A Standardized Terminology for Describing Reproductive Development in Fishes

Author: Brown-Peterson, Nancy J.

Source: Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 3(1) : 52-70

Published By: American Fisheries Society

URL: https://doi.org/10.1080/19425120.2011.555724

Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 3:52–70, 2011

ISSN: 1942-5120 online
DOI: 10.1080/19425120.2011.555724

SPECIAL SECTION: FISHERIES REPRODUCTIVE BIOLOGY

A Standardized Terminology for Describing Reproductive Development in Fishes

Nancy J. Brown-Peterson*
Department of Coastal Sciences, The University of Southern Mississippi, 703 East Beach Drive, Ocean Springs, Mississippi 39564, USA

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

Beverly J. Macewicz
National Marine Fisheries Service, Southwest Fisheries Science Center, 8601 La Jolla Shores Drive, La Jolla, California 92037, USA

Susan K. Lowerre-Barbieri
Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, 100 8th Avenue Southeast, St. Petersburg, Florida 33701, USA

Abstract

As the number of fish reproduction studies has proliferated, so has the number of gonadal classification schemes and terms. This has made it difficult for both scientists and resource managers to communicate and for comparisons to be made among studies. We propose the adoption of a simple, universal terminology for the phases in the reproductive cycle, which can be applied to all male and female elasmobranch and teleost fishes. These phases were chosen because they define key milestones in the reproductive cycle; the phases include immature, developing, spawning capable, regressing, and regenerating. Although the temporal sequence of events during gamete development in each phase may vary among species, each phase has specific histological and physiological markers and is conceptually universal. The immature phase can occur only once. The developing phase signals entry into the gonadotropin-dependent stage of oogenesis and spermatogenesis and ultimately results in gonadal growth. The spawning capable phase includes (1) those fish with gamete development that is sufficiently advanced to allow for spawning within the current reproductive cycle and (2) batch-spawning females that show signs of previous spawns (i.e., postovulatory follicle complex) and that are also capable of additional spawns during the current cycle. Within the spawning capable phase, an actively spawning subphase is defined that corresponds to hydration and ovulation in females and spermiation in males. The regressing phase indicates completion of the reproductive cycle and, for many fish, completion of the spawning season. Fish in the regenerating phase are sexually mature but reproductively inactive. Species-specific histological criteria or classes can be incorporated within each of the universal phases, allowing for more specific divisions (subphases)

Subject editor: Hilario Murua, AZTI Tecnalia, Pasaia (Basque Country), Spain

*Corresponding author: nancy.brown-peterson@usm.edu
Received December 17, 2009; accepted October 4, 2010

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

An accurate assessment of population parameters related to fish reproduction is an essential component of effective fisheries management. The importance of understanding reproductive success and population reproductive potential has recently been summarized (Kjesbu 2009; Lowerre-Barbieri 2009); these reviews do much to advance both our knowledge and our understanding of important reproductive processes as they relate to fisheries. However, the field of fisheries biology and other fish-related disciplines continue to lack a simple, consistently used terminology to describe the reproductive development of fishes. Numerous classifications and associated terminologies have been introduced in the literature to describe reproductive development in fishes (Table 1). Many of these classifications, including the most recently published terminology suggested for use in freshwater fishes (Núñez and Duponchelle 2009), are based on a numbered staging system, the first of which was introduced by Hjort (1914) for Atlantic herring. Unfortunately, this proliferation of terminology has resulted in confusion and has hindered communication among researchers in fish-related disciplines, particularly when different developmental stages are assigned the same number by different scientists (Bromley 2003). Indeed, Dodd's (1986) comment that "ovarian terminology is confused and confusing" is still true today regarding the terminology used to describe reproductive development in both sexes.

The realization that a standardized terminology should be developed to better describe fish reproduction is not a new concept; Hilge (1977) first suggested the importance of a consistent terminology, and there have been several later attempts to provide a more universally accepted gonadal classification scheme (e.g., Forberg 1983; West 1990; Bromley 2003; Núñez and Duponchelle 2009). The wide variations in terminology have no doubt occurred because various disciplines typically need to describe reproductive processes on different levels (e.g., whole-gonadal development in fisheries biology and aquaculture versus gamete development in physiology). Furthermore, since egg production is an important metric in stock assessments, most classification systems have focused on females only. Classification of ovarian development has been based on both macroscopic (e.g., external appearance of the ovary or gonadosomatic index) and microscopic (e.g., whole-oocyte size and appearance or histology) criteria, and each of these methods has its own type of classification scheme (West 1990; Murua et al. 2003). Classification terminology for testicular development is equally diverse and inconsistently used (Brown-Peterson et al. 2002). Reproductive classification based on histological techniques represents the most accurate method and produces the greatest amount of information (Hunter and Macewicz 1985a), but it requires the most time and has the highest cost. In contrast, classification based on the external appearance of the gonad is the simplest and most rapid method, but it has uncertain accuracy and may be too subjective (Kjesbu 2009).

In addition to the existence of multiple terms (e.g., developing, maturing, and ripening) for a specific aspect (e.g., gonadotropin-dependent growth of gametes) of the reproductive cycle, some of the confusion in terminology is the result of terms having been defined multiple times. For example, the term "maturing" has typically been used in the disciplines of fisheries biology and fish biology in reference to the initial, one-time attainment of sexual maturity (i.e., becoming a reproducing adult), but the term has also been used to describe an individual with oocytes that are undergoing vitellogenesis (Bromley 2003). Terms for reproductive classification have apparently been chosen based either on the frequency of occurrence in the literature (e.g., spent or resting) or on how descriptive they are of the process being identified (e.g., developing or spawning); thus, such terms are somewhat subjective and are used inconsistently among studies. In some cases, the name for the reproductive class does not accurately describe the events taking place in the individual fish, which is particularly true for the often-used "resting" classification (Grier and Uribe-Aranzábal 2009).

