% of SL, diameter of eye 25% of HL, body height 11% of TL; 69 myomeres total, 15 preanal, 18 postanal; swim bladder a club-shaped evagination in middle of alimentary canal between myomeres 27 and 31; pectoral fin fan-shaped with rounded margin; black pigment along middle of myomeres in a line and on latero-ventral aspect of myomeres in small patches.

Size range of specimens from Gongshytyan Brook estuary, northern Taiwan between 15 and 24 September 1995 were 20–39 days old ($\bar{x}$ = 28.5 d) and had already begun metamorphosis at 13.6 mm SL; similar in overall appearance to Atlantic tarpon leptocephali of comparable length: translucent with internal structures visible. Length at arrival inshore, 17.8–32.9 mm TL ($\bar{x}$ = 25.6 mm TL, $n$ = 194). Age ($A$) vs. growth ($G$) relationship determined by Tzeng *et al.* (1998: 180):

$$A=58.404e^{-.7886G} \tag{1.1}$$

*Body proportions as percentage of SL*: At 13.6 mm SL, compared with Atlantic tarpon, HL 21.8 vs. 31.3; eye diameter occupying greater proportion of head; differences of other body proportions (e.g. body height at pectoral region, predorsal, preanal) slight. By 24.1 mm SL, HL 10.4, just 0.4 greater than Atlantic tarpon of 21.3 mm SL; indices for body height equal at 6.2 (Pacific tarpon) and 6.1 (Atlantic tarpon). Snout length and horizontal eye diameter, which were 27.8 and 22.2, respectively, in Pacific tarpon larvae of 16.1 mm SL, decrease to 26.8 and 20.0 by 24.1 mm SL.

*Narrative description*: Body nearly identical to Atlantic tarpon's early in Stage 1; that is, ribbon-like, elongated, thin laterally, deep; head small, triangular, pointed, eel-like, wider than body in dorsal aspect; brain clearly visible; eye nearly round; snout sloping gently from top to tip. Central nerve and notochord well developed by 16.1 mm SL, urostyle turned up sharply, seven hypurals visible. Remnants of median finfold apparent in predorsal and postanal regions. Thirteen dorsal and 19 anal-ray bases visible, but fin rays absent. Predorsal and preanal myomere counts 48 and 52, total myomere count 65. Caudal rays 17, two more than Atlantic tarpon of comparable size. Pelvic fin absent, pectoral fin a transparent fleshy bud without rays. Development at 24.1 mm SL comparable to Atlantic tarpon's at ≈26.9 mm SL; position of dorsal fin unchanged, anal fin has moved slightly forward, outline of fins similar in both species. Caudal fin in Pacific tarpon more deeply forked than Atlantic tarpon, each with 19 principal rays. Development of pectoral fin static despite increase in body length of ≈8.0 mm SL; pelvic fin absent. Swim bladder a cylindrical sac arising from gut, pushing dorsally toward central nerve cord. Unidentified structure (kidney?) dorsal to gut extending from myomere 31 to anal area; kidney apparently developing later in Pacific than Atlantic tarpon. At maximum length a few melanophores along ventral abdomen. Stage 1 leptocephali in captivity tend to swim in the middle of the water column.

Head small and rounded when fully developed at ≈ 32 mm SL, body strongly compressed, dorsal and caudal fin rays starting to form; branched melanophores under eye, following along dorsal contour of abdominal cavity, dotting dorsal surface of swim bladder, between posterior-most myomeres; bud of pelvic fin just appearing. Nearly all elements of skull still cartilaginous. Flexion complete, but caudal complex poorly developed; cartilaginous buds of caudal skeleton appearing. Body filled with gelatinous matrix ("mucinous pouch"), which decreases quickly in Stage 2 (Section 1.6). Gills nonfunctional (filaments poorly developed, lamellae absent). Gut straight, esophagus and intestine divided by constriction at anterior ≈ 60% of SL; swim bladder connects immediately anterior to this constriction. At full length, gill filaments still poorly developed; no lamellae present.

Even at end of Stage 1, organismal development of the Pacific tarpon appears retarded compared with leptocephali of other genera (Tsukamoto and Okiyama 1997), and the same could be said for the Atlantic species. Visual and olfactory systems comparatively less advanced in Stage 1. Vision probably excludes formation of images, although differences in illumination are detectable. The nasal cavity is exposed and the anterior and posterior nostrils have not yet formed. Tsukamoto and Okiyama (1997: 31) wrote: "The development of those organs in fully grown leptocephali of Pacific tarpon is similar to that in other marine fish larvae at 2–3 days after hatching, when the yolk-sac is absorbed and the eye pigmented."

