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Reproductive Timing in Marine Fishes: Variability, Temporal Scales, and Methods

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Abstract

Reproductive timing can be defined as the temporal pattern of reproduction over a lifetime. Although reproductive timing is highly variable in marine fishes, certain traits are universal, including sexual maturity, undergoing one or more reproductive cycles, participating in one or more spawning events within a reproductive cycle, release of eggs or offspring, aging, and death. These traits commonly occur at four temporal scales: lifetime, annual, intraseasonal, and diel. It has long been known that reproductive timing affects reproductive success, especially in terms of the onset of sexual maturity and the match or mismatch between seasonal spawning and offspring survival. However, a comprehensive understanding of variability in reproductive timing over species, populations, and temporal scales is lacking. In addition, there is a need to assess how variability in reproductive timing affects a population's resilience. Because natural selection occurs at the individual level, this necessitates an understanding of within-population (i.e., individual) variability in reproductive timing and how fishing may impact it through age truncation and size-specific selectivity or fisheries-induced evolution. In this paper, we review the temporal aspects of reproductive strategies and the four most-studied reproductive timing characteristics in fishes: sexual maturity, spawning seasonality, spawning frequency, and diel periodicity. For each characteristic, we synthesize how it has traditionally been measured, advances in understanding the underlying physiology, its role in equilibrium-based fish population dynamics, and its importance to reproductive success. We then provide a review of emerging methodology—with an emphasis on ovarian histology—to improve our ability to assess variability in reproductive timing both among populations and within populations.

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Reproductive timing, or the temporal pattern of reproduction over a fish's lifetime, plays an important role in reproductive success as it defines the number of reproductive opportunities and the environment in which eggs or offspring are released (Ims 1990; Yamahira 2004). Marine fish species vary widely in their reproductive timing but also exhibit universal reproductive traits, which typically operate over different temporal scales: lifetime, annual, intraseasonal, and diel (Lowerre-Barbieri et al. 2009). At the lifetime scale, fish attain sexual maturity, the life history trait considered to have the greatest impact on fitness (Stearns 1992). Spawning seasonality typically occurs at the annual scale as most fish exhibit seasonality in peak spawning activity and annual reproductive cycles (Bye 1984; Rideout et al. 2005). At this scale, reproductive success is hypothesized to correlate with the match or mismatch between the spawning season and optimal conditions for larval survival (Hjort 1914; Cushing 1973). The intraseasonal scale (i.e., within the spawning season) is associated with birthdate dynamics and spawning (or batch) interval in batch spawners, both of which can impact reproductive success. For example, an individual's birthdate affects other life history traits, such as growth, overwinter survival, and the time of maturation (Cargnelli and Gross 1996; Lowerre-Barbieri et al. 1998). Lastly, egg hydration, mating behavior, and spawning events typically occur at the diel scale, and these affect reproductive success through the probability of fertilization, rates of predation, and dispersion of eggs and larvae (Morgan and Christy 1997; Yamahira 2001; Cowen et al. 2007; Gladstone 2007).

The importance of variability in reproductive timing to population resilience has been recognized (Winemiller and Rose 1992; Winemiller 2005; Anderson et al. 2008; Jager et al. 2008; Wright and Trippel 2009), and demographic effects are increasingly reported (Berkeley et al. 2004; Jørgensen et al. 2006; Wright and Trippel 2009). However, our current knowledge of reproductive timing in fishes is limited. Reproductive timing has traditionally been studied to estimate spawning stock biomass (SSB) or fecundity for a single species, and there is little standardization of methods or terminology (Kjesbu et al. 2003; Brown-Peterson et al. 2011, this special section). The lack of standardization makes it difficult to compare reproductive timing over space, time, or phylogeny. In addition, there is a need to improve our understanding of when fish spawn so that we can assess where they spawn and thus determine how spatiotemporal factors affect recruitment success and the efficacy of spatially explicit approaches for protecting spawning populations (i.e., marine protected areas; Huret et al. 2007; Botsford et al. 2009; Pecquerie et al. 2009). In addition, fitness occurs at the individual level, and modeling results are increasingly indicating that individual variability in reproductive timing affects reproductive success (see James et al. 2003; Jørgensen and Fiksen 2006; Pecquerie et al. 2009). However, individual variability in reproductive timing is typically not assessed in reproductive studies even though demographic trends in spawning seasonality, spawning frequency, and fecundity have been reported (e.g., Murawski et al. 2001; Berkeley et al. 2004; Claramunt et al. 2007; Lowerre-Barbieri et al. 2009; Wright and Trippel 2009), and there is increased concern that some stocks are undergoing fisheries-induced evolution (Law and Grey 1989; Marshall and Browman 2007; Dunlop et al. 2009; Rochet 2009).

The objective of this paper is to review traditional and emerging methods of assessing reproductive timing in marine fishes, emphasizing methods to assess within population variability and demographic effects. We focus primarily on (1) female reproduction, as does most of the fisheries literature, due to the importance of egg production to reproductive potential and reproductive success (Stearns 1992; Murua and Saborido-Rey 2003) and (2) histological techniques as they are considered the most accurate means to assess gonadal development (Kjesbu et al. 2003; Murua et al. 2003; Kjesbu 2009). We begin by reviewing reproductive timing strategies and oocyte development in marine fishes. We then address the four most-studied reproductive timing characteristics: sexual maturity, spawning seasonality, spawning frequency, and diel periodicity. For each characteristic, we review its importance to population dynamics and life history theory and recent advances in understanding the underlying physiological processes and individual variability. We then review methods of assessing each characteristic, including the use of temporal filters, analytical approaches for assessing individual and demographic variability, and future methodological needs.

REPRODUCTIVE TIMING AND OOCYTE DEVELOPMENT

Although most exploited marine teleosts are highly fecund and produce either pelagic or demersal eggs (Murua and Saborido-Rey 2003), their reproductive timing strategies vary widely (Bye 1984; McEvoy and McEvoy 1992; Murua and Saborido-Rey 2003). All fish undergo sexual maturation, participate in one or more reproductive cycles, spawn once or more per cycle, age, and die. However, reproductive timing strategies range from spawning only once during a lifetime (e.g., coho salmon *Oncorhynchus kisutch*) to spawning multiple times within an extended spawning season for many years (e.g., red snapper *Lutjanus campechanus*). Semelparous species undergo the reproductive cycle only once, whereas iteroparous species, which are more common, go through multiple reproductive cycles (Murua and Saborido-Rey 2003). At the annual scale, both semelparous species (e.g., European eel *Anguilla anguilla*; J. Tomkiewicz, National Institute for Aquatic Resources, Technical University of Denmark, Charlottenlund, personal communication) and iteroparous species can exhibit a pattern of total spawning or batch spawning. Most commercially targeted species are iteroparous, batch spawners (Murua and Saborido-Rey 2003). Total spawners spawn either in one event or over a short time period (Pavlov et al. 2009), whereas batch spawners develop and release multiple batches of eggs within a spawning season (Hunter

and Macewicz 1985). Individual spawning periods within a population's spawning season can range from synchronized to asynchronous. Among all fishes, reproductive cycles exhibit similar phases of gonadal development (see Brown-Peterson et al. 2011), including immature, developing, spawning capable, regressing, and regenerating. In addition, the ability of individuals to skip spawning (i.e., to opt out of a reproductive cycle) is increasingly recognized as part of many species' reproductive strategies (Rideout and Tomkiewicz 2011, this special section). Ovulation occurs at the diel scale and typically indicates spawning (i.e., release of eggs from the female; Jackson et al. 2006) as ovulated eggs in most species remain viable for only a short time period (Bobe et al. 2008).

In all fishes, eggs begin as oogonia and go through similar stages of oocyte development (McMillan 2007; Mommsen and Korsgaard 2008), which is commonly divided into primary growth and secondary growth (Figure 1). Secondary growth is typically categorized into the following developmental stages: cortical alveolar stage, vitellogenesis, and oocyte maturation (OM; Matsuyama et al. 1990; Abascal and Medina 2005; Luckenbach et al. 2008). Although we retain the term "cortical alveolar," not all fish develop cortical alveolar vesicles at this stage (Grier et al. 2009); this term is somewhat of a misnomer because it is based on a cytological component common at this developmental stage (as are oil droplets) rather than on functionality. The function of this first stage in secondary oocyte growth, however, is to make the later stage of vitellogenesis possible. Thus, it is associated with an increase in oocyte size and RNA production to prepare organelles that are needed to sequester vitellogen (Morrison 1990), and females with cortical alveolar oocytes typically continue to develop these oocytes through the substages of vitellogenesis (primary [Vtg1], secondary [Vtg2], and tertiary [Vtg3]), OM, and spawning (Wright 2007). Oocyte maturation indicates that spawning is imminent and includes two nuclear events: germinal vesicle migration (GVM) and germinal vesicle breakdown. In some species, OM may also include the formation of large oil droplets or lipid coalescence, yolk coalescence, and hydration. Oocyte maturation ends in ovulation, when the follicle ruptures, releasing eggs into the ovarian lumen. The ruptured follicles are called postovulatory follicles (POFs), and they remain in the ovary until they are resorbed (Hunter and Macewicz 1985).