Unfortunately, previous attempts to introduce standardization and consistency into reproductive classification (i.e., Hilge 1977; West 1990; Bromley 2003) have met with limited to no success due to the reluctance of researchers to adopt an unfamiliar terminology that may not be appropriate for the species under investigation. Thus, rather than erecting a new classification system, communication among researchers studying reproduction in fishes may be improved by describing and naming the major milestones within the fish reproductive cycle. All fishes, regardless of reproductive strategy, go through a similar cycle of preparation for spawning (i.e., the development and growth of gametes), spawning (i.e., the release of gametes), cessation of spawning, and preparation for the subsequent reproductive season (i.e., proliferation of germ cells in iteroparous species). Therefore, the objective of this article is to present a universal conceptual model of the reproductive cycle in fishes that (1) describes the major phases of the cycle by use of a standardized terminology and (2) is applicable to species with differing reproductive strategies (e.g., determinate and indeterminate fecundity; Hunter et al. 1992; Murua and Saborido-Rey 2003). Existing classification schemes and species-specific terminology can then be integrated into this framework while still retaining the standardized terminology under the umbrella of phase names. We have opted to use the term "phase" to describe

TABLE 1. Examples of gonadal classifications for female marine (M) and freshwater (F) fishes (classes = number of classes in each system). Determinate and indeterminate refer to fecundity type; batch and total refer to spawning pattern. All total spawners listed here have determinate fecundity.

Species	Strategy	Classes	Reference	Comments
Atlantic herring *Clupea harengus* (M)	Total	7	Hjort 1914	Macroscopic
Goldfish *Carassius auratus* (F)	Indeterminate, batch	8	Yamamoto and Yamazaki 1961	
European horse mackerel *Trachurus trachurus* (M)	Indeterminate, batch	9	Macer 1974	Two immature classes
Pacific hake *Merluccius productus* (M)	Determinate, batch	8	Foucher and Beamish 1977	Macroscopic, four additional subclasses
Marine teleosts	Various	4	Hilge 1977	No inactive mature class
Eurasian perch *Perca fluviatilis* (F)	Total	9	Treasurer and Holliday 1981	
Capelin *Mallotus villosus* (F)	Total	9	Forberg 1983	Seven additional subclasses
Pacific herring *Clupea pallasii* (M)	Total	8	Hay 1985	Three developing classes
Atlantic cod *Gadus morhua* (M)	Determinate, batch	5	Morrison 1990	No inactive mature class
Red drum *Sciaenops ocellatus* (M)	Indeterminate, batch	8	Murphy and Taylor 1990	
Roundnose grenadier *Coryphaenoides rupestris* (M)	Total	5	Alekseyev et al. 1991	No inactive mature class
Dover sole *Microstomus pacificus* (M)	Determinate, batch	2	Hunter et al. 1992	Based on 15 subclasses of active or inactive spawners
Brighteye darter *Etheostoma lynceum* (F)	Indeterminate, batch	6	Heins and Baker 1993	Macroscopic classes
Atlantic croaker *Micropogonias undulatus* (M)	Indeterminate, batch	7	Barbieri et al. 1994	
Pike icefish *Champsocephalus esox* (M)	Total	6	Calvo et al. 1999	Immature not included
Brazilian hake *Urophycis brasiliensis* (M)	Indeterminate, batch	9	Acuña et al. 2000	Two partially spent classes
Narrowbarred mackerel *Scomberomorus commerson* (M)	Indeterminate, batch	9	Mackie and Lewis 2001	Three spawning classes
Spotted seatrout *Cynoscion nebulosus* (M)	Indeterminate, batch	6	Brown-Peterson 2003	Immature not included
Atlantic cod (M)	Determinate, batch	9	Tomkiewicz et al. 2003	Three spawning classes
Red grouper *Epinephelus morio* (M)	Indeterminate, batch	9	Burgos et al. 2007	Includes transitional and uncertain maturity
Marine teleosts	All	5	ICES Workshop 2007	Includes class for spawn-skipping fish
Freshwater teleosts	Batch and total	6	Núñez and Duponchelle 2009	Different descriptions for total versus batch spawners

the parts of the cycle because (1) this term has historically been used in biology in reference to cyclical phenomena and (2) the term "stage" has been commonly used in recent literature for describing the development of individual gametes (Taylor et al. 1998; Tomkiewicz et al. 2003; Grier et al. 2009) rather than development of the gonad. Our approach will be to (1) introduce the terminology used to describe and name the major phases in the reproductive cycle of fishes, (2) illustrate the application of this framework to female and male gonochoristic marine teleosts with varying reproductive strategies, (3) demonstrate

the applicability of this system to fishes with alternate reproductive strategies (i.e., hermaphroditic and livebearing species), and (4) show how an existing classification system can fit under the umbrella of phase names.

