Received: 29 April 2023 | Revised: 15 September 2023 | Accepted: 6 October 2023

DOI: 10.1002/mcf2.10276

FEATURE ARTICLE

A unified framework and terminology for reproductive traits integral to understanding fish population productivity

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Abstract

Objective: This paper highlights the complexity of marine fish spawner–recruit systems and how they vary across species and ecosystems while providing a universal terminology and framework to evaluate fish reproduction. We emphasize the gonadal development important to assess maturity, fecundity, where and when fish spawn, and transition and sex assignment in protogynous species.

Methods: We review and compare reproductive traits in warmwater and coldwater fishes. Reproductive phases for both sexes and protogynous species are defined and histological micrographs presented. New methods are developed to assess maturity; spawning seasonality; peak spawning; and, for protogynous species, sex assignment.

Result: Protogyny, extended spawning seasons, and indeterminate fecundity are more common in warmwater than coldwater systems. The following reproductive phases are defined as immature, transitional (sex change), early developing (the first stage of entrainment in the reproductive cycle), late developing (stages needed to complete maturational competence), spawning, regressing (spawning season termination), and regenerating (fish that are mature but outside of the spawning season). A method to assess the certainty of maturity assignment based on reproductive phase and the age and size range sampled is presented, as are best practices to estimate size and age at maturity. To remove the subjectivity from current methods to estimate spawning seasonality, we present a new quantitative method to identify the core spawning season and peak spawning months.

Conclusion: A species' ability to adapt to fishing and climate change varies with their reproductive strategy. Improving our understanding of fish reproduction necessitates standardizing methodology and terminology.

KEYWORDS

fish reproduction, fish reproductive strategies, gonadal histology, maturity, protogynous, spawning season

INTRODUCTION

Reproductive success is defined as producing offspring that survive to sexual maturity (Clutton-Brock 1988). It drives species persistence and population growth, making an understanding of fish reproductive biology critical to fisheries management, restoration, and aquaculture. Reproductive parameters are important components of life tables, stock assessments, population dynamics, and ecology, and over the past several decades, multiple large-scale collaborative efforts have addressed fish reproductive biology and improved measures of reproductive potential. These efforts include the book *Fish Reproductive Biology: Implications for Assessment and Management* (Jakobsen et al. 2009); the European Cooperation in Science and Technology action "Fish Reproduction and Fisheries," which resulted in increased awareness that spawning stock biomass may underrepresent total egg production (Marshall 2009; Morgan et al. 2009; Mehault et al. 2010; Murua et al. 2010); and three published articles: "Emerging Issues and Methodological Advances in Fisheries Reproductive Biology" (Lowerre-Barbieri et al. 2011a), "Egg Production Methods in Marine Fisheries: An Introduction" (Bernal et al. 2012), and "Fish Reproduction and Fisheries" (Saborido-Rey and Trippel 2013). More recent work has confirmed that most fish species have hyperallometric scaling (i.e., large individuals produce more eggs by unit body weight than small individuals; Barneche et al. 2018; Marshall et al. 2021), and scientists are increasingly aware that reproductive success in harvested fish may not be as tightly coupled to fecundity as it is in harvested terrestrial animals (Lowerre-Barbieri et al. 2017). Factors in addition to fecundity-at-age relationships affecting fish reproductive success include disproportionately increased reproductive value with age or the "big old fat fecund female fish" effect (Berkeley et al. 2004; Hixon et al. 2014), diversity of spatiotemporal reproductive behavior (Berkeley et al. 2004; Lowerre-Barbieri et al. 2015; Biggs et al. 2021), population structure (Frank and Brickman 2001; Fromentin et al. 2014; Cadrin 2020), and sperm limitation in protogynous species (Brooks et al. 2008).

Reproduction and age or growth are key life history processes integrated into stock assessments and consequent management actions. Because data in stock assessments comes from multiple sources, there is a need to standardize methods and terminology to improve the quality of data and the ease of integrating it. There is also a recognized need to integrate emerging understanding of key life history processes, such as age and growth and reproduction, into our conceptual models. In age and growth, this has focused on agreement of how hard-part indicators are interpreted and a test of their validity to correlate with age (Vitale et al. 2019), as well as an increased focus on understanding individual growth and its plasticity (Lorenzen 2016). Similarly, there is growing awareness of how individual-scale behavior affects reproductive parameters and reproductive success (Lowerre-Barbieri et al. 2013; Zarada et al. 2019) and that reproductive parameters such as age and size at maturity are not invariant over time and may change with fishing mortality (Olsen et al. 2004; Lappalainen et al. 2016). However, the complex processes underlying reproductive success in fish affect the ease with which terminology and methods can be standardized. The core data used to assess growth is age and a measure of size. Core reproductive data includes measures of gonadal development to assess (1) sex ratio, (2) maturity, and (3) fecundity. However, our ability to estimate sex ratio and maturity is affected by a species' sexual system, as, unlike other vertebrates, sequential hermaphroditism—where an individual changes sex—is fairly common in teleost fishes (Todd et al. 2016). Sequential hermaphrodites have a functional primary (i.e., initial) sex and then transition to a functional terminal sex; this includes protogyny (from female to male) and protandry (from male to female). Fecundity in fish is also more complicated than in harvested terrestrial animals, as fish typically produce thousands to millions of eggs and in warmwater species they often spawn multiple batches over extended spawning seasons. Calculating annual fecundity in these species necessitates estimating batch fecundity, spawning fraction (i.e., the proportion of spawning females), and the spawning season (Hunter and Macewicz 1985). Lastly, few species provide parental care and offspring mortality is high, often affected by where and when fish spawn, unlike terrestrial vertebrates.

The objective of this paper is to provide a universal framework and terminology to discuss fish reproduction important to understanding population productivity, with an emphasis on gonadal development important to assess maturity, fecundity, where and when fish spawn, and transition and sex assignment in protogynous species. Traditional stock assessments integrate reproductive success through the stock–recruitment relationship, which typically relates either female mature biomass or total egg

Impact statement

We demonstrate the complexity of fish reproductive strategies and how reproductive traits are species-specific and differ between warmwater and coldwater systems, affecting population productivity. We present a unified framework and terminology to describe fish reproduction and new methods to assess key reproductive parameters.

production to annual recruitment. Here we describe multiple traits within species-specific spawner–recruit systems that have been shown to affect reproductive success (Lowerre-Barbieri et al. 2017; Ospina-Alvarez et al. 2022). This conceptual model provides the means to discuss reproductive traits in terms of their inheritability and plasticity as well as compare latitudinal trends in fixed and ecologically variable traits. To demonstrate patterns in warmwater fishes, we review reproductive traits of federally managed species in the southeastern USA, including egg type, egg size, sexual system, spawning season, and spawning and fecundity type, and compare these to those reported for coldwater species. We use this meta-analysis to help identify areas that need updating in the foundational work of Brown-Peterson et al. (2011), whose criteria and terms to assess gonadal development have been widely adapted by both marine and freshwater researchers worldwide (Figure 1). Specifically, updates address the following needs: (1) universal applicability to warmwater and coldwater species, (2) ease of standardization of historic histological data, (3) identification of spawning events, and (4) additional information to more fully address protogynous species, including transition rates and sex ratio. We give examples of the importance of accurate reproductive phase assignment and emerging concepts to assess maturity, spawning season, and spawning frequency. Multiple methods are briefly mentioned, but the main focus is on histological analysis. Because histological indicators can look quite different depending on embedding medium and stain, we include examples from two commonly used methodologies, paraffin blocks stained with hematoxylin and eosin (H&E) and plastic blocks stained with periodic acid-Schiff (PAS) reagent.

DEFINITIONS AND METHODOLOGY

Spawner–recruit systems

Spawner–recruit systems in fish have evolved under a given regime of natural mortality (Young et al. 2006; Lowerre-Barbieri et al. 2011a), with most species exhibiting a "small egg strategy" (Andersen et al. 2016). This strategy is hypothesized to have evolved to overcome high and unpredictable mortality rates and/or patchiness of prey resources at relatively large spatial scales (Stearns 1992; Winemiller and Rose 1993). Although small eggs and high fecundity are ubiquitous in harvested fish, with most species broadcasting their eggs with no parental care, spawner–recruit systems are species-specific and differ in a number of other traits that affect their resilience to fishing mortality. These include genetically fixed traits (e.g., gestation and egg type, sexual system), behavioral traits (e.g., mating systems and the size of the reproductive unit, ranging from pair spawners to aggregate spawners), and

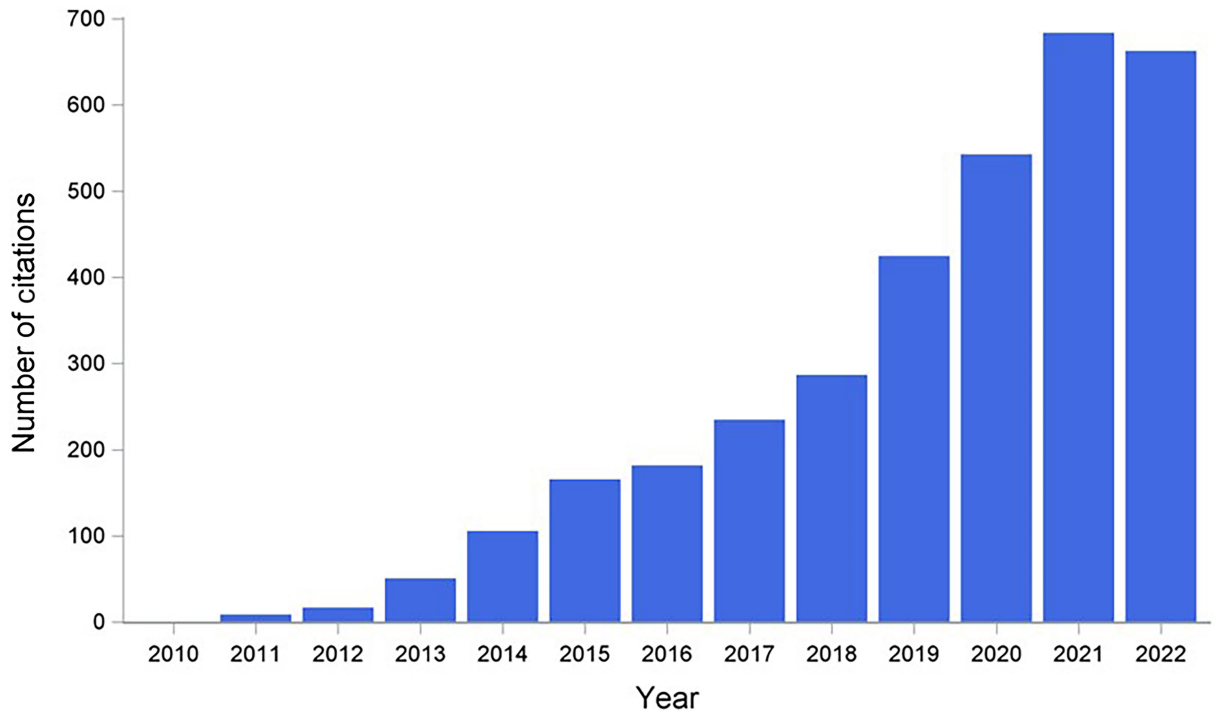

FIGURE 1 Annual citations of the standardized terminology paper (Brown-Peterson et al. 2011) since publication through December 2022, based on citations from the Web of Science core collection. An additional 407 citations occurred from January through August 2023.

variable traits that occur at the individual scale within a given ecological context, such as spawning site selection and sex change (Lowerre-Barbieri et al. 2017).

All oviparous fish need to produce fertilized eggs at a time and place where offspring survival is possible. In species with pelagic eggs and no parental care, offspring survival is affected by where and when fish spawn, since wind and currents will affect the ability for larvae to settle in nursery habitats conducive to survival (Ciannelli et al. 2015). However, important fisheries are also supported by species with demersal eggs, such as Atlantic Herring *Clupea harengus*, Atlantic Salmon *Salmo salar*, and Capelin *Mallotus villosus*. In addition, many rockfish species (subfamily Sebastinae) have internal fertilization and release live larvae (Murua and Saborido-Rey 2003). In these species, offspring survival is still affected by when and where fish spawn but there is no difference between birth site and hatch site.

The sexual systems in marine fish, which produce male and female gametes, range from gonochoristic species (separate sexes, fixed at maturation) to simultaneous hermaphrodites. However, sequential hermaphrodites represent the most common type of hermaphroditism and have been documented in at least 462 fish species (Kuwamura et al. 2020). Protandrous sequential hermaphrodites have a female terminal sex and protogynous species have a male terminal sex, with approximately two-thirds of all hermaphroditic species being protogynous (Casas and Saborido-Rey 2021). The protogynous sexual system is thought to occur in species with mating systems where female choice or territoriality infer increased reproductive success on larger males (Sattar et al. 2008) and an individual will change sex when reproductive success as a male exceeds that of a female at the same size and age (Charnov 1982; Warner 1988; Allsop and West 2004). In contrast, gonochoristic species with dimorphic growth (Lande 1980; Rankin and Kokko 2007) typically have larger females (Corey et al. 2017; Carroll and Lowerre-Barbieri 2019), and it is assumed that this is driven by increased fecundity with body size (Reznick 1983; Magurran and Garcia 2000; Henderson et al. 2003; Keyl et al. 2015).