Oocyte recruitment patterns support the wide range of reproductive timing strategies in fishes. Mature iteroparous females maintain a constant reserve of primary growth oocytes regardless of where they are within the reproductive cycle, whereas semelparous species have no need for such a reserve and exhibit total recruitment of all primary growth oocytes to secondary growth. In addition, iteroparous species exhibit two general temporal patterns of oocyte recruitment from primary growth to secondary growth. In coldwater species, which often have slow oocyte developmental rates (Rideout et al. 2005) and restricted spawning seasons, recruitment from primary to secondary growth will be discontinuous, resulting in determinate fecundity, as can be seen in the Atlantic cod *Gadus morhua* (Kjesbu 2009; Pavlov et al. 2009). In contrast, many batch spawners in warmwater habitats exhibit continuous oocyte recruitment, repeatedly recruiting oocytes from primary to secondary growth, thus increasing their fecundity and their ability to spawn over an extended time period. These species are considered to have indeterminate fecundity (Hunter and Goldberg 1980). Oocyte recruitment rates within secondary growth (i.e., from CA to Vtg1–Vtg3) also fall along a continuum from quite synchronous to completely asynchronous. Total spawners exhibit synchronous development of secondary growth oocytes (e.g., striped mullet *Mugil cephalus*), whereas batch

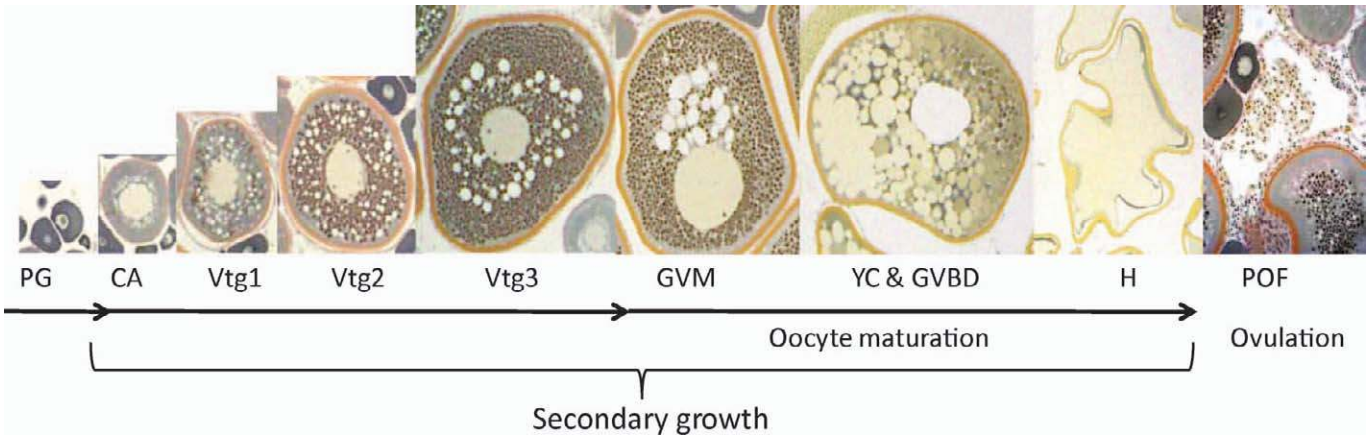

FIGURE 1. Progression of oocyte development from primary growth oocytes (PG), to secondary growth, which begins with the cortical alveolar (CA) stage and then proceeds through vitellogenesis (Vtg), which can be broken into substages associated with the extent of yolk globules or platelets in the ooplasm (primary [Vtg1], secondary [Vtg2], and tertiary [Vtg3]). Oocyte maturation (OM) occurs after the appropriate trigger and can include germinal vesicle migration (GVM), yolk coalescence (YC), germinal vesicle breakdown (GVBD), and in pelagic spawners, hydration (H). At ovulation, the follicle ruptures and the oocyte is released. Postovulatory follicles (POF) remain in the ovary, where they are resorbed.

spawners can exhibit modal development (i.e., each batch develops relatively synchronously) or asynchronous secondary growth development (e.g., Atlantic sardine *Sardina pilchardus* [also known as European pilchard] and red drum *Sciaenops ocellatus*).

Oocyte recruitment patterns and the leading oocyte developmental stage underlie the various methods used to assess ovarian development, including macroscopic characteristics, oocyte size frequency distributions, gonadosomatic indices, and histological assessment (Kjesbu et al. 2003). In this paper, we will focus on histological analysis given that it has been shown to be the most accurate (West 1990; Kjesbu et al. 2003), and we define reproductive phases based on Brown-Peterson et al. (2011) and the following histological criteria. The most developed oocytes in immature fishes are primary growth oocytes, whereas early developing females have cortical alveolar oocytes. Developing females have oocytes undergoing vitellogenesis (e.g., Vtg1 and Vtg2). Spawning capable females are those that will spawn during the current reproductive cycle and thus contain either vitellogenic oocytes or histological indicators of imminent spawning (late GVM, germinal vesicle breakdown, and hydration) or recent spawning (newly collapsed POFs). For species with determinate fecundity and for batch spawners with short spawning intervals, spawning capable females will have fully developed vitellogenic oocytes (i.e., Vtg3). Regressing females are those that are ending their spawning period, as indicated by resorption of residual secondary growth oocytes. Regenerating females are sexually mature but have completed their spawning period and no longer have secondary growth oocytes.

SEXUAL MATURITY

The timing of sexual maturity in fishes is a critical component of population dynamics and life history theory. Age at first maturity affects generation time (e.g., the average age of mature females in a population with a stable age distribution) and thus influences the intrinsic rate of population growth, and it is often used as a de facto biological reference point in an effort to allow fish to reproduce at least once before they are harvested (Beverton and Holt 1957; Caddy and Agnew 2004). Maturity data are also a prerequisite for estimating SSB, which has traditionally been used as an index of reproductive potential (Trippel 1999; Marshall et al. 2006). Although traditional stock assessments have assumed equilibrium conditions and static size and age at maturity, more recent research has highlighted how size and age at maturity may change in exploited populations to compensate for increased mortality associated with fishing (Rochet 2009). These changes can be indicative of a density-dependent compensatory response wherein fish reach a higher average nutritional state (condition) at a younger age (Marshall and McAdam 2007) but similar size (Stearns 1992) or fisheries-induced evolution (Dieckmann and Heino 2007).

The physiological process of maturation begins well before the gonads develop, and an understanding of this process is important for understanding the factors that drive changes in size and age at maturity. In Atlantic salmon *Salmo salar*, the maturation process begins in the fertilized egg and progresses in stages dependent on genetically determined energetic thresholds and the environmental context (Thorpe 2007). Maturational stages are controlled by the brain–pituitary–gonad axis through a suite of hormones, sex steroids, and insulin-like growth factor I (Okuzawa 2002). These stages 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 environmental cues. Maturational stages may also correlate with ontogenetic shifts in habitat usage as many marine species are reported to move from nursery habitat to adult or spawning habitat (Gillanders et al. 2003), which makes it difficult to obtain representative samples of both mature and immature individuals (Tomkiewicz et al. 1997; Hunter and Macewicz 2003; Murua et al. 2003).

Fitting a logistic curve to sex-specific maturity data distributed by size or age is the traditional method of estimating sexual maturity. However, the accuracy of the resulting estimate will be affected by the spatial distribution of sampling, the time period over which samples are collected (see below), and the method used to categorize fish as mature or immature (Hunter and Macewicz 2003). Although maturity classification based on histology has been shown to be more accurate than macroscopic classification (Murua et al. 2003; Tomkiewicz et al. 2003; Vitale et al. 2006), there is no standard level of gonadal development considered representative of "mature," and often the criteria used are not reported. Females with maturationally functional pituitary and gonads but for whom the brain does not respond to environmental cues will have primary growth oocytes. Females with a functional brain–pituitary–gonad axis, which are capable of responding and are responding to environmental cues, will have initiated secondary growth and thus will have ovaries containing cortical alveolar oocytes. Recent research suggests that this developmental stage is mediated through growth hormones (Canosa et al. 2007) and thus is associated with a fish's condition. Females with cortical alveolar oocytes have been categorized as mature in a number of studies (Barbieri et al. 1994; Saborido-Rey and Junquera 1998; Murua and Saborido-Rey 2003; Lowerre-Barbieri et al. 2009) because fish with this level of development typically continue through vitellogenesis and spawn in the upcoming season (Wright 2007). However, fish are not spawning capable until at least some oocytes have completed vitellogenesis (Brown-Peterson et al. 2011), which is the process by which yolk proteins are produced in the liver, transported to the ovary, and stored in the egg to later provide nutrition for the offspring (Senthilkumaran et al. 2004). The presence of vitellogenic oocytes is also commonly used to identify mature females, and this is the criterion for many studies based on macroscopic staging (Kjesbu et al. 2003). It also has

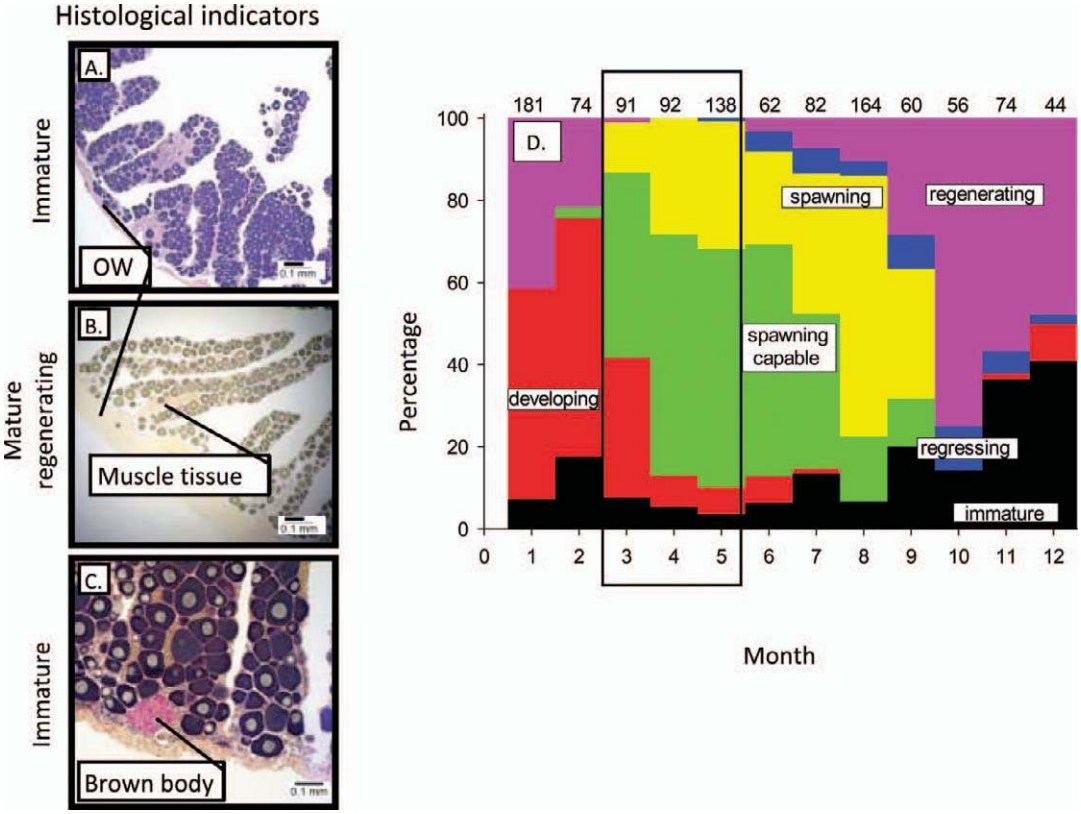

FIGURE 2. Histological indicators used to assess maturity and the monthly proportion of female developmental phases in spotted seatrout *Cynoscion nebulosus*: **(A)** immature female exhibiting a thin ovarian wall (OW) and stroma within the lamellae; **(B)** mature regenerating female with a thick OW and muscle tissue within the lamellae; **(C)** immature female with melanomacrophages or brown bodies; and **(D)** monthly proportions of the developmental phases, illustrating how accuracy of maturity estimates can be improved by using data from only those months (indicated by the black rectangle) when there is little co-occurrence of immature and mature regenerating females. Sample size for each month is indicated at the top of the graph.