METHODS

The terminology presented here was developed during discussions at the Third Workshop on Gonadal Histology of Fishes (New Orleans, Louisiana, 2006) and has been further refined in relation to the reproductive strategies defined by Murua and Saborido-Rey (2003). Total spawners are species with determinate fecundity that synchronously develop and spawn a single batch of oocytes during the reproductive season. Batch spawners can have either determinate or indeterminate fecundity, exhibit various levels of asynchronous oocyte development (including group-synchronous [modal] development), and spawn multiple batches of oocytes during the reproductive season. Oogenesis patterns further reflect fecundity type; species with discontinuous recruitment—usually characterized by a gap in oocyte distribution between primary growth (PG) oocytes and secondary growth oocytes—have determinate fecundity, whereas species with continuous recruitment have indeterminate fecundity, meaning that oocytes are repeatedly recruited into vitellogenesis throughout the spawning season (Murua and Saborido-Rey 2003; Lowerre-Barbieri et al. 2011a, this special section). Batch-spawning species with indeterminate fecundity will have different oocyte developmental patterns depending on how quickly the oocytes are recruited to various stages of vitellogenesis, which drives how asynchronous the oocyte pattern appears (Lowerre-Barbieri et al. 2011a). Terminology associated with various types of viviparity follows that of Wourms (1981). Terminology for oocyte stages, including atresia, follows that suggested by Lowerre-Barbieri et al. (2011a) and is based on a compilation of terminologies presented by Wallace and Selman (1981), Hunter and Macewicz (1985a, 1985b), Matsuyama et al. (1990), Jalabert (2005), and Grier et al. (2009). All vitellogenic oocytes are secondary growth oocytes. Additionally, we consider cortical alveolar (CA) oocytes to be secondary growth oocytes since their formation is gonadotropin dependent (Wallace and Selman 1981; Luckenbach et al. 2008; Lubzens et al. 2010). This inclusion of CA oocytes in secondary growth follows the terminology and rationale presented by Lowerre-Barbieri et al. (2011a) and Lubzens et al. (2010), despite the fact that CA oocytes are not vitellogenic and have been considered PG oocytes by some (Patiño and Sullivan 2002; Grier et al. 2009). Vitellogenesis is normally a long process during which important and visible changes occur within the oocyte: oocyte size increases noticeably, yolk progressively accumulates in the cytoplasm, and several cytoplasmatic inclusions appear (vacuoles, oil droplets, etc.). For this reason, vitellogenesis is normally subdivided into various stages, although these divisions are often based on rather arbitrary features. In this study, vitellogenic oocytes are separated into three stages (primary [Vtg1], secondary [Vtg2], and tertiary [Vtg3] vitellogenesis) based on the diameter of the oocyte, the amount of cytoplasm filled with yolk, and the presence and appearance of oil droplets (in species that have oil droplets) following the work of Matsuyama et al. (1990) and Murua et al. (1998). However, since vitellogenic oocyte growth represents a continuum from Vtg1 to Vtg3, the exact appearance and description of these stages are species specific. In general, oocytes in Vtg1 have small granules of yolk that first appear around either the periphery of the oocyte or the nucleus, depending on the species, whereas Vtg2 oocytes have larger yolk globules throughout the cytoplasm. Both Vtg1 and Vtg2 oocytes may have small oil droplets interspersed among the yolk in the cytoplasm. The key vitellogenic stage is Vtg3, defined here as an oocyte in which yolk accumulation is basically completed; numerous large yolk globules fill the cytoplasm, and oil droplets, if present, begin to surround the nucleus. The Vtg3 oocyte has the necessary receptors for the maturation-inducing hormone and thus is able to progress to oocyte maturation (OM). Oocyte maturation is divided into four stages based on cytoplasmic and nuclear events, beginning with germinal vesicle migration (GVM) and ending with hydration (Jalabert 2005); ovulation is not considered a part of OM. Spermatogenic stages follow those outlined by Grier and Uribe-Aranzábal (2009) and include spermatogonia (Sg), spermatocytes (Sc), spermatids (St), and spermatozoa (Sz), which can be differentiated by a decrease in size and an increase in basophilic staining as development progresses from Sg to Sz. Throughout this paper, the term "phase" is used to indicate gonadal development, whereas the term "stage" is used to define events during gamete development.

The reproductive phase terminology was developed for gonochoristic, oviparous female marine teleosts, which constitute a group of fishes that are the most commonly targeted for commercial and recreational harvest; however, the terminology is applicable to both sexes and all fishes. Although reproductive cycles are commonly annual (Bye 1984), the phases introduced here are also appropriate for species with cycles of longer or shorter duration. Three species with differing oocyte developmental patterns are used to illustrate the phases of the terminology for females: the Atlantic herring, a total spawner with determinate fecundity and oocytes exhibiting synchronous secondary growth; the Dover sole, a batch spawner with determinate fecundity and oocytes exhibiting asynchronous secondary growth; and the spotted seatrout, a batch spawner with indeterminate fecundity and oocytes exhibiting asynchronous secondary growth. The red snapper *Lutjanus campechanus* and vermilion snapper *Rhomboplites aurorubens* are used to illustrate the phases of the terminology for males; these species represent a family (Lutjanidae) with an unrestricted spermatogonial testis, the most common type of testis in higher teleosts (Grier and Uribe-Aranzábal 2009). Specific differences in the reproductive phase terminology that are applicable to species showing alternate reproductive strategies (i.e., hermaphrodites and livebearing fishes) are illustrated with a single representative

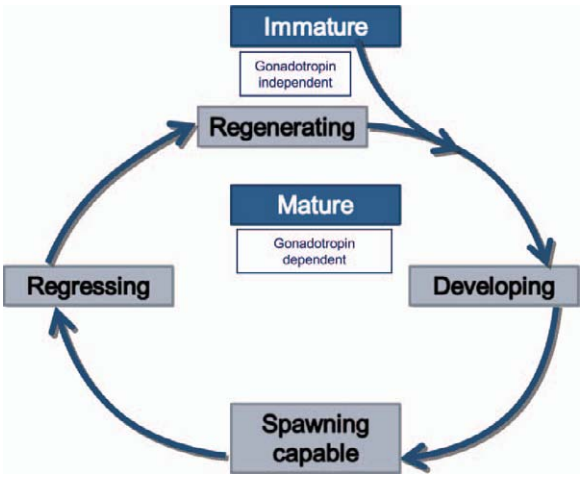

FIGURE 1. Conceptual model of fish reproductive phase terminology.

species from each group: the gag *Mycteroperca microlepis*, a batch-spawning protogynous hermaphrodite with indeterminate fecundity and oocytes exhibiting asynchronous secondary growth; the painted comber *Serranus scriba*, a batch-spawning simultaneous hermaphrodite with indeterminate fecundity; and the deepwater redfish *Sebastes mentella*, a total-spawning livebearer with determinate fecundity.

REPRODUCTIVE PHASE TERMINOLOGY

We have developed a conceptual model to identify the critical phases within the reproductive cycle that are commonly used in fisheries science. These phases apply to all fishes regardless of phylogenetic placement, gender, or reproductive strategy, as they constitute a description of the cyclic gonadal events necessary to produce and release viable gametes (Figure 1). Definition of each phase is based on specific histological and physiological markers instead of on temporal aspects of gamete development. In the immature phase, gonadal differentiation and gamete proliferation and growth are gonadotropin independent (i.e., oogonia and PG oocytes in females; primary spermatogonia [Sg1] in males). Fish enter the reproductive cycle when gonadal growth and gamete development first become gonadotropin dependent (i.e., the fish become sexually mature and enter the developing phase). A fish that has attained sexual maturity will never exit the reproductive cycle and return to the immature phase.

