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Nancy J. Brown-Peterson
University of Southern Mississippi, nancy.brown-peterson@usm.edu

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SPECIAL SECTION: FISHERIES REPRODUCTIVE BIOLOGY

Emerging Issues and Methodological Advances in Fisheries Reproductive Biology

Susan K. Lowerre-Barbieri*

*Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute,
100 8th Avenue Southeast, St. Petersburg, Florida 33701, USA*

Nancy J. Brown-Peterson

*Department of Coastal Sciences, The University of Southern Mississippi, 703 East Beach Drive,
Ocean Springs, Mississippi 39564, USA*

Hilario Murua

*AZTI Tecnalia, Unidad de Investigación Marina, Herrera Kaia Portualde z/g, 20110 Pasaia (Gipuzkoa),
Basque Country, Spain*

Jonna Tomkiewicz

*National Institute of Aquatic Resources, Technical University of Denmark, Jaegersborg Allé 1,
2920 Charlottenlund, Denmark*

David M. Wyanski

*South Carolina Department of Natural Resources, Marine Resources Research Institute,
217 Fort Johnson Road, Charleston, South Carolina 29412, USA*

Fran Saborido-Rey

*Instituto de Investigaciones Marinas de Vigo, Consejo Superior de Investigaciones Científicas,
C/Eduardo Cabello, 6, Vigo, Pontevedra E-36208, Spain*

Abstract

Although incorporating detailed reproductive data into all stock assessments is not a practical goal, the need to understand how reproductive biology affects population productivity is being increasingly recognized. More research focused on reproductive biology—coupled with a shift towards a resilience perspective in fisheries science—is resulting in challenges to many long-held assumptions; the emergence of important new issues; and identification of the need to improve data and methods used in reproductive studies. Typically, data for reproductive studies are based on an assessment of gonadal development, which is most accurately evaluated with histology. This special section of *Marine and Coastal Fisheries* contains contributions from a workshop on the gonadal histology of fishes that was held in Cadiz, Spain, during June 2009. These papers cover a wide range of species and reproductive topics while introducing improved and new histological techniques. In this introduction, we address the following needs: (1) to employ standardization, thereby improving our ability to conduct comparative studies; (2) to better understand patterns of gonadal development and spawning events over time; and (3) to move beyond the spawning stock biomass paradigm. We identify the contributions of special section papers to these topics and conclude by suggesting needs

for future research and integration of reproductive data into both conceptual and quantitative models to better understand how reproductive performance affects population dynamics.

With the recognition that many marine stocks are either fully exploited or overexploited (Hutchings and Reynolds 2004; Grafton et al. 2007), management objectives are shifting from the optimization of yield to achieving conservation and recovery of fish stocks. In addition, the realization that traditional stock assessments are oversimplifications of complex systems has led to a call for a better understanding of biological processes and ecosystems (Walters and Martell 2004; Jakobsen et al. 2009). Although the incorporation of detailed reproductive data into all stock assessments is not a practical goal, the need to understand factors driving population productivity (Worm et al. 2009) and the role reproductive biology plays in this productivity (Kjesbu 2009; Lowerre-Barbieri 2009) is being increasingly recognized. This is evidenced by the number of recent peer-reviewed articles (Figure 1) and books on fish reproductive biology (e.g., Rocha et al. 2008; Jakobsen et al. 2009; Jamieson 2009) as well as key papers highlighting the relationship between reproductive biology and stock sustainability (Winemiller and Rose 1992; Murawski et al. 2001; Berkeley et al. 2004; Marshall and Browman 2007a; Morgan et al. 2009; Murua et al. 2010).

As knowledge of fish reproductive biology rapidly evolves and as fisheries science shifts from an equilibrium perspective to a resilience perspective (Hughes et al. 2005), a number of long-held assumptions are being challenged and important issues requiring more study are emerging. Applied fisheries repro-

ductive biology (AFRB; Kjesbu 2009) has traditionally focused on estimating size and age at sexual maturity and fecundity as important components of life tables (Stearns 1992), whereas there is little focus on assessing reproductive traits at the individual level and how they may impact reproductive success (Lowerre-Barbieri 2009; Wright and Trippel 2009). However, reproductive success is what allows species to persist, and it will depend on both the reproductive output (i.e., egg production) and the factors that affect the survival of that output. A long-held assumption has been that the only adult reproductive trait affecting reproductive success is egg production and that spawning stock biomass (SSB) can be used as a proxy for egg production (Trippel 1999). However, studies have increasingly shown that older, larger females may disproportionately contribute to both egg production and reproductive success (Law 2000; Murawski et al. 2001; Berkeley et al. 2004). In addition, another long-held assumption is that in a species with an annual reproductive cycle, all mature females spawn during each year. However, skipped spawning (i.e., mature individuals not spawning within a reproductive cycle) appears to be more common in fishes than previously thought (Rideout et al. 2005; Jørgensen et al. 2006; Secor 2008; Rideout and Tomkiewicz 2011, this special section). It has also been widely assumed that high fecundity confers greater resilience to fishing pressure, but most exploited marine species are highly fecund (Murua and Saborido-Rey 2003) and many are overfished (Sadovy 2001). However, these same species differ in a range of other reproductive traits, including maturity and longevity, gender and mating systems, spatial attributes (e.g., spawning migrations, spawning site selection, and fidelity), and the temporal pattern of reproduction over a lifetime (i.e., reproductive timing; Murua and Saborido-Rey 2003; Patzner 2008; Lowerre-Barbieri et al. 2011, this special section). Adaptations to offset natural mortality have led to the selection of these traits; that is, regardless of extremely high fecundity and low larval survival rates, certain adult traits have resulted in greater numbers of surviving offspring. Given that a species' reproductive compensatory ability depends on the selection pressures under which it evolved (Garrod and Horwood 1984), we need to better understand these reproductive traits, their genetic basis and phenotypic plasticity, and the role they play in population productivity and resilience to fishing pressure (Lowerre-Barbieri 2009); such an understanding will improve our predictions of population growth and recovery rates of overfished populations.

To achieve this understanding will take collaboration and synthesis of knowledge from various fields as well as improved and standardized means of collecting, analyzing, and discussing reproductive data. Although reproductive data come from a range of sampling techniques, including egg and larval surveys,
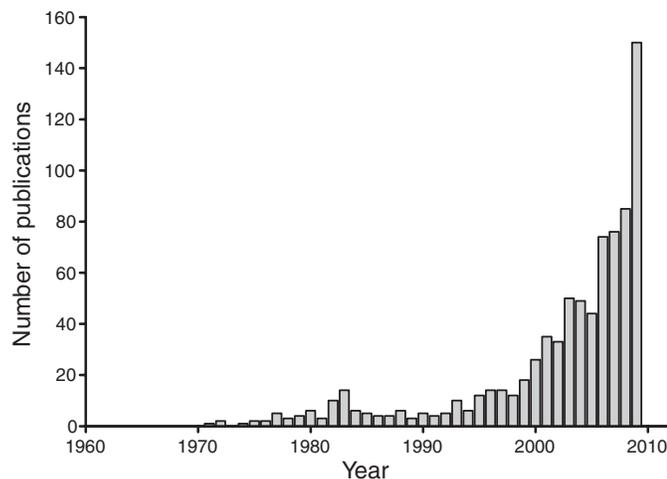

FIGURE 1. Number of peer-reviewed publications by year (1970–2009) that have focused on fish reproductive biology. Data for the figure were generated by using a series of key words (fish reproduction, spawning, fecundity, and oocyte) to search abstract databases (JSTOR, ScienceDirect, and Academic Search Premier). Publications listed in multiple databases were included only once.

visual observation, and tagging, the basis of most reproductive data is a measure of gonadal development or reproductive state (West 1990). Gonadal development can be assessed through macroscopic evaluation, whole-oocyte analysis, the gonadosomatic index, or gonadal histology. Although gonadal histology is expensive and time consuming, it is also considered the most accurate means to assess reproductive state (West 1990; Kjesbu et al. 2003) and is commonly used either to provide data for reproductive parameter estimates or to validate less-costly methods of assessing gonadal development. Thus, similar to recent efforts to review, standardize, and disseminate advances in otolith research and its application to fishery science (Secor et al. 1995; Elsdon et al. 2008), there is a need to review gonadal histology techniques for a wide range of species and regions, to standardize histological indicators and terminology, and to present new applications of these techniques to address emerging issues in fish reproductive biology.