the advantage of occurring closer to the time of actual spawning (Burton et al. 1997; Nieland et al. 2002; Thorsen et al. 2010). A disadvantage of using vitellogenesis as the criterion for maturity is that maturing individuals (i.e., those with cortical alveolar oocytes) are then categorized as immature. Thus, in species with annual reproductive cycles and no reports of large numbers of females resorbing cortical alveolar oocytes, we recommend using this stage of oocyte development to identify maturity because it is more closely associated with the time of the physiological trigger (Wright 2007). However, there is a need to distinguish between "early" and "late" cortical alveolar stages as Arctic cod that opted out of a reproductive cycle (i.e., that skipped spawning) exhibited arrested oocyte development at the early cortical alveolar stage (Skjæraasen et al. 2009). In addition, if it is important that a designation of "mature" correlates to fish that are close in time to spawning, then the vitellogenic stage is preferable; this is especially true for species with slow oocyte developmental rates and reproductive cycles longer than 1 year, such as some deep-sea species (e.g., Greenland halibut *Reinhardtius hippoglossoides*; Junquera et al. 2003).

In addition, it is difficult to distinguish between the lifetime scale of ovarian development and the development associated with the annual reproductive cycle, although this is easier done in coldwater species that take longer to resorb POFs (see Spawning Seasonality section below). Both immature and mature regenerating females (i.e., fish with undeveloped ovaries prior to recrudescence in the next reproductive cycle) have primary growth oocytes as their most developed oocyte stage. Similarly, both first-time spawners and repeat spawners will develop cortical alveolar oocytes early in their reproductive cycles. Because of this, additional histological features are often used to help distinguish between immature and mature regenerating females, including thickness of the ovarian wall (Morrison 1990), lamellar structure, the presence of very-late-stage atretic oocytes, the presence of melanomacrophage centers, and muscle bundles. The thickness of the ovarian wall is expected to be greater in mature females that have expanded and contracted their ovaries in past reproductive cycles (Figure 2A, B). However, this trait can be difficult to quantify because histological slides are often made from partial cross sections of the ovary, meaning that the ovarian wall is no longer representative of its state in situ. In addition, the thickness of the ovarian wall is highly variable even in a full cross section, making it difficult to obtain a representative measurement. Because the attainment of maturational

competence is a continuous process, immature females early in the process of developing functional ovaries will have relatively few primary growth oocytes, a tightly organized lamellar structure, and stroma that are visible within the lamellae (Figure 2A). However, as development progresses, these differences will be less obvious. One potential indicator is the presence of muscle tissue within the lamellae (Shapiro et al. 1993) in mature regenerating females (Figure 2B). However, more work is necessary to evaluate whether this occurs in all individuals and remains identifiable throughout the regenerating phase. Late-stage atretic oocytes are another potential indicator that may remain for extended periods even in tropical fishes (e.g., 2–7 months; Miranda et al. 1999). Melanomacrophage centers also have been suggested as possible indicators of mature regenerating females as they are reported to occur in association with oocyte atresia (Agius and Roberts 2003). However, they function as primitive analogs to mammalian lymph nodes (Schwindt et al. 2008), and because of this role they can be present in both immature (Figure 2C) and mature females.

Temporal filters decrease noise in reproductive timing data and can be used to help standardize methods of estimating maturity. Because individual spawning periods can be highly variable within a population (Wright and Trippel 2009), regenerating females can occur prior to the end of the spawning season (Lowerre-Barbieri et al. 2009) and can potentially be improperly categorized as immature. By assessing the proportion of reproductive phases over time (Figure 2D), it is possible to identify those times when immature females but few regenerating females are present (Hunter and Macewicz 1985, 2003). This time period typically occurs just prior to or early in the spawning season (Murua et al. 2003). Maturity can then be estimated for fishes collected only during this time period, thus improving accuracy. Size and age at maturity estimated with this methodology are usually less than those based on data collected throughout the year without regard to spawning seasonality (Hunter and Macewicz 2003). International bodies performing stock assessments, such as the International Council for the Exploration of the Sea, are adopting this methodology (ICES 2007, 2010).

However, there continues to be a need for methods that can definitively distinguish between mature and immature individuals. Methods associated with other components of the maturation process show promise, such as brain chemistry (Black and Grober 2003), endocrinology (Heppell and Sullivan 1999), and various aspects of the liver due to its role in vitellogenesis (Vitale et al. 2006; Nunes et al. 2011, this special section). An additional advancement is the use of analytical approaches that assess how varying factors affect individual time of maturation. These approaches include probabilistic maturation reaction norms (Marshall and Browman 2007; Perez-Rodriguez et al. 2009), and statistical models, such as generalized additive models and generalized linear models, that assess binomial data and factors affecting the probability of individual maturity (Silva et al. 2006).

SPAWNING SEASONALITY

The duration of a population's spawning season plays a critical role in reproductive success and can be negatively impacted by the age truncation effects of fishing (Anderson et al. 2008; Pecquerie et al. 2009; Wright and Trippel 2009). At the population level, spawning seasonality varies in terms of its duration (restricted or extended); the degree of synchronization among individual spawning periods; and the season of occurrence (e.g., fall–winter or spring–summer). Although restricted spawning seasons are more common in coldwater habitats and extended seasons are more common in warmwater habitats (Pavlov et al. 2009), many factors drive spawning seasonality; in fact, tropical fishes can exhibit a wide range of spawning seasons (Sadovy 1996). Species with restricted spawning seasons produce offspring with a relatively narrow range of birthdates (i.e., hatch dates), and so these species are more apt to (1) fit the match–mismatch theory, (2) demonstrate greater recruitment variability, and (3) potentially suffer a greater impact from climate change (Wright and Trippel 2009). In contrast, species with extended spawning seasons have a wide range of birthdates that can result in differing life history traits associated with early born versus late-born individuals and differing vulnerability to a size-limited fishery (Lowerre-Barbieri et al. 1998). Extended spawning seasons also provide a greater number of reproductive opportunities, which have the potential to increase recruitment (James et al. 2003). Lastly, many species demonstrate demographic differences in spawning periods: older, larger fish spawn sooner and often for longer durations than younger fish (Kjesbu et al. 1996; Wright and Trippel 2009), presumably increasing the reproductive success of these individuals and the population as a whole.

Spawning seasonality is controlled by ultimate factors that select for inheritable components (e.g., endogenous rhythms and energetic thresholds) and by proximate factors, which are exogenous cues used to entrain gonadal development and spawning activity (Munro et al. 1990; Yamahira 2001; Leder et al. 2006). A detailed understanding of the physiological control that allows for temporally appropriate reproductive development and behavior does not currently exist for most species (Milla et al. 2009). However, the selection pressure to synchronize seasonal spawning activity with the optimal time for offspring survival is obvious since this will determine an individual's ability to pass on genes to the next generation (Bye 1984). The duration of the offspring survival window will differ with climate. Thus, cold climates, in which gonadal development is slow (Pankhurst 2008) and in which the optimum time for larval feeding is often restricted to the spring algal bloom (Platt et al. 2003), select for more restricted spawning seasons. Exogenous cues ensure that gonadal development occurs at the appropriate time so that fish are capable of spawning when the conditions favor offspring survival. Common exogenous cues entraining gonadal development in fishes are photoperiod (Bromage et al. 2001), water temperature (Lam 1983), rainfall (Okuzawa 2002), and social interactions (Fricke and Fricke 1977); photoperiod is the

primary cue in coldwater species with restricted spawning seasons. For example, changes in photoperiod alone can entrain the reproductive cycle in salmonids (Pankhurst and Porter 2003). In contrast, for warmwater species with extended spawning seasons, gonadal development tends to be entrained by an interaction between temperature and photoperiod (Pankhurst and Porter 2003).

A population's spawning season is typically determined by the sampling of mature females and assessing where they are within the reproductive cycle based on ovarian development. Although all fish go through similar phases of gonadal development within a reproductive cycle, the use of histological indicators to determine these phases will vary between warmwater and coldwater species (Brown-Peterson et al. 2011). Metabolism is the biological processing of energy and materials, and metabolic rates increase with increasing temperature (Brown et al. 2004). Thus, water temperature will affect rates of gonadal development (Rideout et al. 2005), oocyte atresia, and POF resorption (Hunter and Macewicz 1985). The effect of temperature on POF resorption rates has been the most studied of these aspects; warmwater fishes resorb POFs within 24–48 h of spawning (Hunter and Macewicz 1985; Fitzhugh and Hettler 1995; Yoda and Yoneda 2009), while resorption rates in coldwater fishes are much slower (Saborido-Rey and Junquera 1998; Rideout et al. 2005). For example, POFs are easily identifiable in Flemish Cap Atlantic cod (temperatures typically $< 10^{\circ}$C) approximately 3 months after the spawning season ends. In contrast, POFs in common snook *Centropomus undecimalis* at water temperatures of approximately 29°C reached a similar state of resorption within 18 h postovulation (Figure 3).