The developing phase is a period of gonadal growth and gamete development prior to the beginning of the spawning season. The developing phase can be considered a spawning preparation phase characterized by the production of vitellogenic oocytes in females and active spermatogenesis in the spermatocysts of males. Fish enter this phase with the appearance of CA oocytes in females (Tomkiewicz et al. 2003; Lowerre-Barbieri 2009) or the appearance of primary spermatocytes (Sc1) in males, indicating that the fish has reached sexual maturity. Females with CA oocytes as the most advanced oocyte type are considered to be in the early developing subphase, thereby entering the current reproductive cycle. However, the complete development of CA oocytes may take longer than 1 year in some species (Junquera et al. 2003). Females remain in the developing phase as long as ovaries contain CA oocytes, Vtg1 oocytes, Vtg2 oocytes, or a combination of these but without Vtg3 oocytes or signs of prior spawning; males remain in this phase as long as the testis contains Sc1, secondary spermatocytes (Sc2), St, and Sz within the spermatocysts. Fish in the developing phase do not release gametes. Postovulatory follicle complexes (POFs) are never present in females, and Sz is never found in the lumen of the lobules or in sperm ducts of males. Fish only enter the developing phase one time during a reproductive cycle. Once the leading cohort of gametes has reached the Vtg3 stage in females or once the Sz are present in the lumen of the lobules in males, the fish move into the spawning capable phase.

The spawning capable phase is defined as the fish being capable of spawning within the current reproductive cycle due to advanced gamete development such that oocytes are capable of receiving hormonal signals for OM in females or Sz release occurs in males. Females that are in this phase but that lack signs of prior spawning are used for estimates of potential annual fecundity in species with determinate fecundity. For batch spawners, evidence of previous spawning (POFs in females; Sz in the sperm ducts of males), in combination with the presence of vitellogenic oocytes in females, is also diagnostic of the spawning capable phase as these fish are capable of spawning future batches during the current cycle. Batch fecundity based on fish undergoing OM is estimated in this phase for batch-spawning species. An actively spawning subphase within the spawning capable phase indicates imminent release of gametes and is defined as the presence of late GVM, germinal vesicle breakdown, hydration, ovulation, or newly collapsed POFs in females and spermiation (macroscopic observation of the release of milt) in males.

The end of the reproductive cycle is indicated by the regressing phase (often referred to as "spent"), which is characterized by atresia, POFs, and few (if any) healthy Vtg2 or Vtg3 oocytes in females. The end of the spawning season for the population is indicated by the capture of numerous females in the regressing phase. In males, the regressing phase is characterized by depleted stores of Sz in sperm ducts and the lumen of the lobules, cessation of spermatogenesis, and a decreased number of spermatocysts. Fish remain in the regressing phase for a relatively short time and then move to the regenerating phase (formerly referred to as "resting" or "regressed"). During the regenerating phase, gametes undergo active gonadotropin-independent mitotic proliferation (i.e., oogonia in females; Sg1 in males) and growth (PG oocytes) in preparation for the next reproductive cycle. Fish in this phase are sexually mature but reproductively inactive. Characteristics of the regenerating phase in females include PG oocytes, late-stage atresia, and a thicker ovarian wall than is seen in immature fish (see Morrison 1990), while males in the regenerating phase can be distinguished by the presence

TABLE 2. Macroscopic and microscopic descriptions of the phases in the reproductive cycle of female fishes. Timing within each phase is species dependent. Some criteria listed for phases may vary depending on species, reproductive strategy, or water temperature. Subphases that apply to all fishes are listed; additional subphases can be defined by individual researchers (CA = cortical alveolar; GVBD = germinal vesicle breakdown; GVM = germinal vesicle migration; OM = oocyte maturation; PG = primary growth; POF = postovulatory follicle complex; Vtg1 = primary vitellogenic; Vtg2 = secondary vitellogenic; Vtg3 = tertiary vitellogenic).

Phase	Previous terminology	Macroscopic and histological features
Immature (never spawned)	Immature, virgin	Small ovaries, often clear, blood vessels indistinct. Only oogonia and PG oocytes present. No atresia or muscle bundles. Thin ovarian wall and little space between oocytes.
Developing (ovaries beginning to develop, but not ready to spawn)	Maturing, early developing, early maturation, mid-maturation, ripening, previtellogenic	Enlarging ovaries, blood vessels becoming more distinct. PG, CA, Vtg1, and Vtg2 oocytes present. No evidence of POFs or Vtg3 oocytes. Some atresia can be present. *Early developing subphase*: PG and CA oocytes only.
Spawning capable (fish are developmentally and physiologically able to spawn in this cycle)	Mature, late developing, late maturation, late ripening, total maturation, gravid, vitellogenic, ripe, partially spent, fully developed, prespawning, running ripe, final OM, spawning, gravid, ovulated	Large ovaries, blood vessels prominent. Individual oocytes visible macroscopically. Vtg3 oocytes present or POFs present in batch spawners. Atresia of vitellogenic and/or hydrated oocytes may be present. Early stages of OM can be present. *Actively spawning subphase*: oocytes undergoing late GVM, GVBD, hydration, or ovulation.
Regressing (cessation of spawning)	Spent, regression, postspawning, recovering	Flaccid ovaries, blood vessels prominent. Atresia (any stage) and POFs present. Some CA and/or vitellogenic (Vtg1, Vtg2) oocytes present.
Regenerating (sexually mature, reproductively inactive)	Resting, regressed, recovering, inactive	Small ovaries, blood vessels reduced but present. Only oogonia and PG oocytes present. Muscle bundles, enlarged blood vessels, thick ovarian wall and/or gamma/delta atresia or old, degenerating POFs may be present.

of Sg1 and residual Sz in sperm ducts and the lumen of the lobules in some specimens. Females living in cold water can also have old, degenerating POFs in the regenerating phase, although these structures are often difficult to differentiate from late-stage atresia. As the beginning of the next reproductive cycle approaches, gonadotropin-dependent gamete development (CA oocytes in females; Sc1 in males) is initiated as the fish move to the developing phase to again begin the cycle.

Because the proposed terminology focuses on key steps within the reproductive cycle as defined by specific histological and physiological events rather than any given temporally based staging scheme, it can be modified to fit a wide range of research needs. Furthermore, phase names are applicable for fishes exhibiting either determinate or indeterminate fecundity because the overall reproductive cycle is similar regardless of gamete developmental patterns. In particular, terminology that is grounded in the reproductive cycle has the added advantage of allowing the addition of subphases to describe developmental processes that may be species specific, unique to a reproductive strategy, or important for defining temporal (i.e., daily, seasonal, or annual) events in the reproductive cycle. Additionally, researchers can use subphases such that their original classification system fits neatly under the umbrella of one or more of the newly defined phases, resulting in a common set of phases being used by everyone and eliminating the confusion caused by diverse terminologies. Specific examples of each phase and some proposed subphases in the terminology are presented below for fish exhibiting a variety of reproductive strategies.