These were the objectives of the Fourth Workshop on Gonadal Histology of Fishes, which was held in June 2009 in Cadiz, Spain, and was jointly sponsored by Fish Reproduction and Fisheries (FRESH; European Cooperation in Science and Technology [COST] Action FA0601) and the American Fisheries Society (AFS) Marine Fisheries Section. Presentations from this meeting form the basis of the papers in this special section. Although histological analysis has been widely applied in studies of maturity and fecundity and with the daily egg production method (DEPM), to our knowledge this collection of papers is the first to present novel approaches for improving our ability to study these topics (Ganias et al. 2011, this special section; Nunes et al. 2011, this special section) as well as addressing a number of emerging reproductive topics and histological applications (Alonso-Fernández et al. 2011, this special section; Kjesbu et al. 2011, this special section; Serra-Pereira et al. 2011, this special section; Tomkiewicz et al. 2011, this special section). In addition, these papers cover a wide range of species, and several papers act to bridge the understanding between researchers studying warmwater versus coldwater species (Brown-Peterson et al. 2011, this special section; Lowerre-Barbieri et al. 2011; Rideout and Tomkiewicz 2011), for which the methodology, terminology, and commonly accepted assumptions are often different.

The objective of this article is to address our emerging understanding of fish reproductive biology and its relationship to sustainability. We begin with an overview of universal reproductive traits and milestones within gametogenesis. We then present the need to standardize both the histological indicators used to identify these milestones and the terms used to describe them, which would improve our ability to compare reproductive traits among species, over their spatial range, and under different fishing regimes. To understand the physiological processes underlying reproductive milestones, there is a need to better understand gonadal development and spawning events over time. Thus, in the reproductive timing section, we introduce the range of reproductive timing strategies exhibited in fishes, the relationship between oocyte recruitment pattern and fecundity estimates, and the manner in which advanced histological techniques can be used to study oogenesis and spermatogenesis. Other reproductive traits addressed in this section include hermaphroditism and time of transition in sequential hermaphrodites and the spawning fraction and spawning interval in batch spawners. The importance of moving beyond an SSB-driven conceptual model of reproductive potential is presented in the third section, which addresses three emerging issues: fisheries-induced evolution, the interaction between energetics and reproductive performance, and skipped spawning. We conclude with a section on future needs for research and integration of reproductive data into both conceptual and quantitative models to improve our understanding of population growth and sustainability.

UNIVERSAL REPRODUCTIVE TRAITS AND TERMINOLOGY

Reproductive strategies in marine fishes are extremely diverse (see Balon 1975; Murua and Saborido-Rey 2003; Patzner 2008), yet all strategies contain certain universal reproductive traits. By developing a conceptual model of reproductive systems based on universal traits (Figure 2) and by identifying a common terminology (Brown-Peterson et al. 2011), we can build the necessary framework to improve communication and standardization, which will improve the ability to conduct comparative analyses and to assess individual variability in these traits. For all fish species, individuals reach sexual maturity, participate in one or more reproductive cycles, release gametes or offspring once or more within a given reproductive cycle, reach maximum reproductive age (often synonymous with maximum age), and die. Reproductive cycles represent the gonadal development needed for mature fish to spawn at the appropriate time. In iteroparous species, which go through multiple reproductive cycles in a lifetime, reproductive cycles also include removal of residual oocytes by atresia and regeneration of oocytes for the next spawning season. Although most exploited marine species exhibit annual reproductive cycles (Bye 1984; Rideout et al. 2005), other periodicities also occur. In addition, skipped spawning is increasingly recognized as a component of many species' reproductive strategies (Rideout and Tomkiewicz 2011).

Gametogenesis is also similar for all teleosts, and most studies focus on oogenesis. Spermatogenesis (i.e., the development and growth of sperm) proceeds through universal stages of development, including spermatogonia, spermatocytes, spermatids, and spermatozoa. Oogenesis (i.e., the development and growth of oocytes) is also similar for all fish (McMillan 2007; Mommsen and Korsgaard 2008) and typically shows the following progression: (1) oogonia, (2) primary growth (PG) oocytes, (3) a previtellogenic stage in which oocytes increase in size and often acquire oil droplets and cortical alveolar (CA) vesicles, (4) a largely estradiol-driven vitellogenic stage, and (5) oocyte maturation (OM) and ovulation. We describe oogenesis in detail
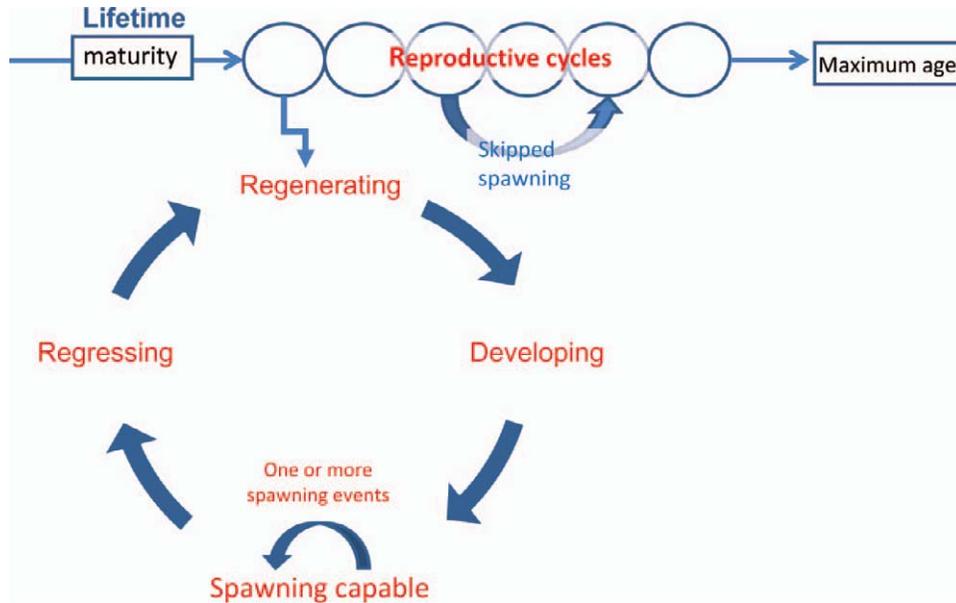
FIGURE 2. Conceptual model of universal reproductive traits in fishes. All fish reach sexual maturity, go through one or more reproductive cycles, release gametes or offspring one or more times within a given reproductive cycle, reach maximum reproductive age, and die.

given that it has been more widely studied than spermatogenesis and the stages are used to assess a number of important reproductive parameters. Oogonia divide by mitosis and form germ cell nests. Once the oogonia initiate meiosis, they enter into the chromatin nucleolus stage of development and are considered oocytes. This stage of development occurs prior to the typically identified basophilic stages of PG, which include the perinucleolar stage, when meiosis is arrested, and the development of the Balbiani body (Wallace and Selman 1981; Grier et al. 2009). Most AFRB studies do not identify specific stages in PG; rather, they classify these stages as PG oocytes, and this is the most developed stage observed in immature females. Secondary growth in exploited marine species is typically identified as beginning with the CA stage and progressing through several substages

of yolk deposition or vitellogenesis (primary [Vtg1], secondary [Vtg2], and tertiary [Vtg3]), OM, and finally ovulation (Figures 3, 4). Oocyte maturation indicates the resumption of meiosis and involves several nuclear and cytoplasmic events (Figure 4): germinal vesicle migration, yolk coalescence (proteolysis of yolk), and germinal vesicle breakdown (Clelland and Peng 2009). In addition, hydration is an important cytoplasmic event that occurs in many species, particularly in marine species with pelagic eggs. Hydration results in a significant and rapid uptake of fluid by the oocyte (Fulton 1898; Wallace and Selman 1981), which causes the oocyte to swell. Ovulation occurs when the follicle ruptures after the completion of OM. These remnant follicles are then called postovulatory follicles (POFs).
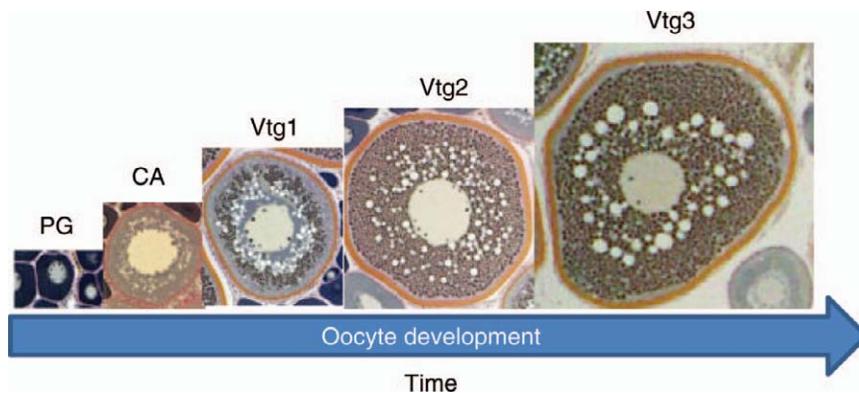