*Duration*: According to Tzeng *et al.* (1998), Stage 1 lasts 20–39 days ($\bar{x}$ = 28.5 days).

## Stage 2 – Shrinking leptocephalus

Range ≈ 32–16 mm SL; body remains transparent until near end of Stage 2. Gill lamellae develop as length diminishes, and most components are present at termination of shrinkage. Length of alimentary canal decreases, especially the esophagus. Alimentary canal still straight, but intestine has thickened; stomach is developing. First uroneural and fifth and sixth hypurals ossify; most of caudal skeleton ossifies. At 27.4 mm SL, the Stage 2 Pacific tarpon closely resembles the Atlantic species of 23.0 mm SL. Head now bullet-shaped, HL 11.1, > 1.8 larger than Stage 1 larvae of 28.0 mm SL and equivalent to HL of Stage 2 Atlantic tarpon of 24.5 mm SL. Eye oval, elongated dorsoventrally and occupying a greater proportion of head compared with an Atlantic tarpon of 23.0 mm SL, becoming well developed as Stage 2 proceeds. Snout length as proportion of HL now decreased to 21.9 and also less than in the 23 mm SL Atlantic tarpon. Jaws larger than largest Stage 1 larva, gape now reduced, single nasal aperture, hindbrain anterior to dorsal half of first myomere. Position of fins similar to Atlantic tarpon. Dorsal fin rays 13–14, anal fin rays 22–24 compared to Atlantic tarpon's respective 12 and 20; branching apparent only for last ray of dorsal and anal fins; all but marginal rays of caudal fin are split. Predorsal and preanal myomere

counts 50 and 51, same as largest Stage 1 larva of 24.1 mm SL. Pelvic fins starting to differentiate at myomere 29 (those of Atlantic tarpon develop in Stage 1). Swim bladder larger, rising straight up from gut at myomere 27. Kidney elongated, still attached posteriorly to gut (same as Atlantic tarpon), extending from myomeres 11–35. Pigmentation similar to Atlantic tarpon's, mainly a line of dashes on gut, kidney, base of anal fin, and appearing as scattered spots on caudal fin.

By 21.0 mm SL, percentages of body parts against SL of body are HL 13.4, body height at pectoral fin 8.4, prepelvic 51.6, predorsal 73.8, preanal 80.0. As percentage HL, snout length now 26.4, horizontal eye diameter 25.2. Myomere count 67, 27 prepelvic, 45 predorsal, 49 preanal.

These trends have continued by 15.6 mm SL. Slope of snout less steep, HL has increased to 21.2. Snout length now decreased to 19.7 of HL, eye diameter increased to 28.8 of HL. Body height at pectoral fin increased to 12.1 of body SL. Nares appear as single opaque areas on snout. At minimum size, viscous matter occupies almost half the body. Four gill arches, branchiostegals forming; pigment spots on upper ocular orbit. Body height now greater anterior of anus; median fins longer and higher, last ray of each branched. Dorsal fin origin has shifted posteriorly, its anterior insertion now increased by one myomere. Standard length has increased 3.8%. Insertion point of anal fin unchanged; pelvic fin has increased in size and shape, although change of positon negligible. Caudal peduncle now deeper, seven hypural plates visible; urostyle slender and pointed; lobes of caudal fin more elongated. Body becoming opaque, unlike Atlantic tarpon of comparable size; separation of gut and kidney still visible, beginning at myomere 32 and extending to anus. Swim bladder occupying large area mostly above and anterior to developing pelvic fins. Pigment spots apparent on dorsal surface of gut, ventral border of developing kidney, bases of dorsal and anal fins, caudal peduncle, along midline of body; one dark spot on every myomere.

The remarkable shrinking that occurs during Stage 2 is mediated by thyroid hormones, which in the Pacific tarpon are required for metamorphosis (Shiao and Hwang 2004, 2006). Thiorurea is an anti-thyroid hormone that inhibits production of thyroxine ($T_4$) and triiodothyronine ($T_3$). Leptocephali just entering Stage 2 treated with thyroxine or triiodothyronine showed slightly accelerated metamorphosis. However, those treated with thiorurea entered a metamorphic stasis lasting > 22 days, or a week beyond the normal interval of transformation to Stage 3. Although similar experiments have not been conducted with Atlantic tarpon leptocephali, there is little reason to believe the outcome would be qualitatively different. Time of development (i.e. rate of shrinkage) is unaffected by the environment's ionic strength. The timing until minimum length is attained correlates with completion of metamorphosis. However, otoliths grow continuously, indicating a decoupling of somatic from otolithic growth. Stage 2 leptocephali in captivity tend to swim lower in the water column compared with larvae in Stage 1, and closer to the bottom.

