Life history demographic parameter synthesis for exploited Florida and Caribbean coral reef fishes

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SEDAR80-RD-08

January 2022

Received: 11 April 2019 | Revised: 31 July 2019 | Accepted: 14 August 2019

DOI: 10.1111/faf.12405

ORIGINAL ARTICLE

FISH and FISHERIES WILEY

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Funding information
Biscayne National Park, Grant/Award Number: P15AC01746; Dry Tortugas National Park, Grant/Award Number: P15AC012441 and P16AC01758; Florida RESTORE Act Center of Excellence, Grant/Award Number: FIO-4710112600B; National Park Service Natural Resource Conservation Assessment Program, Grant/Award Number: H5000105040, PA15AC01547 and PA16AC01758; NOAA Southeast Fisheries Science Center & Coral Reef Conservation Program, Grant/Award Number: NA15OAR4320064-SUB36

Abstract

Age- or length-structured stock assessments require reliable life history demographic parameters (growth, mortality, reproduction) to model population dynamics, potential yields and stock sustainability. This study synthesized life history information for 84 commercially exploited tropical reef fish species from Florida and the U.S. Caribbean (Puerto Rico and the U.S. Virgin Islands). We attempted to identify a useable set of life history parameters for each species that included lifespan, length at age, weight at length and maturity at length. Key aspects of the life history synthesis were development of: (a) a database that characterized study details including sampling region, biological and statistical methods, length range of sampled individuals, sample size, capture gears and sampling time frame; (b) reproducible procedural criteria for parameter identification for a given species; and (c) a reliability metric for each parameter type. Complete life history parameter sets were available for 46 species analysed. Of these, only 16 species had parameter sets meeting the highest standards for reliability, highlighting future research needs.

KEYWORDS

data-limited fisheries, fish population dynamics, growth, lifespan, maturity, stock assessment

1 | INTRODUCTION

Tropical reef fish populations have been commercially fished in Florida and the U.S. Caribbean (i.e. Puerto Rico, U.S. Virgin Islands) for nearly two centuries (GMFMC, 1981). In the early 1980s, declining catch rates and overfishing prompted the first regional management actions that included minimum size limits and gear restrictions for several snapper and grouper species (NOAA, 1983). Additional regulations implemented over the past 30 years have included increased minimum size limits, bag limits, gear restrictions, seasonal and spatial closures, and annual catch limits for an increasing number of reef fishes (GMFMC, 2008; SAFMC, 2018). The reef ecosystem supports more than 50 exploited fish species from many families (snappers, groupers, grunts, porgies, triggerfishes, parrotfishes, etc.), yet only a small portion have undergone formal quantitative stock assessments via the federal SEDAR (SouthEast Data, Assessment, and Review) process (e.g. SEDAR, 2014, 2015b, 2016a). This cooperative review involving scientists, managers, commercial and recreational fishers, and other stakeholders was designed to increase transparency and reliability in assessments, and better inform management strategies for state governments and regional fishery management councils (i.e. Gulf of Mexico, South Atlantic and Caribbean). The lack of quantitative assessments has been mainly due to inherent limitations in resources for sampling and processing catch, effort and life history data needed to conduct assessments (Newman, Berkson, & Suatoni, 2015). Life history demography defining lifespan, growth and reproductive maturity are critical inputs to both conventional stock assessments (e.g. biomass dynamics, statistical catch-at-age models) and data-limited approaches (e.g. mean length estimator) (Ault, Bohnsack, & Meester, 1998; Ault et al., 2019; Haddon, 2011; Quinn & Deriso, 1999). In addition, life history information contributes to other analyses focused on assessing productivity and susceptibility (Patrick et al., 2009), which can be used to guide management decisions or stock assessment prioritization.

Reef fish life history demographic research in the tropical central western Atlantic began in earnest in the 1980s, well after the effects of intensive exploitation by commercial and recreational fisheries were evident. This can be highly problematic for obtaining accurate population dynamics required for stock assessments. A central component of cohort-structured assessment models is a function that describes average lifetime growth of an individual fish, such as the von Bertalanffy (1938) function that models average length from age 0 to the biological maximum age (defined as 'lifespan'). The usual data for developing lifetime growth functions are paired length-age observations for fish sampled from the population. Increasing rates of fishery exploitation lead to decreasing probabilities that individual fish will live to their biological maximum age or grow to their maximum sizes, making a population younger, smaller and less fecund (i.e. juvenescence) compared to its unfished state (Ault et al., 1998; Harris, Wyanski, White, & Moore, 2002; McBride & Richardson, 2007). Developing lifetime growth functions from specimens obtained from fishery-truncated length (and thus age) distributions may give the perception that a species is faster-growing and shorter-lived, when in fact it is a much slower-growing and longer-lived species. This may in turn lead to the perception that exploitation rates are sustainable when they are actually too high and not sustainable, because faster-growing, shorter-lived species are generally more resilient to fishing compared to slower-growing, longer-lived species (Beverton & Holt, 1957; Ricker, 1954).

We reviewed several hundred scientific and technical publications and inventoried all available life history demographic parameters for exploited reef fishes in Florida and the U.S. Caribbean. Characteristics of the various investigations, including time and location of specimen collection, biological and statistical methods, length ranges and sample sizes, were assessed to guide selection of the best available parameters for age, growth and maturity for each species. Potential problems in lifetime growth functions arising from fishery truncation were evaluated by comparing length distributions from length-age studies with those from fishery-dependent sampling data with high temporal and spatial resolution. Analyses of biological and statistical study characteristics were used to develop a species-level reliability metric for the selected life history parameters, providing guidance for use in stock assessments and for focusing future life history research.

2 | METHODS

2.1 | Life history parameters

The life history synthesis was designed to obtain reliable demographic parameters describing lifetime growth, survivorship and reproductive maturity required for size-age cohort-structured stock assessments (Table 1; c.f., Ault et al., 1998; Quinn & Deriso, 1999). Lifetime growth was described by the von Bertalanffy (1938) length dependent on age $L(a)$ growth function,

$$L(a) = L_\infty \left(1 - e^{-K(a-a_0)}\right) \tag{1}$$

where L_∞ is mean asymptotic length, K is the Brody growth coefficient, and a_0 is theoretical age at length zero. Observed maximum age a_λ was used to estimate the mean length at oldest age L_λ from

TABLE 1 Life history demographic parameters compiled for exploited reef fishes

Parameter	Definition	Units
a_λ	Maximum observed age	years
L_λ	Length at maximum age	mm fork length (FL)
L_∞	Asymptotic length	mm FL
K	Brody's growth coefficient	per year
a_0	Theoretical age at length 0	years
α	Weight-length scalar	kg/mm$^\beta$
β	Weight-length power	dimensionless
L_m	Length at 50% maturity	mm FL
a_m	Age at 50% maturity	years
L_{99}	99th percentile of commercial lengths	mm FL
L_{min}	Minimum length sampled	mm FL
L_{max}	Maximum length sampled	mm FL
L_d	Desired length units	mm
W_d	Desired weight units	kg
L_1	Original length units	cm, in, etc.
W_1	Original weight units	g,lb,etc.
u	Weight conversion factor for α	kg/ (g, lb, etc.)
v	Length conversion factor for α	mm/ (cm, in, etc.)
α_1	Original weight-length scalar	W_1/L_1^β
b_0	Length-type conversion intercept	mm FL
b_1	Length-type conversion slope	dimensionless

Equation (1). Oldest age a_λ is the primary input parameter for lifespan estimators of the instantaneous rate of natural mortality M (Alagaraja, 1984; Hewitt & Hoenig, 2005). The parameters L_∞, K and L_λ are inputs for length-based estimators of the instantaneous rate of total mortality Z (Beverton & Holt, 1957; Ehrhardt & Ault, 1992). The allometric weight (W) dependent on length relationship,

$$W(a) = \alpha L(a)^{\beta}, \tag{2}$$

has model-fitting parameters α and β. Equations (1) and (2) are used in conjunction to model lifetime growth of an individual fish in terms of average weight at age.

Length at reproductive maturity L_m was described using the logistic function,

$$p(L) = \frac{e^{\beta_0+\beta_1 L}}{1+e^{\beta_0+\beta_1 L}} \tag{3}$$

where $p(L)$ is the proportion of fish mature at length L, and β_0 and β_1 are model-fitting parameters (Kutner, Nachtsheim, Neter, & Li, 2004; Roa, Ernst, & Tapia, 1999). The parameter L_m was defined as the associated length at $p(L) = 0.5$, that is the length at which 50% of individuals have attained sexual maturity. The corresponding age at 50% maturity, a_m, was computed from L_m using the von Bertalanffy growth function (Equation 1) rearranged to compute age as a function of length,

$$a_m = \frac{-ln\left(1-\left(\frac{L_m}{L_\infty}\right)\right)}{K} + a_0. \tag{4}$$

2.2 | Commercial fleet sampling database, 1983–2016

To guide selection of exploited reef fish species for the life history demographic synthesis, species-specific length composition data were obtained from NOAA's Trip Interview Program (TIP; NOAA Southeast Fisheries Science Center), a dockside intercept statistical survey of the commercial fleet that began in the 1980s. These length data were evaluated for the time period 1983–2016 for two geographic regions, Florida and the U.S. Caribbean (Puerto Rico and the U.S. Virgin Islands). A candidate list of species was developed by cross-matching TIP species against species in regional reef fish fishery management council plans (e.g. Gulf of Mexico, Caribbean), and species observed in fishery-independent monitoring of coral reefs in Florida (Smith et al., 2011) and the U.S. Caribbean (Bryan, Smith, Ault, Feeley, & Menza, 2016). Subsequent selection criteria for exploited reef fishes were developed based on the number of TIP length observations in the two regions.

For species selected for life history synthesis, TIP length composition data were used to develop a measure for expected maximum length. Candidate metrics evaluated included the maximum observed length, the 99th percentile of length observations (L_{99}) and related frequency measures. Estimates of TIP maximum expected length were then compared with the corresponding maximum length reported in available scientific age and growth studies (L_{max}) as a general reliability check for the von Bertalanffy length-age function.