Gonadal development necessary for reproduction occurs over four temporal scales (Lowerre-Barbieri et al. 2011b). These include lifetime, reproductive cycle, spawning season, and diel (Figure 2). All gonochorists reach sexual maturity once in life, participate in one or more reproductive cycles, release gametes or offspring once or more within a given reproductive cycle, have a maximum reproductive age (often synonymous with maximum age), and typically die before reaching that age. Sexual maturation is the trait expected to have the greatest impact on fitness (Stearns 1992), and given the assumption of fecundity-driven reproductive success, female maturation is typically the focus of population dynamics, life history theory, and fish stock assessments. Age at sexual maturity determines generation time (e.g., the average age of mature females in a population with a stable age distribution) and is often used as a de facto biological reference point in marine fisheries (Beverton and Holt 1957; Caddy and Agnew 2004). In sequential hermaphrodites, fish that transition to the terminal sex in fact are assessed for maturity twice, once for each gender. Although the drivers of transition, or maturity in the terminal sex, are poorly understood, it is often associated with social structure (Warner 1988; Godwin 2009; Kobayashi et al. 2013).

A reproductive cycle represents the gonadal development needed for fish to spawn at the appropriate time for offspring to survive (Figure 2). All reproductive cycles are made up of common reproductive developmental phases, and most cycles are annual. The first reproductive cycle in which a fish spawns marks when it becomes sexually mature. Semelparous fishes only go through one reproductive cycle in their lives, while iteroparous species will go through multiple reproductive cycles. Within a reproductive cycle, fish that develop all their oocytes synchronously and spawn once or release eggs over a very short time period are called total spawners, while those spawning more than once over a longer time period are multiple batch spawners. Within each reproductive cycle, fish must fully develop their secondary growth oocytes prior to spawning. Cortical alveolar (CA) oocytes are the first stage of this development, which is followed by vitellogenesis. When vitellogenesis is completed, oocytes have reached maturational competence and can undergo oocyte maturation (OM) if they receive the appropriate cue to commit to an upcoming spawning event. Spawning seasonality varies across species and populations in terms of duration (restricted or extended), the degree of synchronization among individual spawning periods, and the season of occurrence (e.g., fall–winter or spring–summer). Total spawners have determinate fecundity, while most multiple batch spawners have indeterminate fecundity. Multiple spawners with indeterminate fecundity develop and spawn more oocytes than are in the standing stock at the beginning of the spawning season (Murua and Saborido-Rey 2003). In species that spawn in small groups or aggregations, the diel timing of spawning events is often synchronized, resulting in the release of gametes into the water column by multiple fish at the same time. Sperm competition is common in these species and results in males with much larger reserves of sperm than seen in pair spawners (Lowerre-Barbieri et al. 2020b). The degree of synchronization in OM and ovulation (Figure 3) will affect the ability to age postovulatory follicles (POFs; what is left after an egg is ovulated). For species with

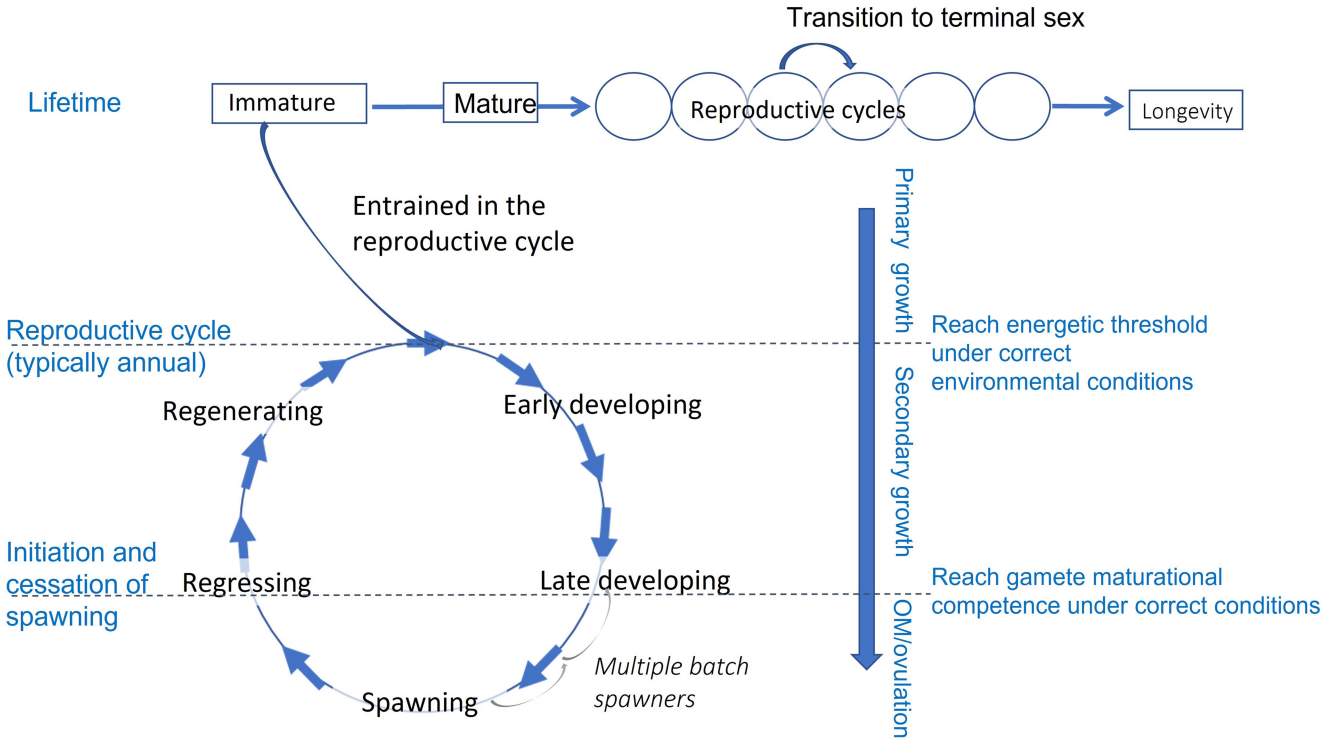

FIGURE 2 Temporal scales of fish reproduction. Fish mature once in a lifetime and participate in one or more reproductive cycles. The reproductive cycle ensures gonadal development needed for spawning to occur when offspring can survive. Fish must reach gamete maturational competence under the correct conditions for spawning to be initiated. Batch spawners spawn multiple times within a spawning season, exhibiting either spawning markers from multiple spawning events or cycling between late developing and spawning within the spawning season. Spawning events (i.e., ovulation) occur at the diel scale after oocyte maturation (OM) is completed and result in postovulatory follicles, which will be resorbed.

strong diel periodicity, POFs can be aged based on field samples. For other species, in-captivity experiments are needed to accurately define the age of POFs. Part of the reproductive cycle in iteroparous species is the removal of residual oocytes or sperm and regeneration of new gametes for the next spawning season.

Recognizing commonalities and differences in reproductive traits of managed species helps identify best measures for reproductive potential and identify species exhibiting uncommon traits that might make them less resilient to fishing, such as parental care or live-bearers. Spawner–recruit systems in coldwater species at moderate depths are often driven by food limitation and exhibit high seasonality with a short window when eggs and larvae can survive (McBride et al. 2015). The lower metabolic rates with cooler water temperatures also affect the timing of gonadal development and histological indicator duration (Lowerre-Barbieri et al. 2011b). Strategies in deepwater species are also affected by colder water temperatures but typically have much lower seasonality due to relatively stable temperatures and a lower effect of light (Barneche et al. 2018). Warmwater species have higher metabolic rates, often mature earlier, and are not as food limited as coldwater or deepwater species. Here we focus on fixed reproductive traits: egg type and size, sexual system (gonochoristic or hermaphroditic), spawning seasonality, spawning type (total or batch), and fecundity type. Fish with a determinate fecundity type recruit all of their secondary growth oocytes prior to an individual's spawning period, whereas fish with indeterminate fecundity continue to recruit secondary growth oocytes throughout the spawning season (Lowerre-Barbieri et al. 2011a, 2011b). We review the fixed reproductive traits for 25 federally managed species in the southeastern United States by assessing working papers for stock assessments, theses, and the primary literature. We then use traits for managed species from Norway (Lønning et al. 1988) to demonstrate similarities and differences with coldwater species.

Universal reproductive states and phases

Correctly assigning reproductive phases underlies our ability to estimate important changes in reproductive state associated with recruitment to the mature population, the spawning population, a spawning event, and the terminal sex in sequential hermaphrodites (Table 1). The reproductive phases presented here are a refinement of those

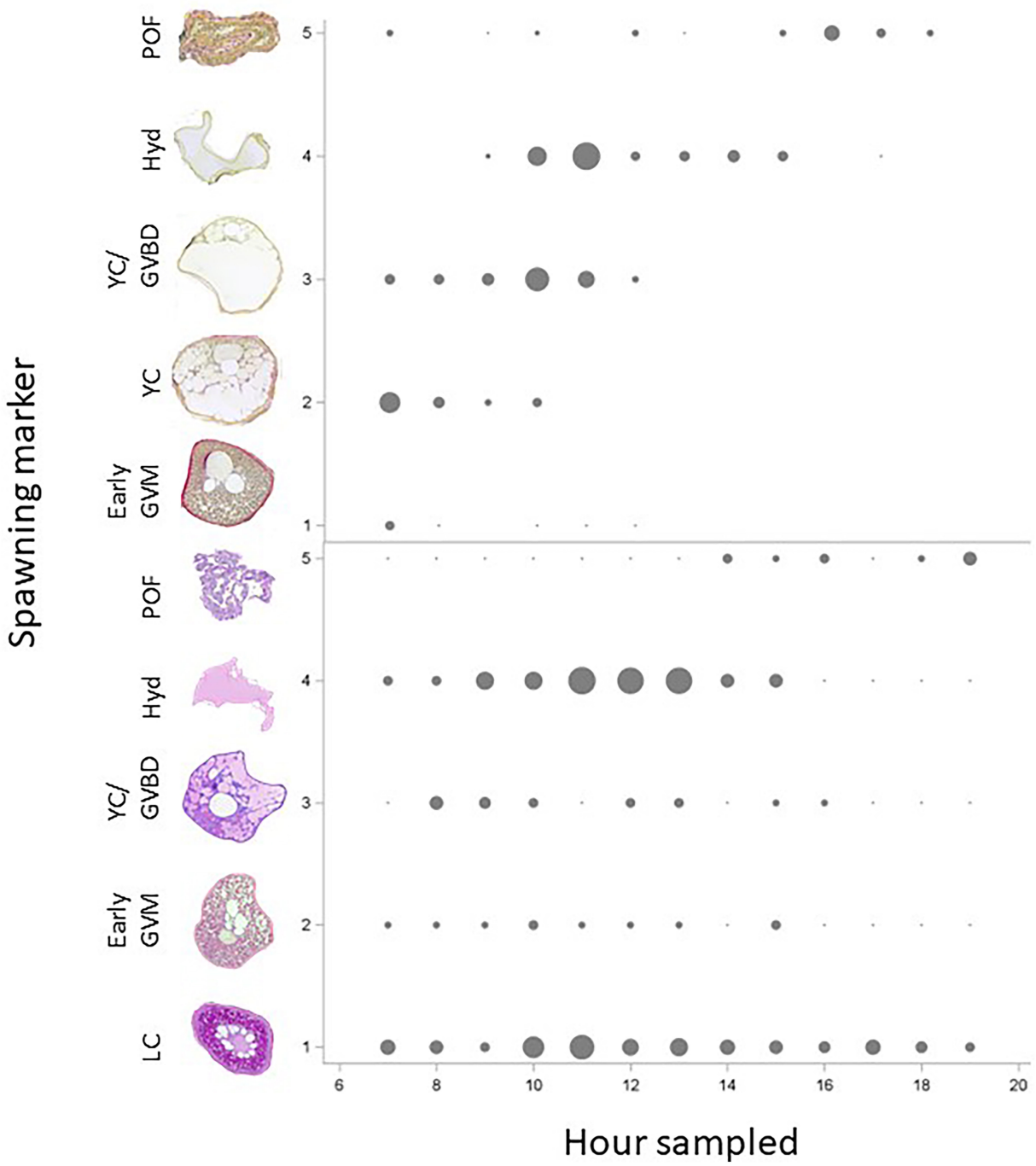

FIGURE 3 Sampling time and histological indicators of the spawning phase in Red Snapper *Lutjanus campechanus*, which have pelagic eggs. The size of the circles indicates the relative number of fish captured at each time. Small gray dots indicate that no fish were captured. The top panel shows Red Snapper from the Florida Atlantic coast stained with periodic acid-Schiff (PAS), showing the progression from indicators of imminent and active spawning. The bottom panel shows Red Snapper from the Gulf of Mexico stained with hematoxylin and eosin (H&E), with the addition of lipid coalescence (LC), which occurs prior to early germinal vesicle migration (GVM). Other abbreviations are as follows: YC = yolk coalescence, GVBD = germinal vesicle breakdown, Hyd = hydrated, and fresh POF = postovulatory follicle.

presented in Brown-Peterson et al. (2011) and include immature; early developing; late developing; spawning; regressing; regenerating; and, in the cases of sequential hermaphrodites, transitioning. These refinements are a result of more than a decade of continued reproductive research and efforts to help integrate reproductive data into stock assessments. Reproductive phases can be assigned based on macroscopic or histological analysis. Macroscopic inspection is often sufficient to assign sex in gonochorists, but it will not be able to identify all the same reproductive phases as histology. Macroscopic inspection of ovaries can identify very undeveloped ovaries,

TABLE 1 Reproductive state, reproductive phase and subphases, histological indicators, and significance to reproductive dynamics. Abbreviations are as follows: CW = coldwater, BFE = batch fecundity estimates, PG = primary growth, CA = cortical alveolar, Vtg = vitellogenic, OM = oocyte maturation, GVM = germinal vesicle migration, YC = yolk coalescence, GVBD = germinal vesicle breakdown, POF = postovulatory follicle, Sg1 = primary spermatogonia, Sg2 = secondary spermatogonia, Sc1 = primary spermatocyte, Sc2 = secondary spermatocyte, St = spermatid, Sz = sperm, rSz = residual sperm, OW = ovarian wall, CGE = continuous germinal epithelium, DGE = discontinuous germinal epithelium, and NA = not applicable.