The larva depicted by van Kampen 1909: 10), presumably 22 mm SL (Fig. 1.11) is toothless and probably on the verge of shrinking. I count ≈68 myomeres on the drawing, the number confirmed in different specimens by others (e. g. Delsman 1926: 408 footnote 1, Hollister 1939).

*Duration*: Stage 2 lasts ≈10–14 days (Chen and Tzeng 2006; Chen *et al.* 2008; Shiao and Hwang 2006; Tzeng *et al.* 1998), or the same length of time required for metamorphosis by the Atlantic tarpon. According to Chen *et al.* (2008), its duration is unaffected by whether leptocephali are fed or starved. However, water temperatures that mimic winter (20°C) and summer (30°C), respectively, slow and accelerate metamorphosis slightly. The process generally takes ≈14 days at the optimal temperature of 25°C.

## Stage 3 – Fry

Range 15–40 mm SL. Body length has briefly stabilized at start of Stage 3, but proportional changes in other characters as percentage of SL continue: HL, *H*, body width increase. Length of gill filaments and numbers of lamellae increase. Fin rays become well developed, last ray of dorsal fin elongates, and dorsal and anal fins move anteriorly. Pigments become denser. The intestine coils, and pyloric caeca start forming. Noticeable changes have occurred by 15.0 mm SL (fry, or Wade's Stage IIIA; Wade 1962: 571 Figure 6b, c; 572–573). Jawbones and most elements of hyoid and branchial regions have ossified. Wade described Pacific tarpon "fingerlings" as 36–72 mm SL, but mentioned the term only once and probably borrowed it from Alikunhi and Rao (1951: 107), who referred to fish exactly within this range from the Cooum River, Chennai (Madras), India as "fingerlings." This suggests a fish in Wade's Stage IIIB (equivalent of Stage 4 here), larger and more developed than a fry.

A fish entering the fry stage (Stage 3) has its greatest height anterior of the pelvic fins, its body tapering toward the anal fin and expanding again at the caudal peduncle. Between 15.6 and 15.0 mm SL, this change is dramatic, *H* now 18.7% of SL. The body is thicker than in stages 1 and 2 but still laterally compressed. Overall appearance more fish-like. Eye large and round and, 31.1% of HL, an increase of 5.2% over a Stage 2 specimen of 15.5 mm SL. Snout 3.3% of HL. Both changes as in Atlantic tarpon, but occurring less rapidly. Head length now 30.0% of SL, an increase of 8.8%. Mandible protrudes ventrally to below posterior edge of ocular orbit. Dentary and maxillary bear single rows of fine teeth. Nares not yet bifurcate, appearing as opaque areas on snout. Fins also showing striking changes with pectorals, pelvics displaying rays and increased surface area, pectorals extending two-thirds distance to pelvic, the pelvics extending two-thirds distance to anus. Origin of pelvic fins now slightly behind mid-point of SL. Outline of dorsal and anal fins similar, except posterior border of anal, which is falcate. The dorsal fin has shifted forward from myomere 46 to 34. Along with this anterior shift of the dorsal, the anal fin is now at myomere 44, having decreased 4.8% in distance from snout. Pigmented areas largely unchanged except for addition of spots on median rays of caudal fin.

By 24.2 mm SL (fry), or still Wade's Stage IIIA (Wade 1962: 571 Figure 6C, 573–574), the body is starting to look like that of a juvenile, notable for its increasing height anteriorly. In lateral view it resembles the torpedo-like shape of a 25.2-mm SL Atlantic tarpon. Snout and eye diameter as proportion of head length are also close to proportions of these measurements in Atlantic tarpons of similar length (1.7 and 0.4, respectively). The mouth is large, the maxillary extending down obliquely to where it aligns vertically with posterior border of pupil. In the Atlantic tarpon, this bone reaches to the level of the eye's posterior margin. Predorsal length has decreased 9.6% of SL, while prepelvic distance is now 10% greater. Anterior shifting of the dorsal fin has been become more obvious by the decrease in the predorsal myomere count to 28. Meanwhile the anal fin has also shifted. Pigment spots now found on every fin and scattered sparsely in a patternless manner over all regions of head and body. Scale formation is apparent below the lateral line from opercula to middle of the caudal peduncle. *Duration*: Not reported, to my knowledge.

## Stage 4 – Juvenile

*Meristic description*: The information I found was too sketchy to assemble and report.