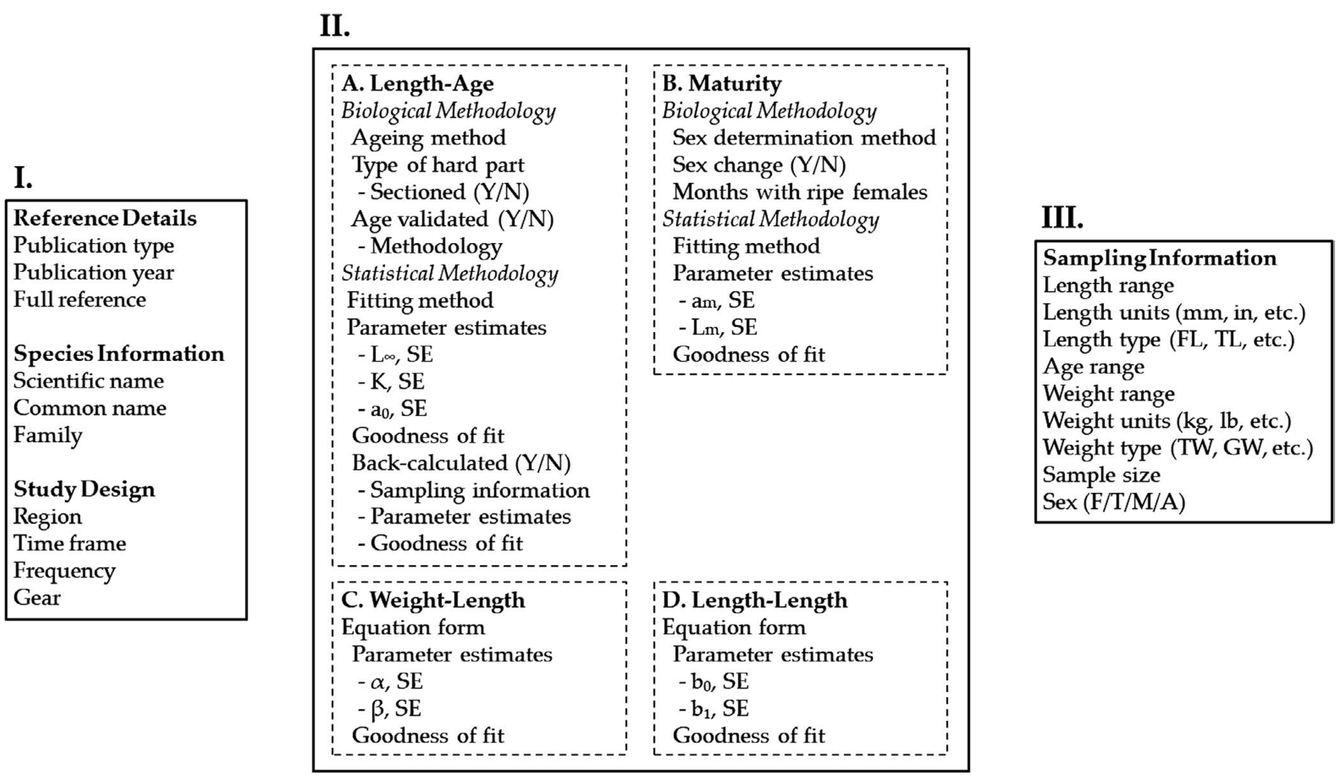

FIGURE 1 Variables of the life history parameter synthesis database for reef fishes in Florida and the U.S. Caribbean. Each table for life history parameters (II:A–D) included general study (I) and sampling (III) information. Abbreviations: Yes (Y), No (No), standard error (SE), fork length (FL), total length (TL), total weight (TW), gutted weight (GW), female (F), transitional (T), male (M) and all sexes (A)

2.3 | Literature synthesis and database for life history studies

An extensive literature review was conducted for exploited reef fish species in Florida and the U.S. Caribbean to assess life history parameter availability and reliability. The review encompassed peer-reviewed publications, dissertations and theses, conference proceedings, published and unpublished technical reports, etc. Relevant information from each source was compiled into a synthesis database, organized into separate tables containing general study information (e.g. publication details, species, location, etc.; Figure 1, Box I), the specifics of biological and statistical methods, parameter estimates and standard errors (Figure 1, Box II), and sampling information (e.g. age and length range of sampled individual fish, sample size, etc.; Figure 1, Box III). These study characteristics were used to develop hierarchical selection criteria for identifying the best available literature references and associated parameters for length-age, weight-length and maturity for each species (Figure 2). For example, studies conducted in Florida and the Caribbean Sea were preferred over studies conducted outside of this focal region (hierarchy level 1). For multiple studies within the focal region reporting von Bertalanffy parameters for the same species, preference was given to length-age models (Equation 1) developed from sectioned otoliths for individual fish that were fit with nonlinear regression over other biological and statistical methods (hierarchy level 2). For maturity, preference was given to studies that employed histological examination of gonads and logistic regression (Equation 3). For competing weight-length functions (Equation 2), preference was given to studies using model-fitting procedures that resulted in homogeneous residual errors for weight along the range of lengths (Kutner et al., 2004). If competing studies were similar with respect to level 2 criteria, then additional criteria including length/age range sampled (hierarchy level 3) and sample size (hierarchy level 4) were considered. Sampling time frame was not considered for the hierarchical selection criteria because throughout 1980s–present, regulations have led to the recovery of some species and increased pressure on other species at varying rates, resulting in a subjective range of ideal sampling years.

2.4 | Units and conversions

Units of length and weight for demographic functions and parameters were millimetre fork length (FL) and kg wet weight (W), respectively. Unit-of-measure conversions for length (e.g. inches to mm) and weight (e.g. pounds to kg) were carried out using.

$$L_d = uL_1 \tag{5}$$

and

$$W_d = vW_1 \tag{6}$$

where subscript d denotes the desired unit of measure, subscript 1 denotes the original unit of measure, u is the length conversion factor, and v is the weight conversion factor. Equation (5) was applied to L_∞ to convert length-age functions to mm; parameters a_0 and K are independent of the unit of measure for length. Length parameters L_λ and L_m were also converted to mm using Equation (5). For the allometric

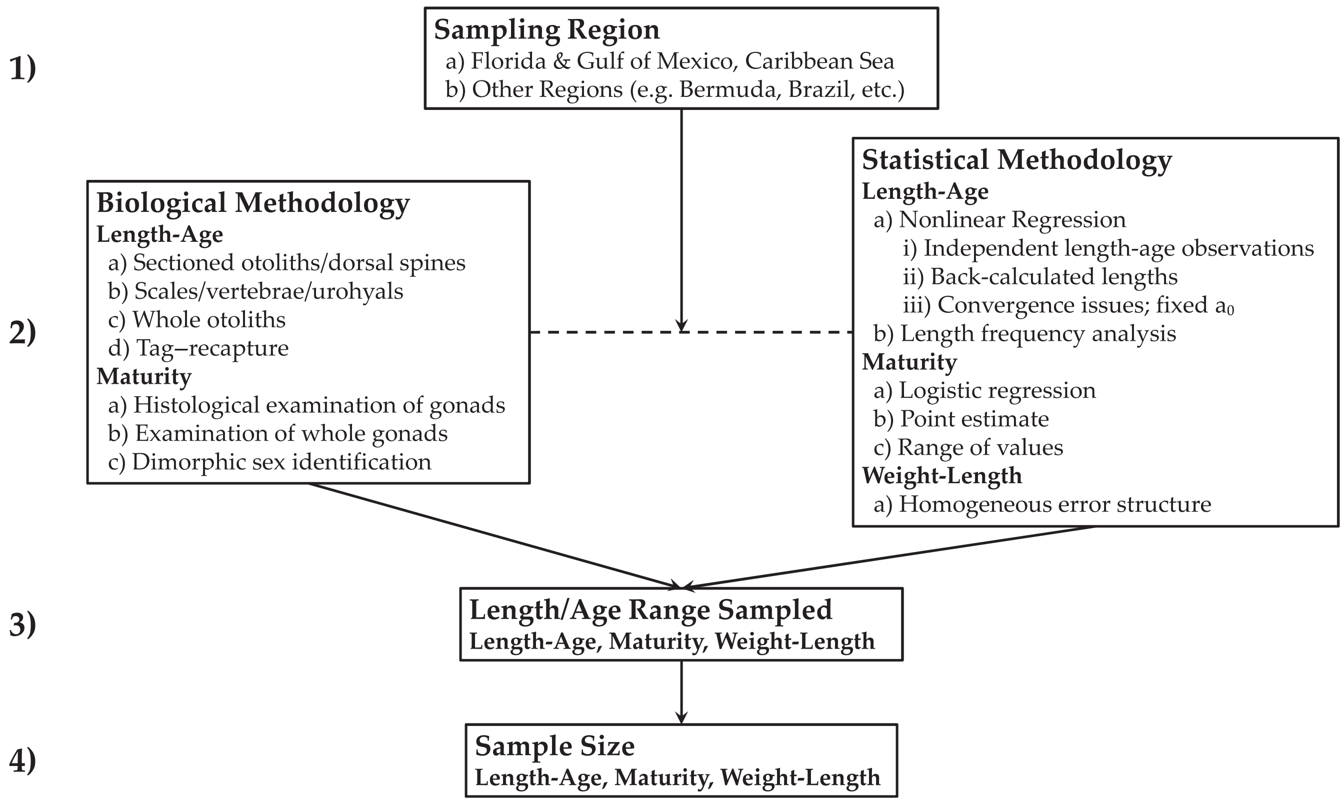

FIGURE 2 Selection criteria for determining a best set of life history parameters from the available scientific literature, arranged in hierarchical levels (1–4) and sublevels (a, b, etc.)