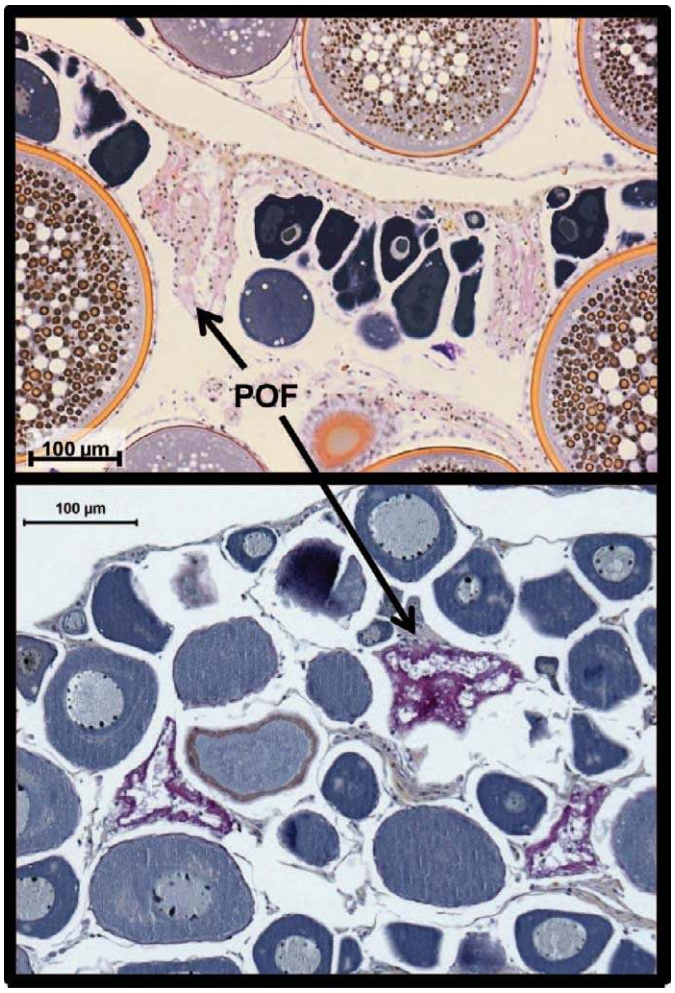

FIGURE 3. Histological section of an ovary showing 18-h-old, degenerating postovulatory follicles (POFs) in a common snook spawned in captivity at 29°C (upper panel; photo provided by R. Taylor, Florida Fish and Wildlife Conservation Commission, St. Petersburg). In comparison, the ovary of a Flemish Cap Atlantic cod shows degenerated POFs that are approximately 3 months old (lower panel). The Atlantic cod was sampled on 8 July 2005; the spawning season is completed by the end of April, and water temperatures are typically less than 10°C.

Even though the effect of temperature on other histological indicators has been less studied, it is recognized that gonadal development is slower in coldwater species than in warmwater species (Rideout et al. 2005), and this difference will affect how histological indicators can be used and the degree of individual synchronization in gonadal development. In warmwater fishes, vitellogenesis begins shortly before the spawning season. Because of this, estimates of spawning season duration are commonly based on any of three indicators: vitellogenic oocytes, OM, and POFs (Figure 4). In addition, individuals of warmwater species often do not exhibit synchronized spawning seasons. The lack of synchronization can result in some species having (1) an extended spawning season, during which some portion of the population is spawning, and (2) a large degree of overlap between spawning capable fish and both early developing individuals and fish that have completed their spawning periods (i.e., regressing or regenerating individuals; Figure 4). For species with this pattern and with fast rates of atresia and POF resorption, it will be difficult to identify females that are exhibiting skipped spawning (Lowerre-Barbieri et al. 2009; Rideout and Tomkiewicz 2011). In contrast, coldwater species have slower metabolic rates and females must begin development well in advance of the spawning season. Because of this, vitellogenic oocytes are present in the ovary well before the spawning season and are not normally used as an indicator of spawning seasonality. This pattern can be seen in the deepwater redfish *Sebastes mentella* from Icelandic waters; the deepwater redfish is ovoviviparous but exhibits the same oocyte developmental stages and ovulation as oviparous species (Figure 5). Although individual variability can be seen in the occurrence of females with cortical alveolar oocytes (early developing) and vitellogenesis, the spawning season is restricted and there is no overlap between ovulating females and early developing or regenerating females. In addition, many individuals with vitellogenic oocytes are observed well in advance of the spawning season.

A standard method to assess the population spawning season and times of peak spawning activity does not exist. This is

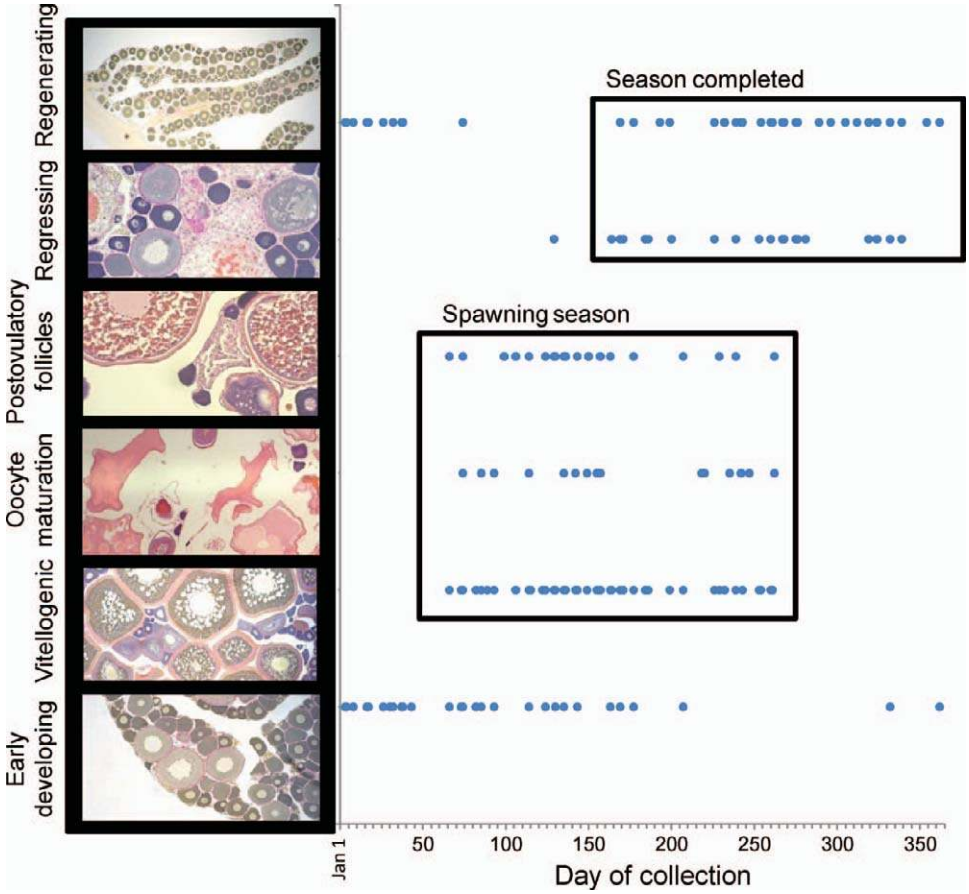

FIGURE 4. Ovarian development of individual spotted seatrout in Florida waters by day of collection during 2001 ($N = 692$; day 1 = January 1).

needed because spawning seasonality has been shown to vary (1) annually due to changes in exogenous cues, primarily temperature; (2) spatially, especially with latitude but also with other habitat factors, such as water depth; and (3) demographically with the size and age of the spawning population (Trippel et al. 1997; Wright and Trippel 2009). For fish with relatively restricted spawning seasons, such as Atlantic cod, annual and latitudinal differences can be assessed by comparing the mean date and range of the population spawning season (Hutchings and Myers 1994). Another approach is to assess the duration of the spawning season based on the time elapsed from the date that 50% of females are in prespawning condition (i.e., advanced vitellogenesis with no signs of prior spawning) to the date that 50% of females are in postspawning condition (Figure 6; Armstrong et al. 2001; Murua et al. 2003; Alonso-Fernández and Saborido-Rey, in press). Studies on species with extended spawning seasons typically report both population spawning seasons and times of peak spawning activity (see review of tropical species by Sadovy 1996). However, without a quantitative definition of peak spawning it is difficult to compare spawning activity among species or populations. As an example, spotted seatrout in Tampa Bay, Florida, could be considered to exhibit no peak, two peaks, or one peak in spawning activity depending on whether the threshold for the percentage of spawning capable females in the population is set at 50, 75, or 80%, respectively (Figure 7). One method to address this is to define the population spawning season based on the first and last occurrences of actively spawning fish and to define peak spawning based on a predefined proportion of spawning capable females (Lowerre-Barbieri et al. 2009).

Methods to effectively assess individual variability and demographic trends in spawning periods will vary with reproductive timing strategies. In total spawners or species with restricted spawning seasons, it is relatively easy to assess age and size effects on the time of spawning simply by evaluating the time over which spawning capable females occur by size and age. However, batch spawners with indeterminate fecundity and extended spawning seasons will maintain a population of vitellogenic oocytes throughout the spawning period, making the assessment of demographic effects more difficult. One way to assess demographic effects in these species is to extend the 50% entry and exit curve analysis presented above to multiple curves based on size-class or age-class (Figure 6). Another method is to select for females in the early developing phase (i.e., those with