*Body proportions as percentage of SL*: At 13.6 mm SL, horizontal eye diameter larger (as percentage of HL) than Atlantic tarpon. *Body proportions as percentage of head length*: At 11.0–21.3 mm HL, snout length 21.8.

*Narrative description*: Stomach enlarges commensurate with decrease in relative length of esophagus. Squamation commences at ≈22 mm SL and spreads anteriorly with growth (Fig. 1.12). At ≈26 mm SL scales develop further,

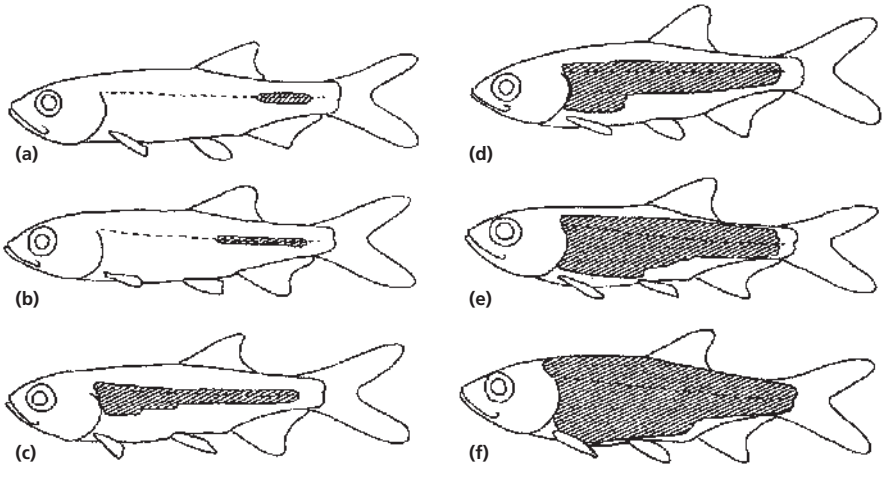


**Fig. 1.12** Sequence of squamation development in Pacific tarpons during the juvenile growth phase. **(a)** 22.4 mm SL. **(b)** 24.3 mm SL. **(c)** 26.2 mm SL. **(d)** 27.0 mm SL. **(e)** 30.0 mm SL. **(f)** 33.5 mm SL. Source: Tsukamoto and Okiyama (1997: 26 Fig. 3).

dorsally and ventrally; by ≈28 mm SL half the body surface is scaled, and squamation is nearly complete at ≈33 mm SL and covering ventral surface by > 35 mm SL; all skull elements ossified by ≈35 mm SL. Shape of head bones as in adult at ≈50 mm SL, but ethmoid still cartilaginous. Most changes in body proportions are finished by ≈20 mm SL, (approximately half the length at which this occurs in Atlantic tarpons), when caudal elements have become ossified and gill formation is complete. Fish now have adult appearance except for incomplete squamation.

*Duration*: Not reported, to my knowledge.

## Stage 5 – Adult Pacific tarpon

*Principal sources used in descriptions:* Boulenger (1909: 27–29); Merrick and Schmida (1984: 53); Pollard (1980: 53).

*Meristic description*: Fin rays: dorsal iv–v 14–16 (total 19–20); anal iii–iv 22–23 (25), total 26–27 (28); pectoral i 14–16; pelvic i 9–10. Gill rakers 14–16 + 29–33 (total 43–49 on first gill arch). Branchiostegal rays 24–27.

*Body proportions as percentage of SL*: Height 26.4–28.6, head length 28.2–30.0, snout length 4.7–7.7, horizontal eye diameter 7.2–7.9, post-orbital 12.6–14.0, inter-orbital 5.1–5.7, upper jaw 13.9–15.9, mandible 15.2–15.3, gular plate length 9.6–11.1, gular plate width 1.3–1.8, pectoral fin 17.1–20.2, pelvic fin 11.1–15.4, predorsal 52.3–57.0, prepelvic 52.3–57.0, preanal 72.4–79.0, last dorsal ray 27.0–30.4.

*Narrative description*: Fins spineless. Body oblong, compressed laterally, eyelids adipose, head moderately sized, snout sharply pointed, mouth large with strongly protruding mandible, tail deeply forked, maxillary extending past posterior border of orbit. Single high dorsal fin with last ray elongated and easily distinguished, about equal to or slightly longer than head length. Pectoral fin long and shallow, pectoral and pelvic fins with long fleshy axillary processes, axillary scales covering approximately two-thirds the length of both fins. Anal fin behind base of dorsal fin and without basal scaly sheath. Pseudobranch not exposed. Lateral line well developed with branched tubes. Scales exceptionally large, cycloid, firmly attached, lateral line distinct with 34–36 scales in lateral series, ≈4 more on caudal peduncle.