TABLE 2 Sample sizes (*n*) of reef fish lengths collected by the commercial Trip Interview Program, 1983–2016, from Florida and U.S. Caribbean, where the 99th percentile of length distributions, L_{99} (mm FL), was calculated for sample sizes ≥ 300, that is a minimum of approximately 10 samples per year on average

		Florida		Caribbean	
Common name	**Scientific name**	***n***	L_{99}	***n***	L_{99}
Groupers	Epinephelidae				
Atlantic Creolefish	*Paranthias furcifer*	469	378	36	–
Black Grouper	*Mycteroperca bonaci*	7,545	1,390	231	–
Coney	*Cephalopholis fulva*	51	–	34,175	639
Gag Grouper	*Mycteroperca microlepis*	91,980	1,268	4	–
Goliath Grouper	***Epinephelus itajara***	**2**	**1,733**	**78**	**2,007**
Graysby	*Cephalopholis cruentata*	536	425	2,404	550
Misty Grouper	***Hyporthodus mystacinus***	**115**	**1,208**	**294**	**1,370**
Mutton Hamlet	*Alphestes afer*	–	–	309	440
Nassau Grouper	***Epinephelus striatus***	**36**	**893**	**1,548**	**798**
Red Grouper	*Epinephelus morio*	230,948	890	191	–
Red Hind	*Epinephelus guttatus*	369	698	41,819	778
Rock Hind	*Epinephelus adscensionis*	749	485	629	725
Scamp	*Mycteroperca phenax*	65,225	858	–	–
Snowy Grouper	*Hyporthodus niveatus*	19,081	1,178	–	–
Speckled Hind	*Epinephelus drummondhayi*	12,870	1,023	–	–
Tiger Grouper	*Mycteroperca tigris*	8	–	3,391	890
Warsaw Grouper	*Hyporthodus nigritus*	1,246	1940	–	–
Yellowedge Grouper	*Hyporthodus flavolimbatus*	40,520	1,080	5	–
Yellowfin Grouper	*Mycteroperca venenosa*	463	973	1,134	920
Yellowmouth Grouper	*Mycteroperca interstitialis*	364	846	92	–
Snappers	Lutjanidae				
Black Snapper	*Apsilus dentatus*	13	–	492	610
Blackfin Snapper	*Lutjanus buccanella*	2,549	778	10,668	640
Cardinal Snapper	*Pristipomoides macropthalmus*	97	–	4,178	608
Cubera Snapper	*Lutjanus cyanopterus*	394	1,223	821	1,200
Dog Snapper	*Lutjanus jocu*	270	–	2,186	1,192
Grey Snapper	*Lutjanus griseus*	41,252	790	1,195	780
Lane Snapper	*Lutjanus synagris*	12,337	686	50,185	560
Mahogany Snapper	*Lutjanus mahogoni*	14	–	2,224	722
Mutton Snapper	*Lutjanus analis*	20,761	889	10,141	914
Queen Snapper	*Etelis oculatus*	1,917	950	13,389	910
Red Snapper	*Lutjanus campechanus*	140,989	920	7	–
Schoolmaster	*Lutjanus apodus*	87	–	8,964	666
Silk Snapper	*Lutjanus vivanus*	4,820	853	37,121	721
Vermilion Snapper	*Rhomboplites aurorubens*	140,855	554	15,524	560
Wenchman	*Pristipomoides aquilonaris*	308	540	2,295	673
Yellowtail Snapper	*Ocyurus chrysurus*	107,147	633	117,290	701
Grunts	Haemulidae				
Barred Grunt	*Conodon nobilis*	–	–	372	401
Black Margate	*Anisotremus surinamensis*	639	700	333	565

(Continues)

TABLE 2 (Continued)

Common name	Scientific name	Florida		Caribbean	
		n	L_{99}	*n*	L_{99}
Bluestriped Grunt	*Haemulon sciurus*	168	–	11,558	450
Burro Grunt	*Pomadasys crocro*	–	–	978	296
Caesar Grunt	*Haemulon carbonarium*	111	–	2,675	320
Cottonwick	*Haemulon melanurum*	89	–	1,161	393
French Grunt	*Haemulon flavolineatum*	29	–	8,734	320
Margate	*Haemulon album*	721	790	737	640
Pigfish	*Orthopristis chrysoptera*	337	430	4	–
Porkfish	*Anisotremus virginicus*	431	331	1,879	352
Sailor's Choice	*Haemulon parra*	520	364	792	410
Tomtate	*Haemulon aurolineatum*	675	306	693	338
White Grunt	*Haemulon plumieri*	12,610	635	78,956	422
Porgies	Sparidae				
Grass Porgy	*Calamus arctifrons*	377	303	–	–
Jolthead Porgy	*Calamus bajonado*	4,206	783	4,784	485
Knobbed Porgy	*Calamus nodosus*	1,632	460	–	–
Littlehead Porgy	*Calamus proridens*	2,423	458	33	–
Pluma Porgy	*Calamus pennatula*	1	–	10,694	446
Red Porgy	*Pagrus pagrus*	29,643	584	1	–
Saucereye Porgy	*Calamus calamus*	194	–	2,974	435
Sheepshead	*Archosargus probatocephalus*	9,042	628	1	–
Sheepshead Porgy	*Calamus penna*	72	–	412	395
Whitebone Porgy	*Calamus leucosteus*	895	690	–	–
Triggerfishes	Balistidae				
Grey Triggerfish	*Balistes capriscus*	22,619	646	146	–
Ocean Triggerfish	*Canthidermis sufflamen*	528	590	317	621
Queen Triggerfish	*Balistes vetula*	522	573	27,650	596
Wrasses and Parrotfishes	Labridae				
Hogfish	*Lachnolaimus maximus*	4,154	803	6,729	765
Princess Parrotfish	*Scarus taeniopterus*	1	–	5,277	377
Queen Parrotfish	*Scarus vetula*	2	–	2,094	420
Redband Parrotfish	*Sparisoma aurofrenatum*	–	–	9,467	335
Redtail Parrotfish	*Sparisoma chrysopterum*	98	–	54,474	500
Spanish Hogfish	*Bodianus rufus*	2	–	600	445
Stoplight Parrotfish	*Sparisoma viride*	20	–	47,121	505
Yellowtail Parrotfish	*Sparisoma rubripinne*	6	–	2,987	394
Barracudas	Sphyraenidae				
Great Barracuda	*Sphyraena barracuda*	752	1,290	596	1,245
Surgeonfishes	Acanthuridae				
Blue Tang	*Acanthurus coeruleus*	15	–	36,696	325
Doctorfish	*Acanthurus chirurgus*	19	–	13,772	378
Ocean Surgeonfish	*Acanthurus bahianus*	–	–	5,232	345
Squirrelfishes	Holocentridae				
Longspine Squirrelfish	*Holocentrus rufus*	21	–	4,796	305
Squirrelfish	*Holocentrus adscensionis*	385	387	5,385	485

(Continues)

TABLE 2 (Continued)

Common name	Scientific name	Florida		Caribbean	
		n	L_{99}	*n*	L_{99}
Goatfishes	Mullidae				
Spotted Goatfish	*Pseudupeneus maculatus*	6	–	14,853	350
Yellow Goatfish	*Mulloidichthys martinicus*	42	–	8,025	418
Boxfishes	Ostraciidae				
Honeycomb Cowfish	*Acanthostracion polygonius*	–	–	12,537	610
Scrawled Cowfish	*Acanthostracion quadricornis*	1	–	6,514	545
Smooth Trunkfish	*Lactophrys triqueter*	–	–	2,644	397
Spotted Trunkfish	*Lactophrys bicaudalis*	–	–	2,361	480
Trunkfish	*Lactophrys trigonus*	6	–	2,089	505
Bigeyes	Priacanthidae				
Bigeye	*Priacanthus arenatus*	1,170	498	243	–

Sample size exceptions were made for three important grouper species (fishing moratoria, etc.; denoted by bold font).

weight-length model, parameter β is independent of the unit of measure for length, but parameter α is dependent on the unit of measure for both length and weight. Conversions of parameter α to millimetres and kilograms were carried out using the general formula.

$$\alpha = \nu u^{-\beta} \alpha_1 \tag{7}$$

using the definitions from Equations (5) and (6). If either length or weight was already in the desired unit of measure, the respective conversion factor was set to 1 in Equation (7).

For life history parameters where length type was different from fork length (e.g. total length, standard length), length-length conversion equations were included as part of the literature search and parameter synthesis database (Table 1 and Figure 1). In contrast to unit-of-measure conversions, parameters of the length-age and weight-length functions are dependent on length type. Thus, parameters for length-age and weight-length functions were reported in the original length type, and a length-length conversion equation was provided where possible. For modelling purposes, the length-length equations can be used in conjunction with length-age or weight-length functions to provide the respective curves in fork length. Values for point estimates of length, L_λ and L_m, were converted to fork length using a length-length equation where possible.

3 | RESULTS

3.1 | Exploited species and maximum lengths

For the period 1983–2016, the Trip Interview Program (TIP) sampled commercial catches during all seasons covering the entire respective coastlines of Florida and the U.S. Caribbean each year. The subset of commercially exploited reef fishes for analysis was defined by a frequency of 300 or more TIP length samples for a given species from either Florida or the U.S. Caribbean, or a minimum of approximately 10 samples per year on average (Table 2). Sample size exceptions were made for three historically important groupers (denoted by bold font; Table 2), two of which have been under fishing moratoria since the early 1990s (Goliath, Nassau). The final list was comprised of 84 reef fish species from 12 families: groupers (Epinephelidae), snappers (Lutjanidae), grunts (Haemulidae), porgies (Sparidae), triggerfishes (Balistidae), wrasses and parrotfishes (Labridae), barracudas (Sphyraenidae), surgeonfishes (Acanthuridae), squirrelfishes (Holocentridae), goatfishes (Mullidae), boxfishes (Ostraciidae) and bigeyes (Priacanthidae). Most of these species are also fished recreationally (NOAA Marine Recreational Information Program).

The TIP length observations were also used to estimate the expected maximum length for each species, an empirical analog to the parameter L_λ, the mean length at maximum observed age. Potential definitions are illustrated in Figure 3 using length frequencies for three species with contrasting sample sizes: Red Grouper (n = 230,948; Figure 3a), Black Grouper (n = 7,545; Figure 3b) and Warsaw Grouper (n = 1,246; Figure 3c). For each species, vertical lines denote the maximum observed length, and the 99.95, 99.90 and 99.50 percentile length observations. Although obvious outliers were removed during the analysis process, it was usually not possible to determine whether extremely large length observations within the tails of the distributions were recording errors or true values. Furthermore, the concept of 'expected maximum length' is an average value with some variation of observations above and below. The following criteria were developed to calculate the 99th percentile of length observations (L_{99}) as a measure for 'expected maximum length' for three different ranges of sample sizes:

$$L_{99} = \begin{cases} \text{99.95th percentile} & \text{if } n \geq 10{,}000 \\ \text{99.90th percentile} & \text{if } 10{,}000 > n \geq 2{,}000 \\ \text{99.50th percentile} & \text{if } n < 2{,}000 \end{cases} \tag{8}$$

The specific definitions for L_{99} are indicated for each species in Figure 3. In each case, the defined L_{99} represents the upper end of