		Histological indicators		
Reproductive state	**Phase**	**Female**	**Male**	**Significance**
Immature				
Never spawned	Immature	Oogonia and PG, no muscle bundles or large blood vessels. Lamellae are well organized. Thin OW	Lobules contain Sg1 and Sg2, no lumens	Virgin, has not yet recruited to the spawning population
Sex change				
Protogynous, sequential hermaphrodites	Transitioning	No sex assigned. Early transitioning: Sg, Sc, occasionally St, CGE, decreasing PG abundance; can have atretic oocytes. Late transitioning: Sg, Sc, and St, can have Sz in spermatocysts, clear male tissue proliferation; can have atretic oocytes		Received cues (often social) that reproductive success would be greater in terminal sex
Mature or first time developing				
Entrained within the gonadal cycle	Early developing	PG and CA, no POFs; can be a few early Vtg and atresia	Sg2 and Sc1, sometimes Sc2. Lumens often obscure	Initiates gamete development due to energetic and environmental cues
Achieve gamete maturational competence	Late developing	Females with Vtg oocytes in any stage or combination and no spawning markers. Can have low levels of atresia	All stages of spermatogenesis (Sg, Sc, St, Sz), but no Sz present in lobule lumens and/or sperm duct	Energy reserves sufficient for Vtg; in warmwater species seasonality of this phase is similar to spawning
Mature				
Recruited to the spawning population	Spawning	OM, hydration, or POFs	Sg, Sc, St, and Sz, Sz in lumens and/or sperm duct	Confirmed mature and within the spawning season
	Early	NA	CGE at terminal end of all lobules; all stages of spermatogenesis; no anastomosing lobules	Early in spawning season
	Late	NA	DGE at the terminal end of some/all lobules, anastomosing lobules	In the second half of the spawning season
	Spawning event: imminent	Early OM (early GVM with little YC)	NA	Has received the cue for oocyte maturation; for warmwater species expected to spawn within 12–24 h
	Spawning event: active	Late OM (GVBD, YC, hydrated), ovulating, or with newly-collapsed POFs	NA	Spawning ± 2 h. If no POFs, use for BFE. Indicators of late OM may need to be modified for CW species
	Spawning event: spawned	POFs older than 2 h	NA	POF duration 1–2 days in warmwater species; longer in CW species
Ending the spawning season	Regressing	≥50% of Vtg oocytes undergoing atresia (alpha and beta). Can have POFs	Few to no spermatocysts, lumens contain Sz, rSz in ducts; spermatogonial proliferation	Cessation of spawning
Between spawning seasons	Regenerating	PG, muscle bundles, blood vessels, thick OW. CW species can have POFs	Sg present, some rSz can be present in lumens	Reproductively inactive

which are presumably immature, larger ovaries that are mature but have small oocytes (including early developing, regressing, and regenerating), and ovaries with yolked oocytes (late developing) and/or hydrated oocytes (spawning) in species with pelagic eggs. In these species oocytes undergo hydration as part of OM, becoming transparent in late OM and approximately doubling in size, making it possible to observe them macroscopically. In addition, the gonadosomatic index, which measures the ratio of gonadal to somatic weight, has been used as a proxy for assigning reproductive phase, particularly to identify a threshold for differentiating between reproductively active and inactive fish (Brown-Peterson et al. 2019; Pensinger et al. 2021), and can be useful when histological data are unavailable. However, the degree to which the gonadosomatic index corresponds to reproductive phase will be sex- and species-specific.

In both sexes, histological analysis is based on the most advanced gamete stage (MAGS) and histological indicators associated with gonadal structure. Both testes and ovaries are made up of interstitial tissue, germinal epithelium (GE) from which germ cells are derived, and a tunica or gonadal wall. In ovaries, germ cells are organized within a lamellar structure where oocytes develop, undergo oocyte maturation prior to ovulation, and are released into a central lumen, resulting in the presence of spawning markers indicative of participation in a spawning event. Testes, rather than having lamellae, have tubules or lobules, and sperm are released into the lumen of these structures and then into either a central sperm duct or, in some protogynous species, into sperm ducts/sinuses within or along the interior surface of the gonadal wall. Males do not have spawning markers, as spermatogenesis provides males with a reserve of sperm throughout the spawning season. However, changes in the GE of males with lobular testis make it possible to assess the progression of individuals throughout an extended spawning period, with important implications for understanding sperm limitation. Here we address phases for the most common testis type in neoteleosts—an unrestricted spermatogonial structure, where spermatogonia are distributed along the length of the lobule (Grier and Uribe-Aranzábal 2009; Uribe et al. 2014).

Gonadal structure is also important for understanding transition in protogynous species, as there are three different patterns associated with the transformation of ovaries into testes: (1) delimited, (2) undelimited and spatially distinct, and (3) undelimited and intermixed (Figure 4). In delimited gonads, male and female tissue are separated by connective tissue, with testicular tissue proliferating and surrounding ovarian tissue during transition (i.e., Red Porgy *Pagrus pagrus*; Kokokiris et al. 2006). In undelimited gonads, male and female tissues may be spatially distinct or intermixed but they are not separated by connective tissue (Sadovy and Shapiro 1987). Spatially distinct transition results when male tissue originates from key areas of the ovary, typically near the wall and at the posterior end of the testes. In species with intermixed undelimited gonads, males retain female gonadal structure, such as ovarian walls and lamellae, and can have remnant populations of female gametes. Because of this remnant ovarian structure, sex is often difficult to assign.

Here we present detailed criteria and micrographs for reproductive phase assignment in females, males, and protogynous species using histological analysis. Images were processed to standardize resolution, image size, and illumination. In most cases, sections from the same individual are used to illustrate differences in stains. For protogynous species, properly determining the sexual system and assigning sex can be challenging, but this information is critical to estimating reproductive potential (Sadovy de Mitcheson and Liu 2008). We present criteria for identifying protogynous species that have undelimited, intermixed gonads and the accuracy of different methods

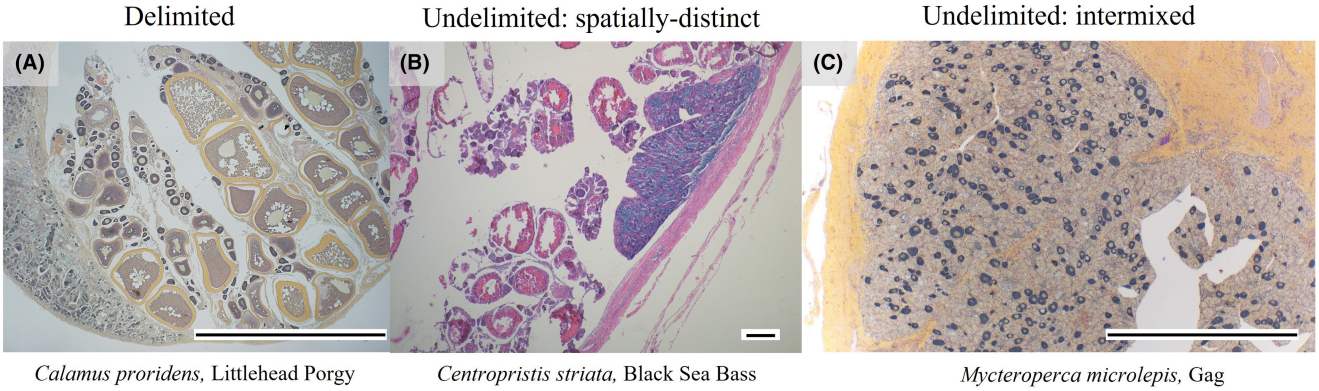

FIGURE 4 Examples of the three gonadal structure patterns associated with transition in protogynous species, showing (A) delimited, (B) undelimited and spatially distinct, and (C) undelimited and intermixed. Histological slides shown in panels (A) and (C) were stained with PAS, and the scale bar = 1 mm; the slide in panel (B) is stained with H&E, and the scale bar = 0.2 mm.

to assign sex in these species, which plays a critical role in estimating sex ratios and potential sperm limitation (Brooks et al. 2008).

Reproductive parameter estimations

We review the accuracy of varying female reproductive phases as indicators of maturity. We develop the concept of the maturation window based on the smallest, youngest mature fish and the largest, oldest immature fish. We then use Red Snapper as an example to demonstrate how assessing where samples fall in comparison to this range can help determine if sampling is representative of both immature and mature individuals. Similarly, we compare the range, and mean size and age of females by reproductive phase, to the maturation window to help identify phases that include both immature and mature fish and thus are of uncertain maturity. We define the maximum spawning season duration, core spawning seasons, and peak spawning months. The maximum spawning season duration is based on the first and last dates females in the spawning phase are observed. To estimate the core spawning season, we use a binomial regression to model the calendar date when 50% of females are developing versus spawning, as well as spawning versus regressing or regenerating (Lowerre-Barbieri et al. 2011b, 2020a). We identify peak spawning months as those within the core spawning season that have a spawning fraction greater than that of the core spawning season as a whole (Lowerre-Barbieri et al. 2022a). In addition, we highlight the role accurate assessment of active spawning plays in understanding spatiotemporal spawning trends and estimating spawning frequency. Lastly, we address the need for accurate assignment of sex and the transitioning phase to understand sex change in protogynous species.

RESULTS AND DISCUSSION

Spawner–recruit systems of managed species

All of the federally managed species in the southeastern USA are highly fecund, and all but one have pelagic eggs and provide no parental care (Table 2). Late OM was characterized by completed germinal vesicle migration (GVM) or germinal vesicle breakdown (GVBD), yolk coalescence (YC), and sufficient hydration that hydrated oocytes were detectable macroscopically. However, Gray Triggerfish have demersal eggs that do not undergo hydration (Lang and Fitzhugh 2015), and after these eggs are fertilized, both sexes protect them (Simmons and Szedlmayer 2012; Kelly-Stormer et al. 2017). Because Gray Triggerfish eggs are approximately the size of tertiary vitellogenic oocytes in pelagic spawners and they do not become translucent with hydration, spawning phase females can only be identified with histology. Fresh POFs remain after ovulation of both pelagic and demersal eggs, although POFs cannot be assessed macroscopically.

Approximately 33% of the federally managed species reviewed are protogynous sequential hermaphrodites (Table 2). Protogynous species can be monandric, where all fish start out as female and later in life some individuals transition to male, or diandric, where some fish initially mature as either female or male with additional females changing sex to male later in life (Sadovy de Mitcheson and Liu 2008). The reproductive unit in protogynous species (i.e., pair, harem, spawning aggregation) and how units are spatially distributed, optimal sex ratio, and cues initiating sex change or transition (Todd et al. 2016; Lowerre-Barbieri et al. 2020b) are important for managing protogynous species but poorly understood.

All warmwater species reviewed were batch spawners with indeterminate fecundity, regardless of sexual system (Table 2). In warmwater species, total spawners are often diadromous (i.e., they migrate to or from freshwater to saltwater to spawn). Several occur in the U.S. southeastern region, but they are not managed federally but rather at a smaller spatial scale. These include Striped Mullet *Mugil cephalus* (McDonough et al. 2003) and Striped Bass *Morone saxatilis* (Gervasi et al. 2019). Calculating annual fecundity and contribution to the spawning stock is much more straightforward, with total spawners compared with batch spawners.

Spawning seasons for most (68%) of the federally managed species in the southeastern United States were extended, five or more months in duration (Table 2). Atlantic Menhaden, Red Drum, Atlantic Goliath Grouper, Gag, and Gray Triggerfish had the shortest spawning seasons, ranging from 3 to 4 months. With the exception of Gray Triggerfish, these species all spawn in the fall or winter. Extended spawning seasons were observed in both highly migratory species, such as King Mackerel (7 months), and highly resident species, such as Red Snapper (5–8 months). Blueline Tilefish and Hogfish had the most extended spawning seasons (10 months)—although this may be due more to low seasonality and synchronicity in spawning than in individuals repeatedly spawning over a longer time period than in other species (Harris et al. 2004; McBride and Johnson 2007).

Reproductive traits of coldwater species often differ from those of warmwater species. This is due to trends in food availability and the strong influence of seasonal changes in temperature on aquatic ectotherm survival, distribution, growth, and reproduction (Trip et al. 2008). The most

TABLE 2 Reproductive traits of managed fish species for federally managed warmwater species from the southern United States, including the southeastern U.S. Atlantic (SEA) and Gulf of Mexico (GOM), and managed coldwater species from Norway. Abbreviations are as follows: OM = oocyte maturation, POF = postovulatory follicle, GSI = gonadosomatic index, Vtg = vitellogenic oocytes, and OD = oocyte diameter. Superscripts indicate citation, listed below, and a question mark indicates that there was no supporting literature. Egg size values represent the whole egg size at or near the terminal stage of development in pelagic eggs (hydration) or demersal eggs (late vitellogenesis/early oocyte maturation).