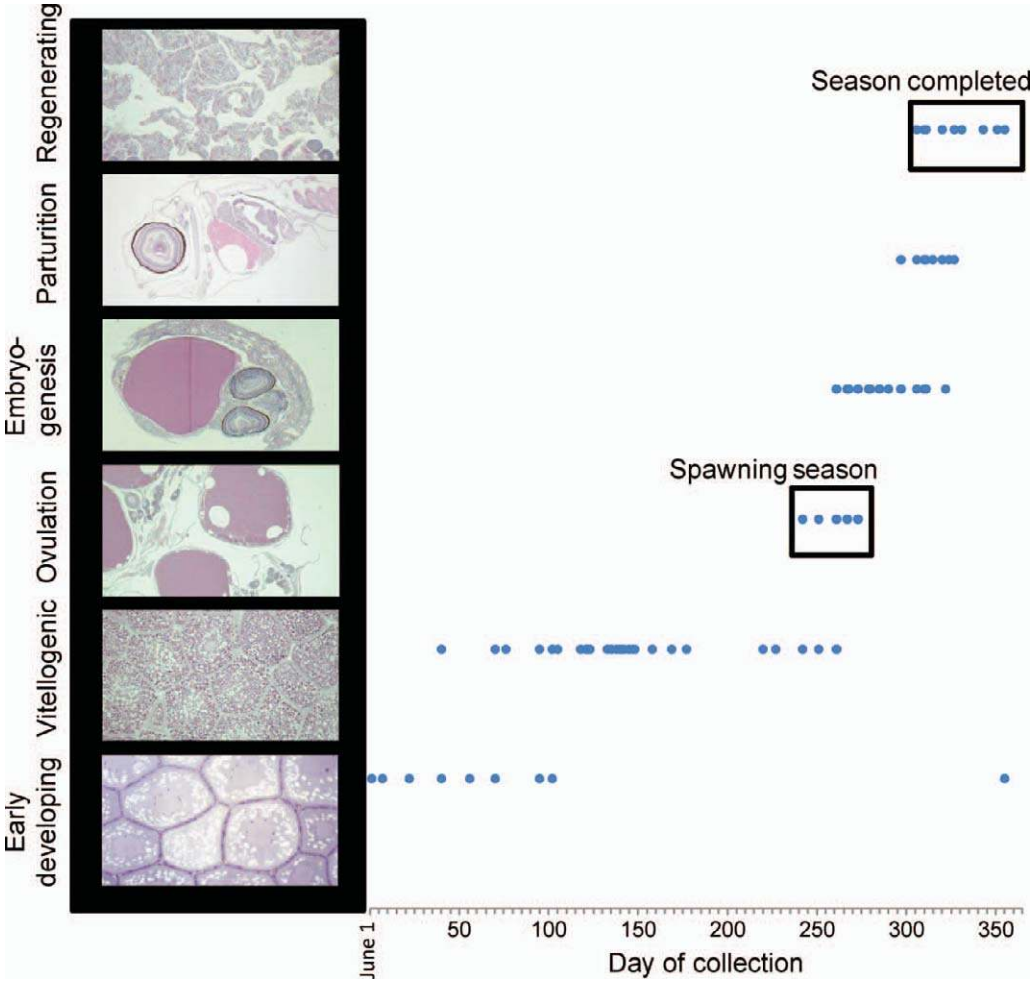

FIGURE 5. Ovarian development of individual ovoviviparous deepwater redfish in Icelandic waters by day of collection during 2001 ($N = 511$; day 1 = June 1). The June 1 start date was chosen to better demonstrate developmental progression. Due to inclement weather, no sampling was conducted from day 177 to day 220. Note that the oocytes show a developmental pattern similar to that in oviparous species

cortical alveolar oocytes) and assess the mean date of occurrence by size-class or age-class (Figure 8). This method works because individuals go through this developmental phase only once prior to the spawning season. Thus, it is possible to determine whether larger, older females develop earlier than their younger counterparts.

However, like all reproductive timing parameters, spawning season estimates can be affected by immigration into or emigration out of the sampled area. In migratory populations, if larger, older fish exhibit more extended spawning seasons, then they may begin their spawning season in one location and finish it elsewhere along their migratory route (Lowerre-Barbieri et al. 1996a). By preselecting data from only the period corresponding to the population spawning season (i.e., the date range over which spawning was possible), hypotheses about recruitment to the spawning population and demographic effects can be tested. First, if recruitment to the spawning population is synchronous and the same population spawns throughout the season, the proportion of spawning capable females should remain relatively constant throughout the spawning season and the mean size of females in the spawning population should either remain constant or increase (Lowerre-Barbieri et al. 2009). Logistic regression can then be used to test whether the probability of a fish being in the spawning population (i.e., spawning capable) at time of capture differs significantly with size-class or age-class. An added benefit of using the logistic regression approach is that it is possible to test the significance of other factors that might affect the proportion of females in the spawning population (e.g., sampling location) and to test their interaction effects (Lowerre-Barbieri et al. 2009; Alonso-Fernández and Saborido-Rey, in press).

Additional and emerging methods to assess spawning seasonality in fishes include plankton surveys, otolith microstructure, passive acoustics, telemetry, and male histological analysis. Egg and larval surveys have long been used to assess spawning seasonality and factors affecting recruitment (Gunderson 1993;

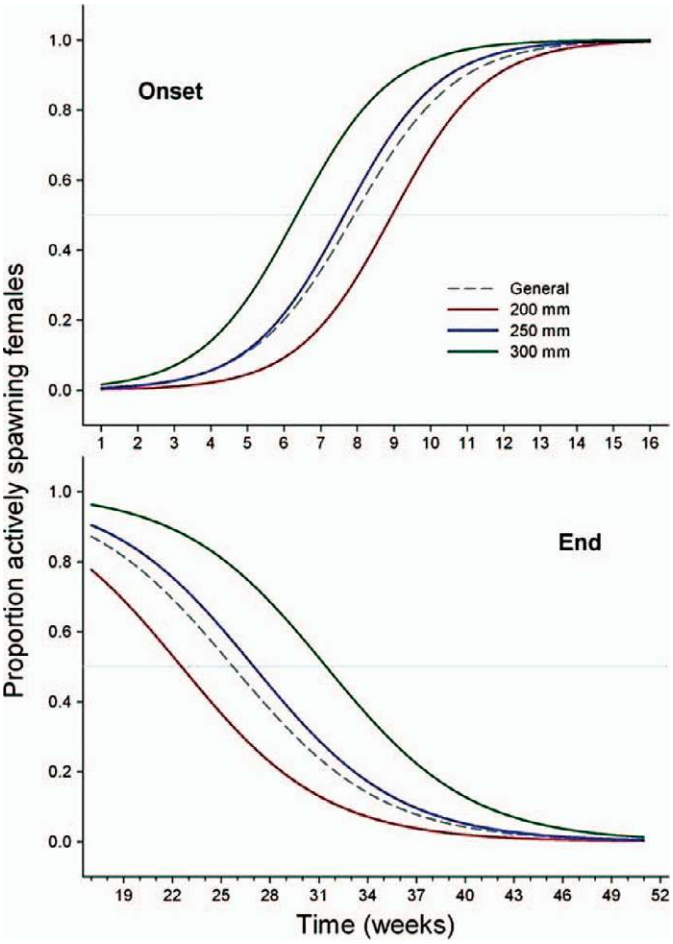

FIGURE 6. Estimated time at which 50% of female bib *Trisopterus luscus* (also known as pouting) are spawning capable at the onset (upper panel) and end (lower panel) of the spawning season in three different size-classes of females (red, blue, and green solid curves) and for all females (gray dashed curves; i.e., all size-classes pooled; $N = 2{,}078$). Proportions were estimated with a general linear model, and female size was entered as a factor. The dates in between where the gray dashed curves and solid horizontal line intersect represent the 18-week season over which 50% of females would be spawning capable. Week 1 in the graph represents week 45 in a calendar year. Figure is modified from Alonso-Fernández and Saborido-Rey (in press).

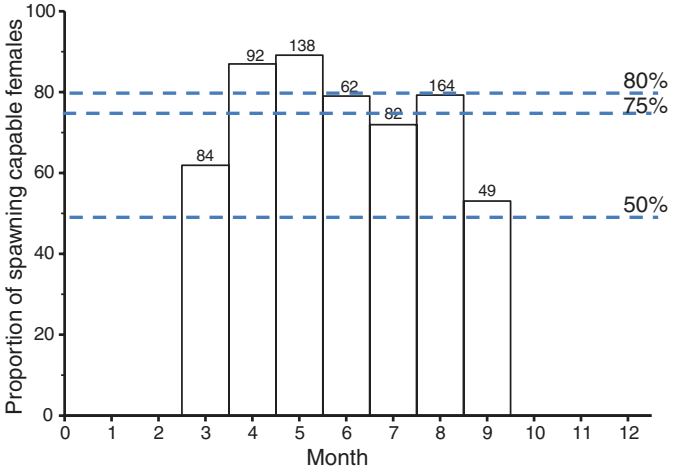

FIGURE 7. Spawning seasonality is typically reported as the months that include spawning activity and the months of peak spawning, without a clear definition of the latter. Spotted seatrout in Tampa Bay, Florida, spawned from mid-March to mid-September in 2001 and 2002. However, the percentage of spawning capable females differed over this period. Thus, peak spawning months also differ depending on the specified threshold for the percentage of spawning capable females in the population: for example, the peak occurs in April–May for the 80% spawning capable threshold; April–June and August for the 75% threshold; and there is no peak for the 50% threshold. Sample sizes are indicated above the bars.

Ibaibarriaga et al. 2007). Integration of these data with information on environment, the age structure and size structure of the spawning population, and estimates of birthdates and locations based on otolith microstructure is improving our understanding of reproductive success in marine fishes (Wieland et al. 2000; Wright and Gibb 2005; Houde 2009). Another emerging method that builds on previous knowledge is the use of passive acoustics. Fishers have located spawning aggregations based on sound production for centuries, but studies that use passive acoustics to assess temporal and spatial patterns have only recently become more common (Gannon 2008). In these species, fish (typically males) make sounds associated with spawning (Rountree et al. 2006; Luczkovich et al. 2008) and passive acoustics at known spawning sites can be used to assess when male sound production begins and ends (Walters et al. 2007; Lowerre-Barbieri et al. 2008). However, seasonality estimates based on male behavior tend to be somewhat longer than those based on ovarian histological analysis because males often arrive on spawning grounds before females and remain after most females have left

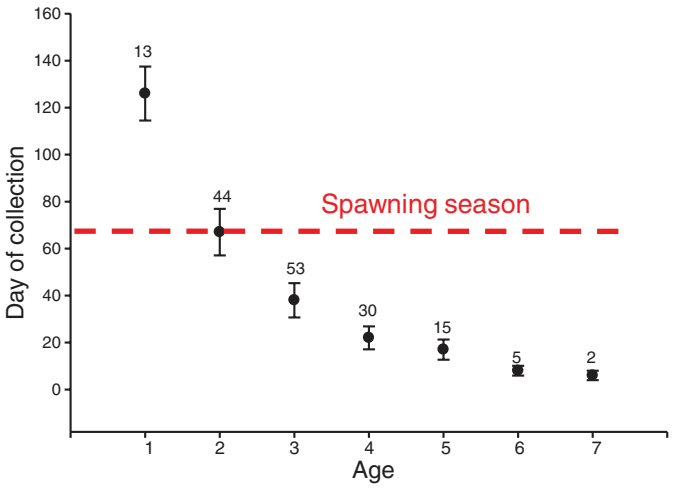

FIGURE 8. Mean (±SE) day of collection by age for females with early developing ovaries (i.e., those with cortical alveolar oocytes as the most developed oocyte stage) among spotted seatrout collected in Tampa Bay, Florida, during 2001 (day 0 = January 1). Only age-3 or older fish had begun the early developing phase prior to the beginning of the spawning season. Thus, fish of ages 1 and 2 would have spawning periods that were shorter than the population's spawning season. Sample size is indicated above each data point.