FIGURE 3. Progression of oocyte growth and developmental stages that are most commonly identified in fishes: primary growth (PG), cortical alveolar (CA), and yolked or vitellogenic (Vtg; Vtg1, Vtg2, and Vtg3 = primary, secondary, and tertiary vitellogenesis, respectively). Species shown is the spotted seatrout *Cynoscion nebulosus*.
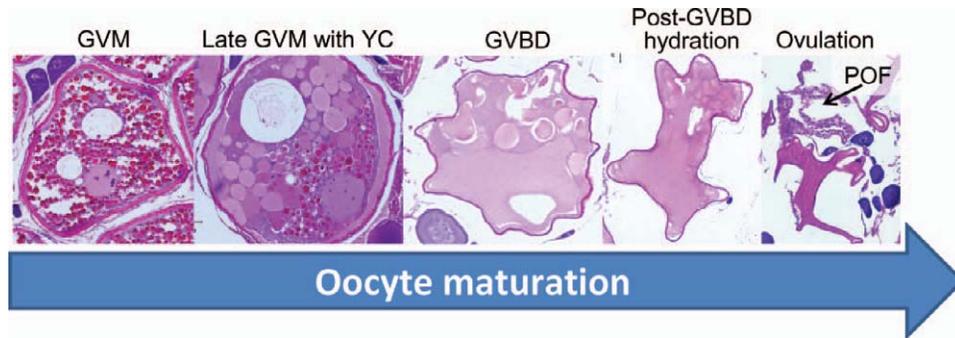
FIGURE 4. Progression of oocyte maturation in fishes: early germinal vesicle migration (GVM), late GVM with yolk coalescence (YC; proteolysis of yolk), germinal vesicle breakdown (GVBD), undergoing hydration after completion of GVBD, and fully hydrated at the time of ovulation. After ovulation, the ruptured oocyte follicle remains in the ovary and is called a postovulatory follicle (POF). Species shown is the spotted seatrout.

Our understanding of the initial stages of secondary growth is still evolving, and the traditional AFRB definition (i.e., the appearance of CA oocytes) differs from other definitions of secondary growth based on initiation of vitellogenesis (Patiño and Sullivan 2002; Grier et al. 2009). Wallace and Selman (1981) defined the CA stage as the first gonadotropin-dependent stage of development, but more recent studies have suggested that it may be mediated through growth hormones (Canosa et al. 2007). Because the neuroendocrine control of this stage of oocyte growth is still not well understood and because not all fish develop cortical alveoli prior to vitellogenic oocytes, Grier et al. (2009) considered the CA stage to be part of PG. However, there are important applications associated with identifying the first developmental stage, which indicates commitment to a given reproductive cycle; these applications include determining fecundity type and assessing maturity. Most, if not all, marine species demonstrate a previtellogenic oocyte developmental stage that occurs only in sexually mature or maturing females. This stage of development is characterized by an increased oocyte diameter; is typically associated with the presence of oil droplets, cortical alveoli, or both; and is commonly called the CA stage. However, in some species such as the bluefin tuna *Thunnus thynnus*, the lipid droplets are the predominant cytoplasmic inclusions; thus, Abascal and Medina (2005) called it the "lipid stage." In addition, for coldwater species this stage is often called "endogenous vitellogenesis" (Murua et al. 2003; Rideout et al. 2005; Vitale et al. 2005). Once fish develop CA oocytes, oogenesis typically continues through vitellogenesis and the fish spawn in the upcoming spawning season (Wright 2007). The CA stage of development identifies those fish that have the necessary energy reserves and have received the appropriate signals to either develop for the first time (sexual maturity) or begin recrudescence for an upcoming spawning season. Thus, we define secondary growth as including the CA stage, as do Murua et al. (2003), Abascal and Medina (2005), and Luckenbach et al. (2008), but we recognize that this area needs further study.

Although there are universal reproductive traits, the terminology used to describe them is diverse and rapidly proliferating. Thus, an emerging issue in AFRB is the need for common terminology. Because many studies have assessed gonadal development to evaluate maturity and fecundity, certain concepts and developmental stages are commonly reported in the reproductive literature. However, the terms employed to describe them are often inconsistent and specific to a study, a species, or a region, making communication and comparative analyses difficult. In an effort to address the need for a common vocabulary, we have developed a list of commonly used reproductive terms and their definitions based on classic and current literature (Table 1). These terms have been used throughout the papers in this special section, indicating their applicability to a wide range of species and topics.

The need for standardized terms to describe gonadal development was the topic of a keynote presentation and the subject of the paper by Brown-Peterson et al. (2011). Brown-Peterson et al. (2011) break the reproductive cycle into a series of developmental phases, including (1) immature, the reproductive phase that precedes sexual maturity and is highly variable in duration; (2) developing, which signals commitment to a given reproductive cycle and occurs in both maturing fish and mature fish undergoing recrudescence; (3) spawning capable, used to identify fish that will spawn during the current reproductive cycle based on advanced gametogenesis (this phase includes the actively spawning subphase); (4) regressing, which signals fish that are completing their spawning period; and (5) regenerating, indicating sexually mature fish that have completed their spawning period and that no longer have secondary growth oocytes, but typically regenerate their reserve of PG oocytes at this time (McMillan 2007). The most developed oocytes in immature females are PG oocytes, whereas early developing females have CA oocytes and developing females have vitellogenic oocytes (Vtg1, Vtg2, or both substages; see Figure 3). The spawning capable phase will have either Vtg3 oocytes or histological indicators of spawning; this phase has different implications depending on whether a fish has determinate or indeterminate fecundity.

TABLE 1.   Definitions of commonly used reproductive terms.

Term	Definition	References
Oogenesis	Development and growth of oocytes from oogonia through maturation. Stages of oogenesis: oogonia (Oo), primary growth (PG), cortical alveolar (CA), vitellogenic (Vtg) or yolked (Yo), and oocyte maturation (OM).	Wallace and Selman 1981; Hunter and Macewicz 1985; Patiño and Sullivan 2002; Kjesbu 2009
Spermatogenesis	Morphological and physiological changes during development of male germ cells. Stages of spermatogenesis: spermatogonia (Sg), spermatocytes (Sc), spermatids (St), and spermatozoa (Sz).	Nagahama 1983; Grier and Uribe-Aranzábal 2009
Primary growth	First stage of oocyte growth in arrested meiosis. Occurs in immature and mature females. Characterized by basophilic staining. Stages include single nucleolus, multiple nucleoli, and perinucleolar.	Wallace and Selman 1981
Secondary growth	Second stage of oocyte growth in arrested meiosis, indicating that oocytes have begun development for an upcoming spawning season. Occurs only in mature or maturing fish. Stages include CA and Vtg; Vtg is often divided into three substages: primary (Vtg1), secondary (Vtg2), and tertiary (Vtg3).	Matsuyama et al. 1990; Abascal and Medina 2005; Luckenbach et al. 2008
Oocyte maturation	Resumption of meiosis and achievement of oocyte maturational competence, ending in ovulation. OM includes two nuclear events: germinal vesicle migration (GVM) and germinal vesicle breakdown (GVBD). In some species, OM may also include the formation of large oil droplets or lipid coalescence (LC), yolk coalescence (YC); and hydration (H).	Jalabert 2005; Grier et al. 2009
Reproductive phases	Phases of gonadal development prior to spawning, associated with spawning, and postspawning that occur in all fishes. Phases are defined as immature; developing; spawning capable, which includes the actively spawning subphase; regressing; and regenerating.	Brown-Peterson et al. 2011, this special section
Determinate fecundity	Recruitment of oocytes from PG to secondary growth occurs prior to an individual's spawning period.	Hunter et al. 1992; Murua and Saborido-Rey 2003
Indeterminate fecundity	Recruitment of oocytes from PG to secondary growth continues throughout an individual's spawning period.	Hunter et al. 1992; Murua and Saborido-Rey 2003
Batch spawner	Females capable of ovulating and spawning multiple batches of oocytes during the individual spawning period. Batch spawners can have determinate or indeterminate fecundity.	Murua and Saborido-Rey 2003
Total spawner	Females ovulate and spawn all developing oocytes in a single event or over a very short time period as part of a single episode.	Murua and Saborido-Rey 2003
Skipped spawning	Failure of sexually mature fish to spawn during a reproductive season. Failure to spawn can be recognized by a lack of ovarian development (Vtg) or by massive atresia prior to the spawning period.	Rideout et al. 2005
Maturation	Synonymous with sexual maturity in both males and females; maturation is attained once in a lifetime.	Rideout et al. 2005

For fish with determinate fecundity and no recent POFs, the spawning capable phase indicates that the spawning period is imminent and fecundity estimates based on fish in this phase are considered the most accurate due to potential downregulation (Thorsen et al. 2006; Witthames et al. 2009). For fish with indeterminate fecundity, the spawning capable phase indicates that the fish are capable of spawning and thus have entered the spawning population. The regressing phase in species with indeterminate fecundity typically is identified by high levels of atresia as the surplus production of secondary growth oocytes is resorbed (Murua et al. 2003; Murua and Motos 2006), whereas coldwater species with determinate fecundity typically have POFs and few residual secondary growth oocytes during this phase (Brown-Peterson et al. 2011). Species-specific histological criteria can be used to develop more specific divisions (subphases) while still preserving the overall reproductive

terminology for comparative purposes. This terminology can easily be modified for teleosts with alternate reproductive strategies, such as sequential hermaphrodites (addition of a transition phase) and livebearers (addition of a gestation phase).