Species	Region	Egg type	Egg size (mm)	Sexual system	Total or batch spawner	Spawning season	Spawning season defined by	Fecundity type
Warmwater species from the southern United States								
Atlantic Menhaden *Brevoortia tyrannus*	SEA	Pelagic	1.35[1]	Gonochoristic	Batch	(SEA) Oct–Dec[2,3]	(SEA) OM/PO	Indeterminate[3]
Black Grouper *Mycteroperca bonaci*	SEA and GOM	Pelagic	~1[4]	Protogynous	Batch	(SEA) Dec–Apr [5,6]; (GOM) Dec–May[6]	(SEA) OM/POF; (GOM) OM/POF	Indeterminate?
Black Sea Bass *Centropristis striata*	SEA	Pelagic	0.86[1]	Protogynous	Batch	(SEA) Dec–Apr[7]	(SEA) OM/POF	Indeterminate[8]
Blueline Tilefish *Caulolatilus microps*	SEA	Pelagic	0.90[9]	Gonochoristic	Batch	(SEA) Feb–Nov[9,10]	(SEA) OM/POF	Indeterminate[9]
Cobia *Rachycentron canadum*	SEA and GOM	Pelagic	1.4[11]	Gonochoristic	Batch	(SEA) Apr–Sep[12]; (GOM) Apr–Sep[13]	(SEA) OM/POF; (GOM) OM/POF	Indeterminate[13]
Gag *Mycteroperca microlepis*	SEA and GOM	Pelagic	1[14]	Protogynous	Batch	(SEA) Dec–May[15]; (GOM) Feb–mid-Apr[16]	(SEA) OM/POF; (GOM) OM/POF	Indeterminate[17]
Tilefish *Lopholatilus chamaeleonticeps*	SEA and GOM	Pelagic	1.25–1.42[18]	Gonochoristic	Batch	(SEA) Mar–Jul[7,18]; (GOM) Jan–Jun[19]	(SEA) OM/POF; (GOM) OM/POF, GSI	Indeterminate?
Atlantic Goliath Grouper *Epinephelus itajara*	SEA and GOM	Pelagic	0.95[20]	Gonochoristic, some protogny[21]	Batch	(SEA) Aug–Oct[20,21,22]; (GOM) Jun–Sep[23,24]	(SEA) OM/POF; (GOM) Vtg/OM	Indeterminate[20]
Gray Snapper *Lutjanus griseus*	GOM	Pelagic	0.85[25]	Gonochoristic	Batch	(GOM) May–Sep[26,27]	(GOM) OM/POF	Indeterminate?
Gray Triggerfish *Balistes capriscus*	SEA and GOM	Demersal	0.5–0.6[28]	Gonochoristic	Batch	(SEA) May–Aug[29]; (GOM) May–Aug[28,30]	(SEA) OM/POF; (GOM) POF	Indeterminate/ group synchronous[28]
Greater Amberjack *Seriola dumerili*	SEA and GOM	Pelagic	1[31]	Gonochoristic	Batch	(SEA) Jan–Jun[32]; (GOM) Feb–Jun[33,34]	(SEA) OM/POF; (GOM) GSI/OM	Indeterminate[32]
Gulf Menhaden *Brevoortia patronus*	GOM	Pelagic	1.2[35]	Gonochoristic	Batch	(GOM) Oct–Mar[36]	(GOM) OM/POF	Indeterminate[36]
Hogfish *Lachnolaimus maximus*	SEA and GOM	Pelagic	1.2[37]	Protogynous	Batch	(SEA) Mar–Jun, Nov[38]; (GOM) all but Aug and Sep[39]	(SEA) OM/POF; (GOM) POF	Indeterminate?
King Mackerel *Scomberomorus cavalla*	SEA and GOM	Pelagic	1[40]	Gonochoristic	Batch	(SEA) and (GOM) Apr–Oct[40,41]	(SEA) and (GOM) late Vtg, OD	Indeterminate?

TABLE 2 (Continued)

Species	Region	Egg type	Egg size (mm)	Sexual system	Total or batch spawner	Spawning season	Spawning season defined by	Fecundity type
Mutton Snapper *Lutjanus analis*	SEA and GOM	Pelagic	0.78[42]	Gonochoristic	Batch	(SEA) Apr–Sep[43]; (GOM) Apr–Sep[43,44]	(SEA) GSI and OM/POF; (GOM) GSI & OM/POF	Indeterminate?
Red Drum *Sciaenops ocellatus*	SEA and GOM	Pelagic	0.8[1]	Gonochoristic	Batch	(SEA) Aug–Oct[45,46]; (GOM) Aug–Oct[47,48]	(SEA) GSI, hydroacoustic; (GOM) OM/POF, hydroacoustic	Indeterminate[47]
Red Grouper *Epinephelus morio*	SEA and GOM	Pelagic	0.95[49]	Protogynous	Batch	(SEA) Feb–Jun[50]; (GOM) Mar–Jul[51]	(SEA) OM/POF; (GOM) OM/POF	Indeterminate[51]
Red Porgy *Pagrus pagrus*	SEA and GOM?	Pelagic	1[52]	Protogynous	Batch	(SEA) Nov–May[53,54]; (GOM) Nov–Mar[55,56]	(SEA) OM/POF; (GOM) OM/POF	Indeterminate[54]
Red Snapper *Lutjanus campechanus*	SEA and GOM	Pelagic	0.82[57]	Gonochoristic	Batch	(SEA) May–Oct[53,58]; (GOM) Mar/Apr–Oct[59,60,61]	(SEA) OM/POF; (GOM) OM/POF	Indeterminate[61]
Scamp *Mycteroperca phenax*	SEA and GOM	Pelagic	1[14]	Protogynous	Batch	(SEA) Feb–Aug[53,62]; (GOM) Jan–Jun[63,64]	(SEA) OM/POF; (GOM) OM/POF	Indeterminate[62]
Snowy Grouper *Hyporthodus niveatus*	SEA and GOM	Pelagic	1?	Protogynous	Batch	(SEA) Jan–Oct[65]; (GOM) Apr–Sep[66,67]	(SEA) OM/POF; (GOM) OM/POF	Indeterminate?
Spanish Mackerel *Scomberomorus maculatus*	SEA and GOM	Pelagic	1.14[35]	Gonochoristic	Batch	(SEA) May–Aug[68]; (GOM) May–Sep[69]	(SEA) OM; (GOM) GSI	Indeterminate?
Vermilion Snapper *Rhomboplites aurorubens*	SEA and GOM	Pelagic	1.25[70]	Gonochoristic	Batch	(SEA) Apr–Sep[7,70]; (GOM) Apr–Sep[71]	(SEA) OM/POF; (GOM) OM/POF	Indeterminate[70]
Yellowedge Grouper *Hyporthodus flavolimbatus*	SEA and GOM	Pelagic	1?	Protogynous	Batch	(SEA) Apr, Jul–Sep[72]; (GOM) Mar–Sep[73]	(SEA) HO; (GOM) OM	Indeterminate?
Yellowtail Snapper *Ocyurus chrysurus*	SEA and GOM	Pelagic	0.82[74]	Gonochoristic	Batch	(SEA) Apr–Aug[75]; (GOM) Apr–Aug[76]	(SEA) GSI; (GOM) GSI	Indeterminate?
Coldwater species from Norway								
American Plaice *Hippoglossoides platessoides*	Norway	Pelagic	2.6[77]	Gonochoristic	Batch	Spring, 1.5 months[77,78]	Ichthyoplankton survey	Determinate[78]
European Plaice *Pleuronectes platessa*	Norway	Pelagic	2[77]	Gonochoristic	Batch	Spring, 2 months[77,78]	Ichthyoplankton survey	Determinate[78]
European Flounder *Platichthys flesus*	Norway	Pelagic	0.8–0.9[79]	Gonochoristic	Batch	Summer, 3 months[77,79]	Ichthyoplankton survey, Vtg	Determinate[79]
Atlantic Halibut *Hippoglossus hippoglossus*	Norway	Pelagic	3[81]	Gonochoristic	Batch	Winter, 2 months[77,81]	Ichthyoplankton survey	Determinate?

(Continues)

TABLE 2 (Continued)

Species	Region	Egg type	Egg size (mm)	Sexual system	Total or batch spawner	Spawning season	Spawning season defined by	Fecundity type
Capelin *Mallotus villosus*	Norway	Demersal	1[77]	Gonochoristic	Total (semelparous)	Spring, ~1 month[77,78]	Ichthyoplankton survey	Determinate[78]
Atlantic Herring *Clupea harengus*	Norway	Demersal	1[77]	Gonochoristic	Total	Spring, ~1 month[77,78]	Ichthyoplankton survey	Determinate[78]
Lumpfish *Cyclopterus lumpus*	Norway	Demersal	2.3[82]	Gonochoristic	Batch	Summer, ~2 months[77,82]	Ichthyoplankton survey	Determinate[82]

[1]Lewis et al. (2016); [2]Gartland et al. (2019); [3]Southeast Data Assessment and Review [SEDAR] (2020); [4]Teixeira et al. (2004); [5]SEDAR (2017a); [6]Crabtree and Bullock (1998); [7]Sedberry et al. (2006); [8]Danson (2009); [9]Harris et al. (2004); [10]SEDAR (2017b); [11]Arnold et al. (2002); [12]Lefebvre and Denson (2012); [13]Brown-Peterson et al. (2001); [14]S. K. Lowerre-Barbieri, personal communication; [15]McGovern et al. (1998); [16]Lowerre-Barbieri et al. (2020b); [17]Collins et al. (1998); [18]Erickson et al. (1985); [19]Lombardi-Carlson (2012); [20]Koenig et al. (2017); [21]Murie et al. (2023); [22]Koenig and Coleman (2013); [23]Mann et al. (2009); [24]Bullock et al. (1992); [25]Allen (1985); [26]SEDAR (2018); [27]Kim (2022); [28]Lang and Fitzhugh (2015); [29]Kelly-Stormer et al. (2017); [30]SEDAR (2015); [31]Sarih et al. (2019); [32]Harris et al. (2007); [33]Murie and Parkyn (2008); [34]Beasley (1993); [35]Barneche et al. (2018); [36]Brown-Peterson et al. (2017); [37]Colin (1982); [38]D. M. Wyanski and K. J. Kolmos, personal communication; [39]McBride and Johnson (2007); [40]Finucane et al. (1986); [41]Beaumariage (1973); [42]Watanabe et al. (1998); [43]Barbieri and Colvocoresses (2003); [44]SEDAR (2008); [45]Ross et al. (1995); [46]Lowerre-Barbieri et al. (2008); [47]Bennets et al. (2019); [48]Lowerre-Barbieri et al. (2018); [49]Collins et al. (1996); [50]Burgos et al. (2007); [51]Lowerre-Barbieri et al. (2014); [52]Mihelakakis et al. (2001); [53]Farmer et al. (2017); [54]Daniel (2003); [55]Devries (2006); [56]Hood and Johnson (2000); [57]Rabalais et al. (1980); [58]Lowerre-Barbieri et al. (2015); [59]Brown-Peterson and Millender (2022); [60]Lowerre-Barbieri et al. (2022a, 2022b); [61]Collins et al. (1996); [62]Harris et al. (2002); [63]Lombardi-Carlson et al. (2012); [64]Lowerre-Barbieri et al. (2020a); [65]Kolmos et al. (2019); [66]Wyanski et al. (2000); [67]SEDAR (2016); [68]Schmidt et al. (1993); [69]Finucane and Collins (1986); [70]Cuellar et al. (1996); [71]Moncrief et al. (2018); [72]Keener (1984); [73]Cook (2007); [74]Gutiérrez-Sigeros et al. (2018); [75]McClellan and Cummings (1998); [76]Collins and Finucane (1989); [77]Lønning et al. (1988); [78]Murua and Saborido-Rey (2003); [79]Maddock and Burton (1998); [80]Van der Veer et al. (1994); [81]Brown et al. (2006); [82]Kennedy (2018).

common differences between warm- and coldwater managed species are the prevalence of sequential hermaphrodites, spawning duration, and fecundity type (Table 2). Hermaphroditism is more common in warmwater species, with sequential hermaphroditism and protogyny most common in shallow, tropical reef habitats (Pla et al. 2021). Although some hermaphroditic species are found in colder waters (Aasen 2019), none support a managed fishery. Because of the associated slower metabolism, gonadal development is also slower in coldwater species than in warmwater species (Rideout et al. 2005). The slower gonadal development, in conjunction with shorter windows of time when larval food is abundant, results in most coldwater species having more restricted (i.e., shorter) spawning durations than warmwater species, which typically have extended and asynchronous spawning seasons (Pavlov et al. 2009). These same processes result in coldwater managed species often being capital breeders (i.e., storing energy prior to the spawning season and then drawing on it; McBride et al. 2015) and having determinate fecundity. In contrast, warmwater managed species typically have indeterminate fecundity and are income breeders, using resources obtained during the reproductive season to continue to recruit and grow oocytes (Stevens et al. 2009). Proximate cues to entrain gonadal development also vary, with photoperiod as the primary cue in coldwater species such as salmonids, whereas spawning seasonality and gonadal development tend to be entrained by an interaction between temperature and photoperiod in warmwater species (Pankhurst and Porter 2003). Lastly, egg size exhibits a relationship with water temperature and current, with fish living in warm waters often producing smaller pelagic eggs than coldwater fishes (Martin et al. 2017; Barneche et al. 2018).