Color of back bluish-green to olive, head dark olive, sides silvery, ventral surface white, caudal yellowish, other fins greenish-yellow, dorsal fin with a dusky margin. Fresh specimens from different locations in eastern Africa have been described as having warmer colors: top of head dark brown, fins brownish, caudal and dorsal margins dark, pectoral and pelvic axillary scales speckled light brown. A dark patch on posterior edge of operculum has been reported by some observers, but not others.

*Maximum size and longevity*: According to Ley (2008: 8) the current angling record (weighed but apparently not measured) is a fish ≈611 mm FL (2.99 kg) caught near Gladstone, Queensland, but Ley also reported a 525-mm FL specimen

from the Russell River estuary, Queensland and mentioned a specimen of 610 mm FL caught in the Calliope River near Gladstone. Barnard (1925: 105), without presenting evidence, listed Pacific tarpons as reaching 500 mm. Losse (1968: 81) reported the size of a female specimen from Tanga, Tanzania as 480 mm SL and 5.5 lb (≈2.5 kg). Bell-Cross and Minshull (1988: 42, 91) noted a specimen of 1.361 kg caught by angling at the confluence of the Save and Runde rivers, Zimbabwe, but did not provide a length, and they referred to another caught by an angler in Kenya that weighed 1.8 kg, again without stating its length. Rahman (1989: 236) mentioned adult lengths of Pacific tarpons in Bangladesh as 75–150 cm TL, but provided neither data nor a citation; 1500 mm TL is more than twice the maximum length typically stated. Without citing a source, Munro (1967: 41) wrote that Pacific tarpons reach "at least 40 inches," or ≈1016 mm. Pollard (1980: 53), without presenting evidence, claimed that lengths >1500 mm are attained, echoing Rahman and probably using him as an uncited source. Roughley (1953: 7) claimed that Pacific tarpons in Australian waters grew to 5 ft (≈1525 mm), but did not cite a source. Coates (1987) recorded 440 mm SL (1.5 kg) as the maximum size of specimens obtained from the Sepik River system, northern Papua New Guinea. The smallest was 103 mm (10 g). These lengths were repeated by Allen and Coates (1990: 52–53). Norman and Fraser (1938: 93–97) claimed that Pacific tarpons grow to 3 or 4 ft (≈914–1219 mm) without citing a source. Alikunhi and Rao (1951: 100) mentioned adult specimens >18 in. long (≈457 mm) in the Tamil Nadu region of southeastern India. Thomas (1887: 168) claimed to have seen Pacific tarpons in India measuring one cubit (≈460 mm). According to Shen *et al.* (2009), Pacific tarpons > 600 mm TL are rare in Taiwan. Kulkarni (1983, 1992) described growth of juvenile Pacific tarpons released into two freshwater Indian lakes in 1939. The specimens were not tagged, but intermittent seining over the years showed a near cessation of growth. Some fish caught in 1970 after 32 years were 650 mm TL (2.8 kg). In 1983, after 44 years, seined specimens were 670 mm TL (2.75–3.1 kg). A tarpon subsequently taken in 1991 after 53 years was 670 mm TL (3 kg), indicating no discernible growth in length. I could not find evidence that tarpons of either species living permanently in freshwaters are stunted, and according to Kulkarni (1992), the lakes from which these specimens came contained abundant food. Based largely on his information, I place the maximum length of Pacific tarpons at ≈ 700 mm TL.

## 1.6 Leptocephalus physiology

The leptocephalus is notable in many ways, but its physiology is truly remarkable. During the planktonic, or pre-metamorphic, phase it actually accumulates energy reserves as lipids and glycosaminoglycans, these last formerly called

mucopolysaccharides (Pfeiler 1996). The unusual nature of this adaptation – perhaps unique among fish larvae – is hard to overstate. Although energy budgets of tarpon leptocephali have yet to be studied specifically, those of other species make illuminating proxies, with qualifications. Bishop and Torres (1999) evaluated how energy was partitioned between metabolism and excretion by leptocephali of four species of eels: margintail conger (*Paraconger caudilimbatus*), bandtooth conger (*Ariosoma balearicum*), honeycomb moray (*Gymnothorax saxicola*), and shrimp eel (*Ophichthus gomesii*).