(Morgan and Trippel 1996; Rhodes and Sadovy 2002). Similarly, remote telemetry can be used to assess both the first occurrence of fish on the spawning grounds and the individual variability in arrival time (Douglas et al. 2009). It can also be used to evaluate differential use of spawning habitat based on fish sex or size and the time spent on the spawning grounds (Robichaud and Rose 2002, 2003; Alonso et al. 2009; Bansemer and Bennett 2009). In addition, histological analysis of testes can be used to help evaluate variability in individual spawning seasons. Spermatogenesis can be identified based on the presence of germinal epithelium in the testicular lobules (Grier and Taylor 1998). Because the majority of spermatogenesis occurs early in the spawning season and because sperm is stored in and released from the lobules for the remainder of the season (Grier and Taylor 1998; Brown-Peterson et al. 2002; Brown-Peterson 2003), spermatozoa stores can be used in combination with the presence of germinal epithelium in the testicular lobules to determine whether an individual is in the early, middle, or late portion of the spawning season (Brown-Peterson et al. 2011). In addition, Tomkiewicz et al. (2011, this special section) have developed a method to quantify individual testicular development, thus improving our ability to assess individual variability of spawning seasonality in males.

SPAWNING FREQUENCY

Estimation of spawning frequency is essential for quantifying fecundity in species with indeterminate fecundity, and spawning frequency has been studied for the past several decades in a wide range of species, especially clupeoids (Hunter and Macewicz 1985; Murua et al. 2003; Stratoudakis et al. 2006; Ganias 2009). However, the terminology associated with reproductive activity at this scale can be confusing as the same term is often used to mean different things. “Spawning frequency” has been used to refer to the number of spawning events occurring daily (Hunter and Macewicz 1985; Murua et al. 2003), the number of spawning events occurring over a spawning season (Lowerre-Barbieri et al. 1996b; McBride and Thurman 2003), and the time interval between spawning events (Claramunt et al. 2007; Lowerre-Barbieri et al. 2009). In an effort to improve clarity, we present and use unique terms for each of the components involved in determining the number of annual spawning events in batch spawners. We use “spawning fraction” to indicate the proportion of mature females spawning daily (Hunter and Macewicz 1985; Murua et al. 2003, 2010; Stratoudakis et al. 2006; Ganias 2009). “Spawning interval” is used to refer to the time period between spawning events (Almatar et al. 2004; Murua and Motos 2006) and at the population level is estimated as the reciprocal of the spawning fraction. We define "spawning frequency" as the number of spawning events within a spawning period (for an individual) or the spawning season (for the population). Spawning frequency for a population is estimated by dividing the number of days in the spawning season by the average spawning interval (Lowerre-Barbieri et al. 1996b; Murua et al. 2003, 2006).

The most studied aspect of spawning frequency has been spawning fraction because of its use in the daily egg production method (DEPM) of estimating SSB and in estimating spawning intervals at the population level (Hunter and Macewicz 1985; Murua et al. 2003, 2006). The advantage of DEPM is that it allows estimates of SSB independent of commercial landings and provides important data on egg production and reproductive biology (Lasker 1985; Somarakis et al. 2004; Stratoudakis et al. 2006; Murua et al. 2010). The development of DEPM changed how we understand fecundity in fishes (Hunter and Macewicz 1985; Hunter et al. 1985) and highlighted that most marine epipelagic spawners are batch spawners with indeterminate fecundity. Because body cavity size limits the number of oocytes that can be hydrated and spawned at one time (Sadovy 1996), a batch-spawning reproductive strategy allows for increased annual fecundity and birthdate range, which can affect offspring survival rates (Lowerre-Barbieri et al. 1998; Wright and Gibb 2005).

Within-population variability at this temporal scale has rarely been assessed (Claramunt et al. 2007) but has important implications for fecundity estimates, maintenance of spawning stock age structure, and spatial management. Although studies assessing individual spawning frequency are rare, several have shown that spawning intervals vary over a spawning period and by sex (Asoh 2003; Curtis 2007; Patzner 2008) and that population estimates without the resolution to assess this variability may lead to overestimation of spawning frequency and fecundity (Curtis 2007). Similar to reproductive timing at the other temporal scales, spawning frequency in species with indeterminate fecundity has been shown to increase with size and age (Ganias et al. 2003; Claramunt et al. 2007) and temperature (Curtis 2007; Ganias 2009) and to be energetically constrained (Hunter and Leong 1981; Pecquerie et al. 2009). Also, like other aspects of reproductive timing, the degree to which individuals synchronize the timing of multiple spawning events differs widely among species. California grunion *Leuresthes tenuis*, silversides *Menidia* spp., and the Japanese grass puffer *Takifugu niphobles* exhibit synchronized spawning intervals (Helfman et al. 1997; Yamahira 2001), as do a number of reef fishes (Claydon 2004; Takemura et al. 2004). This synchronization often results in dense aggregations occurring in discrete locations, making the fish spatially more vulnerable to overfishing (Sadovy 1996; Claydon 2004).

Our ability to accurately estimate spawning frequency depends on how well the population spawning season represents the average duration of individual spawning periods and whether sampled spawning fractions accurately represent the spawning activity of a population. As demonstrated above, many species have highly variable individual spawning periods. Thus, if fish move to and from specific locations to spawn and if sampling occurs only on the spawning grounds, the population spawning season may overestimate the average individual spawning

period. Similarly, spatial and temporal factors can affect the accuracy of spawning fraction estimates if they influence the proportion of active spawners at a given location or if the complete spawning population (i.e., all mature fish) is not representatively sampled (Hunter and Macewicz 1985; Stratoudakis et al. 2006). In addition, there must be a means to accurately identify the daily cohort of spawning females.

Spawning females are those in which spawning is imminent, occurring, or recently concluded (Hunter and Macewicz 1985; Murua et al. 2003). When the daily cohort of spawning females is identified based on imminent spawners, this is called the hydrated oocyte method; when identification is based on recent spawners with POFs, this is called the POF method (Hunter and Macewicz 1985). Oocytes will undergo yolk coalescence and hydration in species with pelagic eggs, and oocytes that have sufficiently progressed in the hydration process are macroscopically identifiable through ovarian inspection (Hunter and Macewicz 1985) or by an elevated gonadosomatic index (Claramunt et al. 2003). However, histological analysis is necessary to identify earlier stages of OM (see Diel Periodicity section) and POFs. In addition to identifying spawning females, it is necessary to "age" the chosen morphological indicator in relation to the actual time of spawning (i.e., hours prior to spawning or hours postspawning), and this requires prior knowledge of diel periodicity or spawn times as well as the ability to identify clear histomorphological stages in OM and POF resorption (Hunter and Macewicz 1985; Stratoudakis et al. 2006; Ganias et al. 2007). Definition of these stages and estimation of their ages require a series of ovarian samples taken at regular intervals both before and after spawning. This can be accomplished by spawning the fish in the laboratory (Leong 1971; Fitzhugh and Hettler 1995; Alday et al. 2008) or, more commonly, by using field estimates of the interval between the time of capture and average spawning time (DeMartini and Fountain 1981; Alheit et al. 1984; Goldberg et al. 1984).

The POF method to estimate spawning fraction is commonly used in the DEPM. Ages of POFs are based on structural changes. For example, Atlantic sardine POFs exhibit changes that can be used to identify females that spawned the same day (i.e., the day of capture; Figure 9A, day 0), the previous day (Figure 9B, day 1), 2 d prior to capture (Figure 9C, day 2), or three or more days prior to capture (Figure 9D, day 3+). However, POF resorption is continuous and adult samples are often collected opportunistically throughout the day. This leads to difficulties in assigning daily cohorts based on morphological stages of POF resorption. One method to improve POF age assignment is to measure the cross-sectional area of POFs (see Ganias et al. 2007 for details on this method). An emerging modification of this method is to perform 3-D volume reconstruction of POFs (Korta et al. 2010) by adding the *Z*-dimension measurement to perimeter measurements of POFs based on histological slides (Ganias et al. 2007). Both methods provide a means of validating morphologically based POF ages and produce a continuous variable that can also be used to assess other factors affecting POF resorption, such as embedding medium and temperature.

Spatial reproductive behavior of a species (e.g., spawning migrations, aggregate spawning, and spawning site selection) is often unknown and thus can bias samples used to estimate spawning frequency estimates. Individuals of many species change their location and habitats upon maturity (Hunter and Macewicz 2003) and to participate in spawning events (Claydon 2004; Okunishi et al. 2009). Spawning fraction estimates will be affected if immature females are included (Rogers et al. 2003) rather than just the mature population (Stratoudakis et al. 2006). Also, many species aggregate in spawning migrations (Jørgensen et al. 2008), at spawning locations within a region (Sadovy 1996; Claydon 2004), or in the water column (Ganias 2008), affecting the density of active spawners in these locations. This can cause biased results from the hydrated oocyte method (Hunter and Macewicz 1985; Ganias 2008), wherein the direction of the bias is dependent on the proximity of sampling to the spawning site. Given that the POF method is based on females that have recently completed spawning, it has the potential to be less biased because spawning aggregations should have dispersed (Ganias 2008). However, its accuracy will depend on how well the postspawning individuals mix with the remainder of the population and, if mixing occurs, where and when such mixing happens with respect to sampling. For most species, this type of data is unavailable. However, in spotted seatrout the proportion of females with hydrated oocytes and females with POFs varied with sampling location and

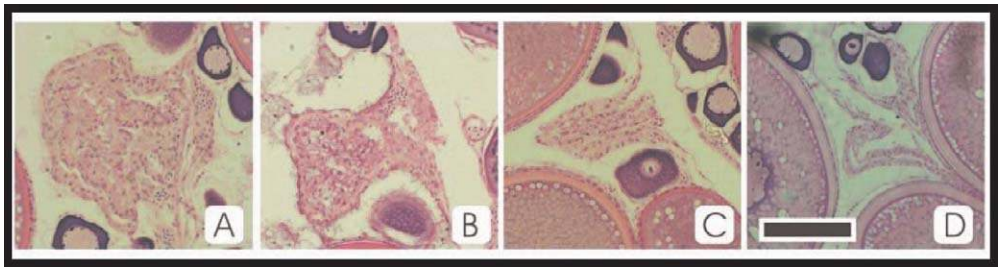

FIGURE 9. Appearance of Atlantic sardine postovulatory follicles (POFs) at the following POF ages: **(A)** day 0, **(B)** day 1, **(C)** day 2, and **(D)** day 3+. Scale bar is 50 μm.