Reproductive traits for commonly fished species in northern Norway (Lønning et al. 1988) exhibit many of these differences as compared with warmwater species (Table 2). Although none of the species reviewed in Lønning et al. (1988) were sequential hermaphrodites, two sequential hermaphroditic species are common to Norway: the Ballan Wrasse *Labrus bergylta* and the Cuckoo Wrasse *Labrus mixtus* (Aasen 2019). Demersal eggs were more common (40% compared with 4% in our review of warmwater species; Table 2). Egg diameter and chorion thickness differed in both demersal and pelagic eggs in the coldwater species, with ~50% of species having eggs larger than the 1 mm diameter common in warmwater fishes. The largest pelagic eggs were 2–3 mm and occurred in European Plaice and Atlantic Halibut, respectively. Spawning seasons reported in Lønning et al. (1988) were based on the presence of eggs in the plankton and thus not directly comparable to the methods used to assess spawning season in the warmwater species we reviewed. However, spawning seasons appear more constricted,

with the longest of them being approximately the duration of the shortest seasons seen in warmwater species: 3 months in Atlantic Cod *Gadus morhua* and 4 months in European Flounder *Platichthys flesus*. Given the broad geographic range of many of the coldwater species reported, stock-specific variations in egg size and spawning duration are expected. For instance, Atlantic Herring from the U.S. Gulf of Maine have a 2 month fall–winter spawning season, with evidence of some individuals spawning during spring (Wuenschel and Deroba 2019), compared with the April and May spawning season in Norway reported in Lønning et al. (1988). Atlantic Cod in the U.S. Gulf of Maine also have a winter–spring spawning season but one that can extend to 4 months (Zemeckis et al. 2014) compared with the 3-month season in Norway (Lønning et al. 1988).

Universal reproductive phases and reproductive state

Females

Physiologically, female maturation is a complex process that begins in the brain (hypothalamus) and pituitary and is finalized through gonadal development, ending in fish participating in their first spawning event. In conjunction there are often ontogenetic habitat shifts associated with this process (Lowerre-Barbieri et al. 2011b), resulting in fish receiving the needed cues both to develop their gonads and to move to spawning habitat. The development within the immature reproductive phase occurs in stages that are controlled by the brain–pituitary–gonad axis, which in turn regulates the multiple and complex hormonal and neuroendocrine interactions that regulate gonadal development. The hypothalamus produces gonadotropin-releasing hormone, which regulates the release of gonadotropins, follicle-stimulating hormone, and luteinizing hormone from the pituitary. The pituitary also releases growth hormones, which affect the liver and insulin-like growth factor. Follicle-stimulating hormone and luteinizing hormone regulate early gametogenesis and the production of sex steroids in the gonads. The stages of maturation include (1) completely immature, (2) the pituitary is maturationally functional but the gonad and brain are not, (3) the pituitary and gonad are maturationally functional but the brain does not yet respond to environmental cues, and (4) the brain–pituitary–gonad axis is maturationally functional, resulting in the occurrence of maturation given the appropriate cues (Okuzawa 2002). The immature phase begins with birth, with important developmental milestones including gonadal differentiation, the production of oogonia, and recruitment of primary growth (PG) oocytes, and ends with a fully developed population of PG oocytes in the perinucleolar stage (Grier et al. 2009). Females in the last stage are capable of being entrained into a reproductive cycle if they receive the correct cues (Lowerre-Barbieri et al. 2015). Immature fish have the same MAGS as regenerating females but can be distinguished by smaller cross sections, thinner ovarian walls, and well-organized lamellae (Table 1; Figure 5A,G).

The MAGS used as histological indicators in females include PG, CA, and primary, secondary, and tertiary vitellogenic (Vtg1, Vtg2, and Vtg3, respectively) stages of OM. The first stage of gonadotropin-dependent development, indicating entrainment into the reproductive cycle, is the development of CA oocytes. In the original Brown-Peterson et al. (2011) phases, the developing phase was made up of females with CAs and early vitellogenic oocytes (Vtg1 and Vtg2) and the spawning-capable phase included fully grown vitellogenic oocytes (Vtg3) and/or POFs. Differentiating between vitellogenic oocyte stages is difficult, can be somewhat subjective, and often is not done in historic data sets, where oocytes were simply identified as vitellogenic. Thus, we propose an early developing phase for ovaries with PG and CA and occasionally a few Vtg1 oocytes (Table 1; Figure 5B) that identifies females that have responded to the cues to develop secondary growth oocytes but are typically not undergoing vitellogenesis. Females with large populations of vitellogenic oocytes, regardless of stage, are within the newly defined late-developing phase. This phase represents the period when gametes achieve maturational competence and can respond to cues to spawn (Table 1; Figure 5C). The late-developing phase can also include atresia of secondary growth oocytes, as occasionally environmental changes may result in atresia of most or all of a batch of vitellogenic oocytes, typically Vtg3 oocytes (Lowerre-Barbieri et al. 1996), but it does not include females with any spawning markers. Females with spawning markers (i.e., OM, hydration, or POFs of all ages) are now placed within a spawning phase (Table 1; Figure 5D, E), with three subphases: imminent, active, and spawned. We do not retain the "spawning capable" phase as it was not as easily applied to coldwater species with slower oocyte growth than warmwater species. However, we do retain it as an important concept for understanding spawning in warmwater multiple batch spawners, where females with spawning intervals of greater duration than that of POF resorption (typically ~2 days) will not contain spawning markers and therefore be assigned as late developing, even though they are within the spawning season and thus spawning capable.

The spawning phase includes three subphases to identify an individual's proximity to a spawning event (imminent, active, or spawned). These help with assessing diel

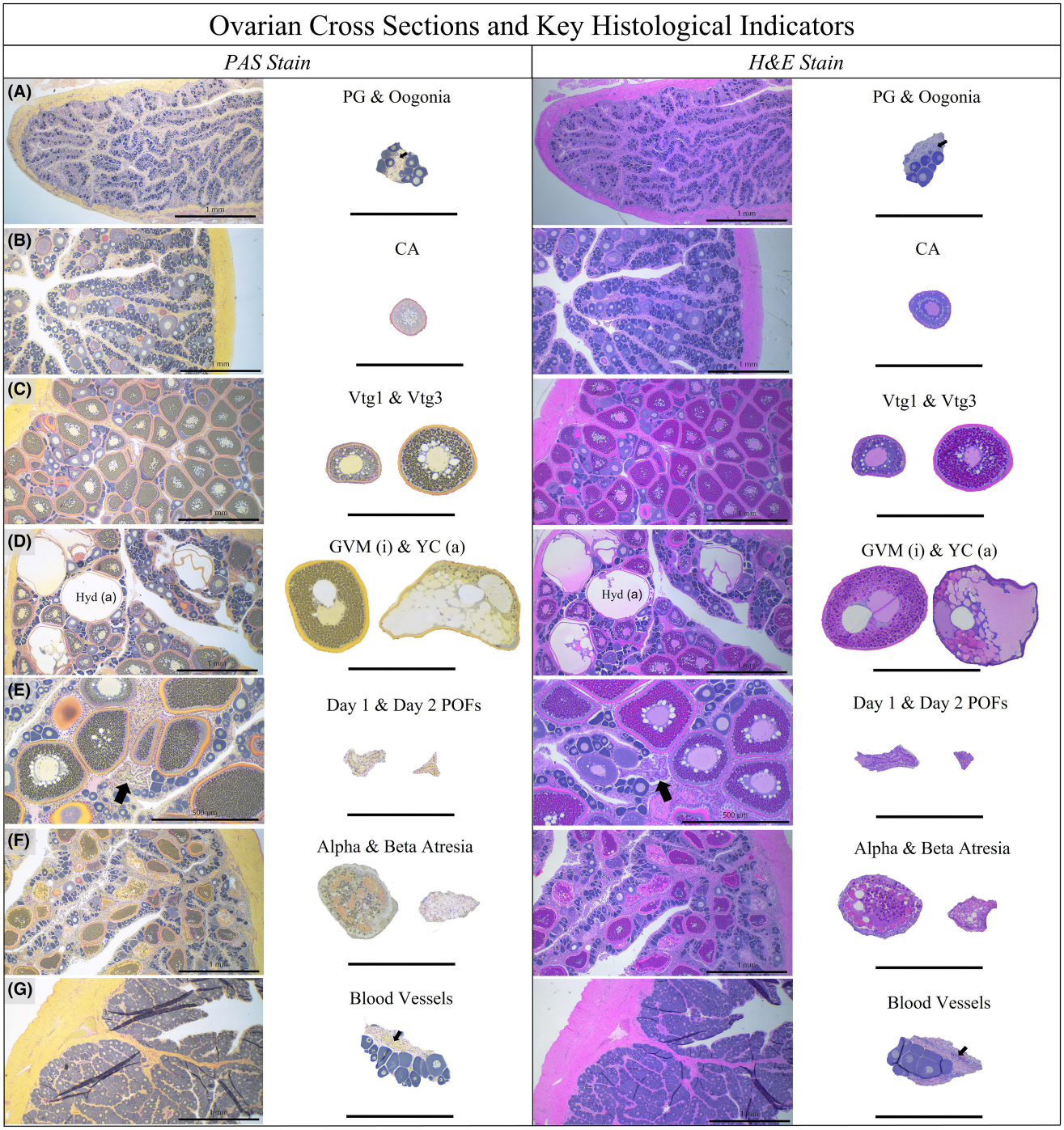

FIGURE 5 Histological indicators for female reproductive phases of Red Snapper, showing an ovarian cross section and the most advanced oocyte stage or the key histological indicator (scale bars are 0.5 mm), using PAS stain (left panels) and H&E stain (right panels). The rows show the following phases: (A) immature phase, where the arrow indicates oogonia; (B) early developing phase; (C) late-developing phase; (D) spawning phase with indicators of active (a) and imminent (i) subphases; (E) spawning phase with indicators of the spawned subphase (arrow shows POFs); (F) regressing phase; and (G) regenerating phase, with arrows indicating blood vessels. Individual variability is observable, as images are not from the same ovary in row (E). Abbreviations are as follows: PG = primary growth, CA = cortical alveoli, Vtg1 = primary vitellogenic, Vtg3 = tertiary vitellogenic, GVM = germinal vesicle migration, YC = yolk coalescence, and POF = postovulatory follicle.

periodicity, spawning habitat, and spawning frequency (Table 1; Figure 5D, E). The imminent subphase includes females undergoing early stages of OM (i.e., lipid coalescence and GVM; see Figure 3). Females in this subphase have received the cue to initiate OM and thus are committed to an upcoming spawning event. The active

subphase of spawning is used to identify fish within 2 h of spawning (Lowerre-Barbieri et al. 2009). In warmwater fishes this includes females with late OM (i.e., completed GVM or GVBD, YC, and hydration; see Figure 3). Hydrated oocytes in this subphase can be distinguished macroscopically and, if unovulated, are at the developmental stage appropriate for batch fecundity estimation. However, this subphase also includes females that are ovulating or have fresh POFs (up to 2 h old). Because histological indicators have longer durations in coldwater fishes, the indicators used to identify the actively spawning subphase (i.e., within 2 h of spawning) may need to be modified. The spawned subphase includes females with POFs older than 2 h. Batch spawners in this subphase typically have POFs and vitellogenic oocytes, as fish that have spawned are capable of spawning future batches during the current reproductive cycle. In batch spawners, resorption of secondary growth oocytes indicates the end of the spawning season. In contrast, for total spawners, POFs will indicate the end of the spawning season. Since females in the spawning phase definitely contribute to the spawning stock in the current season, they can be considered functionally mature. In contrast, late-developing females do not contain any spawning markers. Historically, females in this phase (i.e., with vitellogenic oocytes) have been considered mature, but recent research highlights the importance of maturity being based on both gonadal development and movement to the spawning grounds (Prince et al. 2022).

Histological indicators used to identify the immature, regressing, and regenerating phases are not different from Brown-Peterson et al. (2011). However, it is important to note that the regressing phase does not occur in all species. Because fish with indeterminate fecundity recruit secondary growth oocytes throughout the spawning season, as the spawning season ends they typically resorb unneeded developed oocytes resulting in high levels of atresia and a range of MAGS and can also have POFs (Table 1; Figure 5F). Cessation of spawning for total spawners will be indicated by the spawned subphase (i.e., presence of POFS), as can be the case for some determinate batch spawners; these species will move directly from the spawned subphase to the regenerating phase. Due to ovaries stretching to accommodate hydrated oocytes, changes in gonadal structure can be used to differentiate between immature and regenerating phase females, although these work best to distinguish young immature females without a full PG population from older regenerating females (Table 1). These indicators include large ovarian cross sections, decreased interstitial tissue, poorly organized lamellar structure, muscle bundles, and thick ovarian walls (Figure 5G), and in coldwater species, some (but not all) regenerating females will have late-stage POFs. There is no conclusive single histological indicator that can reliably distinguish between older immature females and those that are regenerating.