To further demonstrate the applicability of this new terminology, it was adapted to describe the reproductive cycle of oviparous elasmobranchs, and this is presented by Serra-Pereira et al. (2011). For females, progression of oocyte development in the ovary and changes in the oviducal glands and uterus are incorporated into the terminology. For males, a combination of spermatogenic stages and changes in sperm ducts and claspers is used to define reproductive phases. All five reproductive phases described for teleosts can be identified in oviparous female elasmobranchs, although the duration of the phases varies by species. In contrast, the regressing and regenerating phases do not seem to occur in all oviparous male elasmobranchs, whereas the other three reproductive phases can be identified (Serra-Pereira et al. 2011).

REPRODUCTIVE TIMING: GONADAL DEVELOPMENT AND SPAWNING

A necessary step in evaluating the processes underlying observed patterns in reproductive biology is a better understanding of gonadal development and spawning over time. This was the topic of a keynote address and the review paper by Lowerre-Barbieri et al. (2011). Reproductive timing occurs over four temporal scales: lifetime, annual, seasonal, and diel. An understanding of development at these different scales and the interactions between them can improve our understanding of fish reproduction. For example, although sexual maturation occurs at the lifetime scale, there is an interaction effect with the reproductive cycle, meaning that maturing fish must recruit oocytes to secondary growth at the appropriate time of the year to be capable of spawning at the beginning of the spawning season. Most species recruit oocytes from PG to secondary growth and complete the secondary growth of oocytes in less than 1 year (Rideout et al. 2005). However, some fishes, such as the Greenland halibut *Reinhardtius hippoglossoides*, have such slow oocyte growth rates that CA oocytes are recruited a year prior to the season in which they will be spawned (Junquera et al. 2003).

Reproductive timing strategies in marine fishes fall along a continuum from semelparous total spawners to iteroparous batch spawners with extended spawning seasons and long reproductive life spans. Oocyte developmental patterns reflect these timing strategies in terms of oocyte recruitment from PG to secondary growth and within secondary growth (Figure 5). At the lifetime scale, semelparous species, which participate in only one reproductive cycle and then die, recruit all of their oocytes into secondary growth. In contrast, iteroparous species, which are more common and have the potential to participate in multiple reproductive cycles, constantly maintain a reserve of PG oocytes (Murua and Saborido-Rey 2003). For both semel-

parous and iteroparous species, two spawning patterns within a reproductive cycle are demonstrated: (1) total spawners, which spawn either in one event or over a short time period and thus have relatively synchronous secondary growth oocyte development (e.g., Atlantic herring and coho salmon; Figure 5); and (2) batch spawners, which develop and release multiple batches of eggs within a spawning season (e.g., European eel, Atlantic cod, Atlantic sardine [also known as European pilchard], and spotted seatrout; Figure 5).

Iteroparous batch spawners, in turn, demonstrate different oocyte recruitment patterns, and these are affected in part by oocyte developmental rates and their relationship to metabolic rates and water temperature. However, temperature is only one component of a fish's environment, and the selection of spawning pattern and duration of the spawning season may be driven by other factors; in fact, tropical fish species can range from spawning a few times per year to repeatedly over many months (Sadovy 1996). Nevertheless, coldwater species exhibit slower oocyte developmental rates (Rideout et al. 2005) and often have short spawning seasons, resulting in discontinuous recruitment from PG to secondary growth and determinate fecundity, as observed in the Atlantic cod (Kjesbu 2009; Pavlov et al. 2009). In contrast, many batch spawners in warmwater habitats exhibit continuous oocyte recruitment, repeatedly recruiting oocytes from PG 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 through the substages of vitellogenesis) also fall along a continuum from quite synchronous to completely asynchronous (Figure 5).

Although conceptual definitions of determinate and indeterminate fecundity are easy to understand, our ability to prove these recruitment patterns is more difficult. The traditional method of distinguishing between determinate and indeterminate fecundity has been based on whether oocyte size distributions demonstrate a significant gap between secondary growth oocytes and PG oocytes (Hunter and Macewicz 1985; Murua et al. 2003; Pavlov et al. 2009). Other criteria have also been used in conjunction with the gap to indicate determinate fecundity: most notably a decrease in the number or size of advanced vitellogenic oocytes as the season progresses (Hunter et al. 1992; Greer-Walker et al. 1994; Murua and Saborido-Rey 2003). However, to conclusively demonstrate discontinuous recruitment, it is necessary to evaluate oocyte development in individual fish over time; this is now possible with advanced histological quantification techniques and in-captivity studies (see Advanced Histological Techniques section below).

Methodology used to estimate annual fecundity in marine fishes differs depending on fecundity type. In species with determinate fecundity, potential annual fecundity is estimated based on the number of developing oocytes just prior to spawning (Murua et al. 2003). Because the accuracy of this method is
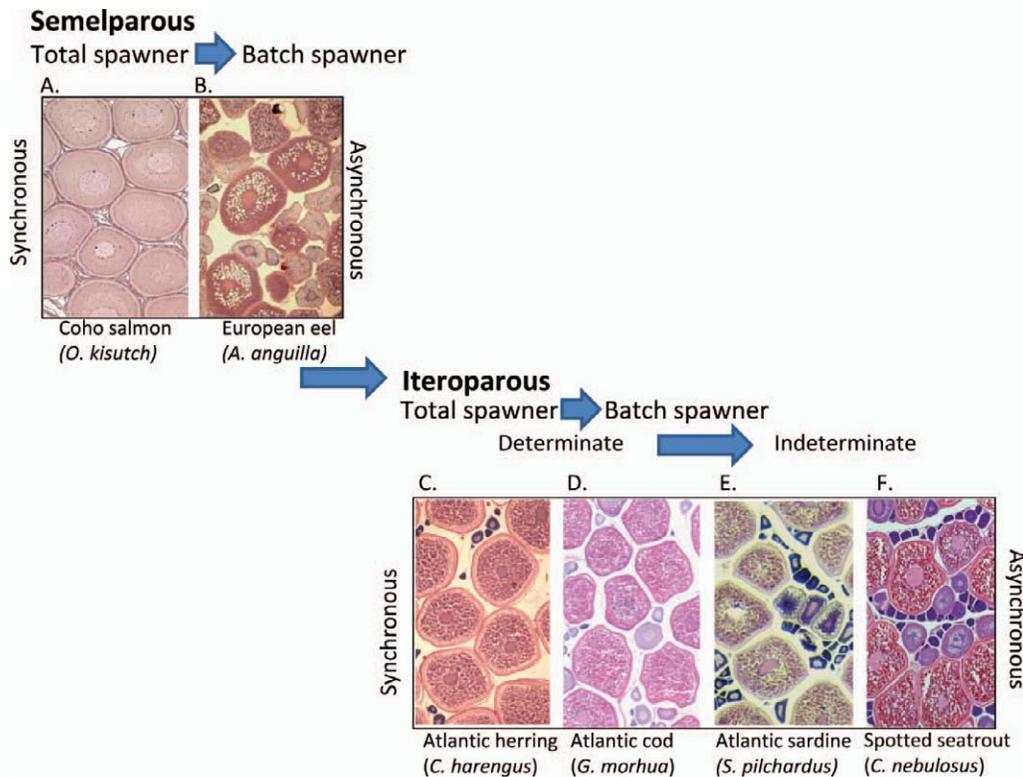
FIGURE 5.   Oocyte dynamics drive the availability of fully developed oocytes for recruitment to oocyte maturation and thus are correlated with spawning patterns. Spawning patterns fall along a continuum from **(A)** semelparous total spawners with synchronous development of all oocytes to **(F)** iteroparous batch spawners with asynchronous development of secondary growth oocytes. Semelparous species die after participating in one reproductive cycle and do not maintain a reserve of primary growth (PG) oocytes. However, they can be either **(A)** total spawners with synchronous oocyte development, such as the coho salmon *Oncorhynchus kisutch* (demonstrated here with all oocytes in the perinucleolar stage), or **(B)** batch spawners with asynchronous secondary growth development, such as the European eel *Anguilla anguilla*. All iteroparous species maintain a reserve of PG oocytes (C–F). However, **(C)** iteroparous total spawners have synchronous development of secondary growth oocytes, as seen in the Atlantic herring *Clupea harengus*. Iteroparous batch spawners can exhibit **(D)** discontinuous oocyte recruitment and determinate fecundity wherein all oocytes to be spawned in a season are recruited to secondary growth prior to the first spawning event, such as in the Atlantic cod *Gadus morhua*, or **(E)**, **(F)** continuous oocyte recruitment throughout the spawning season and indeterminate fecundity. Oocyte recruitment rates within secondary growth also differ, ranging from **(E)** relatively synchronous development of batches, such as in the Atlantic sardine *Sardina pilchardus* (also known as European pilchard), to **(F)** asynchronous development, exhibiting a wide range of secondary growth stages at any given time, such as in the spotted seatrout.

dependent on the underlying oocyte recruitment pattern, oocyte recruitment has been more intensely studied in species that are suspected to have determinate fecundity, and these are often fishes from coldwater habitats (Pavlov et al. 2009). However, species with indeterminate fecundity are more common (Murua and Saborido-Rey 2003). In these species, estimation of the standing stock of advanced oocytes in the ovary or potential annual fecundity is meaningless because oocytes are continuously recruited to this stock. Thus, the annual fecundity of species with indeterminate fecundity is calculated by estimating the number of oocytes spawned per batch, the percentage of females spawning per day (spawning fraction), and the duration of the spawning season (Hunter et al. 1985; Murua and Saborido-Rey 2003). Because accurate estimates of batch fecundity and spawning frequency will give accurate estimates of annual fecundity regardless of fecundity type, indeterminate fecundity for many warmwater species is assumed but not proven.