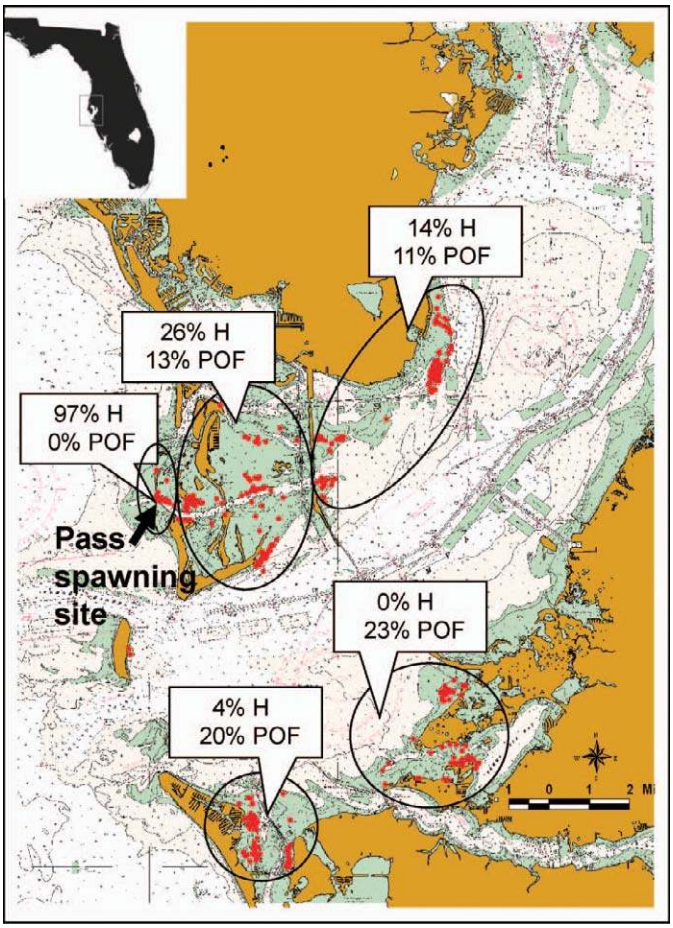

FIGURE 10. Spatiotemporal patterns of spawning activity can be complex, as demonstrated here for spotted seatrout, which spawn near dusk in lower Tampa Bay, Florida (N = 2,034). Two reproductive patterns were observed: (1) fish moving nightly to a high-intensity spawning site (Pass) and (2) low-intensity spawning in three of four estuarine zones. Zones are indicated by ovals, and individual red dots indicate the locations of sampled individuals (H = percentage of females in PM samples that were undergoing oocyte maturation or ovulating [i.e., females with hydrated oocytes]; POF = percentage of females in AM samples that had approximately 12-h-old postovulatory follicles [POFs]). No females were captured in AM samples at the Pass site.

proximity to a spawning aggregation site (Lowerre-Barbieri et al. 2009; Figure 10).

Spawning intervals and consequent spawning frequencies can vary among individuals, over time, and by sex (Asoh 2003; Patzner 2008; S. K. Lowerre-Barbieri, unpublished data) but are difficult to study. Increased interest in aquaculture has led to a greater number of reproductive studies on fish in captivity (Rocha et al. 2008), allowing for direct observation and measurement of individual spawning activity over time. Similar observations are possible in the field on species that spawn in discrete locations over a relatively small geographic range (Patzner 2008). For example, males of the Hawaiian dascyllus *Dascyllus albisella* make nests 1–2 d prior to spawning and the females spawn demersal eggs. By marking both nests and individuals, Asoh (2003) was able to describe individual spawning intervals and the population spawning frequency; mean spawning intervals (over the season) ranged from 6.4 to 11.7 d in 1997 and from 5.5 to 29.0 d in 1998. A similar approach can be taken with remote telemetry at a spawning site if it has been shown that fish move to that site exclusively to spawn (Lowerre-Barbieri, unpublished data). A number of other methods are also emerging that are not dependent on following individuals over time. For species with highly synchronized diel patterns and that aggregate to spawn, the interval between aggregations may indicate spawning interval (e.g., silver pomfret *Pampus argenteus*: Almatar et al. 2004; rabbitfishes [family Siganidae]: Takemura et al. 2004). For species with short spawning intervals, ovarian histology can be used since ovaries will show signs of both imminent and recent spawning (Uriarte et al. 2010). Another approach to understanding spawning intervals is the evaluation of vitellogenic oocyte growth rates (Ganias et al. 2011, this special section) based on the fact that individuals cannot have spawning intervals of shorter duration than the time needed to develop the next batch of oocytes. Lastly, the concept underlying the spawning fraction method (i.e., that the probability of spawning is represented by the proportion of spawning females in the spawning population) can be applied to logistic regression to assess the probability of spawning and how it may vary over spatial, temporal, and demographic scales (Lowerre-Barbieri et al. 2009).

DIEL PERIODICITY

Knowledge of the diurnal period during which fish spawn and the level of individual variability is needed to assess the spatial distribution of spawning sites (Walters et al. 2009) and how source dynamics affect reproductive success. The timing and site of egg release determine the environment first encountered by an egg and thus determine physical factors (e.g., salinity, temperature, and current), the presence of potential predators, and the probability of fertilization. Individual spawn time within a given environment also determines when eggs hatch (Kokita and Nakazono 2000; Asoh and Yoshikawa 2002). Thus, spawn time directly affects survival and dispersion. The synchronicity of individual spawn times, or diel periodicity, varies with species. Although studies of diel periodicity have been conducted most extensively on tropical coral reef fishes (Doherty 1983; Ross 1983; Foster 1987; Asoh 2003) or clupeoids to estimate the spawning fraction (see above), other marine pelagic spawners have also been reported to exhibit diel periodicity (Ferraro 1980; Holt et al. 1985; McBride et al. 2002). However, the drivers of synchronized diel spawning activity are not fully understood, and some marine species with pelagic eggs do not show this pattern, such as the European hake *Merluccius merluccius* (Murua and Motos 2006) and Atlantic mackerel *Scomber scombrus* (Priede and Watson 1993).

Spawn times are dependent on when and how OM is initiated and how long it takes. For example, in the warmwater spotted

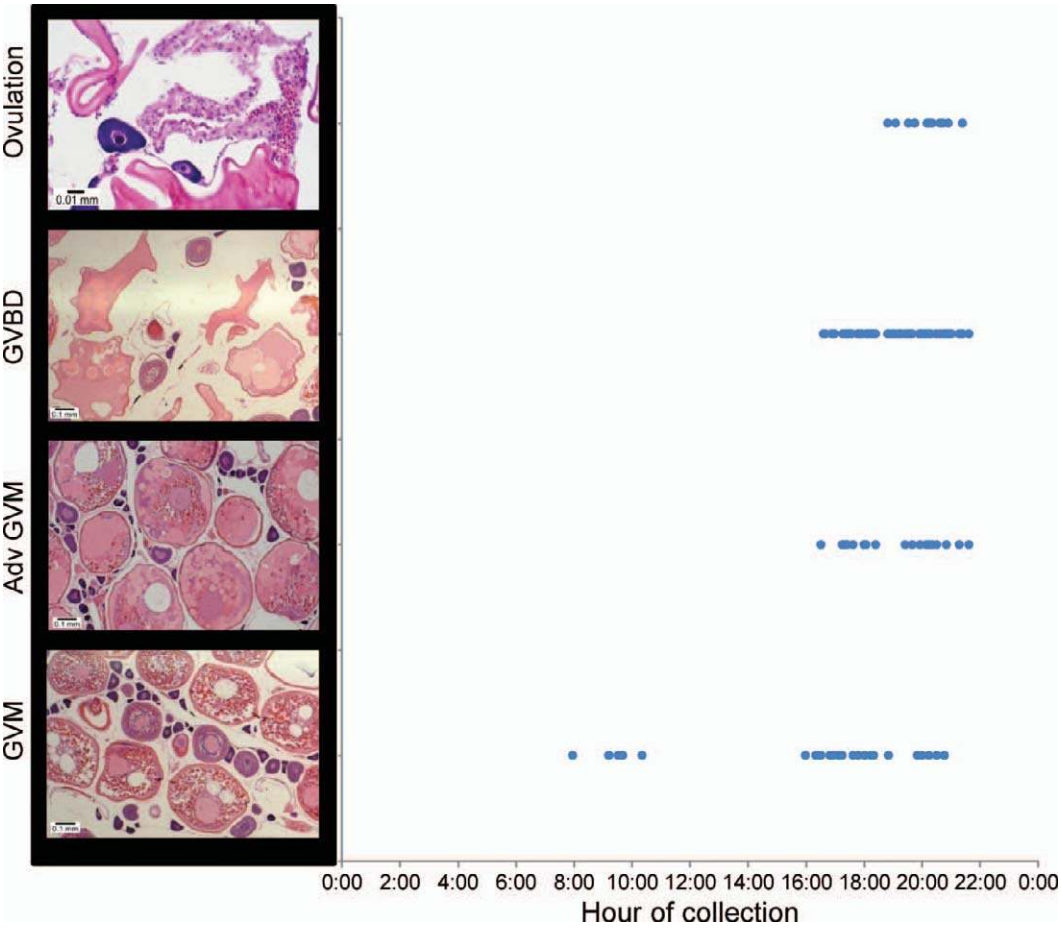

FIGURE 11. Individual spotted seatrout undergoing oocyte maturation by hour of capture from Tampa Bay, Florida, in 2001 and 2002; sampling did not occur after 2136 hours ($N = 193$; GVM = germinal vesicle migration has begun; Adv GVM = GVM is close to completed and oocytes are hydrated enough to be visible macroscopically; GVBD = germinal vesicle breakdown).