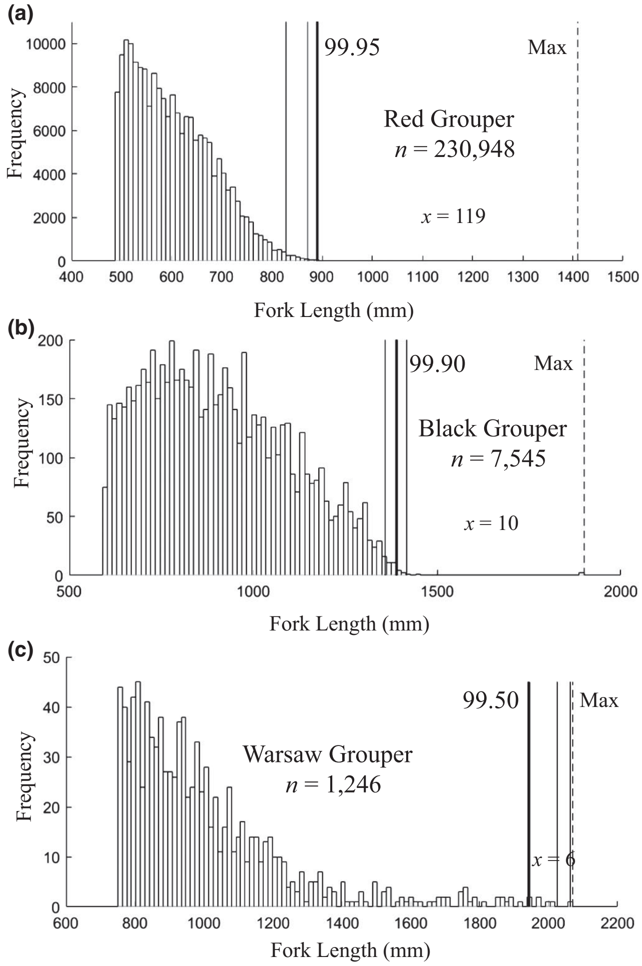

FIGURE 3 Florida TIP length distributions for (a) red, (b) black and (c) warsaw groupers with sample size (n) from 1983 to 2016. Vertical lines from right to left show the maximum length observation (dashed), and the respective 99.95, 99.90 and 99.50 percentiles. Bolded and labelled vertical lines indicate the L_{99} based on sample size criteria defined in Equation 8; x is the number of lengths above L_{99}

the TIP length distribution, accounting for percentiles falling closer to the mean with increasing n and guarding against potential outliers. The criteria of Equation (8) were used to estimate L_{99} for the list of commercially exploited species (Table 2).

3.2 | Life history synthesis and parameter selection

The literature synthesis of life history parameters identified over 300 references dating from 1916 to the present for the species listed in Table 2. The full list of citations is provided in Appendix S1. Examples of the completed data tables and variables for the synthesis database (Figure 1) are provided in Appendix S2 for five species: Black Grouper, Coney, Dog Snapper, Mutton Snapper and Hogfish.

Application of the hierarchical process for selecting the best available life history parameters (Figure 2) is illustrated in Table 3 for length-age of two example species, Mutton Snapper and Coney. Nine different sets of length-age parameters were obtained for Mutton Snapper, and seven sets were obtained for Coney. Information pertaining to hierarchy level 1 (region), level 2 (biological and statistical methodology) and so forth was summarized for each parameter set. Proceeding left to right from region (level 1) to sample size (n, level 4) criteria, brackets denote the point in the selection process at which a parameter set was excluded from further consideration. For example, Mutton Snapper length-age parameters reported in Burton (2002) were excluded because independent length-age observations were preferred for fitting with nonlinear regression over back-calculated lengths, whereas the parameters reported in SEDAR (2008) were excluded because they fit the model using a smaller sample size and narrower length range compared to O'Hop, Muller, and Addis (2015).

The example species in Table 3 had many length-age studies available for consideration. In both cases, the studies selected as having the best available length-age parameters were conducted in the preferred region (Figure 2, criterion level 1a) and utilized the most robust biological and statistical methodologies (sectioned otoliths, independent length-age observations and nonlinear regression, respectively; Figure 2, criterion level 2a). The objective was to identify the single study with the best parameters for use in assessment, not to create a 'blended' set of parameters from different studies. For some species, length-age parameters were only available from a single study; accordingly, these parameters were selected as the best available, even though the study may not have been conducted in the preferred region or employed the most preferable biological and statistical methods.

A further consideration of the robustness and reliability of length-age parameters, beyond biological and statistical methods, was the range of age and length observations in a growth study (Figure 1, Hierarchy Level 3; Table 3). Of particular concern was how well the oldest and largest fishes in a length-age study corresponded with the maximum age (e.g. a_λ) and length (e.g. L_λ, TIP L_{99}) for a species, in the light of the potential for truncated age and length distributions due to exploitation. For length, the largest length in a study ($L_{\max}$) was compared with the L_{99} estimated from the TIP data (Figure 4). As illustrated for Mutton Snapper, the L_{max} (906 mm) reported by O'Hop et al. (2015) corresponded well with the TIP L_{99} from Florida (889 mm; Table 2) and the U.S. Caribbean (914 mm). There was no comparable sampling programme for age composition (e.g. TIP) that might provide an independent estimate of maximum age for all exploited reef fishes; thus, the maximum observed age a_λ for a species was obtained from among the same set of length-age studies that provided the parameters of the von Bertalanffy growth function. For Mutton Snapper, as was typical for most species, the study reporting the oldest age (O'Hop et al., 2015) was also the study reporting the largest length and the highest sample size of aged fish. An interesting finding for Mutton Snapper and other species was that as the geographic extent and sample sizes for length-age studies have increased over the past several decades, estimates of maximum age a_λ have also increased, doubling or even quadrupling in some cases (Figure 5).

Evaluating length- and age-range criteria for parameter selection was less straightforward for Coney (Table 3). The studies by de Araujo and Martins (2006; Brazil) and Trott (2006; Bermuda),

TABLE 3 Examples of the process for selecting the most representative length-age study (and parameters) for Mutton Snapper and Coney following the flow chart from Figure 2

Reference	1. Region	2. Biol.	2. Stats.	3. Age (yr)	3. Length (mm FL)	4. *n*
Mutton Snapper						
Montes (unpub) (1975)	Cuba	–	–	[–]	[–]	[–]
Pozo (1979)	NE Cuba	U	–	[1–9]	[–]	[2,587]
Claro (1981)	SW Cuba	O	–	[1–9]	[–]	[–]
Claro (1981)	NW Cuba	O	–	[1–8]	[–]	[–]
Mason and Manooch (1985)	E Florida	O	[NLR, BC]	[1–14]	[142–764]	[878]
Palazon and Gonzalez (1986)	N Venezuela	U	–	[1–8]	[–]	[274]
Burton (2002)	E Florida	O,S	[NLR, BC]	[1–29]	[170–817]	[1,395]
SEDAR (2008)	Florida	O,S	NLR	0–40	84–896	[7,172]
O'Hop et al. (2015)	**Florida**	**O,S**	**NLR**	**0–40**	**84–906**	**13,052**
Coney						
Randall (1962)	St. John, USVI	[TR]	[LF]	[–]	[295max]	[–]
Thompson and Munro (1978)	–	[TR]	[LF]	[–]	[–]	[–]
Potts and Manooch (1999)	Florida, S Atlantic	O,S	[NLR, CP]	[2–11]	[150–397]	[55]
Potts and Manooch (1999)	Florida, S Atlantic	O,S	[NLR, BC]	[2–11]	[150–397]	[55]
de Araujo and Martins (2006)	[Brazil]	[O,S]	[NLR]	[2–25]	[172–428]	[705]
Trott (2006)	[Bermuda]	[O,S]	[NLR]	[2–28]	[151–384]	[997]
Burton et al. (2015a)	**Florida, S Atlantic**	**O,S**	**NLR**	**1–19**	**217–430**	**353**

Note: For each species, studies are listed by publication date. Biological methodology included urohyal bones (U), otoliths (O), otoliths specified as sectioned (O,S), and tag & release (TR). Statistical methodology included nonlinear regression (NLR) with and without back-calculated lengths (BC), and length frequency analysis (LF); CP denotes convergence problems with model fitting. Proceeding left to right from level 1 (region) to level 4 (sample size *n*) criteria, brackets denote the point in the selection process at which a parameter set was excluded from further consideration. The selected study with the best available length-age parameters is denoted by bold font.

conducted respectively south and north of the focal region, sampled older fish (25–28 years) compared to the Florida–South Atlantic study of Burton, Potts, and Carr (2015a; 19 years), but the L_{max} in the Brazil and Bermuda studies (384–428 mm) was similar to or smaller than Burton et al. (2015a; 430 mm). Likewise, the minimum age of sampled fish was younger, but the minimum length was larger in the Florida–South Atlantic study compared to the Brazil and Bermuda studies. This suggests that growth differs between the focal region and outside the focal region. The Coney length-age parameters from Burton et al. (2015a) were considered to be the most representative for the target region of this synthesis.

There were some exceptions to the region criterion (hierarchy level 1). An example case was Dog Snapper. Length-age curves are shown in Figure 6 for the Cuba study by Claro, Sierra, and Garcia-Arteaga (1999) and the Brazil study by Previero, Minte-Vera, Freitas, Moura, and Tos (2011). Claro et al. (1999) developed sex-specific growth functions, which showed that the average length at age of males was larger than females at older ages (>10–15 years). The pooled-sex growth model of Previero et al. (2011) predicted mean length at age between the respective male and female curves at older ages. While it is possible to account for sex-specific growth in stock assessments, more data are required (e.g. sex-specific catch composition) than are typically available. Weighing practical considerations over increased biological realism, the length-age parameters of Previero et al. (2011) were selected as the best available set.

The specific sampling area within the focal region was given lower priority in the selection process. This was based in part on the information shown in Figure 4. There were 19 species meeting the following conditions: (a) the range of lengths was reported for the length-age study selected as having the best available parameter set; and (b) the TIP L_{99} was estimated for both Florida and the U.S. Caribbean. For comparison purposes, the TIP L_{99} was standardized to the Florida value (i.e. Florida L_{99} = 100%). The U.S. Caribbean L_{99} was within 10% of the Florida value for 10 of the 19 species, was greater than 10% above the Florida value for five species (Rock Hind, Red Hind, Graysby, Wenchman, Tomtate) and was less than 10% below the Florida value for 4 species (Nassau Grouper, Blackfin Snapper, Lane Snapper and White Grunt). U.S. Caribbean species within 5% of the Florida L_{99} included mostly snappers (Mutton, Vermilion, Grey, Cubera, Queen Snappers; Queen Triggerfish; Hogfish; Great Barracuda) and were more evenly distributed between the two regions when compared to groupers, with the exception of Queen Triggerfish (Table 2). There was no discernible trend in expected maximum length between Florida and the U.S. Caribbean populations, but further investigations are needed to distinguish potential differences in species-specific growth within the focal region.