Advanced Histological Techniques

Traditionally, histological "staging" has been applied to females to understand their developmental state at the time of capture. However, histological techniques are rapidly improving with greater application of quantitative techniques to understand oocyte dynamics, finer temporal resolution of histological indicators, and greater application to males and hermaphrodites. Stereology is a method that is increasingly used in fish reproductive studies to extract quantitative information about three-dimensional structures from two-dimensional images based on systematic plane sections separated by a known distance (Sterio 1984; Gundersen 1986; Gundersen et al. 1988; Anderson 2003). The autodiametric method is based on predicting the number of vitellogenic oocytes per gram of ovary (i.e., oocyte packing density) from the mean diameter of vitellogenic oocytes (Thorsen and Kjesbu 2001; Alonso-Fernández et al. 2009; Witthames et al. 2009). The physical disector, a

stereological method, is used to calibrate estimates of oocyte density from image analyses and to adjust for atresia (Kjesbu et al. 2010a; Korta et al. 2010c). These methods can then be used to rapidly estimate fecundity in species with determinate fecundity based on ovarian histological slides (Thorsen and Kjesbu 2001; Witthames et al. 2009; Kjesbu et al. 2011). It is more difficult to use stereological methods to estimate batch fecundity in indeterminate species (Witthames et al. 2009; Kjesbu et al. 2010b), but oocyte-stage-specific algorithms for oocyte packing density and oocyte diameter can be developed to improve our ability to do so (Kurita and Kjesbu 2009; Korta et al. 2010c). Design-based stereology is a newer method that does not require information about the geometry of the objects being quantified. Thus, when design-based stereology is combined with the disector and fractionator methods and used along with statistical sampling methods (e.g., systematic uniform random sampling), it is possible to obtain unbiased estimates of the number of oocytes in all developmental stages (Korta et al. 2010b).

These advanced histological techniques are being used to better understand oocyte dynamics within the PG stage. Although the developmental stages within PG have been previously described (Wallace and Selman 1981; Tyler and Sumpter 1996), there is renewed interest in identifying and quantifying these stages (Grier et al. 2007, 2009; Korta et al. 2010c; Kjesbu et al. 2011). Using design-based stereology, Korta et al. (2010b) quantified chromatin nucleolar, and perinucleolar oocytes in the European hake *Merluccius merluccius* showing that the number of chromatin nucleolar oocytes increased at the end of the spawning season. This suggests that recruitment to the primary growth for the next spawning season may occur even as the present spawning season is ending. The ecophysiological significance of oocyte recruitment patterns in these very early developmental stages is not yet known but potentially can help us to better understand oocyte developmental stages associated with the sexual maturation process (Okuzawa 2002), their relationship to energetic thresholds (Thorpe 2007), and shifts in habitat usage (see Moving Beyond Spawning Stock Biomass section). Similarly, Kjesbu et al. (2011) used simple oocyte packing density theory to quantify PG oocytes and secondary growth oocytes in the Atlantic cod, a species with determinate fecundity. By following individuals in captivity over time, Kjesbu et al. (2011) were able to demonstrate that only maturing females or mature females undergoing recrudescence developed the circumnuclear ring stage of PG. In addition, some individuals showed arrested oocyte development at this stage, whereas CA oocytes occurred in all females that were developing for the upcoming reproductive cycle. Kjesbu et al. (2011) also demonstrated that the diameter of CA oocytes was smaller than previously believed, which has important implications for fecundity estimates based on the standing stock of secondary growth oocytes. In addition, these studies quantifying the number of oocytes in various stages of PG will help to improve our understanding of PG recruitment and the significance of the size of the PG reserve in iteroparous species over the reproductive cycle.

Although less research has been conducted on spermatogenesis, this field is also evolving (Trippel 2003; Grier and Uribe-Aranzábal 2009). The male reproductive phases cannot be based solely on the presence of spermatozoa in the testes (Grier and Taylor 1998; Brown-Peterson et al. 2002) but rather must take into account the amount of active spermatogenesis along the germinal epithelium (Grier and Uribe-Aranzábal 2009; Brown-Peterson et al. 2011). The presence of a continuous or discontinuous germinal epithelium provides a temporal marker for estimating whether males are in the early, intermediate, or late portion of the spawning season (Brown-Peterson 2003; and see Brown-Peterson et al. 2011), thus allowing a level of individual assessment that is not possible for females. However, there is also a need to develop a quantifiable measure of spermatogenesis. Tomkiewicz et al. (2011) present the spermatogenic maturity index, a novel quantification of testis development based on weighted area fractions of different gamete and somatic tissues. The index results in a development score ranging from 0 to 1, which can then be used to assess temporal patterns in testicular development or can be examined for correlation with morphological and physiological parameters.

Hermaphroditism

Histological analysis is also used to identify hermaphroditic species (Sadovy and Shapiro 1987). Hermaphroditism in fishes is widespread and often misdiagnosed, leading to the need for more conclusive diagnostic criteria and clarified terminology (Sadovy de Mitcheson and Liu 2008). Two patterns of hermaphroditism have been identified in fishes: (1) sequential hermaphroditism, in which fish have a functional primary (i.e., initial) sex and then transition to a functional terminal sex (including protogyny [from male to female] and protandry [from female to male]); and (2) simultaneous hermaphroditism, in which functional testicular and ovarian tissues occur in the same individual at the same time or within a short time period. Sadovy de Mitcheson and Liu (2008) presented the following criteria for diagnosis: (1) direct observations of individuals spawning first as one sex and later as the other sex in the field or laboratory; (2) simultaneous occurrence of mature testicular and ovarian tissues in gonads (i.e., mature gametes); or (3) a detailed gonadal histological series depicting the sex change process in mature fish.

The appearance of gonadal tissue from sequential hermaphrodites in transition will differ depending on the type of hermaphroditism and gonadal structure (Sadovy and Shapiro 1987). In sequential hermaphrodites, small amounts of nonfunctional terminal sex gametes (i.e., PG oocytes or spermatogonia) typically appear long before transition (Smith 1965; Reinboth 1982, 1988). However, fish in the transition phase demonstrate a clear proliferation of terminal sex gametes and atresia of the primary sex gametes (Brown-Peterson et al. 2011). In delimited gonads, there is a membrane of connective tissue separating male from female tissues. This is the pattern seen in the protogynous red porgy *Pagrus pagrus*, wherein male tissue develops outside of the ovary. At transition, testicular tissue proliferates while

ovarian tissue regresses and is no longer identifiable in the functional male (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). For example, the protogynous red grouper *Epinephelus morio* exhibits crypts of male tissue interspersed within ovarian tissue (Brulé et al. 1999). Histological appearance of terminal sex gonads also varies in the amount of remnant gonadal structure retained from the primary sex. The ovarian lumen is retained in the testes of some protogynous species (see Brown-Peterson et al. 2011); is greatly reduced and not clearly visible in others, such as the Mediterranean rainbow wrasse *Coris julis*, a protogynous labrid (Alonso-Fernández et al. 2011); or is not retained at all, as seen in some serranid species (Sadovy and Domeier 2005). In addition, the ovaries of many protandrous species with undelimited germinal tissue retain no trace of the earlier testicular structure, appearing similar to ovaries from gonochoristic species (Moore 1979).