Males

Male gonadal development in both gonochorists and protogynous species can be assigned to the same reproductive phases as females, although there are some differences in gonadal structure. In gonochorists with an unrestricted spermatogonial testis type, the orientation of the lobules is such that the terminal or blind end (i.e., distal to the sperm duct) is located at the testes wall and spermatozoa in the lobules drain toward the centrally located sperm duct (Figure 6A). The same lobule orientation is present in protogynous hermaphrodites in which testicular tissue develops on the outer surface of the ovary wall. For example, in Red Porgy, the terminal end is located at the testis wall and the spermatozoa in lobules drain into sperm ducts within the former ovarian wall, which is now internally located (Figure 6B, C). In contrast, testicular tissue develops within the ovarian lamellae of other protogynous hermaphrodites, such as many groupers (family Epinephelidae), and the testes retain the lamellar organization (Sadovy de Mitcheson and Liu 2008). The terminal end of lobules in this case is located at the outer (distal) margin of the lamellae, with the spermatozoa in lobules draining toward the center of the lamellae, then to ducts in the former ovarian wall (Figure 6D).

The MAGS used as histological indicators in males include spermatagonia (Sg), spermatocytes (Sc), spermatids (St), and spermatozoa (Sz). However, an understanding of the lobular structure and sperm ducts is also needed as spermatogenesis is directional along the lobules. Additional histological indicators for correct phase assignment include characterization of the GE continuity (Grier 2002; Brown-Peterson et al. 2011) and the presence or absence of the lumen of the lobule and anastomosing lobules (neighboring lobules with discontinuous GE that have merged into a single, larger lobule filled with Sz).

The lobules of males in all reproductive phases consist of a germinal compartment, which contains the germ cells and the Sertoli cells, as well as an interstitial compartment, which contains Leydig cells and connective tissue elements, including myoid cells (Schulz and Nobrega 2011). Males in both the immature and regenerating phases have lobules with germ cells in the Sg stage. However, histological indicators to distinguish immature males include a small testicular cross section, the absence of lumens in the lobules, and the absence of residual Sz in the testis (Table 1; Figure 7A). In contrast, regenerating-phase

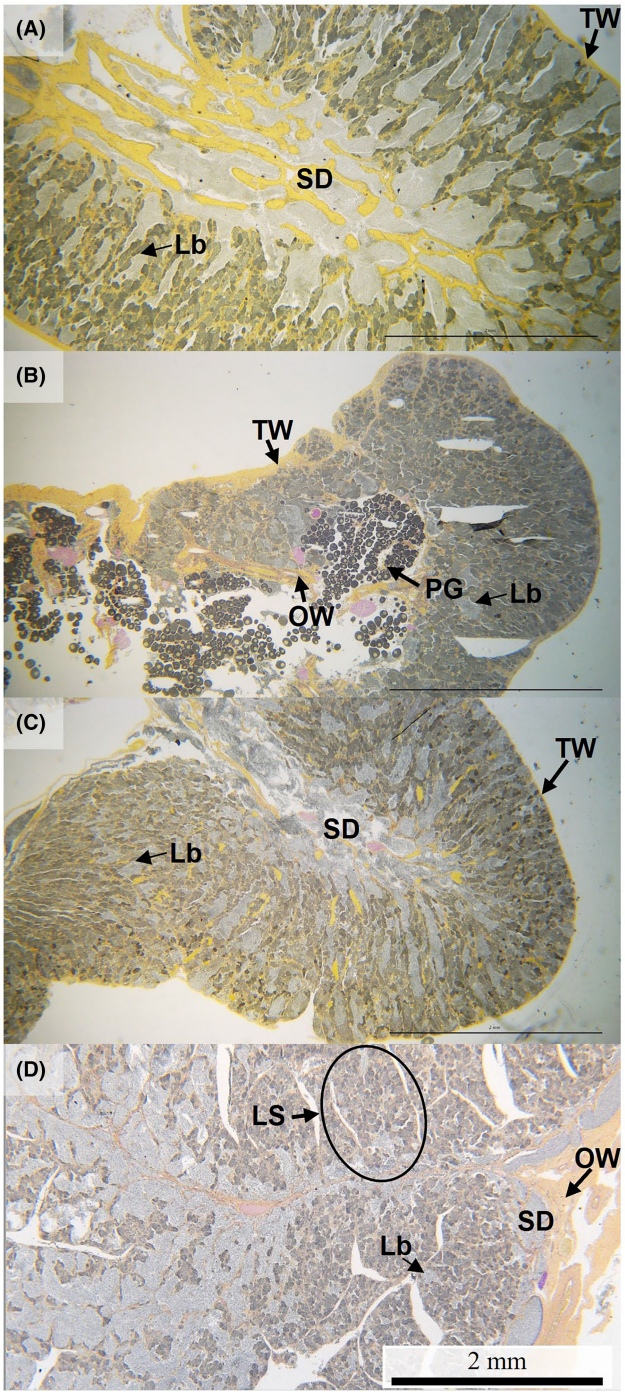

FIGURE 6 The orientation of the lobules and sperm ducts in gonochoristic versus hermaphroditic male fish, showing examples of (A) gonochoristic Red Snapper, (B) protogynous Red Porgy with delimited gonads, displaying female tissue and ovarian wall internally located, (C) a fully transitioned protogynous Red Porgy male (note lobule orientation), and (D) protogynous Gag with an undelimited, intermixed gonad. Abbreviations are as follows: Lb = lobule, LS = lamellar structure, OW = ovarian wall, PG = primary growth oocytes, SD = sperm duct, and TW = testis wall. Histological slides were stained with PAS stain, and the scale bar = 2 mm.

males can have some residual Sz in the lobule lumens as well as empty sperm ducts that are relatively easy to distinguish (Table 1; Figure 7G).

The lobules of males in the early developing phase are characterized by a predominance of secondary spermatogonia (Sg2) and some spermatocysts containing primary spermatocytes (Sc1) (Figure 7B). Early developing males that are repeat spawners (i.e., mature fish entering the reproductive season from the regenerating phase) can also have a few spermatocysts containing secondary spermatocytes (Sc2), and minimal amounts of residual Sz are occasionally present. The late-developing phase has all stages of spermatogenesis in the spermatocysts, but there are no Sz in the lobule lumens or the sperm duct (Table 1; Figure 7C); the late-developing phase is synonymous with what was previously called the developing phase (Brown-Peterson et al. 2011).

The spawning phase is identified by the presence of Sz in the lobule lumens and/or in the sperm ducts and by the presence of spermatocysts lining the lobules; spermatogenesis within the spermatocysts can range from Sg2 through Sz (Figure 7D, E). In nonpair spawning species, the presence of milt in the lumens and/or sperm ducts can be used as a macroscopic indicator of the spawning phase. Once spermatogenesis is complete in a spermatocyst and spermiation occurs, the spermatocyst collapses, resulting in a discontinuous GE (DGE). An increasing amount of DGE, and the resulting appearance of anastomosing lobules, can be used to identify the progression of males through an extended spawning season (Figure 7E). Here, we simplify the male subphases from those presented in Brown-Peterson et al. (2011) by elimination of the mid-GE subphase (Table 1). The changes in the GE allow definition of the early and late portions of the spawning season. The early GE subphase, found in the early portion of the spawning season, is identified by the presence of a continuous GE at the terminal end of all lobules and active spermatogenesis, with many spermatocysts lining the lobules throughout the testis (Figure 7D). If the terminal end of lobules is not present in sections, the early GE subphase can be identified by the following: (1) <25% of the lobules with a DGE near the sperm duct, (2) active spermatogenesis as evidenced by many spermatocysts, (3) lumens filled with Sz, and (4) the lack of anastomosing lobules. The late-GE subphase is identified by a DGE at the terminal end of some, or all, lobules (Figure 7E). Some active spermatogenesis continues in the late-GE subphase, but spermatocysts typically do not contain Sg2. If the terminal end of lobules is not present in sections, the late subphase can be identified by the following: (1) >25% of the lobules with a DGE near the sperm duct, (2) a reduced number of spermatocysts, (3) lumens filled with Sz, and (4) typically the presence of anastomosing lobules.

Regressing males are identified by a DGE throughout the testis, anastomosing lobules, and few spermatocysts, indicating little to no active spermatogenesis (Table 1; Figure 7F). Spermatocysts in regressing males

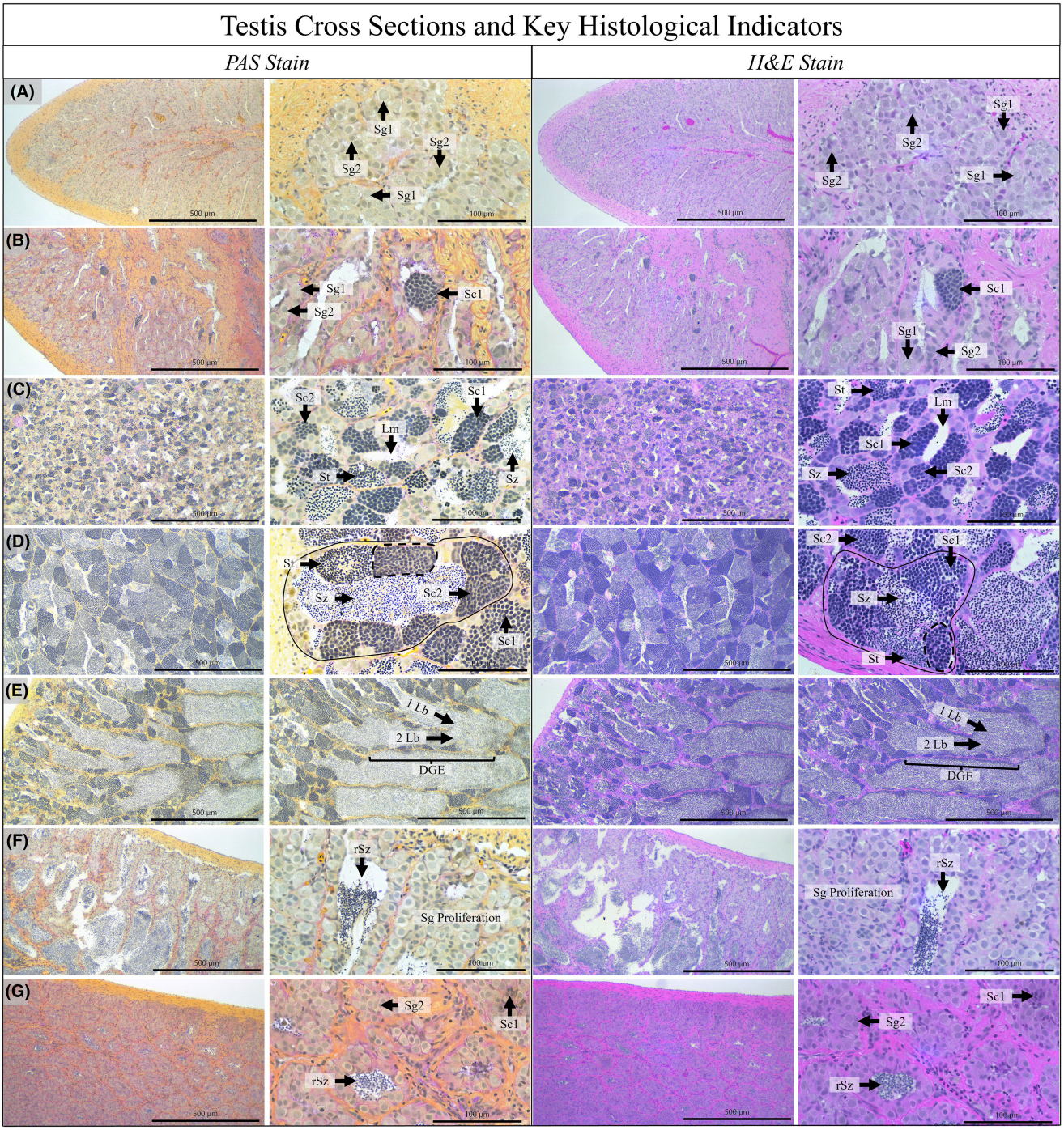

FIGURE 7 Examples of histological criteria for male reproductive phases of Red Snapper, showing a testicular cross section and the most advanced spermatogenic stage or the key histological indicator and stained using PAS (left panels) and H&E (right panels). Histological indicator size may vary between PAS and H&E due to individual variability in testes. The rows show the following phases: (A) immature phase; (B) early developing phase; (C) late-developing phase; (D) spawning phase in the early GE subphase, showing spermatocyst (dotted line) and lobule with a CGE (solid line); (E) spawning phase in the late-GE subphase, with DGE and arrows showing anastomosing lobules; (F) regressing phase; and (G) regenerating phase. Abbreviations are as follows: CGE = continuous germinal epithelium, DGE = discontinuous germinal epithelium, Lb = lobule, Lm = lumen, rSz = residual spermatozoa, Sg1 = primary spermatogonia, Sg2 = secondary spermatogonia, Sc1 = primary spermatocyte, Sc2 = secondary spermatocyte, St = spermatid, and Sz = spermatozoa.

typically contain advanced stages of spermatogenesis (i.e., St or Sz). Many species have spermatogonial proliferation (i.e., nests of Sg) at the terminal end of lobules. Spermatozoa are often still present in the lumen of the lobules and sperm ducts in regressing males but will likely not be released.

