TARPONS

BIOLOGY, ECOLOGY, FISHERIES

STEPHEN SPOTTE

WILEY

Tarpons

Tarpons

Biology, Ecology, Fisheries

Stephen Spotte

Mote Marine Laboratory
Sarasota, Florida, USA

WILEY

This edition first published 2016, © 2016 by John Wiley & Sons, Ltd

Registered Office
John Wiley & Sons, Ltd, The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK

Editorial Offices
9600 Garsington Road, Oxford, OX4 2DQ, UK
The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK
111 River Street, Hoboken, NJ 07030-5774, USA

For details of our global editorial offices, for customer services and for information about how to apply for permission to reuse the copyright material in this book please see our website at www.wiley.com/wiley-blackwell.

Library of Congress Cataloging-in-Publication Data

Names: Spotte, Stephen, author.
Title: Tarpons : biology, ecology, fisheries / Stephen Spotte.
Description: Chichester, UK ; Hoboken, NJ : John Wiley & Sons, 2016. | Includes bibliographical references and index.
Identifiers: LCCN 2016003051| ISBN 9781119185499 (cloth) | ISBN 9781119185703 (epub)
Subjects: LCSH: Tarpon. | Tarpon fisheries.
Classification: LCC QL638.M33 S66 2016 | DDC 597.5/7–dc23
LC record available at http://lccn.loc.gov/2016003051

A catalogue record for this book is available from the British Library.

Wiley also publishes its books in a variety of electronic formats. Some content that appears in print may not be available in electronic books.

Cover image: Atlantic Tarpon © 1992, Diane Rome Peebles

Set in 9.5/13pt Meridien by SPi Global, Pondicherry, India

1 2016

Contents

Preface

Two species of tarpons exist today, one in the Atlantic (*Megalops atlanticus*), the other *(M. cyprinoides*) in the Indo-West Pacific region. The name "tarpon," or "tarpom," is apparently of New World origin. The Englishman William Dampier encountered tarpons on his first voyage to the Bay of Campeche (which he called Campeachy), México, and his mention of the Atlantic tarpon is one of the earliest. Dampier wrote about the fish in his journals in 1675 and later included these entries in the account of his voyages around the world. The copies of *Dampier's Voyages* cited here are early twentieth-century editions edited by the poet John Masefield, but earlier versions were published in the seventeenth and early eighteenth centuries. In Volume II, Dampier (1906: 117–118) stated: "The Tarpom is a large scaly Fish, shaped much like a Salmon, but somewhat flatter. 'Tis of a dull Silver Colour, with Scales as big as a Half Crown. A large Tarpom will weigh 25 or 30 Pound." Because of their extensive distributions, both species have numerous other common names in many languages.[1] For simplicity, I refer to them as Atlantic and Pacific tarpons. The Pacific species is also called the Indo-Pacific tarpon and oxeye (or ox-eye), or sometimes oxeye (ox-eye) tarpon or herring.

Atlantic tarpons grow large, reaching 2.5 m and weighing 150 kg. The Pacific species is comparatively small, attaining only 0.6 m and 3 kg, although unsubstantiated reports exist of specimens three times this length (Seymour *et al.* 2008 and references). Despite the size disparity, their morphology, physiology, ecology, developmental biology, and other life-history features are so similar that I often found little justification for separate treatments, although I have separated them when possible for clarity. In some instances, such as discussion of distributions, I was handicapped by limited access to literature on the Pacific form.

Previous books have concentrated on just a few aspects of tarpon biology or restricted discussion to the Atlantic tarpon recreational fishery. My objective is to cover these and other topics without being too tiresome. The angling aspect presented (Chapter 8) is not about how to catch tarpons but how to conserve them and, if you must catch them, how best to do so with minimal stress to the fish and then release it in a manner offering the best chance of long-term survival.

My presentation of tarpon biology derives from a broad perspective, one in which I hope to assess the tarpon's unique life-history in terms of fishes generally.