All leptocephali have certain common features. Notable is the transparent, laterally compressed body consisting mainly of gelatinous material. The flattened shape provides a high surface-to-volume ratio, perhaps augmenting physiological exchange processes with the external environment (e.g. gas transfer, exchange of water and ions), and, in at least some species the possible uptake of dissolved organic matter, or DOM (Otake *et al.* 1990, 1993), common in many marine invertebrates (Pfeiler 1986). Uptake of DOM could thus be *per os*, by passive transfer across the integument, or through active carrier-mediated transfer linked with $Na^+$ (Fig. 1.13). A thin epidermis only a few cells thick possibly facilitates these functions (Pfeiler 1999 and references). Evidence of exogenous feeding, however, has been mostly inferred: in the Japanese eel (*Anguilla japonica*) leptocephalus, starvation after a certain amount of time appears to stimulate onset of metamorphosis (Okamura *et al.* 2012).

Fish larvae typically absorb the yolk sac soon after hatching and start to feed. Growth then continues to the juvenile stage. Alternatively, after yolk-sac absorption,

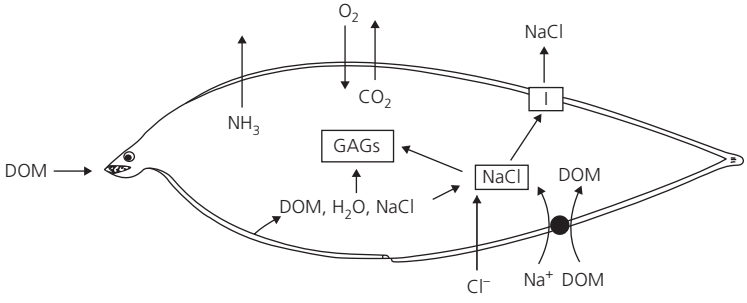


**Fig. 1.13** Model postulating mechanisms of nutrient acquisition, $Na^+$ and $Cl^-$ fluxes, and gas exchange in elopomorph Stage 1 leptocephali. The large, laterally-compressed body offers a high surface-to-volume ratio, favoring cutaneous respiration (the gills are not yet developed) and different pathways for possible uptake of dissolved organic matter (DOM). A portion of the $Na^+$ and $Cl^-$ that enter passively by diffusion, including via $Na^+$-DOM cotransport involving specific carrier proteins (filled circles), and by intestinal absorption (along with water and ingested DOM, is bound to acidic glycosaminoglycans (GAGs). Some NaCl is probably transported actively out of the body by means of ionocytes (I) in the integument (see Chapter 6.3). Water and NaCl of leptocephali increase as GAG concentrations in the extracellular gelatinous body matrix rise during Stage 1 growth. The integument is also an important site of ammonia (designated here as $NH_3$) excretion. Source: Pfeiler (1999: 118 Fig. 2).

the larva grows unusually fast, often without an evident source of nutrients or sensory and anatomical systems sufficiently developed to locate and process food. Proposed energy sources include dissolved and particulate organic matter (Pfeiler 1986). Depending on species, leptocephali can remain in the plankton for days, months, or years, and they comprise the Albuliformes (bonefishes), Anguilliformes (eels), Elopiformes (tarpons and ladyfishes), Notacanthiformes (spiny eels), and Saccopharyngiformes (gulper eels). After absorbing the yolk sac the planktonic leptocephali of these five related orders, like other larvae, grow to species-specific, pre-metamorphic sizes. *However, unlike "conventional" fish larvae they accumulate energy reserves instead of expending them for immediate use*.

According to Pfeiler (1986), these reserves consist of a gelatinous matrix, or "mucinous pouch," extending almost the whole length of the body and comprising lipids and glycosaminoglycans. During Stage 1 the matrix serves as structural support in place of the absent vertebral column. During Stage 2 shrinkage, metamorphosis consumes these compounds, and they serve as the foundation for developing bones and muscles (Pfeiler 1984, 1986, 1996, 1999 and references) in a metabolic sequence apparently universal in leptocephali regardless of species (Deibel *et al.* 2012). The gelatinous matrix might also serve in buoyancy regulation during Stage 1, considering that the swim bladder does not become functional until metamorphosis (Pfeiler 1999 and references).

The normal situation is for organisms to experience a rise in whole-body respiration with increased body weight, but not leptocephali, for which no correlation is evident between mass and any index of metabolism, making them unique. Production of feces would seem unlikely for a life-stage that lacks the ingestion-digestion-excretion apparatus to process solid food. Most fishes are ammonotelic, excreting waste nitrogen as ammonia (Chapter 6), and leptocephali are no different (Bishop and Torres 1999; Pfeiler 1996). Bishop and Torres (1999) reported the rate of ammonia excretion to decline with increasing body weight and was highest in larvae ≤ 0.50 g ($n$ = 51). Heavier larvae demonstrated excretion rates that were specific to wet weight and stayed more or less constant as weight increased.