The transitioning phase in protogynous hermaphrodites

Fish are defined as transitioning (i.e., no sex assigned) if they are actively undergoing sex change, do not have fully formed gametes of either sex, and cannot release gametes. The appearance of transitioning in protogynous species with undelimited gonads differs by species due to differing prevalence of terminal sex gametes prior to transition, as well as gonadal structure (Sadovy and Shapiro 1987). Because small amounts of nonfunctional terminal sex gametes (i.e., PG oocytes in protandrous species or Sg in protogynous species) can appear long before transition in some species (Figure 8B) (Smith 1965; Reinboth 1982, 1988), it is important to assess a priori how common this is for a study species and identify clear species-specific criteria for assignment of the transitioning phase. Here we demonstrate the progression for Gag from functional female to functional male (Figure 8).

For fish undergoing sex change, we define a transitioning phase and break this down into early- and late-transition subphases (Table 1; Figure 8C, D). Early transition in protogynous species is defined as those fish with relatively few spermatocysts, decreased female gamete abundance, and continuous GE. Spermatocysts can contain Sg, Sc, and some St. Mid to late transition shows clear proliferation of male tissue with St or Sz, with no nonatretic secondary growth oocytes. These criteria are similar to those reported for two protogynous groupers, the Honeycomb Grouper *Epinephelus merra* (Bhandari et al. 2003) and Orange-spotted Grouper *E. coioides* (Wu et al. 2015). However, they differ from Sadovy and Shapiro (1987), whose criteria includes "observation of degeneration of primary sex tissue," which will not be observed in species who transition after secondary growth oocytes have been resorbed and retain some level of PG oocytes in males. Being able to accurately identify transitional fish is important to understanding when and where fish are undergoing sex change, if sex change is driven by a size or age threshold, and transition rates. This is critical to evaluating how fishing may impact male recruitment to the spawning population and potential sperm limitation.

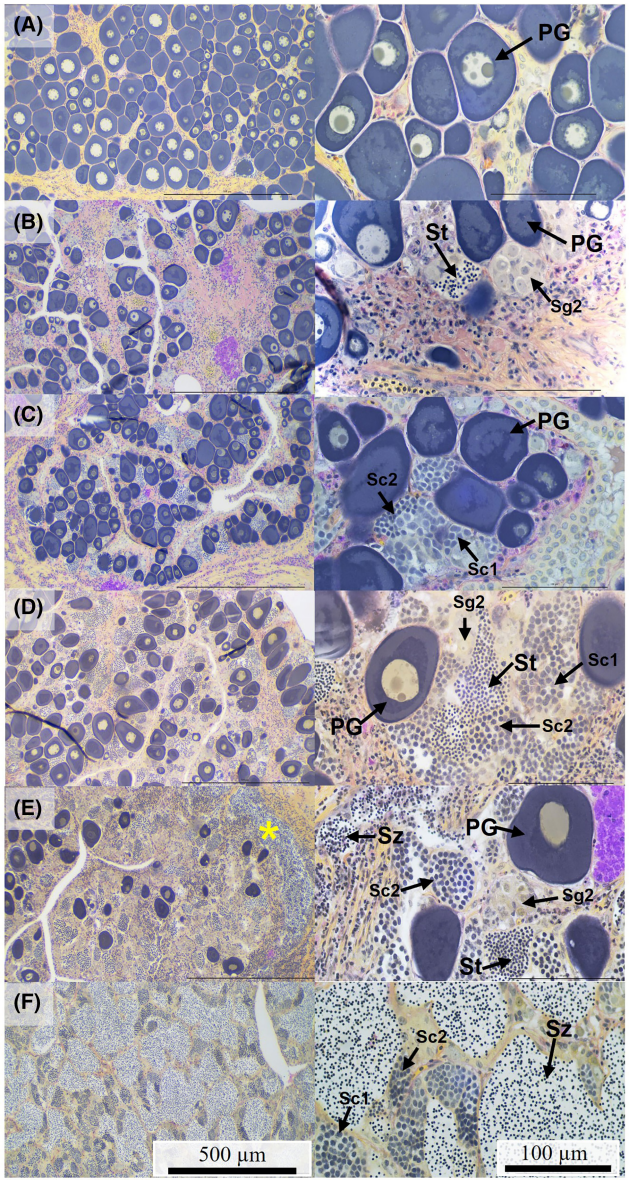

FIGURE 8 Histological progression in Gag from functional female to functional male. The panels on the left show cross sections, and panels on the right show histological indicators to help in defining transition. The rows show the following: (A) functional female, (B) functional female showing small amounts of nonfunctional terminal sex gametes present prior to transition, (C) transitioning fish in the early transition subphase, (D) transitioning fish in the late-transition subphase, (E) functional male with Sz in sperm ducts (yellow asterisk) and remnant populations of female gametes, and (F) functional male, fully transitioned. Abbreviations are as follows: PG = primary growth, Sc1 = primary spermatocyte, Sc2 = secondary spermatocyte, Sg2 = secondary spermatogonia, St = spermatids, and Sz = spermatozoa. Histological slides were stained with PAS stain. Scale bars are 500 µm (left panels) and 100 µm (right panels).

Sexual systems

Sexual systems in most species are easy to identify with proper histological analysis. However, gonochorists can have ovaries or testes with crypts of tissue of the other sex, juvenile bisexuality (Sadovy de Mitcheson and Liu 2008), and dimorphic growth, and as such, all these occurrences need to be ruled out prior to assuming a fish is a sequential hermaphrodite. Protogynous species can be identified macroscopically in species with delimited gonads, such as seen in Red Porgy, or undelimited and spatially distinct,

such as in Black Sea Bass. Because of the spatial orientation of the male sex tissue, if histology is used to assign transition rates, it is important to ensure that sections of gonadal tissue are representative of posterior, mid, and anterior parts of the gonad. However, protogyny in species with an undelimited, intermixed gonadal structure can only be identified through histological analysis (Figure 8A–F).

Sex assignment

Although sex assignment in juvenile gonochorists can be difficult, macroscopic sex assignment for mature gonochorists sampled in or close to the spawning season is accurate based on the shape of the gonad and the presence of vitellogenic oocytes or milt. It is more difficult to macroscopically identify sex in mature specimens of gonochoristic species outside of the spawning season, although the shape and color of the gonad (triangular shape, whitish in males; tubular and yellowish in females) are good indicators. Macroscopic sex assignments should be tested for accuracy through a comparison with histologically assessed gonad tissue from the same fish.

Although correct sex assignment is critical if there is concern for sperm limitation (Brooks et al. 2008), it is not possible through macroscopic assessment in pair-spawning protogynous species with undelimited, intermixed gonads, even in the spawning season. This difficulty is illustrated for the protogynous Gag (Figure 9). In a recent study on Gag, only 45% ($n = 49$) of males sampled during the spawning season released milt when strip-spawned and the percent agreement between sex assignment based on macroscopic evaluation versus histology was 35% (Lowerre-Barbieri et al. 2022b). Other secondary sex characteristics, such as coloration, can help distinguish sexes macroscopically in hermaphrodites, but the efficacy depends on whether the color change is permanent or ephemeral. For example, most Gag exhibit dimorphic pigmentation (Collins et al. 1998). Males develop black-pigmented scales on the ventral area (Figure 9A versus Figure 9B) that are retained year-round and postmortem. However, the physiological process that leads to this change is unknown, and consistency varied by sampling region, from 3% unpigmented males (Figure 9C) to 10% (Lowerre-Barbieri et al. 2022b).

Protogynous pair-spawning species can change sex within the spawning season, resulting in the need for histological criteria for sex assignment. The amount of the remnant gonadal structure retained from the primary sex differs with species (Figure 4). The ovarian lumen is retained in the testes of some protogynous species; is greatly reduced and not clearly visible in others, such as the labrid Mediterranean Rainbow Wrasse *Coris julis* (Alonso-Fernández et al. 2011); or is not retained at all, as seen in some serranid species (Sadovy and Domeier 2005). A fish is assigned as a male if the gonad has a sperm duct, DGE, and Sz during the spawning season (Figure 8E, F). Although Sadovy and Shapiro (1987) define transitional gonads as those with degenerating tissue of one sex and proliferating tissue of the other sex, the observation of primary sex tissue degeneration will be dependent in part on how fast transition occurs and when transition occurs (i.e., only during the spawning season versus during the regenerating reproductive phase). Gag transition during most months of the year (Lowerre-Barbieri et al. 2020a, 2020b) and take a relatively long time to do so—150 days to reach late transition in captivity (Roberts and Schleider 1983). Gag with proliferating male tissue and atretic oocytes occur during the spawning season but are fairly rare (Lowerre-Barbieri et al. 2020a, 2020b). Gag undergoing transition as regenerating females is more common. These fish have already resorbed all of their secondary growth oocytes in the regressing phase. In addition, male Gag

FIGURE 9 Examples of pigmentation, whole gonads, and histological micrographs in Gag, a protogynous hermaphrodite with undelimited, intermixed gonads, showing (A) female, (B) male, and (C) male with atypical pigmentation. Histological slides were stained with PAS stain; the scale bar in the histological image = 2 mm.

can contain remnant primary growth oocytes in relatively large numbers (Figure 8E). In species like these, fish are considered female if there is no sign of decreased production of female gametes and no sperm, even if there are crypts of male tissue (Figure 8B).

Reproductive parameter estimations

Maturity

Female maturity is arguably the most important reproductive state for understanding population dynamics and fitness, and when female spawning stock biomass is used as the measure of reproductive potential, it is the only reproductive metric integrated into stock assessments. Although the analytical approach is typically standardized (i.e., fitting a logistic curve to maturity data distributed by size or age; Lowerre-Barbieri et al. 2011b), standardization of the reproductive phases considered to be mature has not been addressed. In addition, results can be affected by a number of sampling issues. Because the maturation process is often accompanied by ontogenetic habitat shifts, this includes where and when samples are taken and if they are fishery dependent and thus affected by minimum size limits (Lowerre-Barbieri et al. 2011b). The maturation window based on the smallest, youngest mature fish and the largest, oldest immature fish for Gulf of Mexico Red Snapper was 196 mm FL to 542 mm FL, and 99% of the samples fell within or above this size range (Figure 10; Lowerre-Barbieri et al. 2022a), indicating in most years immature fish were undersampled.

Standardizing the method of assigning reproductive phases to the categories of immature, mature, and uncertain maturity is the critical first step in standardizing methods to estimate maturity. Historically, females with Vtg oocytes have been considered to be mature, even if they do not contain spawning indicators, and for species with extended spawning seasons, it was often assumed that early developing females that occurred in peak spawning months were developing for the first time and would not have time to finish the development needed to spawn and

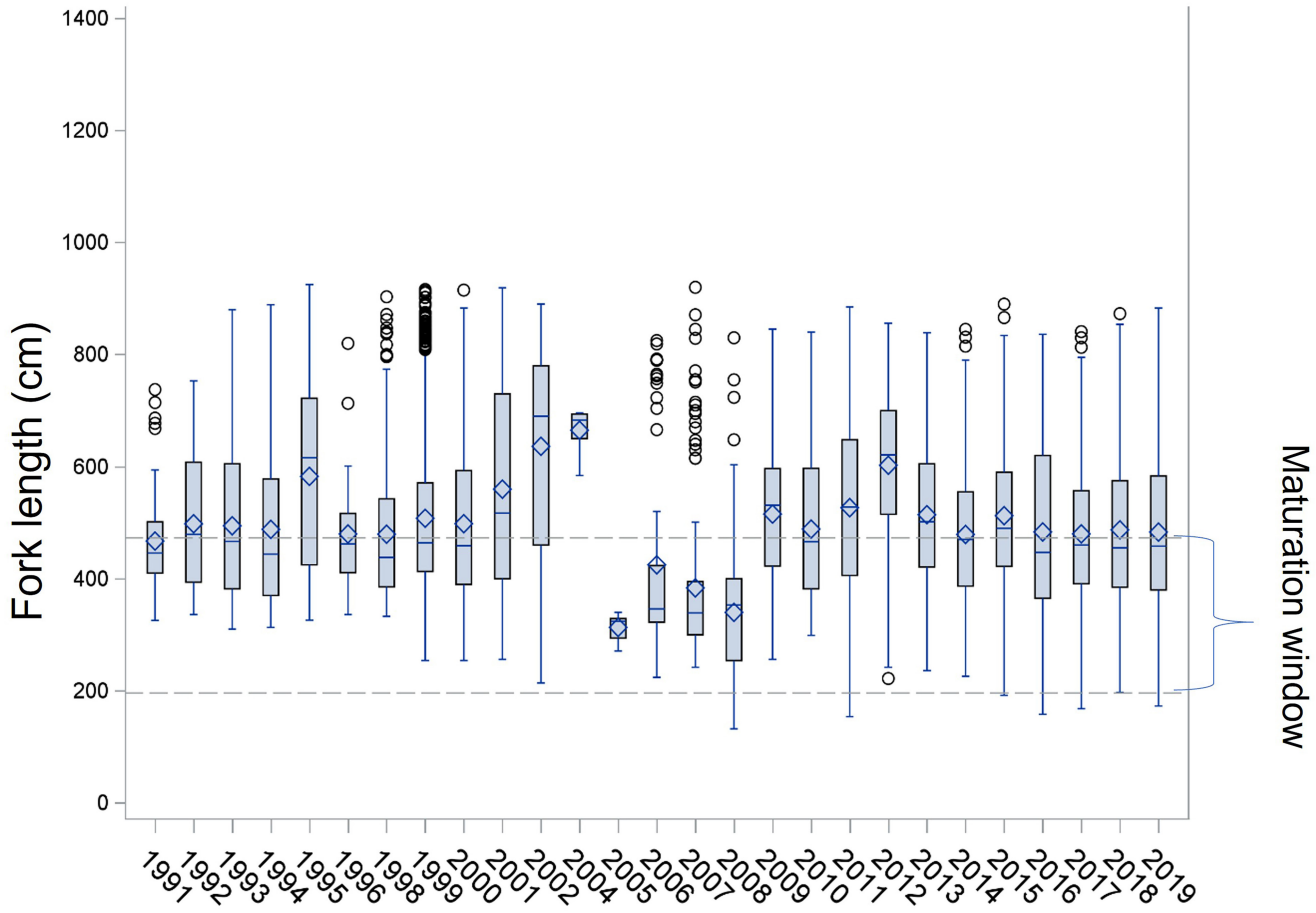

FIGURE 10 Annual size distribution of female Gulf of Mexico Red Snapper samples from 1991 to 2019 in relation to the maturation window, which is based on the smallest, youngest mature female and the largest, oldest immature female captured over the time period being analyzed. Boxes represent the 25th to 75th quantiles, and whiskers are the range. Diamonds represent the means, and horizontal lines are the medians.