---

[1]See, for example: http://www.catalogueoflife.org/col/details/species/id/17963572; http://eol.org/pages/339927/names/common_names; http://www.catalogueoflife.org/col/search/all/key/Megalops

Books like this are usually written by groups of specialists, the result being a series of chapters in which different aspects are partitioned, handed to separate authors, and subsequently treated in isolation. The result is often uneven, redundant, incompletely integrated, and fails to view the subjects themselves – tarpons in this case – as entities ruled by common natural forces for which data from more extensively studied species can sometimes apply just as well. Every biography is, in the end, a narrative of heritage and commonality.

My objective as a single author is to provide a cohesive picture of tarpon biology, ecology, and fisheries in which specialty aspects usually compartmentalized (e.g. physiology, larval development) blend at the edges and reinforce one another. I hope to accomplish this without loss of accuracy. For example, variations on the cube law used to practical advantage in fishery biology for predicting length and weight of individual fishes and assessing the condition of populations also apply theoretically to certain facets of water circulation in the buccal cavity (i.e. lamellar length scales isometrically with body weight). To receive full benefit of this integrative approach, chapters need to be read in sequence. This book, like my others, has been designed to be read, not consulted. Skipping through the text and examining sections out of sequence is guaranteed to be less satisfying. The reader has been duly advised, and I offer no apologies.

Symbols and abbreviations are generally defined at first use, but a roster of them is provided in the book's front matter. Background information necessary to understand certain concepts is given either superficially in the text or, if more detail is necessary, in occasional footnotes. The presentation overall assumes a certain advanced level of knowledge.

An early anonymous reviewer made the reasonable suggestion that I include a section on tarpon evolution. However, not being an ichthyologist I felt uncomfortable doing so. I therefore left this subject and certain other avenues of specialization (e.g. detailed aspects of tarpon skeletal anatomy) to the experts. I take a systems approach instead, integrating functional biology with ecology, and discussing both disciplines in terms of effects caused by humans in the recreational and commercial fisheries at both the individual and population level. Only a few reports exist on tarpon physiology, although other species can safely be used as proxies at the system and even cellular level, at which point any differences are of degree, not kind.

Tarpons are distributed widely throughout subtropical and tropical waters around the world. Appendix A at the end of the book comprises a partial list of countries from which both species have been recorded in the literature. Pusey *et al.* (2004) provided an outstanding short summary of the Pacific tarpon's natural history. Nothing I found on the Atlantic species in the recent literature matches it for brevity and completeness. Hildebrand's (1963) treatment came closest, but his information is outdated.

The Atlantic tarpon ranges north to Nova Scotia and south to Brazil. Some authors extend its southern range to the coast of Argentina (e.g. Castro-Aguirre

et al. 1999: 89; Gill 1907: 36; Hildebrand 1963: 119), although I was unable to find a published record of its presence in either Uruguay or Argentina (e.g. Bouyat 1911 did not mention it). The warm, south-flowing Brazil Current stops at the mouth of the Río de la Plata, and the sea beyond, including off Patagonia, is temperate. It seems that any Atlantic tarpons found there could only be stragglers from Brazil.

Reports about the tarpon in the eastern Atlantic are uncommon in the refereed literature, aside from its inclusion in species lists or as notes mentioning its appearance in regional ichthyofauna. Tarpons in the eastern Atlantic range north to the Formigas, a group of small islands in the eastern Azores (Costa Pereira and Saldanha 1977) and the inshore waters of continental Europe including the Tagus River estuary of Portugal (Costa Pereira and Saldanha 1977), the Lee River of Cork County, Ireland (Twomey and Byrne 1985; Wheeler 1992), and the French Basque coast (Quero *et al.* 1982: 1022–1025). I could not find specific mention of Atlantic tarpons entering the Mediterranean, but surely they have.

Minimum water temperatures probably influence the distributions of Atlantic tarpons (Killam (1992: ix). Costa Pereira and Saldanha (1977) pointed out that north of Sénégal and south of Angola sea temperatures begin to cool and salinity rises, conditions they believed restrict the tarpon's latitudinal range in the eastern Atlantic. These regions are characterized by heightened rates of surface evaporation, lower seasonal rainfall, and weak fluvial flow into the Atlantic, factors that combine to keep coastal salinity values high and perhaps discourage inshore migration of metamorphosing tarpon larvae. Lower sea temperatures both to the north and south are the result of increasing latitude. The only elopiform listed by Penrith (1976) from Namibia and all of South Africa's western coast was the bonefish (*Albula vulpes*). Evidently this region falls outside the Atlantic tarpon's southern latitudinal range.