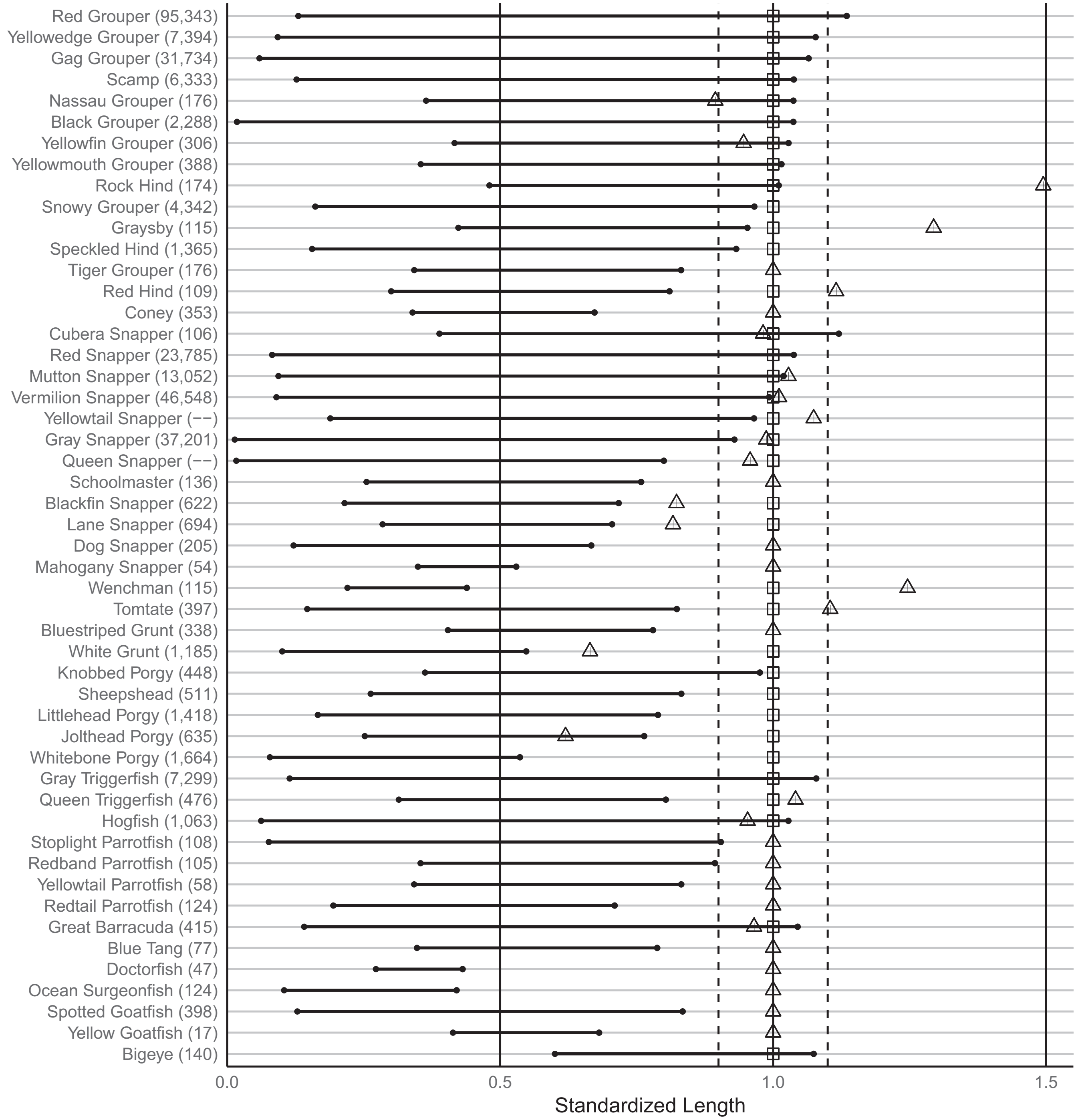

FIGURE 4 Comparison of length ranges from length-age studies (L_{min} to L_{max}, horizontal solid line) with the maximum expected length (L_{99}) from TIP sampling (open squares and triangles). Lengths were standardized to the TIP L_{99} (Table 2) from Florida (square), or to the U.S. Caribbean (triangle) if Florida data were not available. Sample sizes of length-age observations are given in parentheses for each species. Length-age parameter reliability was assessed based on whether a study's L_{max} exceeded 90% of the TIP L_{99}. Vertical dashed lines denote lengths 10% below and above the TIP L_{99}

After selection of the best available parameters for length-age, weight-length and maturity, a species-level score (LH) was assigned to distinguish the completeness and reliability of the parameter set as a whole (Table 4). An initial score was given based on the completeness of the parameter sets (LH = 0 for incomplete, LH = 1 for complete). Complete sets were further distinguished with respect to the robustness of the biological and/or statistical methodologies used to develop the length-age, weight-length and maturity parameters. A score of LH = 2 was given if fish were aged from sectioned otoliths or spines, maturity was based on histological examination of gonads, length-age functions (Equation 1) were fit to independent length-age observations using nonlinear regression, weight-length

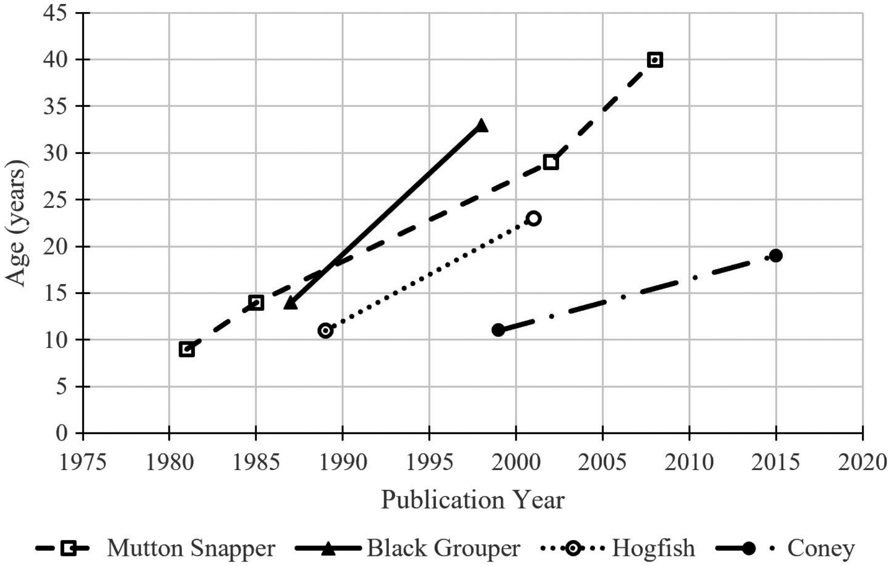

FIGURE 5 Maximum age estimates by publication year for Mutton Snapper (Burton, 2002; Claro, 1981; Mason & Manooch, 1985; SEDAR, 2008), Black Grouper (Crabtree & Bullock, 1998; Manooch & Mason, 1987), Hogfish (Claro, Garcia-Cagide, & Alaiza, 1989; McBride, 2001) and Coney (Burton et al., 2015a; Potts & Manooch, 1999)

functions (Equation 2) were based on sample sizes of $n \geq 30$, and maturity functions (Equation 3) were fit using logistic regression. For species meeting the criteria for LH = 2, the highest score (LH = 3) was given if the L_{max} of the length-age study was greater than 90% of the expected maximum length (TIP L_{99}; Figure 4). A pre-condition of the LH = 3 score was that the length range was reported for the length-age study; this was not always the case.

3.3 | Best available life history parameters

The life history parameters selected across all the literature reviewed as the best currently available are provided in Table 5 for 84 species. The associated references for length-age, weight-length and maturity parameters are listed in Table 6. Length parameters are provided in mm, and weight parameters are provided in kg, converted from the original units where necessary using Equations (5–7). Parameters for the length-age growth function (L_∞,K,a_0) and weight-length function (α, β) are given in the original length type. If length type differed from fork length, length-length conversion equations are provided in Table 7 where possible. The length type for parameters L_λ and L_m was converted to fork length if necessary.

Of the 84 species in Table 5, 46 had a complete set of life history parameters (LH ≥ 1). Of these, 20 species were given a reliability score of LH ≥ 2, and 16 species met the criteria for the highest score of LH = 3. The LH reliability scores of [n-1-2-3] for all n species can be reported as [84-46-20-16] and itemized by family: groupers [20-16-11-9], snappers [16-10-5-5], grunts [13-3-1-0], porgies [10-5-1-0], triggerfishes [3-2-1-1], wrasses and parrotfishes [8-4-1-1], barracudas [1-1-0-0], surgeonfishes [3,3,0,0], squirrelfishes [2-0-0-0], goatfishes [2-1-0-0], boxfishes [5-0-0-0] and bigeyes [1-1-0-0]. Designation of LH values by species and parameter type (length-age, weight-length and maturity) is noted with the references in Table 6.

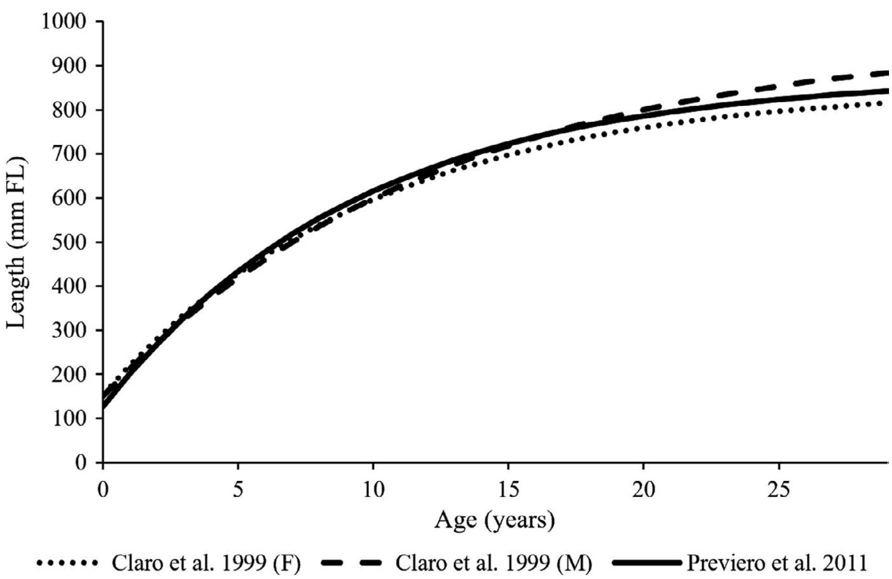

FIGURE 6 Comparison of Dog Snapper sex-specific growth curves from Cuba (Claro et al., 1999) with the pooled-sex growth curve from Brazil (Previero et al., 2011)