This variability in gonadal structure makes conclusive identification of hermaphroditism difficult. Sadovy de Mitcheson and Liu (2008) reported that misdiagnoses are most often due to (1) a lack of histological analysis to rule out possible juvenile bisexuality in gonochores or nonfunctional hermaphrodites; (2) the assumption that a testis with a lumen is indicative of a terminal sex male; or (3) an inappropriate definition of the transition phase. Nonfunctional hermaphroditism is defined as a species or population in which individuals can possess both ovarian and testicular tissue but only reproduce as either a male or a female throughout their lifetime; such species or populations are thus functionally gonochoristic (Sadovy de Mitcheson and Liu 2008). Alonso-Fernández et al. (2011) use histological analysis to evaluate hermaphroditism in three species: the Mediterranean rainbow wrasse, which demonstrates a sequential pattern; painted comber *Serranus scriba*, which is a simultaneous hermaphrodite; and annular sea bream *Diplodus annularis*, which is a rudimentary or nonfunctional hermaphrodite.

Spawning Fraction and Interval

Estimates of how frequently fish spawn are important for understanding both egg production and reproductive success. New quantitative techniques are improving our understanding of oocyte growth rates, spawning fractions, and spawning intervals in species with indeterminate fecundity (see Ganias et al. 2011; Uriarte et al. 2010) and have important implications for the DEPM of estimating SSB. Traditionally, estimates of spawning fraction are based on the proportion of collected females undergoing OM or with POFs, but there can be problems with actively spawning females being contagiously distributed—aggregating and thus occurring in higher proportions at the time and place of spawning than in the overall population. Using a decade of DEPM survey data, Uriarte et al. (2010) showed how high-temporal-resolution data on OM stages and degeneration of POFs can be used to develop a matrix system that defines the probability of these stages belonging to a specific spawning cohort. Using this method on the European anchovy *Engraulis encrasicolus* in the Bay of Biscay, Uriarte et al. (2010) identified five spawning cohorts (i.e., from 1 d prior to spawning to 3 d postspawning) and validation of their method was assisted through the use of individuals with both OM and POFs. The resulting spawning fraction estimate was considerably higher than previous estimates, which implies that the SSB of Bay of Biscay European anchovy may be lower than previously estimated.

In a similarly novel approach, Ganias et al. (2011) used oocyte growth rates to study the spawning interval in Atlantic sardine. If oocyte growth rates remain consistent and if there is no lag time between the completion of vitellogenesis and initiation of OM, then the growth rate of vitellogenic oocytes should reflect the time between spawning events (i.e., the spawning interval). Ganias et al. (2011) estimated oocyte growth rates based on temporal parameters typically estimated for the DEPM: (1) time difference between various stages of OM and time of spawning and (2) known ages of POFs based on the stage of degeneration. Ganias et al. (2011) then used these measures of time to estimate how long it should take for an oocyte in the earliest stage of vitellogenesis to complete the process of vitellogenesis and OM. Spawning interval estimates based on this approach were quite similar to those based on the more labor-intensive DEPM.

MOVING BEYOND SPAWNING STOCK BIOMASS

Our understanding of how fishing impacts populations is changing, as evidenced by a paradigm shift from single-species to ecosystem-based approaches (Walters and Martell 2004; Francis et al. 2007) and a concurrent shift from an equilibrium perspective to a resilience perspective (Hughes et al. 2005). Stock assessment models are used to estimate sustainable yields and to develop management objectives associated with harvest control measures (i.e., minimum size limits, closed seasons, closed areas, bag limits, etc.) that are typically based on biological reference points associated with the level of fishing at which there would be negative consequences (Marshall et al. 2003). Reproductive success has been integrated into this traditional framework through the stock–recruitment relationship, which attempts to evaluate how current stock abundance (i.e., SSB) relates to future abundance of catchable fish (Mehault et al. 2010); the population's maximum reproductive rate or compensatory reserve is represented by the slope of the spawner–recruit curve near the origin (Myers et al. 1999). Data used to estimate SSB for iteroparous species include estimated abundance of mature females at age, mean weight at age, the proportion of females that are mature at a given age, and estimates of natural mortality and fishing mortality to predict survivorship in any given year (Murawski et al. 2001). Although this is a useful paradigm based on basic life history tables, it is also clearly an oversimplification. Stocks do not exist in a vacuum. Natural mortality is stochastic and is affected by life stage, other species within the ecosystem, and fishing mortality.
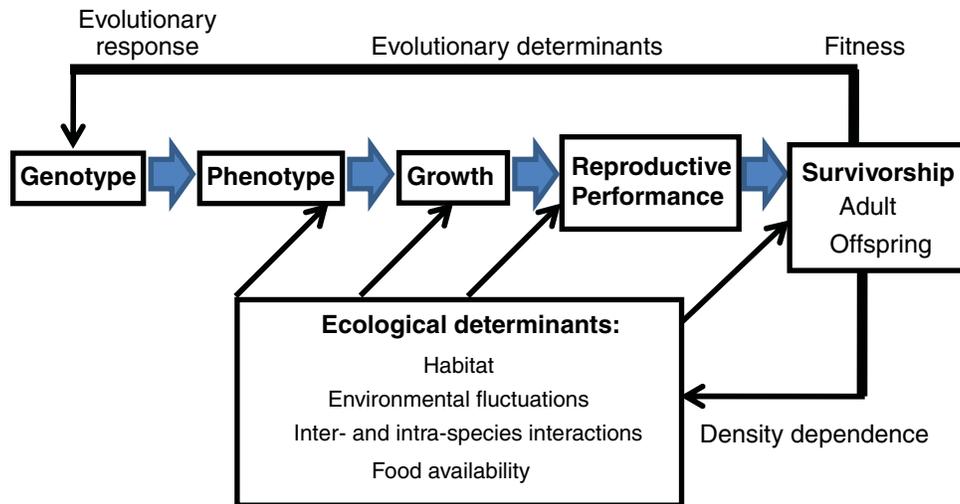
FIGURE 6. Reproductive performance includes egg or offspring production and behavior and is associated with density-dependent and fitness feedback loops. An individual's genotype and phenotype and a number of ecological factors affect its reproductive performance, which in turn influences adult and offspring survival. Ecological determinants depend on spatiotemporal factors, including a stock's abundance, and physiology drives an individual's response to them. Changes in the ecological determinants affect which phenotypes demonstrate the greatest reproductive success. This figure was adapted from Ricklefs and Wikelski (2002) and Young et al. (2006).

In addition, reductions in fishing mortality are often insufficient to produce the necessary population growth and stock recovery of overfished species (Hutchings and Reynolds 2004).

There is also a need to distinguish between stock yield, which is usually well correlated with year-class strength, and stock resilience, which should be more closely linked to factors associated with reproductive success (Lowerre-Barbieri 2009). Reproductive success is accomplished through trade-offs between the rate of reproductive output and the survivorship rate associated with that output. To integrate the concept of reproductive success or parental fitness into stock assessment processes, Trippel (1999) introduced the term "stock reproductive potential," defined as the "annual variation in a stock's ability to produce viable eggs and larvae that may eventually recruit to the adult population or fishery." It has been increasingly shown that SSB is an insensitive index of stock reproductive potential (Marshall 2009), and total egg production has been suggested as an alternative index (Marshall 2009; Morgan et al. 2009; Mehault et al. 2010; Murua et al. 2010). Reproductive characteristics such as sex ratio, annual variation in size and age at sexual maturation, and fecundity will affect total egg production. Because population fecundity varies among species (Pitcher and Hart 1982; Wootton 1984; Helfman et al. 1997), for a given species within its range (Beacham and Murray 1993; Witthames et al. 1995; Korta et al. 2010a), over time (Healey and Heard 1984; Bailey and Almatar 1989; Rijnsdorp 1991; Zwolinski et al. 2001), and with demographics (Murawski et al. 2001; Berkeley et al. 2004; Lowerre-Barbieri et al. 2009), achieving an understanding of reproductive potential necessitates a better understanding of the relationships among stock structure, total

egg production, and population growth (Lowerre-Barbieri et al. 1998). In addition, new information on factors affecting offspring survival as related to the age, reproductive history, and condition of their parents holds important implications for the development of effective fishery management strategies (Jakobsen et al. 2009). These factors include egg quality (Kamler 2006), where and when fish spawn (Begg and Marteinsdottir 2002; Rowe and Hutchings 2003; Lowerre-Barbieri 2009), depensation or the Allee effect (Frank and Brickman 2000; Hutchings and Reynolds 2004), and size-specific fishing mortality, which has the potential to act as a selection agent, thereby leading to fisheries-induced evolution (Dunlop et al. 2009).