Costa Pereira and Saldanha (1977) did not mention that between Sénégal and Angola, where the "skull" of the African continent curves eastward, are sandwiched 13 countries with coastlines characterized by warm seas, high seasonal rainfall supporting tropical forests, mostly strong fluvial flow, an abundance of swamps and brackish lagoons, and other environments favorable for tarpons. The Atlantic tarpon's range is likely to be extended to southeast Asia at some future time now that specimens have been imported into Thailand and released into recreational fishing reservoirs (Chapter 7.2). Some individuals will inevitably escape into coastal waters or be released there. Atlantic tarpons are already established on the Pacific coasts of Panamá and Costa Rica,[2] having traversed the Panamá canal after its opening in 1914 (Anonymous 1975; Hildebrand 1939).

The Atlantic tarpon is essentially a straggler outside the subtropics, but the Pacific tarpon's normal range north and south seems broader, perhaps extending

[2] http://www.ticotimes.net/2011/07/06/tarpon-on-the-pacific-coast-you-betcha. Downloaded 18 July 2015.

Table 0.1 Length-length, length-weight, and otolith weight-age regressions for Atlantic tarpons from south Florida waters. Values of length in mm, weight (*W*) in kg, otolith weight (O*W*) in g, age in years (y). Length range for length-length regressions = 106–2045 mm FL; length range for length-weight regressions = 102–2045 mm FL; age range for O*W* weight-age regressions = 1–55 years (females) and 1–43 years (males). Source: Crabtree *et al.* (1995: 624 Table 2).

y	*x*	*n*	*a*	SE	*b*	SE	r^2
FL	SL	1342	10.8404	±0.6339	1.0423	±0.0007	0.999
FL	TL	1061	–10.8096	±0.8084	0.8967	±0.0007	0.999
SL	FL	1342	–9.9770	±0.6131	0.9588	±0.0007	0.999
SL	TL	1051	–21.1779	±1.0181	0.8606	±0.0009	0.999
TL	FL	1061	12.6345	±0.8937	1.114	±0.0009	0.999
TL	SL	1051	25.5839	±1.1622	1.1607	±0.0012	0.999
$\log_{10}W$	$\log_{10}$FL	1262	–7.9156	±0.0124	2.9838	±0.0045	0.997
$\log_{10}$O*W* (females)	$\log_{10}$*Age*	193	–1.2083	±0.0199	0.5476	0.0152	0.872
$\log_{10}$O*W* (males)	$\log_{10}$*Age*	106	–1.1734	0.0183	0.4614	0.0162	0.886

routinely into temperate waters. Wade (1962: 593) gave a latitudinal range in the western Pacific as Hamana Lake, Totomi Province, Japan (34.7°N, 137.6°E) to Victoria, Australia (≈37.0°S, 144.0°E). East to west, the species ranges halfway across the globe, from Tahiti in the Society Islands (17.7°S, 149.4°W) to Durban, South Africa (29.9°S, 31.0°E). Wade (1962: 594) gave its epicenter of abundance as the region encompassing "India, Ceylon, the Malay Archipelago, East Indies, southern Philippine Islands, and Polynesia." Ley (2008: 3) offered a similar range: 28°N (Japan) to 35°S (southern Australia and South Africa) and 25°E (east African coast) eastward to 171°W (Samoa). Most records of Pacific tarpons in the literature are from the Philippines and India (35% combined).

How the length of a fish is determined requires comment, because the terms defined in this paragraph are used throughout the book. A fish can be measured and its length expressed in several ways: *standard length*, SL (tip of the snout to end of the last vertebra); *fork length*, FL (tip of the snout to where the center-most rays of the caudal fin terminate); *total length*, TL (tip of the snout to end of the caudal fin, sometimes with the lobes compressed so they extend to maximum length); and *notochord length*, NL in early larvae, equivalent to standard length before skeletal development. If enough specimens of a species have been measured using SL, FL, and TL, any of these measures can be converted to the others, as shown for the Atlantic tarpon (Table 0.1). To Breder (1944: 219), TL was measured with the caudal fin lobes spread, and *overall length* was the term he used when they were compressed. I consider this to be TL too. In either case, TL includes the length of the caudal fin, and the literature is seldom specific about which method was used.