Female Reproductive Cycle

Morphological and histological criteria used to distinguish the reproductive phases of female teleost fishes are presented in Table 2. This table includes previously used terminology that is synonymous with the new phase terminology. Universal subphases (i.e., those that occur in all species) are included in Table 2.

The immature phase (Figure 2A) appears histologically similar in all teleosts. This phase can be distinguished histologically by the presence of oogonia and PG oocytes through the perinucleolar stage (Grier et al. 2009). Additionally, there is scarce connective tissue between the follicles, little space among oocytes in the lamellae, and the ovarian wall is generally thin. There is no evidence of oil droplets in PG oocytes or

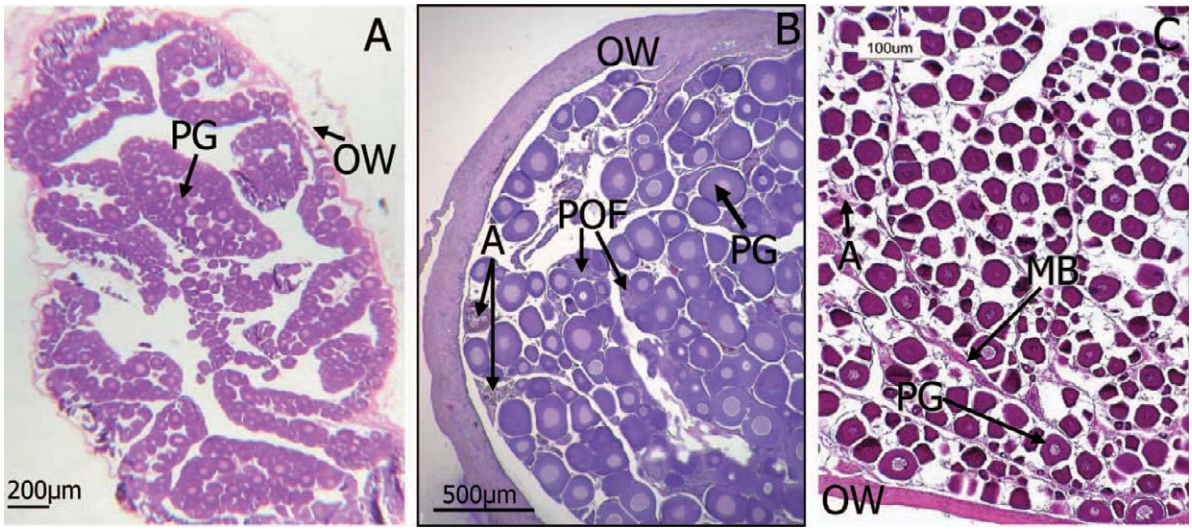

FIGURE 2. Photomicrographs of ovarian histology, illustrating the reproductive phases of fishes: **(A)** immature phase in the Dover sole, a batch-spawning species with determinate fecundity and oocytes exhibiting asynchronous but discontinuous secondary growth (PG = primary growth oocyte; OW = ovarian wall); **(B)** regenerating phase in the Atlantic herring, a total-spawning species with determinate fecundity and oocytes exhibiting synchronous, discontinuous secondary growth (A = atresia; POF = postovulatory follicle complex); and **(C)** regenerating phase in the spotted seatrout, a batch-spawning species with indeterminate fecundity and oocytes exhibiting asynchronous and continuous secondary growth (MB = muscle bundle).

muscle bundles in immature ovaries. Rarely, atresia of PG oocytes may be present.

As females move into the gonadotropin-dependent developing phase, they can be histologically distinguished by the initial appearance of CA oocytes and the later appearance of Vtg1 and Vtg2 oocytes (Figure 3). The initiation of the reproductive cycle is indicated by females in the early developing subphase, when only PG and CA oocytes are present (Figure 3C). While new data for some species suggest that the formation of CA oocytes is regulated by insulin-like growth factor rather than by gonadotropin (Grier et al. 2009), the appearance of CA oocytes and the physiological initiator for their formation nevertheless provide the definitive marker for entry into the developing phase. The early developing subphase within the developing phase encompasses previously used terms, such as early or very early maturation (Brown-Peterson 2003), stage II or one-fourth ripe (Robb 1982), and stage III or early developing (Treasurer and Holliday 1981).

Secondary vitellogenic oocytes are the most advanced stage present in the developing phase; oocytes in this phase do not

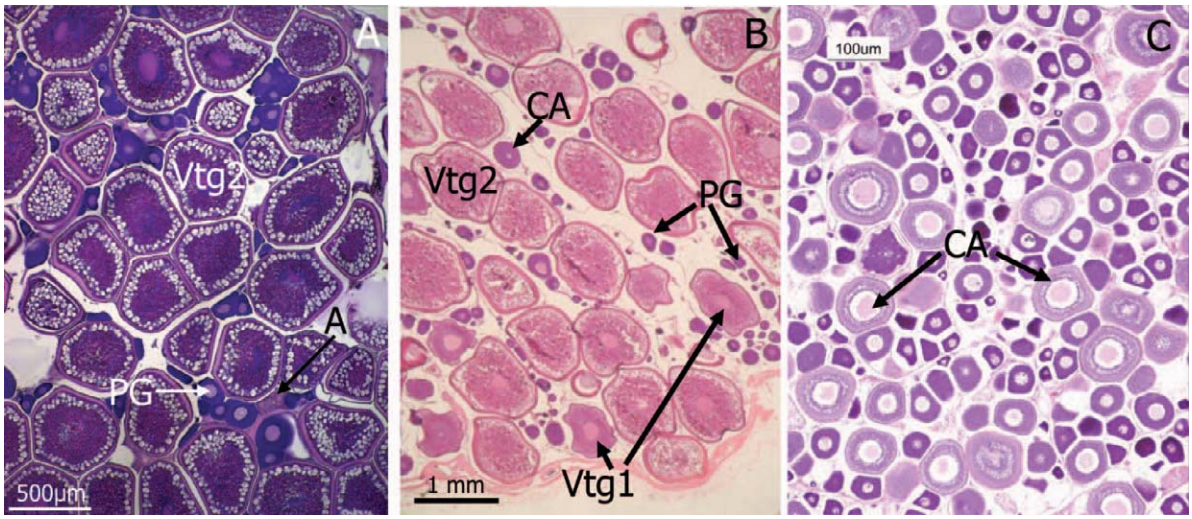

FIGURE 3. Photomicrographs of ovarian histology, illustrating the developing reproductive phase of fishes: **(A)** Atlantic herring (note synchrony of secondary vitellogenic oocytes [Vtg2]; A = atresia; PG = primary growth oocyte); **(B)** Dover sole (note multiple stages of oocyte development; Vtg1 = primary vitellogenic oocyte); and **(C)** spotted seatrout in the early developing subphase, characterized by only PG oocytes and cortical alveolar oocytes (CA).