seatrout, which has eggs with a 1-mm diameter, initiation of OM can occur 6–14 h prior to spawning (Brown-Peterson 2003). In contrast, Atlantic halibut *Hippoglossus hippoglossus* live in deep water and have relatively large eggs (3 mm in diameter), and in this species it can take 35–55 h to complete hydration (Finn et al. 2002). Triggers for OM are also species specific, and two general patterns have been described for fishes: (1) OM in response to the completion of vitellogenesis or (2) OM as a rapid response to external stimuli (Stacey 1984). Triggers and endocrine interactions are unknown for most species, but the physiological control described for goldfish *Carassius auratus* (Kobayashi et al. 2002) provides insight into the process. Male goldfish are in a state of spawning readiness throughout the spawning season, and reproductive timing is driven by the female. During vitellogenesis, the female releases a recrudescent pheromone that attracts males. Once vitellogenesis is completed, the endocrine system becomes primed to respond to environmental cues and can remain in this state for months until encountering the proper exogenous ovulatory cues, such as warm water, spawning substrate, or the odor of ovulating conspecifics (Stacey and Peter 1979; Stacey et al. 1979). Once female goldfish are cued, they will initiate OM, which lasts approximately 15 h. The precise timing of ovulation is mediated by a circadian clock that is set by the ambient photoperiod. Under typical spawning conditions, OM is initiated close to dusk and goldfish spawn synchronously in the low light of early morning (Kobayashi et al. 2002).

A number of methods are used to assess the time of spawning at the diel scale, including collection of newly fertilized eggs, visual observation of spawning behavior, examination of female gonadal development, and histological analysis, which can be used to assess the progression of OM, ovulation, and POF degeneration (Hunter and Macewicz 1985; Scott et al. 1993; Alday et al. 2008). In spotted seatrout, OM exhibits the following progression: (1) early GVM, (2) advanced GVM, (3) germinal vesicle breakdown and hydration, and (4) ovulation (Lowerre-Barbieri et al. 2009). By evaluating these OM characteristics and their time of occurrence, it is possible to assess

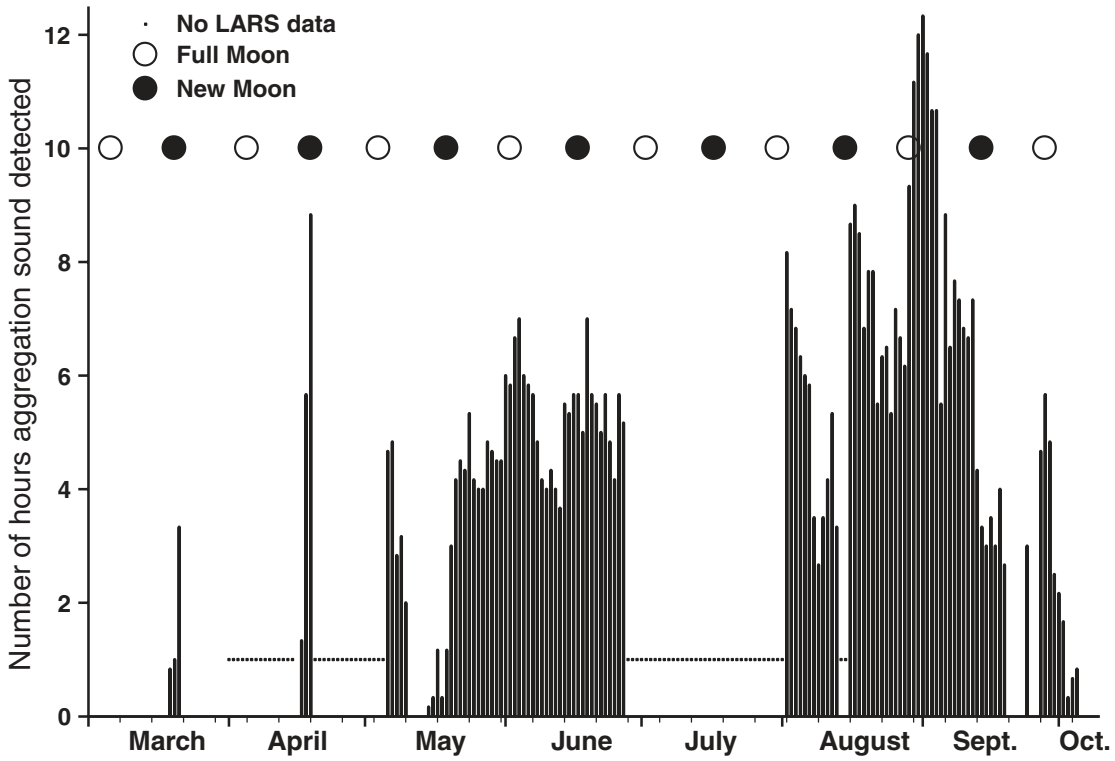

FIGURE 12. Daily duration of spotted seatrout aggregation sound during 2004 at the Pass spawning site (see Figure 10) in lower Tampa Bay, Florida. Aggregation sounds were recorded with a long-term acoustic recording system (LARS).

individual variability and to identify OM characteristics that occur in close proximity to spawning (Figure 11). Early GVM in spotted seatrout occurred over a wide range of times, suggesting either that individual rates of OM show large temporal variability or that spotted seatrout spawn over a wider range of times than previously reported (roughly 2–3-h period close to dusk; Holt et al. 1985; Brown-Peterson 2003). However, to assess the full range of times over which fish spawn, the fish must be sampled at given intervals over 24–48 h (Hunter and Macewicz 1985; Matsuyama et al. 1990; Scott et al. 1993). Red snapper sampled with this method were found to take approximately 10 h to fully hydrate, and ovulating females occurred from 1330 to 1830 hours (Jackson et al. 2006).

Remote sampling methods, such as passive acoustic recordings and fixed-receiver arrays for telemetry, deployed at known spawning sites can provide 24-h coverage, often throughout the spawning season (Lowerre-Barbieri et al. 2008; Douglas et al. 2009; Fudge and Rose 2009). This higher temporal resolution makes it possible to estimate central tendencies and variability in spawn time. Males of many sciaenid species produce distinct courtship sounds, which can be categorized based on the number of fish drumming (Mok and Gilmore 1983) and in some species (e.g., red drum) can also be used to assess proximity to spawning (Lowerre-Barbieri et al. 2008). Walters et al. (2007) used passive acoustics at a known spawning site to estimate the diel periodicity of spotted seatrout over their spawning season based on the hours of large-aggregation sound (Figure 12). Aggregation-level sound occurred daily but varied both in the time of initiation (from 1600 to 2104 hours EST) and in its duration (from 3.0 to 12.3 h); the greatest durations were associated with the full and new moons. In contrast, red drum, which spawn in the fall, initiated aggregation sound earlier in the day (from 1500 to 1730 hours EST) and demonstrated less variability in aggregation sound duration (1–4 h). Another method of assessing spawn times is through visual inspection of spawning activity (Asoh and Yoshikawa 2002). With this method, Asoh and Yoshikawa (2002) were able to demonstrate that over the spawning season, Hawaiian dascyllus modified their time of peak spawning with changing temperatures to maintain a consistent window of hatch times. Asoh (2003) also demonstrated that larger female Hawaiian dascyllus had earlier spawn times than smaller females on any given date, suggesting that—similar to other scales of reproductive timing—there are demographic effects associated with spawn time.

CONCLUSIONS

Evaluating reproductive timing in fishes and its effect on reproductive success at the population and individual levels necessitates both new and standardized methodology. This is an exciting area of life history research as most reproductive parameters have not yet been assessed in terms of central patterns

or individual variability or in relation to size and age (Wright and Trippel 2009). Technological advances, such as remote telemetry, are giving us new insight into reproductive behavior over temporal and spatial scales (Loher and Seitz 2008), and the need for a better understanding of recruitment overfishing and recovery rates has led to increased interest in understanding fish reproductive biology and how it impacts population productivity and resilience (Jakobsen et al. 2009). Much has already been done to meet this objective (Marshall et al. 2003; Murua and Saborido-Rey 2003; Murua et al. 2003; Jakobsen et al. 2009; Kjesbu 2009; Lowerre-Barbieri 2009; Morgan et al. 2009). However, variability in reproductive timing and its effect on reproductive success are still relatively unstudied. Only recently has it become widely recognized that reproductive parameters such as size and age at maturity should be evaluated over time (Rijnsdorp 1993; Trippel 1995; Dieckmann and Heino 2007; Domínguez-Petit et al. 2008) and that fishing mortality has the potential to cause evolution in these parameters over short time scales (Law 2000; Marshall and Browman 2007; Dunlop et al. 2009). Similarly, age truncation has recently been recognized as a factor affecting a population's reproductive success (Anderson et al. 2008), and demographic trends in reproductive timing have been reported at annual (Wright and Trippel 2009), intraseasonal (Claramunt et al. 2007), and diel scales (Asoh 2003).

Although there are many reports of reproductive timing parameters in the literature, there is a need to integrate current knowledge of reproductive timing in marine fishes over the four temporal scales and to evaluate how drivers and constraints differ with habitat and affect the level of synchronization among individuals and, thus, population resilience. Our understanding of the processes underlying reproductive timing in marine fish can be improved through collaborative efforts among reproductive biologists, reproductive physiologists, and scientists studying recruitment processes. Estimates of reproductive timing parameters can also be improved through the use of histology and temporal filters. Hunter and Macewicz (1985) and Hunter et al. (1985) did much to begin this process, and we hope this review will serve as an update to their work by highlighting new and standardized methods of assessing variability in reproductive timing.

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