Acknowledgements

I thank the authors and publishers who allowed me to reproduce their figures and tables, and I thank Mote Marine Laboratory for use of facilities. I am grateful to Patricia E. Anyanwu of the Nigerian Institute for Oceanography and Marine Research for information on aquaculture of Atlantic tarpons, Michael Spotte for assisting with preparation of the figures, and Lucia Spotte for her patience and good humor while this work progressed. Special thanks is extended to Alyson Gamble, former Librarian at Mote's Arthur Vining Davis Library and Archives for her unwavering enthusiasm about all things academic, and for energetically tracking down obscure references, pursuing some of them literally to the ends of the Earth.

Symbols and abbreviations

≈	approximately
<	less than
≠	unequal
>	greater than
≤	less than or equal to
≥	greater than or equal to
°C	degree(s) Centigrade
µ	micro
µm	micrometer (micron)
µmol	micromole
A	age (days)
ABO	air-breathing organ (physostomous swim bladder)
AC(s)	accessory cell(s)
ASB	aquatic surface-breathing
bp	(years) before present
CC(s)	chloride cell(s)
CFTR	cystic fibrosis transmembrane conductance regulator
CI	confidence interval (statistics)
cm	centimeter(s)
COX2	cyclooxygenase type 2
d	day(s)
df	degrees of freedom (statistics)
DOM	dissolved organic matter
dph	day(s) post-hatch
F	fecundity
f_{ab}	air-breathing frequency (per unit time)
f_H	heart rate (beats per unit time)
fl	femtoliter(s) (10^{-15} l)
FL	fork length
g	gram(s)
G	growth (somatic)
GH	growth hormone
GSI	gonadal-somatic index
H	body height at its highest point
h	hour(s)
HA	H^+-ATPase
Hb	deoxygenated hemoglobin (g/l)

HbO_2	oxygenated hemoglobin (g/l)
Hct	hematocrit (%)
HL	head length
H_o	mean observed heterozygosity
H_s	genetic diversity value[1]
IGF-1	insulin-like growth factor 1
in.	inch(es)
kg	kilogram(s)
kPa	kilopascal(s)
L	body length (as FL, NL, SL, or TL)
L	liter(s)
lb	pound(s)
m	meter(s)
M	molar
MCH	mean cell hemoglobin (pg)
MCHC	mean corpuscular hemoglobin concentration (g/l)
MCV	mean corpuscular volume (fl)
min	minute(s)
mL	milliliter(s)
mm	millimeter(s)
mmol	millimole
$\dot{M}O_{2air}$	rate of oxygen uptake from air or ABO (mL/kg/min
$\dot{M}O_{2w}$	rate of oxygen uptake from water (mol/kg/min)
mol	mole
mOsm	milliosmole
MRC(s)	mitochondria-rich cell(s)
mRNA	messenger ribonucleic acid
ms	millisecond(s)
n	sample size
ng	nanogram
NHE	Na^+/H^+ exchanger
NKA	Na^+/K^+-ATPase
NKA1	secretory form of NKA
NKCC	$Na^+/K^+/2Cl^-$ co-transporter
NKCC1	secretory isoform of NKCC
NL	notochord length
Osm	osmole
OSTF1	osmotic transcription factor 1
OW	Otolith weight
oz	ounce
P	partial pressure
p	probability

[1] Nei's unbiased gene diversity across all loci.