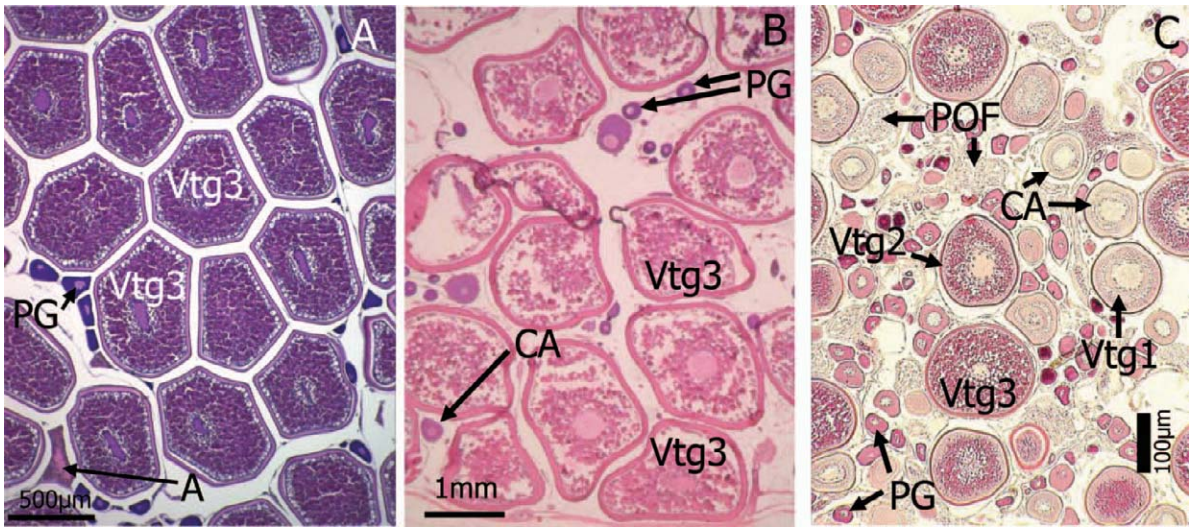

FIGURE 4. Photomicrographs of ovarian histology, illustrating the spawning capable reproductive phase of fishes: **(A)** Atlantic herring with only two stages of oocytes present (PG = primary growth oocyte; Vtg3 = tertiary vitellogenic oocyte; A = atresia); **(B)** Dover sole (CA = cortical alveolar oocyte); and **(C)** spotted seatrout, showing asynchronous continuous oocyte development with oocytes in all stages of development as well as evidence of previous spawns (i.e., postovulatory follicle complex [POF]; Vtg1 = primary vitellogenic oocyte; Vtg2 = secondary vitellogenic oocyte).

exhibit the amount of lipid accumulation or the size of a Vtg3 oocyte. In species with asynchronous oocyte development, such as most batch spawners, oocytes in several developmental stages are present in the ovary during the developing phase (Figure 3B), whereas species with synchronous oocyte development, such as total spawners, tend to have oocytes in only one stage of development beyond PG (Figure 3A). Postovulatory follicles are never seen in the developing phase, although atresia (Hunter and Macewicz 1985b) of vitellogenic and CA oocytes may be present (Figure 3A).

Entry into the spawning capable phase is characterized by the appearance of Vtg3 oocytes (Figure 4); fish in this phase are capable of spawning during the current reproductive cycle due to the development of receptors for maturation-inducing hormone on the Vtg3 oocytes. Fish undergoing early stages of OM (i.e., GVM) are also considered to be in the spawning capable phase. Any fish with Vtg3 oocytes is assigned to the spawning capable phase, yet histological differences between batch spawners and total spawners and between synchronous and asynchronous species are most pronounced in this phase. In total spawners, Vtg3 or early OM and PG oocytes are the only oocyte stages present (Figure 4A). Total spawners complete the sequestration of yolk into all growing oocytes during the spawning capable phase, and the time required for this process is species specific. Similarly, in batch spawners with group-synchronous oocyte development typical of coldwater species (e.g., Atlantic cod; Murua and Saborido-Rey 2003), most oocytes complete vitellogenesis at the beginning of the spawning capable phase. However, since this phase is normally prolonged in batch spawners, a small portion of the oocytes can still be in Vtg2 upon first entry into the actively spawning subphase for batch spawners with group-synchronous oocyte development. Batch-spawning species with determinate fecundity, such as the Dover sole, will complete recruitment of CA or Vtg1 oocytes into Vtg3 oocytes during the spawning capable phase; CA oocytes can be found in ovaries of these species shortly after entry into this phase (Figure 4B). The stock of Vtg3 oocytes will decrease with successive spawning batches. In contrast, species with asynchronous oocyte development, which are always batch spawners, produce successive batches of oocytes multiple times during the spawning season. Batch spawners with indeterminate fecundity, such as the spotted seatrout, continue to recruit oocytes into CA oocytes and then into vitellogenesis throughout the spawning capable phase. Thus, ovaries of these species may have CA oocytes as well as a variety of vitellogenic oocyte stages in the spawning capable phase (Figure 4C).