TABLE 4 Criteria for a reliability score, LH, for the complete set of length-age, weight-length and maturity life history parameters for a given species

LH	Criterion
0	Missing life history information for length-age, weight-length or maturity
1	Complete set of life history parameters: length-age, weight-length and maturity
2	Conditions for LH = 1; parameters for both length-age and maturity developed from the most robust biological and statistical methodologies (Figure 2, hierarchy level 2a); and weight-length sample size ≥ 30 (hierarchy level 4)
3	Conditions for LH = 2 and L_{max} of length-age study > 90% of TIP L_{99} (Figure 4)

TABLE 5 Life history parameter estimates (defined in Table 1) for exploited reef fishes in Florida and the U.S. Caribbean; lengths are in mm fork length and weights are in kg

		Length-Age					Weight-Length		Maturity	
Species	LH	a_λ	L_λ	L_∞	K	a_0	α	β	L_m	a_m
Groupers										
Atlantic Creolefish	0	–	–	314.0	0.28	0.00	–	–	–	–
Black	3	33	1,289.4[c]	1,334.0[a]	0.14	−0.90	8.75E−09	3.08	834.4[c]	6.48
Coney	1	19	372.8	377.0	0.20	−3.53	1.45E−08	3.03	220.0	0.85
Gag	3	31	1,259.7	1,278.0	0.13	−0.67	1.17E−08	3.02	543.0	3.50
Goliath	1	37	2,156.1	2,221.1	0.09	−0.68	6.49E−09	3.15	1,200.0	6.50
Graysby	1	13	378.4	446.0	0.13	−1.51	8.81E−09	3.12	165.0	2.04
Misty	0	150	–	–	–	–	–	–	–	–
Mutton Hamlet	0	–	–	–	–	–	–	–	180.0	–
Nassau	3	22	844.9	932.0	0.10	−1.70	4.17E−09	3.20	435.0	4.59
Red	3	29	810.0	829.0	0.13	−1.20	5.46E−09	3.18	292.0	2.27
Red Hind	2	18	514.9	571.0	0.11	−3.10	6.17E−09	3.14	215.0	1.20
Rock Hind	0	33	498.1	499.4	0.17	−2.50	1.39E−08	3.03	–	–
Scamp	3	31	740.1	772.0	0.09	−4.40	2.46E−08	2.91	332.0	1.85
Snowy	3	35	1,034.7	1,065.0	0.09	−2.88	4.63E−08	2.82	585.1	5.60
Speckled Hind	3	35	859.6[c]	888.0[a]	0.12	−1.80	1.10E−08[a]	3.10	520.5[c]	6.60
Tiger	2	18	680.9[a]	758.0[a]	0.12	−1.88	7.13E−09[a]	3.12	342.0	3.34
Warsaw	1	41	2,182.6	2,394.0	0.05	−3.62	2.09E−08	2.98	1,188.8	9.00
Yellowedge	3	85	950.3[c]	1,004.5[a]	0.06	−4.75	1.73E−08	2.96	527.3[c]	8.00
Yellowfin	3	31	935.1	958.0	0.11	−2.94	2.89E−08	2.91	540.4[c]	4.66
Yellowmouth	1	31	747.0	755.0	0.14	−1.42	8.89E−09	3.07	420.0	4.38
Snappers										
Black	0	–	–	560.0	0.30	0.00	–	–	420.0	4.62
Blackfin	1	27	524.8[c]	579.0[a]	0.16	−1.60	9.54E−09	3.11	240.0	2.17
Cardinal	0	–	–	–	–	–	–	–	180.0	–
Cubera	1	55	1,362.5[c]	1,495.0[a]	0.05	−3.33	4.90E−09[a]	3.16	536.0	5.98
Dog	1	33	854.7	878.0	0.11	−1.49	2.15E−08	2.97	476.0	5.94
Grey	3	32	543.8	546.9	0.15	−1.46	1.45E−08	3.02	253.0	2.56
Lane	1	17	432.9	449.0	0.17	−2.59	5.92E−08	2.86	240.0	1.91
Mahogany	0	18	308.5[c]	334.0[a]	0.31	−1.19	5.40E−09[a]	3.15	–	–
Mutton	3	40	798.0[c]	861.0[a]	0.17	−1.23	1.48E−08	3.03	323.0[c]	2.07
Queen	0	–	–	1,020.0[a]	0.40	−0.29	4.02E−08	2.83	–	–
Red	3	48	800.1[c]	856.4[a]	0.19	−0.39	1.87E−08	2.95	455.8[c]	4.00
Schoolmaster	1	42	479.8[a]	482.0[a]	0.12	−2.79	9.26E−09[a]	3.11	250.0[a]	3.30
Silk	0	–	–	756.7	0.10	−2.08	1.66E−08	3.03	500.0	8.73

(Continues)

TABLE 5 (Continued)

Species	LH	Length-Age					Weight-Length		Maturity	
		a_λ	L_λ	L_∞	K	a_0	α	β	L_m	a_m
Vermilion	3	26	344.0	344.0	0.33	−0.80	2.19E−08	2.92	140.9	0.82
Wenchman	0	14	231.8	240.0	0.18	−4.75	3.00E−08	2.91	–	–
Yellowtail	3	23	474.2[c]	618.0[a]	0.13	−3.13	6.14E−08	2.78	232.1[c]	1.70
Grunts										
Barred	0	–	–	325.0	0.43	0.00	–	–	–	–
Black Margate	0	–	–	–	–	–	2.39E−09	3.39	–	–
Bluestriped	1	23	313.9	314.0	0.32	−1.80	9.31E−09	3.13	204.8	1.50
Burro	0	–	–	–	–	–	2.16E−08	2.93	–	–
Caesar	0	–	–	–	–	–	–	–	–	–
Cottonwick	0	–	–	350.0	0.32	−0.10	2.52E−08	2.95	190.0	2.35
French	0	–	–	350.0	0.24	0.00	9.06E−09	3.16	160.0	2.55
Margate	0	–	–	730.0	0.19	−0.30	1.52E−08	3.04	310.0	2.61
Pigfish	0	4	–	–	–	–	9.71E−09	3.19	210.0	–
Porkfish	0	–	–	–	–	–	1.01E−08	3.17	–	–
Sailor's Choice	0	–	–	388.0	0.24	−0.27	2.02E−08	2.99	–	–
Tomtate	1	9	242.1[c]	310.0[a]	0.22	−1.28	6.19E−09	3.21	131.6[c]	1.75
White	2	18	280.9[c]	323.1[a]	0.52	−0.58	8.49E−08	2.75	167.0	1.16
Porgies										
Grass	0	–	–	–	–	–	–	–	–	–
Jolthead	1	13	569.8[c]	737.0[a]	0.14	−2.02	4.20E−08	2.90	300.0	1.71
Knobbed	0	21	358.7[c]	412.0[a]	0.20	−1.97	7.99E−08	2.79	–	–
Littlehead	2	10	290.3	306.0	0.25	−1.69	6.61E−08	2.82	132.0	0.53
Pluma	0	–	–	–	–	–	1.35E−08	3.11	–	–
Red	1	14	424.4[c]	510.0[a]	0.21	−1.32	2.70E−08[a]	2.89	197.6[c]	1.50
Saucereye	0	–	–	–	–	–	6.78E−08	2.80	–	–
Sheepshead	1	14	478.9	490.4	0.26	−0.42	4.40E−08	2.89	229.0	2.00
Sheepshead Porgy	0	–	–	376.0	0.28	0.00	2.81E−07	2.54	–	–
Whitebone	1	12	304.7	331.0	0.17	−2.64	4.30E−08	2.91	256.8	6.00
Triggerfishes										
Grey Triggerfish	3	14	523.9	589.7	0.14	−1.66	2.16E−08	3.01	210.8	1.50
Ocean Triggerfish	0	–	–	–	–	–	1.55E−08	3.06	–	–
Queen Triggerfish	1	14	393.0	441.3	0.14	−1.80	8.64E−08	2.78	215.0	2.97
Wrasses and Parrotfishes										
Hogfish	3	23	784.3	849.0	0.11	−1.33	9.50E−08	2.75	176.8	0.88
Princess	0	–	–	–	–	–	5.95E−07	2.39	175.0	–
Queen	0	–	–	–	–	–	–	–	–	–
Redband	1	7	176.4[b]	178.0[b]	0.67	0.00	8.35E−08	2.74	140.0	–
Redtail	1	5	246.8[b]	258.0[b]	0.63	0.00	8.89E−07	2.32	235.0	–
Spanish Hogfish	0	–	–	–	–	–	–	–	100.0[b]	–
Stoplight	1	9	350.9[b]	357.0[b]	0.45	−0.06	3.70E−08	2.91	205.0	–
Yellowtail	0	7	237.2[b]	238.0[b]	0.81	−0.05	–	–	170.0[b]	1.49
Barracudas										
Great Barracuda	1	19	1,229.0	1,236.4	0.26	−0.71	7.94E−09	2.97	800.0	3.30

(Continues)

TABLE 5 (Continued)

		Length-Age					Weight-Length		Maturity	
Species	**LH**	a_λ	L_λ	L_∞	K	a_0	α	β	L_m	a_m
Surgeonfishes										
Blue Tang	1	27	219.0	219.0	0.88	−0.15	1.50E−06	2.26	130.0	0.87
Doctorfish	1	12	210.0	210.0	1.10	−0.12	9.23E−08	2.74	170.0	1.38
Ocean Surgeonfish	1	13	183.0	183.0	1.06	−0.15	2.51E−08	2.98	110.0	0.72
Squirrelfishes										
Longspine Squirrelfish	0	–	–	188.0	0.48	0.00	–	–	135.0	2.64
Squirrelfish	0	–	–	261.0	0.23	0.00	2.39E−07	2.56	145.8	3.56
Goatfishes										
Spotted Goatfish	1	5	241.9	332.3	0.27	0.09	2.29E−08	2.96	175.0	2.91
Yellow Goatfish	0	–	–	300.0	0.40	0.00	1.10E−08	3.09	160.0	1.91
Boxfishes										
Honeycomb Cowfish	0	–	–	–	–	–	1.08E−07	2.68	–	–
Scrawled Cowfish	0	–	–	–	–	–	9.56E−07	2.26	222.0	–
Smooth Trunkfish	0	–	–	–	–	–	1.82E−06	2.23	–	–
Spotted Trunkfish	0	–	–	–	–	–	–	–	–	–
Trunkfish	0	–	–	–	–	–	1.43E−07	2.66	–	–
Bigeyes										
Bigeye	1	18	644.5	665.0	0.17	−2.90	1.19E−08	3.04	138.0	−1.52

Note: Exceptions for length type are denoted by superscripts: *a*, length type is total length; *b*, length type is standard length; *c*, length type was converted to fork length using corresponding equations in Table 7. Life History (LH) denotes the reliability score (Table 4).