were therefore considered immature. These assumptions and the impact of using only data from peak spawning months are rarely evaluated. Filtering the female Gulf of Mexico Red Snapper data for historic peak spawning months (June through August) reduced the sample size of female histological samples by 56% ($n = 6476$) and those assigned as immature by 42% ($n = 146$; Lowerre-Barbieri et al. 2022a). Similarly, it affected the maturation window, decreasing the maximum observed length and age of immature fish from 542 mm FL to 473 mm FL and from 8 to 5 years old (Lowerre-Barbieri et al. 2022a). The age range of early developing females was 1 to 24 years old, refuting the assumption that they were all immature; rather, it is a mixture of fish entering the reproductive cycle from the immature phase for the first time, while others are repeat spawners reentering the reproductive cycle from the regenerating phase. There is potential in some species to address this by distinguishing between virgin and mature females in the early developing phase (Reed et al. 2023). However, the only reproductive phase with 100% accuracy in identifying mature females is the spawning phase, as these females can be confirmed as having recruited to the spawning population. Therefore, we recommend that the most accurate, and likely conservative, maturity estimates be made using only immature and spawning fish. Previously, for fish with extended spawning seasons, it was recommended to censor months not in peak spawning to decrease overlap between regenerating and immature fish (Hunter and Macewicz 2003). For species with restricted spawning seasons, this can still be very effective. However, for species with extended spawning seasons, we recommend censoring the reproductive phases of unknown maturity (i.e., use only immature and spawning phase females for estimates of size and age at maturity) rather than censoring sampling months.

Spawning seasonality

Spawning seasonality affects reproductive success and resilience, and because it is often exogenously triggered by water temperature, it can be affected by climate change. Estimates of spawning season duration are important for (1) mean biological birth date used in fractional ages, (2) temporal filters used to increase accuracy in maturity assignments, and (3) estimating spawning frequency and thus annual fecundity in species with indeterminate fecundity. Although the proportion of reproductive phases by month is commonly used to show spawning seasonality (Figure 11A), there is no standardized method to quantify the duration of the spawning season or peak spawning months.

We recommend that spawning seasonality be based on females, given that they have spawning markers, and the following be estimated and reported: (1) maximum spawning duration, (2) core spawning season, and (3) peak spawning months. Here, we use Gulf of Mexico Red Snapper, which are multiple batch spawners with few skip spawners, as an example. The Red Snapper maximum spawning duration was 337 days from January 16 to December 18 (Figure 11A; Lowerre-Barbieri et al. 2022a), but the spawning season is shorter, 218 days from March 17 to October 21 (Figure 11B). The spawning fraction within the core spawning season was 48%, and peak spawning

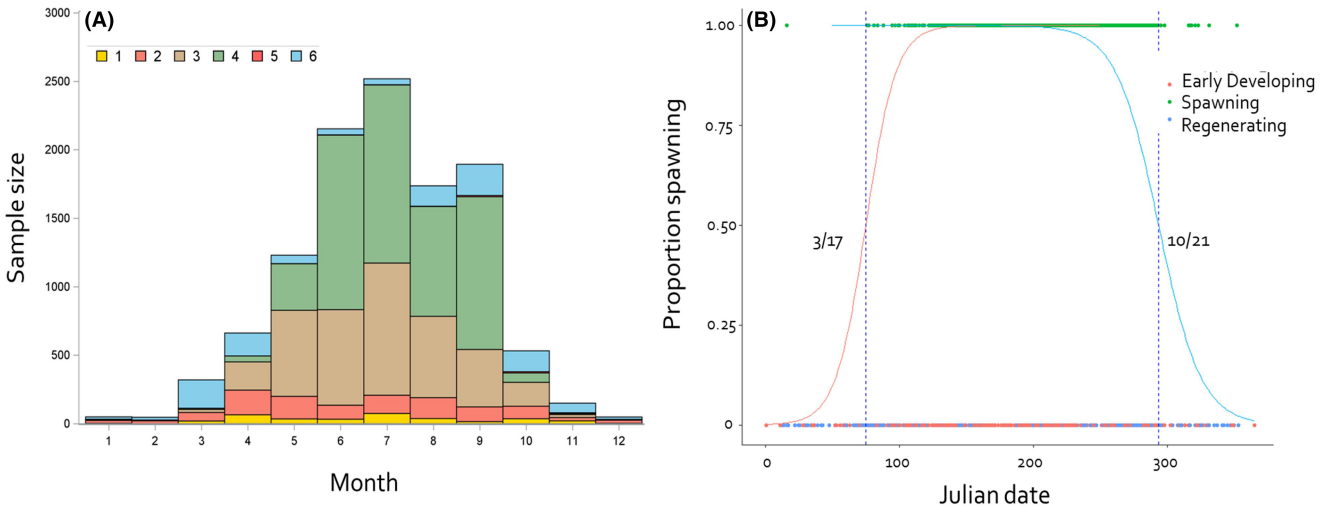

FIGURE 11 Determination of Gulf of Mexico Red Snapper spawning seasonality, showing (A) the number of females captured each month in each reproductive phase, with years and locations combined (1 = immature, 2 = early developing, 3 = late developing, 4 = spawning, 5 = regressing, and 6 = regenerating) and (B) determination of the core spawning season. Because late-developing females occur within the spawning season, the onset of the core spawning season is based on 50% occurrence of early developing and spawning. Because Red Snapper have few to no skip spawners, the end of the core spawning season is based on 50% spawning and regenerating fish.

months were June (60%), July (54%), August (49%), and September (59%). It is important to note when calculating the core spawning season that the reproductive phases chosen to indicate initiation of development and ending of the spawning season are species-specific and dependent on what phases occur within the spawning season. For example, in warmwater multiple batch spawners where the seasonality of late-developing females is similar to that of spawning females, it would be important to estimate the beginning of the core spawning season based on the date associated with 50% early developing and spawning. Similarly, for species with a large number of skip spawners, resulting in regenerating females occurring within the spawning season, it is important to use regressing and spawning to reflect the end of the core spawning season.

Identifying spawning activity and estimating spawning frequency

Females that have participated in spawning events can be identified based on their spawning markers, with subphases used to denote the proximity to the event (i.e., imminent, active, or spawned). These subphases are used to assess spawning activity and are important for batch fecundity estimates and to evaluate diel periodicity, spawning location, and spawning frequency. Batch fecundity estimates should be conducted on females with hydration that has progressed sufficiently to separate the batch of oocytes to be spawned from yolked oocytes but prior to ovulation (Ganias et al. 2014), as defined in the new active subphase. To evaluate the best indicators of spawn time and potential field-based criteria to age OM and POFs, we recommend plotting time of capture against GVM, YC, GVBD, beginning of hydration, full hydration, and fresh POFs. If fully hydrated and fresh POFs occur over a wide range of times, as seen in Red Snapper (Figure 3), then the species does not have a synchronized spawn time and field-based estimates of POF ages will be somewhat subjective. Because fish can move rapidly, we recommend choosing indicators that fall within 2 h of spawning to map spawning grounds, which for warmwater species are late OM (i.e., YC to hydration) and fresh POFs.

Spawning frequency is based on the reciprocal of the spawning fraction (proportion of spawning fish in a given 24-h period) times the number of days in the spawning season (Hunter and Macewicz 1985). Because the proportion must be based on the daily temporal scale, using markers of unknown or poorly calibrated duration can increase uncertainty in spawning frequency estimates. This is especially important when using all spawning markers (i.e., all subphases of the spawning phase) and standardizing to 24 h with a correction factor (Porch et al. 2015). Another source of uncertainty is how the duration of the spawning season is defined (maximum duration, core, or peak spawning months) and how representative the population estimate is of individual spawning periods.

CONCLUSIONS

Fish evolved life history strategies that differ greatly from marine mammals or harvested terrestrial animals (Sharma et al. 2019), resulting in the need for a conceptual model that captures how reproductive behavior and output affect offspring survival, as well as standardization of terms, core reproductive data, and methods. Obviously, this is beyond the scope of any one paper. Here we build on efforts from the European Fish Reproduction and Fisheries Cooperation in Science and Technology initiative from approximately a decade ago, participation by coauthors in providing reproductive data to stock assessments, and ongoing efforts in the United States by Maturity Assessment and Reproductive Variability of Life Strategies to advance the knowledge of reproductive information and communicate its importance in the management of marine fish and invertebrates.

Fully documenting the complexity of spawner–recruit systems for all fish is not a reasonable goal, but we need a conceptual model and terms to discuss these systems and how they drive transgenerational productivity (i.e., population growth). Traditional stock–recruit relationships assume a strong relationship between adult abundance and/or fecundity and offspring survivorship, although this relationship rarely occurs (Vert-pre et al. 2013). There is growing awareness that where and when fish spawn affects productivity (Ciannelli et al. 2015; Kerr et al. 2017; Lowerre-Barbieri et al. 2019) and that all spawning sites are not created equal, with the integration of dispersal models improving our understanding of sources and sinks (Karnauskas et al. 2022). Reproductive behavior and mating strategies are documented in the ecology literature but typically ignored in efforts to predict productivity (Kindsvater et al. 2020). The reproductive resilience paradigm provides a conceptual model of traits affecting fish reproductive success in addition to fecundity, highlighting that spawner–recruit systems are multifaceted and species-specific and have density-dependent and fitness feedback loops (Lowerre-Barbieri et al. 2017). Traditional reproductive studies can do much to better understand these complex systems with data already collected, such as egg size based on the diameter of hydrated oocytes used in batch fecundity estimates and where and when active spawners are sampled.

Feedback loops in species-specific spawner–recruit systems result in changed productivity with fishing mortality and climate change, emphasizing the importance of standardized data and methodology to be able to identify these changes and manage for sustainability. A well-documented example of a feedback loop is decreased size and age at maturity with high fishing pressure due to (1) a density-dependent compensatory response where food availability and nutritional state (i.e., condition) increases with decreased relative population size, resulting in earlier maturation (Marshall and McAdam 2007) or (2) fisheries-induced evolution due to overharvesting of the spawning stock (Dieckmann and Heino 2007). Because earlier maturation can indicate a stressed stock (Olsen et al. 2004), we need to recognize that size or age at maturation is not invariant and track changes over time. Having a consistent approach to what is considered immature or mature is critical for this effort. Similarly, in protogynous species we need to be able to assess if they can adapt their size and age at transition to fishing pressure or if low abundance of the terminal sex will limit productivity (Alonzo et al. 2008; Easter and White 2016). Lastly, climate change is affecting phenology, with important implications for productivity of fish stocks and ecosystems (Staudinger et al. 2019). This includes documented changes in distribution and spawning sites, as well as earlier onset of spawning and hatching with warmer temperatures in species that support important fisheries, thus impacting productivity (Hare et al. 2016). The conceptual model, terms, and standardized reproductive data and analytical approaches presented here are one step in an iterative process to provide the means to compare spawner–recruit systems across species and regions as well as to track important changes over time.

ACKNOWLEDGMENTS

We thank the many histologists and reproductive biologists who contributed to the data used in this paper, including Laura Crabtree, Gary Fitzhugh, Hope Lyon, Alan Collins, William Walling, Veronica Beech, Ashley Pacicco, Michelle Duncan, Anna Millender, and Andrea Leontiou, as well as Noretta Perry and Yvonne Waters (Florida Fish and Wildlife Conservaton Commission/Fish and Wildlife Research Institute histology laboratory) and Lin Bustamante and Chaitali Mukherjee (Texas A&M University histology laboratory), Wiley Sinkus and Homer Hiers IV (South Carolina Department of Natural Resources histology), Cheryl Crowder (Crowder Histology), Mass Histology Service, and Saffron Scientific for histological processing. We are grateful to Erik Lang and the Life History Panel participants in the SEDAR 74 workshop, as the report from that workshop laid the foundation for this publication. We also thank each of our institutions for their financial support throughout this collaborative project.

CONFLICT OF INTEREST STATEMENT

The authors state that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

ETHICS STATEMENT

All ethical guidelines were followed and no animals were handled in the development of this study.

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