Although entry into the spawning capable phase is defined as the presences of Vtg3 oocytes, batch spawners in this phase can have oocytes in any stage of vitellogenesis—including but not restricted to Vtg3—after the initial spawning event (indicated by the presence of POFs). Thus, batch-spawning species with asynchronous oocyte development, such as the Atlantic sardine *Sardina pilchardus* (also known as European pilchard), may have only Vtg1 or Vtg2 oocytes present immediately after spawning (Ganias et al. 2004), but the presence of POFs indicates that the fish have previously spawned during the current reproductive cycle and should thus be considered spawning capable. Fish with POFs could be placed into a past-spawner subphase, which is equivalent to the "partially spent" (Macer 1974; Murphy and Taylor 1990; Lowerre-Barbieri et al. 1996; Acuña et al. 2000) and "spawned and recovering" (Núñez and Duponchelle 2009) terminology previously used for batch-spawning species. Additional subphases could also be assigned for batch spawners based on the age of POFs; these further divisions may be useful

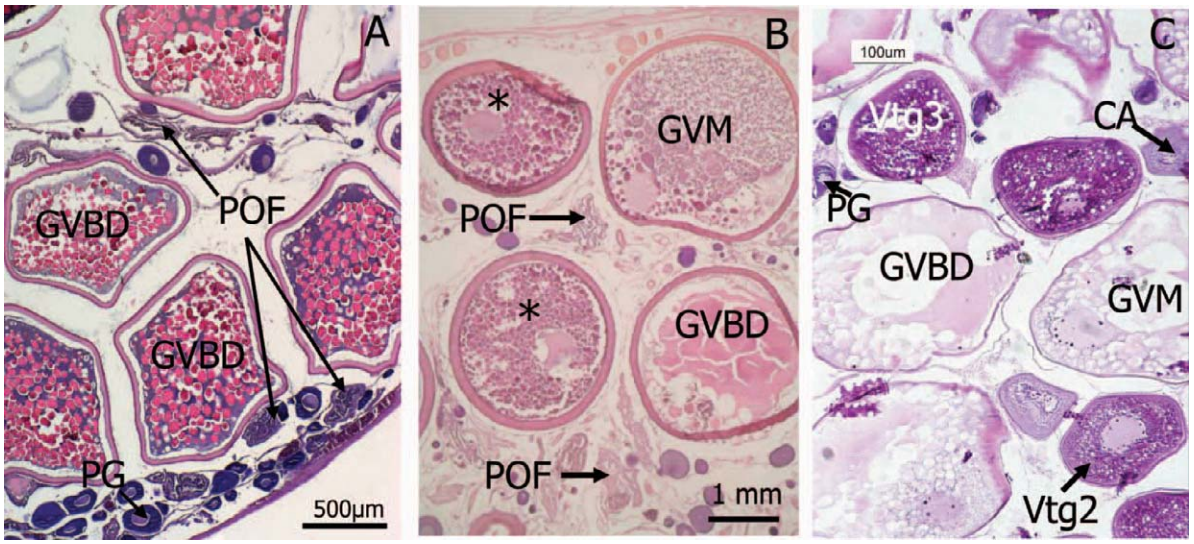

FIGURE 5. Photomicrographs of ovarian histology, illustrating the actively spawning subphase of the spawning capable reproductive phase of fishes: **(A)** Atlantic herring with only two types of oocytes present and recent postovulatory follicles (POFs) from previous release of ova (PG = primary growth oocyte; GVBD = germinal vesicle breakdown); **(B)** Dover sole, for which oocytes in early germinal vesicle migration (indicated by asterisks) are a different batch than oocytes in late germinal vesicle migration (indicated by "GVM") and GVBD (note the presence of recent POFs); and **(C)** spotted seatrout, for which oocytes undergoing late GVM and GVBD are in the same batch (note oocytes in multiple stages of development; CA = cortical alveolar oocyte; Vtg2 = secondary vitellogenic oocyte; Vtg3 = tertiary vitellogenic oocyte).

for the identification of spawning fractions that could be applied to the daily egg production methodology (Uriarte et al. 2010).

Potential annual fecundity estimates for species with determinate fecundity are made in the spawning capable phase, since all oocytes to be released for that year have been recruited into vitellogenesis and since downregulation of fecundity due to atresia occurs during this phase (Kjesbu 2009). However, in batch-spawning species with determinate fecundity, these estimates must be made when no POFs are present (i.e., prior to the release of the first batch of oocytes). A prespawner subphase, which is equivalent to stage IV (late developing) described by Tomkiewicz et al. (2003), could be defined to generate potential annual fecundity estimates for species with determinate fecundity. Batch fecundity estimates for species with indeterminate fecundity also occur in the spawning capable phase; these estimates are typically made with fish that are undergoing OM or that have completed hydration but not ovulation.

An actively spawning subphase can be used to identify those fish that are progressing through OM (i.e., late GVM, germinal vesicle breakdown, or hydration) or ovulation or that are exhibiting newly collapsed POFs, indicating that they are close to the time of ovulation (see Lowerre-Barbieri et al. 2009). When Vtg3 oocytes are fully grown, they become maturationally competent (i.e., membrane receptors are capable of binding maturation-inducing hormone), and OM is initiated (Patiño and Sullivan 2002). Meiosis resumes once OM is initiated and then is once again arrested after ovulation (Patiño and Sullivan 2002). Because the time from initiation to completion of OM will differ with species, we define the actively spawning subphase (Figure 5) based only on the later stages of OM or on the observation of either ovulation or recently collapsed POFs (i.e., fish that have just completed spawning). Hydration is a typical event in this subphase for marine species that spawn pelagic eggs, but it does not occur in all species (Grier et al. 2009). In total spawners, ovaries in the actively spawning subphase will normally have only two types of oocytes: PG and late OM (Figure 5A). However, some total spawners may take several consecutive days to ovulate and release all mature oocytes in the ovary (Pavlov et al. 2009); thus, POFs are often present in these fish (Figure 5A). Occasionally, a small proportion of Vtg3 oocytes may coexist for a short time alongside oocytes undergoing OM. In contrast, batch spawners typically have vitellogenic oocytes and OM oocytes present simultaneously during the actively spawning subphase (Figure 5C) and can also demonstrate the presence of POFs, indicating previous spawns (Figure 5B). For coldwater batch spawners with determinate fecundity, such as the Dover sole, the presence of recent POFs during the actively spawning subphase may not indicate daily spawning (Hunter et al. 1992). However, in warmwater batch spawners with indeterminate fecundity, the presence of recent POFs in the same ovary with oocytes undergoing OM can suggest daily spawning (Hunter et al. 1986; Grammer et al. 2009) since for these species all oocytes in a batch normally undergo rapid OM and are released in the same single spawning event (Brown-Peterson 2003; Jackson et al. 2006).