Reproductive strategies are complex, adaptable systems that have evolved to overcome a given regime of natural mortality (Lowerre-Barbieri 2009). An emerging concept in reproductive biology is the physiology–life history nexus paradigm, which was proposed by Ricklefs and Wikelski (2002) and applied to fish by Young et al. (2006). Within the context of this paradigm, the observed spawning pattern of an individual or population is dependent on reproductive performance, which will be affected by how environmental parameters and past experiences have driven the phenotypic expression of the underlying genotype (Figure 6). Reproductive performance, in turn, can impact other individuals in the population through density-dependent compensatory mechanisms as well as by affecting fitness, thus determining which genotypes remain in the population. In other words, the behavior associated with any given spawning event will have both a fitness effect and a density-dependent effect that can influence future spawning events at the individual and population levels. Gamete developmental patterns, endogenous

rhythms affecting reproductive timing, and gender systems are all part of a species' genotype. However, the phenotypic expression of when an individual will mature, when a sequential hermaphrodite will undergo transition, and when (or whether) an individual will opt out of a reproductive cycle (i.e., skipped spawning) will be affected by exogenous factors, such as environment (e.g., photoperiod, temperature, etc.), energy supply, and population density. Similarly, there will be genetic attributes that restrict the range of environments within which a species can spawn, but the phenotypic expression that drives individual site selection and fidelity to a given site in consequent spawning events will be affected by short-term environmental cues and past experience. Thus, a species' resilience to fishing will depend on its genotypically determined traits, the degree of phenotypic plasticity in these traits, and the factors that drive individual plasticity in the traits. Emerging issues associated with this ecophysiological paradigm and addressed in this section include (1) fisheries-induced evolution, (2) the interaction between energetics and reproductive performance, and (3) skipped spawning.

Fisheries-Induced Evolution

Fisheries-induced evolution refers to the rapid evolution of biological attributes in response to selective and high fishing mortality (Law and Grey 1989). The capacity for such rapid genetic change has been confirmed through controlled selection experiments (Conover and Munch 2002). The reproductive attributes that are most commonly assessed in association with fisheries-induced evolution are the onset of sexual maturity (Law and Grey 1989; Hutchings and Myers 1993; De Roos et al. 2006); tradeoffs between reproductive performance and energy allocation, including migratory behavior (Jørgensen et al. 2008); and sex allocation in hermaphrodites (Sattar et al. 2008). However, it is difficult to assess the impacts of selective fishing pressure on fitness without a better understanding of how ecological determinants will affect phenotypic plasticity and thus reproductive performance.

A good example of this is the complex process of sexual maturation. This ontogenetic shift from an immature state, where all energy is allocated to survival and somatic growth, to a reproductively mature state, where energy will be required for gametogenesis and reproductive behavior, is multifaceted and associated with biochemical, physiological, behavioral, and ecological shifts (Okuzawa 2002). In addition, the size and age at which a fish matures are postulated to profoundly affect its reproductive success (Roff 1992; Stearns 1992). There is currently concern that the number of highly exploited stocks demonstrating decreases in size and age at maturity may be indicative of fisheries-induced evolution (Marshall and Browman 2007b; Rochet 2009; Dunlop et al. 2009). Probabilistic maturation reaction norms, which describe the probability of maturing as a function of age and size, have been proposed as a statistical tool to distinguish between ecological and evolutionary determinants of maturation. However, the ecological factors affecting the process of sexual maturation are not well understood (Marshall and Browman 2007b), and the underlying biological data used to estimate maturity differ depending on the sampling design, the method used to assess ovarian development, and the stage of development considered to be indicative of maturity (Lowerre-Barbieri et al. 2011).

Although maturity estimates play an important role in understanding fisheries-induced evolution and in stock assessment, a standardized method to produce these estimates is still lacking. Representative samples can be difficult to obtain due to differential habitat usage of immature and mature fish (Tomkiewicz et al. 1997). In addition, although histological gonadal evaluation has been shown to be more accurate than macroscopic evaluation (Murua et al. 2003; Tomkiewicz et al. 2003; Vitale et al. 2006), there is no clear histological indicator that can be used to separate immature females from mature regenerating females in those species for which POFs from a past spawning season cannot be identified at the time of recrudescence. Thus, Hunter and Macewicz (1985, 2003) and Murua et al. (2003) recommended using data for maturity analysis only from those times when there are few or no regenerating females—typically just prior to or early in the spawning season. Estimates of size at sexual maturity based on this technique are usually smaller than those based on data collected throughout the year (Hunter and Macewicz 2003), highlighting the importance of standardized biological methods for assessing maturity. The International Council for the Exploration of the Sea has recognized the need for improved and standardized methods to estimate size and age at maturity and the importance of histological analysis for confirming gonadal state (ICES 2006). In an effort to meet these needs, the council has conducted a series of eight workshops covering 18 species over the last 3 years. Guidelines for the workshops and for collecting maturity data and histological analyses for maturity workshops have been developed (ICES 2010), and the need to standardize terminology was also highlighted in these workshops.

Gender system also affects a species' resilience to fishing and potential for fisheries-induced evolution (Sattar et al. 2008). Sequential hermaphroditism is a life history pattern that is potentially more susceptible to fisheries-induced evolution given that (1) fish in the terminal sex have already undergone natural selection in the primary sex and (2) the larger size of the terminal sex often results in greater fishing pressure due to size-selective fishing practices. The relative impact of fishing will depend in part on the factors driving sexual transition (Armsworth 2001; Heppell et al. 2006). Heavy fishing on species with low phenotypic plasticity in the timing of transition can result in skewed adult sex ratios and sperm limitation, leading to lower population productivity (Koenig et al. 1996; Vincent and Sadovy 1998; Alonzo and Mangel 2004; Brooks et al. 2008). In species with greater plasticity, fishing pressure can result in decreased size and age at transition (Armsworth 2001; Rochet 2009). Other behaviors in hermaphroditic reef fishes can also affect their resilience to fishing (e.g., hermaphroditic species that aggregate to

spawn) and sex-specific differences in catchability (Rowe and Hutchings 2003).

Within this special section, several papers either directly or indirectly address reproductive and histological issues that are important to understanding fisheries-induced evolution in terms of sexual maturity and gender system. Lowerre-Barbieri et al. (2011) review the underlying physiology affecting reproductive timing at varying temporal scales (i.e., lifetime, annual, intraseasonal, and diel) and discuss potential implications for fitness. Two papers present methods that might help improve our ability to distinguish immature females from mature inactive females. Kjesbu et al. (2011) demonstrate that for Atlantic cod, the circumnuclear ring stage can be used to distinguish between immature and mature inactive females. There is potential for similar transitional oocyte developmental phases in other species, and this is an important area for future research. Nunes et al. (2011) present results on liver tissue histology differences that are associated with the spawning season and that may have future application for assessing sexual maturity. Changes in the size and age of sexual transition are a special case of sexual maturity and are important to assessing fisheries-induced evolution in sequential hermaphrodites. Histological analysis plays an important role in identifying gender type and size and age at transition, as shown by Alonso-Fernandez et al. (2011) for the Mediterranean rainbow wrasse.

Energetics and Reproductive Performance

Because reproductive activity has an energetic cost (Roff 1983), females are limited in the time and resources they can devote to producing offspring as these expenditures can decrease future growth, condition, survival, and reproductive output. A species' life history strategy is driven by how much and when energy is allocated to these various components (Trivers 1972). Thus, the trade-off between survival, reproduction, and growth determines (1) the size and age at the onset of sexual maturity in relation to maximum body size and (2) a species' reproductive life span, which can be from 1 year (semelparity) to more than 30 years in iteroparous rockfishes *Sebastes* spp. This was the topic of a keynote address by Saborido-Rey et al. (2010b) and is an emerging issue in reproductive biology. Optimal energy allocation is dependent on inherited components (energetic thresholds and endogenous rhythms) and on the environment encountered by the individual (e.g., food, environmental proximate cues, and temperature because of its effect on metabolic rates), as is seen in Iberian Atlantic sardine (Nunes et al. 2011). Within a reproductive cycle, the temporal pattern of energy gain with respect to reproductive behavior and spawning is species specific and falls somewhere between two extremes: capital breeders and income breeders (Houston et al. 2007). Capital breeders build their energy reserves by feeding prior to the spawning season and then use this stored energy for reproduction. In addition, they often expend energy on reproductive traits other than egg production, such as extensive spawning migrations or parental care (Jager et al. 2008). In contrast, a pure income breeder would continuously replenish energy reserves throughout the spawning season without the need for energy storage. Within a population, energy reserves can also drive demographic differences in reproductive timing and fecundity. For example, in many species, the larger, older females are reported to develop earlier, spawn more frequently, and have longer individual spawning seasons than younger, smaller fish (Kawaguchi and Yamamoto 1990; Ganias et al. 2003; Wright and Trippel 2009). In addition, there is a strong relationship between body size and fecundity; thus, older females may disproportionately contribute to egg production (Berkeley et al. 2004).

Skipped Spawning

Although we do not yet fully know what factors or interactions cause an individual fish to opt out of spawning in a reproductive cycle, the rapid increase in research on skipped spawning is greatly improving our understanding. This was the topic of a keynote address and is an important emerging issue that links energetics and reproductive performance (Rideout and Tomkiewicz 2011). Increasing evidence suggests that skipped spawning is part of the reproductive strategy of many species if they cannot meet or maintain necessary energy and may be more common in long-lived species that have either temporally restricted food availability (e.g., capital breeders) or high energetic costs associated with reproduction, such as extensive spawning migrations (Jørgensen et al. 2006; Jager et al. 2008; Secor 2008; Rideout and Tomkiewicz 2011). Recent in-captivity studies have evaluated the physiological attributes associated with skipped spawning in Atlantic cod in the northeast Arctic and have demonstrated that females opting out of a reproductive cycle had lower condition, smaller livers, and lower plasma 17β-estradiol levels than normally developing females and exhibited arrested oocyte development in the early CA stage (Skjæraasen et al. 2009).