4 | DISCUSSION

This study synthesized life history information for 84 exploited tropical reef fish species from Florida and the U.S. Caribbean. Only a handful of these species have undergone formal assessments via the SEDAR (SouthEast Data, Assessment, and Review) process to estimate stock status and inform management strategies. The study's focus was to identify reliable life history demographic parameters (i.e. lifespan, length at age, weight at length and maturity at length) that are required for age- or length-based stock assessments, and also for use in ecosystem modelling and ecological risk assessments. Key aspects of the life history synthesis included construction of a database that characterized relevant aspects of a given study (e.g. sampling region, statistical and biological methods, length range, sample size), procedural criteria for selecting parameters for a given species, and a species-level reliability metric.

The life history synthesis database (Figure 1, Appendix S2), developed concurrently with the hierarchical selection criteria (Figure 2), was instrumental for identifying the best available parameters and evaluating their reliability for a given species. In general, the reporting of study details such as time and location of specimen collection, biological and statistical methods, sample size was more complete in life history investigations of the past decade or so compared to previous studies. However, it was surprising that basic information such as the length range of specimens was still occasionally not reported in recent studies. Work is underway to convert the prototype synthesis database compiled in this study to a publicly available online version maintained by NOAA's Southeast Fisheries Science Center. Along with providing our compilation of life history study details for the full suite of exploited reef fish species, the online database will also enable researchers to submit information from new life history studies as they become available. In the interim, our prototype database will be provided to researchers upon request.

A complete set of life history parameters was available for 46 of the 84 species analysed. In terms of reliability, the 16 species receiving the highest score (LH = 3) were mostly groupers and snappers. This metric was only possible to achieve where length-age studies had reported length ranges of species. The reliability metric can be used to guide future life history research, especially for species with reliability scores of LH ≤ 2. For example, reliability scores of many snappers could be improved markedly by focusing on estimates of length at maturity. Future life history research should employ robust biological and statistical methods, satisfying the criteria for obtaining a reliability score of at least LH = 2 in the present study. Our analysis found that more recent studies generally employed the most robust methods—sectioned otoliths paired with nonlinear regression for length-age, histological examination of gonads paired with logistic regression for maturity at length—indicating that these

TABLE 6 Citations for the selected life history parameters in Table 5 with Life History (LH) reliability scores for each parameter type noted in parentheses based on criteria defined in Figure 2 and Table 4

Species	Length-age	Weight-length	Maturity
Groupers			
Atlantic Creolefish	Posada and Appeldoorn (1996) (1)	(0)	(0)
Black	SEDAR (2010) (3)	SEDAR (2010) (2)	SEDAR (2010) (2)
Coney	Burton et al. (2015a) (2)	Burton et al. (2015a) (2)	Trott (2006) (1)
Gag	SEDAR (2014) (3)	SEDAR (2014) (2)	SEDAR (2014) (2)
Goliath	SEDAR (2016b) (2)	SEDAR (2016b) (2)	SEDAR (2016b) (1)
Graysby	Potts and Manooch (1999) (3)	Potts and Manooch (1999) (2)	Nagelkerken (1979) (1)
Misty	(0)[a]	(0)	(0)
Mutton Hamlet	(0)	(0)	Marques and Ferreira (2011) (1)
Nassau	Cushion (2010) (3)	Cushion (2010) (2)	Cushion (2010) (2)
Red	SEDAR (2015b) (3)	SEDAR (2015b) (2)	SEDAR (2015b) (2)
Red Hind	Cushion (2010) (2)[a]	Sadovy, Figuerola, and Roman (1992) (2)	Sadovy, Rosario, and Roman (1994) (2)
Rock Hind	Potts and Manooch (1995) (1)[a]	Burton, Potts, and Carr (2012) (2)	(0)
Scamp	Lombardi, Cook, Lyon, Barnett, and Bullock (2012) (3)	Matheson, Huntsman, and Manooch (1986) (2)	Lombardi et al. (2012) (2)
Snowy	SEDAR (2013) (3)	SEDAR (2013) (2)	SEDAR (2013) (2)
Speckled Hind	Ziskin, Harris, Wyanski, and Reichert (2011) (3)	Ziskin (2008) (2)	Ziskin et al. (2011) (2)
Tiger	Garcia, Sierra, and Claro (1999) (2)	Garcia et al. (1999) (2)	Caballero, Brule, Noh-Quinones, Colas-Marrufo, and Perez-Diaz (2013) (2)
Warsaw	Manooch and Mason (1987) (1)	Manooch and Mason (1987) (2)	Manooch (1984) (1)
Yellowedge	SEDAR (2011) (3)	SEDAR (2011) (2)	SEDAR (2011) (2)
Yellowfin	Burton, Potts, and Carr (2015b) (3)	Burton et al. (2015b) (2)	Cushion (2010) (2)
Yellowmouth	Burton, Potts, and Carr (2014) (3)	Burton et al. (2014) (2)	Bullock and Murphy (1994) (1)
Snappers			
Black	Thompson and Munro (1983) (1)	(0)	Thompson and Munro (1983) (1)
Blackfin	Burton, Potts, and Carr (2016) (2)	Burton et al. (2016) (2)	Thompson and Munro (1983) (1)
Cardinal	(0)	(0)	Thompson and Munro (1983) (1)
Cubera	Burton and Potts (2017) (3)	Burton and Potts (2017) (2)	Baisre and Paez (1981) (1)
Dog	Previero et al. (2011) (2)[a]	Previero et al. (2011) (2)	Claro and Garcia (1994) (1)
Grey	SEDAR (2018) (3)	SEDAR (2018) (2)	SEDAR (2018) (2)
Lane	SEDAR (2016c) (2)	SEDAR (2016c) (2)	SEDAR, 2016c) (1)
Mahogany	Potts and Burton (2017) (2)	Potts and Burton (2017) (2)	(0)
Mutton	O'Hop et al. (2015) (3)	SEDAR (2008) (2)	SEDAR (2008) (2)
Queen	Murray and Moore (1993) (1)	Gobert et al. (2005) (2)	(0)
Red	Cass-Calay et al. (2013) (3)	Cass-Calay et al. (2013) (2)	Cass-Calay et al. (2013) (2)
Schoolmaster	Potts, Burton, and Myers (2016) (2)	Potts et al. (2016) (2)	Thompson and Munro (1983) (1)
Silk	Poso and Espinosa (1982) (2)	Poso and Espinosa (1982) (2)	Poso and Espinosa (1983) (1)
Vermilion	SEDAR (2016a) (3)	SEDAR (2016a) (2)	SEDAR (2016a) (2)
Wenchman	Anderson, Lombardi-Carlson, and Hamilton (2009) (2)	Anderson et al. (2009) (2)	(0)
Yellowtail	O'Hop, Murphy, and Chagaris (2012) (3)	O'Hop et al. (2012) (2)	O'Hop et al. (2012) (2)
Grunts			
Barred	Garcia and Duarte (2006) (1)	(0)	(0)
Black Margate	(0)	Bohnsack and Harper (1988) (1)	(0)

(Continues)

TABLE 6 (Continued)

Species	Length-age	Weight-length	Maturity
Bluestriped	Pitt, Trott, and Luckhurst (2010) (2)	Pitt et al. (2010) (2)	Garcia-Cagide (1986) (1)
Burro	(0)	Claro and Garcia (2001) (1)	(0)
Cottonwick	Nelson, Manooch, and Mason (1985) (2)	Bohnsack and Harper (1988) (2)	Billings and Munro (1974) (1)
French	Dennis (1988) (1)	Bohnsack and Harper (1988) (2)	Billings and Munro (1974) (1)
Margate	Garcia-Arteaga (1983) (2)	Bohnsack and Harper (1988) (1)	Garcia-Cagide (1986) (1)
Pigfish	(0)[a]	Bohnsack and Harper (1988) (2)	Hildebrand and Cable (1930) (1)
Porkfish	(0)	Bohnsack and Harper (1988) (2)	(0)
Sailor's Choice	Claro, Lindeman, and Parenti (2001) (2)	Bohnsack and Harper (1988) (2)	(0)
Tomtate	Manooch and Barans (1982) (2)	Bohnsack and Harper (1988) (2)	Manooch and Barans (1982) (1)
White	Murphy, Murie, and Muller (1999) (2)	Murie and Parkyn (2005) (2)	Murphy et al. (1999) (2)
Porgies			
Jolthead	Burton, Potts, Page, and Poholek (2017) (2)	Burton et al. (2017) (2)	Liubimova and Capote (1971) (1)
Knobbed	Burton, Potts, Poholek, Ostrowski, and Page (2019) (3)	Burton et al. (2019) (2)	(0)
Littlehead	Tyler and Torres (2015) (2)	Tyler and Torres (2015) (2)	Tyler and Torres (2015) (2)
Pluma	(0)	Claro and Garcia (1994) (2)	(0)
Red	SEDAR (2006) (2)	SEDAR (2006) (2)	SEDAR (2006) (1)
Saucereye	(0)	Bohnsack and Harper (1988) (2)	(0)
Sheepshead	Dutka and Murie (2001) (2)	Dutka and Murie (2001) (2)	Render and Wilson (1992) (1)
Sheepshead Porgy	Garcia and Duarte (2006) (1)	Bohnsack and Harper (1988) (2)	(0)
Whitebone	Waltz, Roumillat, and Wenner (1982) (2)	Waltz et al. (1982) (2)	Waltz et al. (1982) (1)
Triggerfishes			
Grey	SEDAR (2015a) (3)	SEDAR (2015a) (2)	SEDAR (2015a) (2)
Ocean	(0)	Bohnsack and Harper (1988) (2)	(0)
Queen	Albuquerque, Martins, Leite Junior, Araújo, and Ribeiro (2011) (2)	Albuquerque et al. (2011) (2)	Aiken (1975) (1)
Wrasses and Parrotfishes			
Hogfish	Cooper, Collins, O'Hop, and Addis (2013) (3)	Cooper et al. (2013) (2)	Cooper et al. (2013) (2)
Princess	(0)	Bohnsack and Harper (1988) (1)	Reeson (1975a) (1)
Redband	Choat and Robertson (2002) (1)	Bohnsack and Harper (1988) (2)	Reeson (1975a) (1)
Redtail	Choat and Robertson (2002) (1)	Bohnsack and Harper (1988) (2)	Figuerola, Matos, and Torres (1998) (1)
Spanish Hogfish	(0)	(0)	Robertson and Warner (1978) (1)
Stoplight	Choat, Robertson, Ackerman, and Posada (2003) (3)	Bohnsack and Harper (1988) (2)	Figuerola et al. (1998) (1)
Yellowtail	Choat and Robertson (2002) (2)	(0)	Robertson and Warner (1978) (1)
Barracudas			
Great Barracuda	Kadison, D'Alessandro, Davis, and Hood (2010) (3)	Kadison et al. (2010) (2)	Kadison et al. (2010) (1)
Surgeonfishes			
Blue Tang	Mutz (2006) (2)	Bohnsack and Harper (1988) (2)	Reeson (1975b) (1)
Doctorfish	Mutz (2006) (2)	Bohnsack and Harper (1988) (2)	Reeson (1975b) (1)
Ocean Surgeonfish	Mutz (2006) (2)	Bohnsack and Harper (1988) (2)	Reeson (1975b) (1)
Squirrelfishes			
Longspine Squirrelfish	Munro (1999) (1)	(0)	Wyatt (1983) (1)