P_{50}	PO_2 at which 50% of Hb is bound to O_2 (HbO_2)
P_a	partial pressure in arterial blood
Pa	pascal(s)
PAT(s)	pop-up archival transmitting tag(s)
pg	picogram (10^{-12} g)
pH_{cv}	caudal venous pH
ppt	parts per thousand
P_v	partial pressure in venous blood
PVC(s)	pavement cell(s)
P_w	partial pressure in water
$\dot{Q}$	cardiac output (ml/min/kg)
r^2	coefficient of determination
RBC	red blood cells (10^6/μl)
Rh(cg)	rhesus glycoproteins
Rhag	Rh-associated glycoprotein (ammonia transporter)
Rhbg	Rh-associated glycoprotein (ammonia transporter)
Rhcg	Rh-associated glycoprotein (ammonia transporter)
RSI	ram-suction index
S	salinity (mg/kg of seawater)
s	second(s)
S_A	absolute salinity scale (mg/kg of seawater)
SA	body surface area
SD	standard deviation
SE	standard error (slope of the regression)
SEM	standard error of the mean
SEM	standard error of the mean
SL	standard length
S_P	practical salinity scale (no units)
Su	Survivorship
TF2B	(osmotic) transcription factor 2B
TL	total length
TTPG	time to peak gape
U_{crit}	critical swimming speed (l/s)
V_{ab}	volume of a single breath of air
V_{ABO}	ABO volume (ml/kg)
vol%	vol/total vol × 100
V_R	(aquatic) ventilation rate (opercular pumps/min)
V_S	cardiac stroke volume (ml)
W	body weight, or mass (g)
W_r	relative weight (g)
y	year(s)
Σ	sum
$\overline{X}$	mean, or average
Z	Rayleigh's test of circular distributions

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

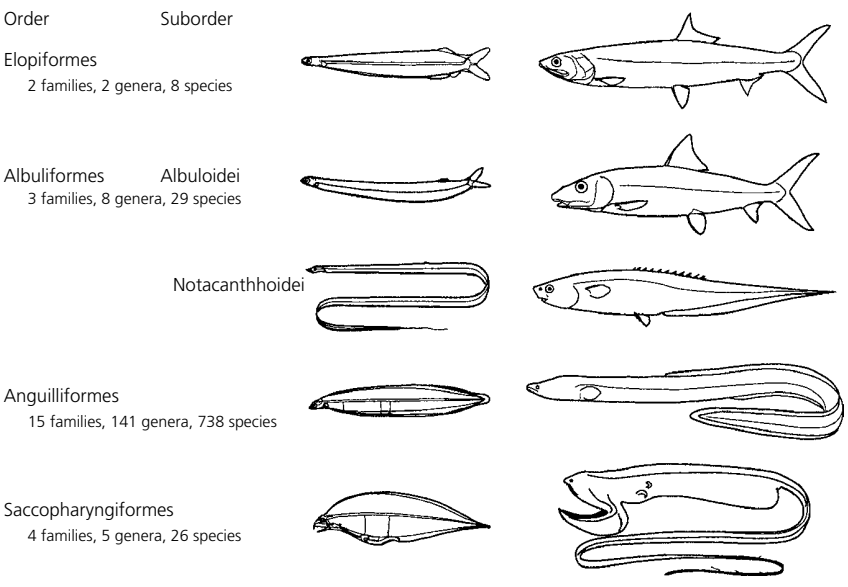

Fig. 1.1 Higher-level classification of orders in the Elopomorpha along with numbers of taxa presently included. Representative larval and adult body forms are illustrated for each group. The Elopiformes, to which the two extant species of tarpons (*Megalops atlanticus* and *M. cyprinoides*) belong,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