Histological analysis plays an important role in assessing skipped spawning (Rideout et al. 2005), which is proving to be more common than previously believed and may be an adaptive trait (i.e., resulting in increased lifetime reproductive output) rather than an abnormality (see Rideout and Tomkiewicz 2011). Our ability to identify skipped spawning will depend on the duration of the spawning season in comparison with the duration of histological indicators of spawning activity (Lowerre-Barbieri et al. 2009). Many temperate and high-latitude species have determinate fecundity (Pavlov et al. 2009), and low water temperature in these habitats affect ovarian processes, such as the resorption rates of POFs (Fitzhugh and Hettler 1995; Lowerre-Barbieri et al. 2011). Resorption of POFs typically occurs within a span of several days in warmwater species (Hunter and Macewicz 1985), but POFs can remain identifiable for months in coldwater species (Saborido-Rey and Junquera 1998). Thus, for determinate species, skipped spawning can be identified by (1) the presence of POFs but without the development of secondary growth oocytes during the time of year when females

typically exhibit recrudescence or (2) high rates of atresia at any of the oocyte developmental stages (Rideout et al. 2005; Saborido-Rey et al. 2010a; Rideout and Tomkiewicz 2011). Although sexually mature fishes collected during the spawning season either with no ovarian development or with resorption of all vitellogenic oocytes have been thought to indicate skipped spawning in warmwater species with indeterminate fecundity (Brown-Peterson et al. 2008; Zupa et al. 2009), skipped spawning in these species is harder to prove. This is because these species typically have extended population spawning seasons with variable individual spawning periods, have faster POF resorption rates (Lowerre-Barbieri et al. 2011), and can exhibit high levels of oocyte atresia (i.e., resorbing a batch of oocytes) that is not indicative of the end of the spawning season (Lowerre-Barbieri et al. 1996; Rideout and Tomkiewicz 2011).

CONCLUSIONS AND FUTURE DIRECTIONS

Ovarian histology became more commonly used in fisheries science after it was described in several classic papers and after the development of the POF method to assess spawning fraction (Wallace and Selman 1981; Hunter and Macewicz 1985; West 1990). As demonstrated by the papers in this special section, gonadal histology is now frequently applied to a wide range of reproductive issues and species, and new techniques and applications are rapidly evolving and improving our ability to study reproductive processes at the cellular level. In addition to the applications covered by the papers in this special section, an issue that was discussed at the workshop but that is not represented in these papers is our ability to identify gonadal abnormalities associated with perturbed aquatic ecosystems (see Rice 2003; Curya and Christensen 2005; Strand et al. 2009). Given the recent BP Deepwater Horizon oil spill in the Gulf of Mexico and efforts to assess its impact on living resources (Marscarelli 2010), this is an especially relevant issue. Commonly observed gonadal abnormalities in perturbed ecosystems include changes in the expected timing of development (Thomas and Rahman 2009; Zhang et al. 2009), intersex (the occurrence of primary oocytes in testicular tissue or the occurrence of spermatocytes in ovarian tissue in nonhermaphroditic species; see Strand et al. 2009; Sun and Tsai 2009), and increased levels of oocyte atresia (Johnson et al. 2008). Other gonadal abnormalities that potentially indicate stressed fish include a high prevalence of inflammatory lesions (Johnson et al. 2008) and an increased occurrence of bacterial infections in ovaries, as was observed in red drum *Sciaenops ocellatus* (R. M. Overstreet, University of Southern Mississippi, personal communication).

Although gonadal histology has many useful applications, it is time consuming, expensive, and limited to providing data on germ cell development. Thus, there is a need to leverage its use and, where possible, to combine histological methods with less-expensive approaches and with methods that can be used to assess reproductive behavior. Two less-costly methods to assess gonadal development are the gonadosomatic index and squash mounts of whole oocytes; if they can be validated with histological analysis, these methods will have wide application for assessing gonadal development (Witthames et al. 2009). Other indices also have important applications in terms of assessing the relationship between energetics and reproductive biology (Marshall et al. 1999); these include the hepatosomatic index, condition indices, and direct measures of tissue energy storage (Domínguez-Petit and Saborido-Rey 2010; Nunes et al. 2011). However, the reproductive strategy of a population is defined as much by its behavior as by its egg production; thus, there is a need to better integrate knowledge of reproductive state with reproductive behavior, and several key methods are emerging that will improve our ability to do so. Remote sampling techniques, such as passive acoustics (Roundtree et al. 2006; Gannon 2008; Luczkovich et al. 2008), bioacoustics (Lawson and Rose 2000; Macchi et al. 2005), and telemetry (Robichaud and Rose 2002, 2003), are allowing us to monitor reproductive behavior over time and space in ways that were not previously possible. Passive acoustics can be used to identify the spatial distribution of spawning sites and to monitor reproductive timing based on courtship sounds at known spawning sites (Walters et al. 2007, 2009; Lowerre-Barbieri et al. 2008). Similarly, remote telemetry can be used to assess 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 by sex or size and time spent on spawning grounds (Robichaud and Rose 2002, 2003; Alonso et al. 2009; Bansemer and Bennett 2009).

Although conserving sufficient reproductive or spawning potential for a stock to maintain or rebuild itself is a fundamental goal of fisheries management (Goodyear 1993), we do not yet fully understand the species-specific aspects of reproductive strategies that drive reproductive potential (i.e., the production of eggs that survive to become juveniles). However, this is rapidly changing as our understanding of reproductive processes and their importance to sustainability improves (Kjesbu et al. 2010b), and management strategy evaluation frameworks are increasingly being used to assess alternative measures of reproductive potential (Murua et al. 2010). A fundamental shift in population dynamics research is the recognition that reproductive performance can affect recruitment and thus population growth and resilience (Murawski et al. 2001; Berkeley et al. 2004; Jakobsen et al. 2009). This realization has led to an increased awareness of reproductive dynamics and strategies, and particular emphasis has been given to the importance of larger and older females for reproductive output and reproductive success, as age truncation is expected to decrease a stock's resilience (Caddy and Agnew 2004) and increase its recruitment variability (Anderson et al. 2008). Reproductive traits exhibiting demographic trends will vary with species but include fecundity (Berkeley et al. 2004; Murua et al. 2006; Mehault et al. 2010; Thorsen et al. 2010), reproductive timing (Wright and Trippel 2009; Lowerre-Barbieri et al. 2011), skipped spawning (Rideout et al. 2005; Jørgensen

et al. 2006; Secor 2008; Rideout and Tomkiewicz 2011), and egg quality (Kamler 2006). Thus, traditional stock assessments based on SSB and fishing mortality-based reference points will underestimate the impacts of age truncation and overestimate a stock's resilience (Trippel 1999; Murawski et al. 2001; Marshall 2009).

Reproductive strategies are complex, integrated systems (Lowerre-Barbieri 2009); reproductive performance includes egg or offspring production and behavior and is associated with density-dependent and fitness feedback loops (Figure 6). This improved conceptual model of fish reproduction provides the basis for assessing fisheries-induced evolution (Dunlop et al. 2009) and the potential for depensation due to density-dependent mating strategies (Frank and Brickman 2000; Caddy and Agnew 2004; Rowe et al. 2004). In addition, genetic studies of highly fecund marine species suggest that the population of successful breeders may be much smaller than the adult population and that success is associated with spawning at the right time and place (Hedgecock 1994; Hauser et al. 2002; Gomez-Uchida and Banks 2006); thus, there is a need to better understand spatial components of reproductive strategies. This is especially important given the increased use of marine protected areas as management measures (Botsford et al. 2009), the increased evidence for natal homing (Thorrold et al. 2001; Robichaud and Rose 2004; Svedang et al. 2007), and the awareness of spatial effects on recruitment success (deYoung and Rose 1993; Begg and Marteinsdottir 2002). Lastly, it has been suggested that a stock's resilience to fishing pressure may increase with intraspecific diversity (Frank and Brickman 2000). Thus, there is a need to assess a stock's reproductive biology in terms of bottlenecks and variability over time, space, and demographics (Lowerre-Barbieri et al. 2009). To gain this level of reproductive knowledge and to better integrate it into management practices will necessitate standardized reproductive methods and terminology, a better understanding of internal and external factors affecting reproductive success in fishes, and the sharing of results and techniques across geographic regions, as was done at the Fourth Workshop on Gonadal Histology of Fishes and in the papers in this special section.

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