Weight-specific consumption of oxygen (i.e. relative oxygen consumption rate, $\dot{M}O_{2w}$) fell steeply with increasing body weight when a power function was applied:

$$\dot{M}O_{2w} = aW^{b} \tag{1.2}$$

Here $a$ is a scaling constant (i.e. the allometric coefficient, or intercept), $W$ represents body weight, and $b$ is the scaling exponent. Larvae < 0.20 g wet weight showed the greatest changes in $\dot{M}O_{2w}$. Depending on the value of $b$, relative metabolic rate as $\dot{M}O_{2w}$ regressed against body weight is either allometric and curved ($b \neq 1$) or isometric and linear ($b = 1$). In isometric relationships, metabolic rate and body weight scale in direct proportion; that is, in a straight line.

In conventional fish larvae, energy taken in is mostly expended with little being stored, making large and small larvae about equal in vulnerability to starvation. Overall, according to Bishop and Torres (1999: 2490), "a lower proportion of the mass of the leptocephalus is invested in metabolizing tissue than in other larval fish." This is certainly unusual, to which can be added that the energy reservoir (glycosaminoglycans) doubles as a pseudo-skeleton, permitting efficient propulsion in the absence of a bony scaffold, "and without appreciable metabolic costs other than that needed for acquiring and depositing the glycosaminoglycans." These authors found a sharp negative relation between increasing body weight and the weight-specific rate of $O_2$ consumption, excretion rate, and enzymatic activity in four species of eel leptocephali. The result was a substantial drop in metabolic rate with increasing size. They wrote (Bishop and Torres 1999: 2485): "The result suggests that the proportion of actively metabolizing tissue also declines with size, being replaced in large measure by the metabolically inert energy depot, the glycosaminoglycans." Their conclusion was that, "Leptocephali can thus grow to a large size with minimal metabolic penalty, which is an unusual and successful developmental strategy."

The combination of glycosaminoglycans and lipids is the impetus for rapid, low-budget growth, providing a fuel dump poised to fund the metabolic expense of impending metamorphosis. Mercado Silgado (1971: 14) speculated correctly when stating, "*Se cree pueda ser por ósmosis o reabsorción de tejidos, en todo caso, existe una disminución de tamaño, cuando no se ha formado su sistema digestivo, lo que hace pensar en el autoconsumo.*" [It (feeding) is thought to be by osmosis or reabsorption of tissues, although in any event size decreases before the digestive system has formed, indicating self-consumption.] Death by starvation is less likely when you *are* your own food, a situation that only gets better with increasing size when metabolism declines drastically instead of increasing as expected. For a leptocephalus, bigger is unquestionably better.

Atlantic tarpons in Stage 1 and early Stage 2 apparently do not feed exogenously (Dahl 1965; Harrington 1966). Feeding does not commence until Stage 2 (Phase VIII of Mercado Silgado 1971 and Mercado Silgado and Ciardelli 1972), or the approximate equivalent of Wade's (1962) Stage IIIA (also see Chapters 1.6, 7.7, Appendix B). This occurs at or near the end of metamorphosis during drastic shrinkage when the ribbon-like form becomes torpedo-shaped, simultaneously losing much of its surface area.

Stage 2 reveals enhanced development of organ, sensory, and structural systems; the epidermis thickens and becomes less permeable. The gelatinous matrix that served as structural support in Stage 1 is replaced by bony vertebrae and muscles; stiffening fin rays have attained their adult numbers. Stage 2 is relatively short, and during its progression the gelatinous matrix is quickly resorbed. Some leptocephali (those of the white-spotted conger eel, *Conger myriaster*, for example) convert the glycosaminoglycan component hyaluronan (which aids in control of water content) to glucose during metamorphosis, which might

then be metabolized to glycogen and stored for use in further ontogenesis (Kawakami *et al.* 2009).

The matrix of bonefishes (*Albula* spp.) early in Stage 2 consists of sulfated keratan glycosaminoglycan (Pfeiler 1984, 1986, 1996; Pfeiler *et al.* 1991) in the form of repeating disaccharide chains displaying dominant anionic charge densities. Its complement in the Atlantic tarpon is heparan glycosaminoglycan and, in the ladyfish (*Elops saurus*), a form of chondroitin sulfate (Pfeiler *et al.* 1991). Glycosaminoglycans cause water retention and influence the distribution of ions, including sodium. Water content of some Stage 1 leptocephali is therefore >90% of total weight (Pfeiler 1986 and references). In bonefishes undergoing metamorphosis and not yet feeding, water and carbohydrate content both decrease ≈80% over 10 days or so in step with simultaneous loss of the gelatinous matrix (Pfeiler 1986, 1999). Although protein remains constant, the amount of collagen, lipid, and ash diminish by half. These events are indication of water accumulation during Stage 1. As Pfeiler (1986: 7) stated: "To argue otherwise would require that the recently hatched leptocephalus contain an amount of water equal to that of a fully developed Phase [stage] I leptocephalus …." In other words, 10 times the whole-body wet weight at hatching.