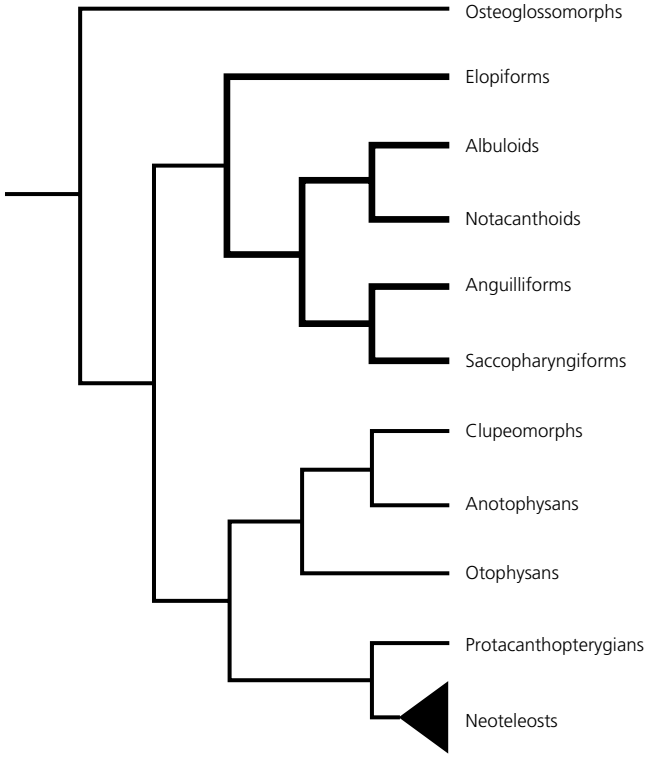

Fig. 1.2 A modern phylogenetic hypothesis about the monophyly of Elopomorpha. See source publication for history and details. Source: Inoue *et al.* (2004: 276 Fig. 2B).

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.

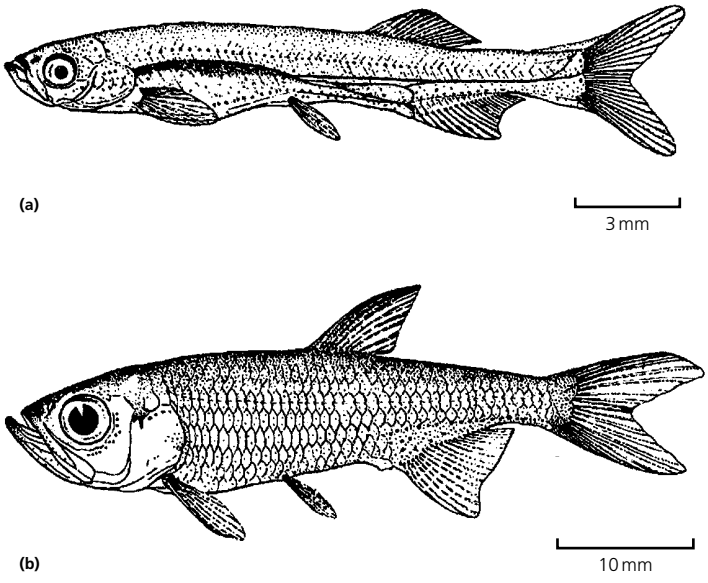

Fig. 1.3 **(a)** Atlantic tarpon fry, Stage 3 phase X (16.9 mm SL). **(b)** Atlantic tarpon in late Stage 3 (41.0 mm SL) approaching the end of allometric growth. Source: Mercado Silgado and Ciardelli (1972: 181, Fig. 10A, B).

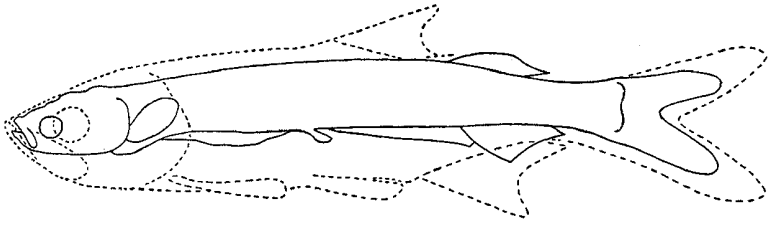

Fig. 1.4 Profiles of an Atlantic tarpon 36.8 mm SL (broken lines) and an earlier specimen of 16.0 mm SL (solid lines), the second superimposed onto the first and enlarged proportionately so that standard lengths of the two illustrations coincide. Source: Harrington (1958: 5 Fig. 2).

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).

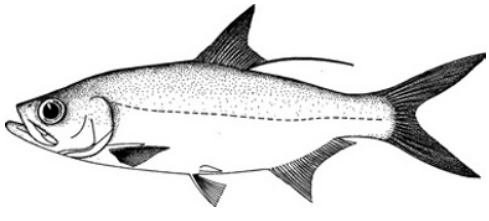

Fig. 1.5 Illustration of an adult Pacific tarpon showing the elongated last ray of the dorsal fin. Source: Food and Agriculture Organization of the United Nations. 1984. Bianchi (1984: 3). *Field Guide: Commercial Marine and Brackish Water Species of Pakistan* by G. Bianchi. FAO Species Identification 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.