(Continues)

TABLE 6 (Continued)

Species	Length-age	Weight-length	Maturity
Squirrelfish	Munro (1999) (1)	Bohnsack and Harper (1988) (2)	Mendes, Hazin, Oliveira, and Carvalho (2007) (2)
Goatfishes			
Spotted	Santana, Morize, and Lessa (2006) (2)	Bohnsack and Harper (1988) (2)	Munro (1976) (1)
Yellow	Munro (1976) (1)	Bohnsack and Harper (1988) (2)	Munro (1976) (1)
Boxfishes			
Honeycomb Cowfish	(0)	Bohnsack and Harper (1988) (2)	(0)
Scrawled Cowfish	(0)	Bohnsack and Harper (1988) (2)	Ruiz, Figueroa, and Prieto (1999) (2)
Smooth Trunkfish	(0)	Bohnsack and Harper (1988) (2)	(0)
Trunkfish	(0)	Claro and Garcia (2001) (2)	(0)
Bigeyes			
Bigeye	Ximenes, Fonteles, and Paiva (2009) (3)	Bohnsack and Harper (1988) (2)	Tapia, Yanez-Arancibia, Sanchez-Gil, and Garcia-Abad (1995) (1)

[a]Citations for maximum age estimates when the maximum age estimate was not obtained from the preferred length-age study: Misty grouper (Luckhurst & Dean, 2009); Red hind (Sadovy et al., 1992); Rock hind (Burton et al., 2012); Dog snapper (Potts & Burton, 2017); Pigfish (Taylor, 1916)

have become the standards for scientific best practice. Tag–recapture growth studies were quite rare in our literature search, even though this approach has proven useful for developing length-age functions for tropical fishes that are inherently difficult to accurately age from otoliths and other hard parts (Francis, 1988; Laslett, Eveson, & Polacheck, 2002; Welsford & Lyle, 2005). Likewise, we did not encounter length-age studies utilizing Bayesian model-fitting procedures (c.f., Dortel et al., 2015), although this may change in the future.

Reporting of model-fitting details such as regression diagnostics and parameter standard errors was more common in recent length-age and weight-length studies. This information allows for the uncertainty in length at age and weight at age to be incorporated into stock assessments along with the respective expected (i.e. mean) values (Ault et al., 2019; Carruthers et al., 2014; Methot & Wetzel, 2013; Sagarese et al., 2018). In contrast, parameter values (i.e. mean + *SE*) for the maturity-at-length function (Equation 3) were rarely reported. The standard practice seems to be to simply report the point

TABLE 7 Length-length conversions utilized to standardize all lengths from standard length (SL), total length (TL) or maximum total length (TL_m) to fork length (FL)

Species	Conversion	Units	References
Black Grouper	TL = −1.40 + 1.028 FL	mm	SEDAR (2010)
Speckled Hind	FL = −1.88 + 0.982 TL	mm	Ziskin (2008)
Yellowedge Grouper	FL = 15.87 + 0.935 TL	mm	SEDAR (2011)
Yellowfin Grouper	FL = 18.63 + 0.93 TL	mm	Burton et al. (2015b)
Blackfin Snapper	FL = 3.38 + 0.91 TL	mm	Burton et al. (2016)
Cubera Snapper	FL = −9.65 + 0.97 TL	mm	Burton and Potts (2017)
Mahogany Snapper	FL = 12.01 + 0.89 TL	mm	Potts and Burton (2017)
Mutton Snapper	TL = 10.02 + 1.065 FL	mm	SEDAR (2008)
Queen Snapper	FL = −1.003 + 0.837 TL	cm	Gobert et al. (2005)
Red Snapper	TL_m = 0.39 + 1.06 FL	in	Cass-Calay et al. (2013)
Yellowtail Snapper	FL = 25.85 + 0.75 TL	mm	O'Hop et al. (2012)
Tomtate	TL = −1.82 + 1.154 FL	mm	Manooch and Barans (1982)
White Grunt	TL = 1.15 FL	cm	Gaut and Munro (1974)
Jolthead Porgy	FL = −14.26 + 0.90 TL	mm	Burton et al. (2017)
Knobbed Porgy	FL = −12.54 + 0.91 TL	mm	Burton et al. (2019)
Red Porgy	TL = 6.07 + 1.14 FL	mm	SEDAR (2006)
Whitebone Porgy	FL = −2.0 + 0.86 TL	mm	Waltz et al. (1982)
Stoplight Parrotfish	SL = 0.83 FL	mm	Choat et al. (2003)

value for L_m, the length at 50% maturity, whereas the length-at-maturity function and its uncertainty would be of much higher utility for stock assessments. This is especially critical for data-limited stock assessment packages such as DLMtool, which include data-limited approaches that require estimates of 50% and 95% maturity as well as estimates of their uncertainty (Carruthers et al., 2014; Sagarese et al., 2018). Future growth and maturity studies could also greatly benefit by employing parameter estimate procedures that minimize size-selection bias (Gwinn, Allen, & Rogers, 2010).

Perhaps the more challenging requirement for new life history research will be to include specimens encompassing the full range of expected lengths for a particular species. Sampling the entire length range of a population is critical to accurately model the early period of rapid growth (K, Equation 1) as well as the approach to mean asymptotic length (L_∞, Equation 1). This is obfuscated when high exploitation rates have truncated the upper bounds of the population length structure (Ehrhardt & Ault, 1992). Often, fishery-independent studies are required to obtain samples in the lower bounds of length distributions due to minimum size limits, gear selectivities or both. We focused on reliability criteria pertaining to the upper bounds of length distributions, gauging representativeness of maximum size and age estimates. Current researchers are at a disadvantage in this regard due to the likelihood of truncated length and age distributions resulting from centuries of exploitation. For length-age studies in particular, the expected maximum length (L_{99}) estimated from Trip Interview Program data provides a target for the largest specimens (L_{max}) needed for ageing. The comparability between L_{max} and L_{99} was the basis for obtaining a reliability score of LH = 3. This highest reliability score indicates that the length-age function (Figure 6) was representative of the growth of a species up to the asymptotic portion of the curve, which includes the full range of expected lengths (ordinate axis). What remains unknown is how far the asymptotic portion of the curve extends with respect to the maximum age of a species (abscissa axis). This uncertainty in lifespan, however, extends in one direction. Recent work by Ault et al. (2019) incorporated this uncertainty property for maximum observed age into length-based stock assessments of reef fishes.

The analyses of Figures 4 and 5 provide some insights for alleviating the length-age truncation problem in life history studies. The discrepancy between L_{max} and L_{99} (Figure 4) for many species likely stems from the longer time frame, wider geographic distribution and higher intensity of TIP sampling of the commercial fleets in Florida and the U.S. Caribbean compared to length-age studies which are usually more limited in time, geographic scope and sampling effort. Likewise, the maximum observed age has generally increased over time for a number of species (Figure 5) as ageing studies have progressively widened their geographic scope, increased sample sizes and refined ageing techniques. For an exploited fish population, the probability of individuals reaching their biological maximum length and age decreases with increasing fishing intensity (Ault et al., 1998, 2019; Ault, Smith, & Bohnsack, 2005). It seems that increasing the sampling intensity of life history studies is a viable strategy to counteract these low probabilities and obtain specimens of larger, older fishes. The TIP survey provides an opportunity for life history scientists to subsample larger fishes for ageing to fill in gaps in length-at-age observations.

A parallel strategy would be to focus specimen collections (with proper permitting) in areas with low to no fishing pressure. One possibility is the Dry Tortugas region in southern Florida, which includes several large no-take marine reserves as well as other management areas that limit fishing (e.g. no commercial fishing, no spearfishing) that have been in place since 2001 or earlier (Ault et al., 2006). Fishery-independent surveys have shown that this region harbours a disproportionately higher number of spawning adults of exploited snapper and grouper species compared to other areas of the southern Florida coral reef ecosystem (Ault et al., 2013). Furthermore, species of parrotfishes, surgeonfishes, goatfishes and boxfishes (Table 5) are routinely observed in fishery-independent diver visual surveys in southern Florida (Smith et al., 2011), where they are either not targeted or prohibited from fishing, in contrast to the U.S. Caribbean (Table 2). These areas present an opportunity to more accurately describe lifetime growth of exploited species using data without truncation from fishing, a largely ignored and confounding issue in fisheries stock assessments.

ACKNOWLEDGEMENTS

This paper would not have been possible without the assistance and input from Adyan Rios and Dr. Skyler Sagarese. Adyan Rios has been leading NMFS efforts to create an online life history parameter database. Lawrence Beerkircher provided processed Trip Interview Program data. We also appreciate the assistance from Gulf of Mexico Fishery Management Council and National Marine Fisheries Service employees in the literature review for species assessed in SEDAR 46 and SEDAR 49, particularly Dr. Linda Lombardi. Funding for this research was provided by NOAA Southeast Fisheries Science Center & Coral Reef Conservation Program Grant No. NA15OAR4320064-SUB36, National Park Service Natural Resource Conservation Assessment Program Grant No. H5000105040-PA15AC01547-PA16AC01758, Dry Tortugas National Park Grant No. P15AC012441-P16AC01758, Biscayne National Park Grant No. P15AC01746, and Florida RESTORE Act Center of Excellence Grant no. FIO-4710112600B.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Stevens MH, Smith SG, Ault JS. Life history demographic parameter synthesis for exploited Florida and Caribbean coral reef fishes. *Fish Fish*. 2019;20:1196–1217. https://doi.org/10.1111/faf.12405