Total glycosaminoglycans in bonefishes declines ≈87% during Stage 2 (Pfeiler 1984), which probably accounts for the substantial losses of water, sodium, and chloride. This reasoning assumes that glycosaminoglycans are synthesized during Stage 1, which they almost certainly are. As Pfeiler (1986: 7) wrote: "Again, to argue otherwise would require a high [glycosaminoglycan] content in recently hatched embryos which remains constant during the time when larvae form an extensive amount of gelatinous matrix."

Pfeiler (1986) outlined a hypothetical model. After the yolk sac has been consumed, Stage 1 leptocephali generate large quantities of gelatinous material, presumably a result of glycosaminoglycan synthesis. One consequence is water loading without altering the percentage of water to total wet weight (i.e. it remains balanced at ≈ 90%). Salt loading occurs simultaneously. Both are probably associated with the synthesis of polyanionic glycosaminoglycans (Pfeiler 1986, 1999). The strong anionic charge in the matrix drives the uptake and accumulation of sodium and chloride from the surrounding seawater. As Stage 2 ends and metamorphosis begins, glycosaminoglycans are catabolized, destabilizing tissue water and salt concentrations, which are then diminished through loss to the external environment.

But what about front-end loading? What serves as raw material for glycosaminoglycan synthesis, and where does it originate? As Pfeiler argued, that such large amounts of finished glycosaminoglycans could be retained in the yolk sac throughout Stage 1 until onset of Stage 2 is unlikely. As mentioned, DOM is the most likely raw material, its uptake enhanced by a high surface-to-volume ratio of the leptocephalus' flattened form. The conspicuous teeth, which Pfeiler (1986: 8) rightly called "enigmatic structures," warrant mention too. Their size and shape

could easily mark them as the teeth of a planktonic predator, but this is apparently not the case. The teeth are resorbed or lost prior to metamorphosis when feeding on live prey starts. A function has not been identified (Pfeiler 1999).

The Stage 1 leptocephalus of tarpons has yet to acquire functional digestive and excretory systems, and identifiable food material that might properly be called "prey" (e.g. live plankton) has not, to my knowledge, been found in the gut of a first-stage leptocephalus of either species of tarpon. Leptocephali of some eels that remain in the plankton for extended periods are suspected of consuming "marine snow," including discarded appendicularian houses rich in microorganisms, zooplankton fecal pellets, and other forms of particulate organic matter (Deibel *et al.* 2012; Miller *et al.* 2011, 2013; Otake *et al.* 1990, 1993). In other words, those leptocephali that feed do so at a lower trophic level at which minimal energy is expended (Pfeiler 1999). Stage 1 leptocephali in general have low metabolism, meaning their demand for energy is low too (Pfeiler and Govoni 1993). Whatever their source of energy – dissolved or particulate organic matter, stored lipids or glycosaminoglycans – little is required to sustain metabolic functions. In any case, that bonefish, ladyfish, or tarpon Stage 1 leptocephali ingest exogenous matter is doubtful.

The contribution of free amino acids to energy reserves of larval bonefishes is minor (Pfeiler 1996). The combination of endogenous carbohydrate (principally keratan glycosaminoglycans) and lipid fuels metamorphosis during Stage 2, contributing, respectively, ≈ 20% and ≈ 80% of the overall energy budget (Pfeiler 1984, 1986, 1996). This adaptation diverges from the typical situation in which the yolk provides stored energy as lipid and protein until feeding begins, and carbohydrate contributes little (Pfeiler 1986). Growth in these other fishes is minimal through the yolk-sac phase, seemingly held in abeyance, commencing once feeding begins and proceeding uninterrupted to the juvenile stage. And DOM? Any contribution to metamorphosis is doubtful, at least to metamorphosing bonefish larvae. Unfed specimens kept in nutrient-free artificial seawater containing only inorganic compounds survived and developed normally (Pfeiler 1996). Whether dissolved organic compounds are taken up from the sea during Stage 1 and used as precursors of glycosaminoglycans or immediate energy sources is yet to be determined.