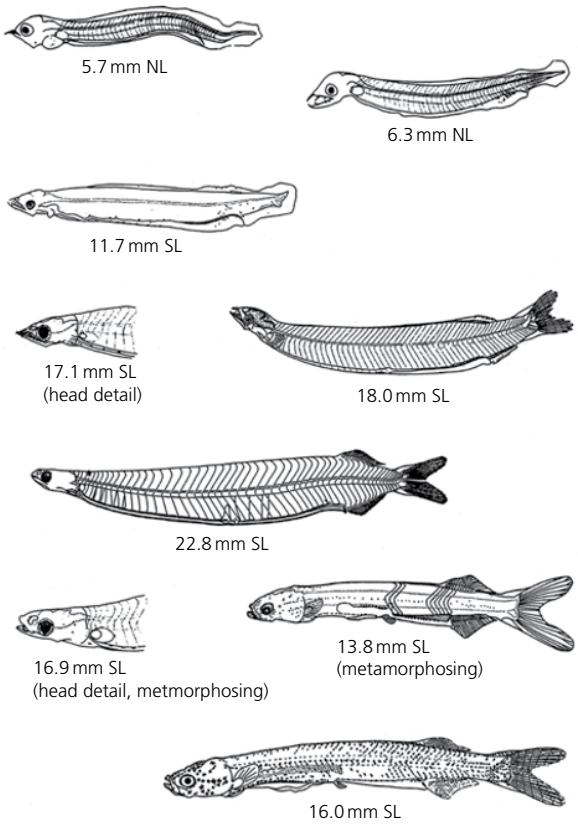

Fig. 1.6 Stages 1 and 2 Atlantic tarpon larvae. Source: Fahay (2007: 13). © Northwest Atlantic Fisheries Organization. Reproduced with permission.

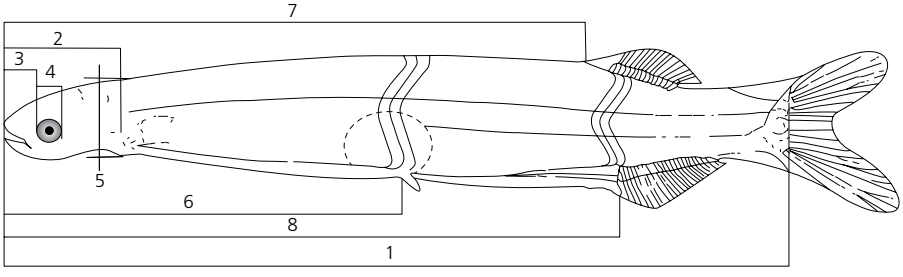

Fig. 1.7 Atlantic or Pacific tarpon larva, depicting where some (but not all) measurements are typically taken. Numbers indicate the following measurements (mm) or counts (9–15 not illustrated): 1 – *standard length* (SL); 2 – *head length* (HL) tip of snout to posterior fleshy margin of operculum; 3 – *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).

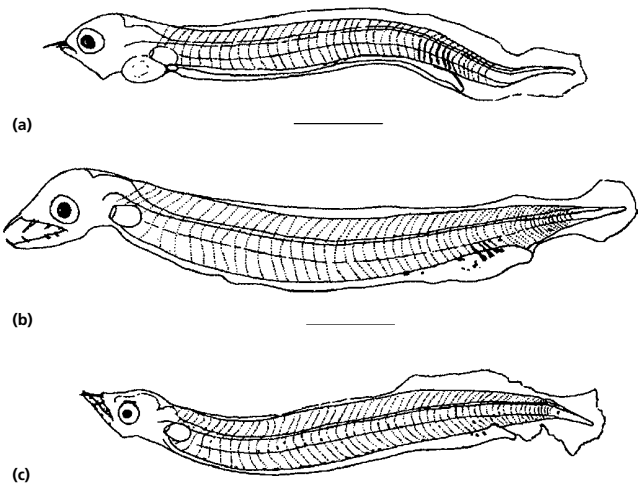

Fig. 1.8 Early Stage 1 Atlantic tarpons from the Yucatán Channel, Mexican Caribbean, and Gulf of Mexico (exact collection locations unclear). **(a)** 5.7 mm NL, **(b)** 6.3 mm NL, **(c)** 8.1 mm NL). Scale bars = 1 mm. Source: Smith (1980: 138 Fig. 2).

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