Differences in reproductive strategies (including the time that it takes individual species to complete OM) and differing research objectives related to the dynamics of spawning may necessitate the adjustment or creation of subphases within the spawning capable phase in addition to the actively spawning

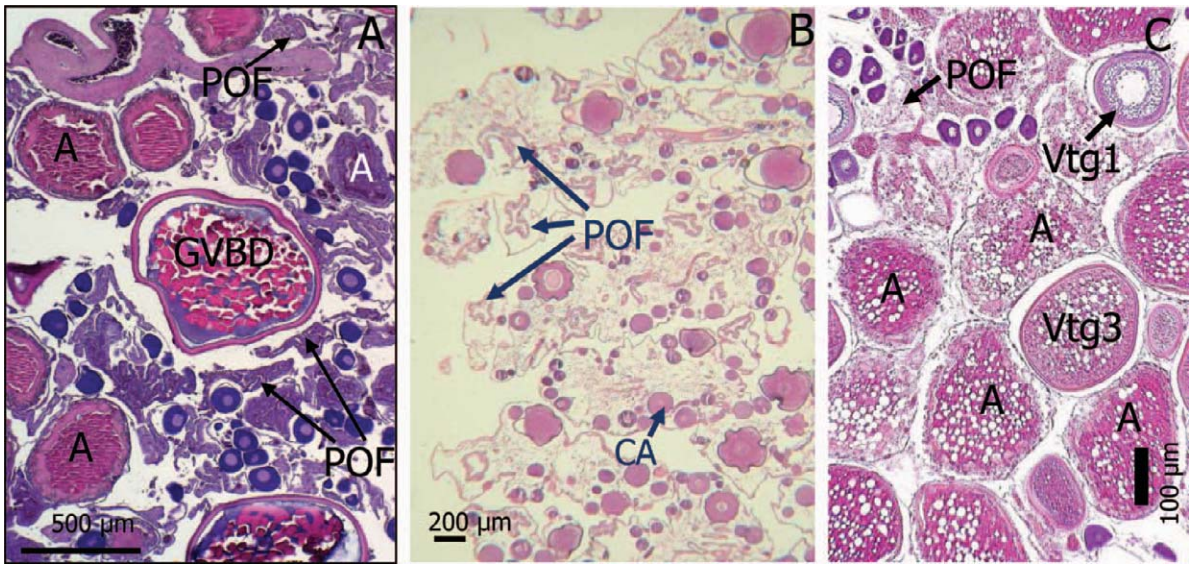

FIGURE 6. Photomicrographs of ovarian histology, illustrating the regressing reproductive phase of fishes: **(A)** Atlantic herring with some atretic vitellogenic oocytes and many 24-h postovulatory follicle complexes (POF) present (note the presence of a residual oocyte undergoing germinal vesicle breakdown [GVBD]; A = atretic oocyte); **(B)** Dover sole, showing many POFs, many empty spaces in the ovary, and some cortical alveolar oocytes (CA); and **(C)** spotted seatrout, showing massive atresia of vitellogenic oocytes and some oocytes that have not yet undergone atresia (Vtg1 = primary vitellogenic oocyte; Vtg3 = tertiary vitellogenic oocyte).

subphase we present here. For instance, maturationally competent oocytes in warmwater batch spawners with indeterminate fecundity (e.g., spotted seatrout) begin OM and progress through hydration and ovulation in less than 24 h (Brown-Peterson 2003); thus, the appearance of any stage of OM could be considered to indicate the actively spawning subphase for these species (Figure 5C). In contrast, coldwater batch spawners with determinate fecundity (e.g., Dover sole) can have oocytes in early and late stages of OM (early GVM and germinal vesicle breakdown–late GVM; Figure 5B) that represent several batches (Hunter et al. 1992). Thus, a Dover sole with ovaries containing early GVM as the most advanced oocyte stage would be considered spawning capable but not as belonging to the actively spawning subphase.

As the reproductive cycle ends, fish move into the regressing phase, which is recognized by the presence of oocyte atresia, a reduced number of vitellogenic oocytes, and, in some species, POFs. In total spawners (Figure 6A), some atretic vitellogenic oocytes and many POFs in varying stages of degeneration characterize this phase and only PG oocytes are present. In batch spawners with determinate fecundity (Figure 6B), POFs are commonly seen and there are typically few or no vitellogenic oocytes undergoing atresia. Some CA and Vtg1 oocytes may still populate the ovary, particularly in coldwater species like the Dover sole. These oocytes either undergo atresia at a later time or, in some coldwater species, may represent preparation for the next reproductive cycle. In these species, the presence of POFs indicates that a fish is in the regressing phase rather than the developing phase, since POFs never occur in the developing phase. Due to the slower POF degeneration rate in colder waters, the occurrence of POFs in the regressing phase is more common in coldwater species than in warmwater species regardless of reproductive strategy. In contrast, atresia of vitellogenic oocytes is common in batch spawners with indeterminate fecundity (Figure 6C), and some oocytes at different developmental stages may still populate the ovary, particularly at the beginning of the regressing phase.

The regenerating phase (Figure 2B, C) is characterized by ovaries containing only oogonia and PG oocytes, similar to the immature phase (Figure 2A). In marine species that produce pelagic oocytes, circumnuclear oil droplets can be seen in PG oocytes during the regenerating phase, a step of PG that is not present in immature fish (Grier et al. 2009). Additionally, the regenerating phase can be differentiated from the immature phase by (1) a thicker ovarian wall (see difference in Figure 2A, B); (2) the presence of more space, interstitial tissue, and capillaries around PG oocytes (see difference in Figure 2A, C); and (3) the presence of late-stage (gamma or delta) atresia and "muscle bundles" (Figure 2C). Muscle bundles are defined as blood vessels (usually arteries) surrounded by connective and muscle tissue (Shapiro et al. 1993); these structures can be prominent in the regenerating ovaries of some species, such as groupers *Epinephelus* spp., but are more difficult to discern in other species. Finally, coldwater species, such as the Atlantic herring, can have old, degenerating POFs present in the ovary during the regenerating phase (Figure 2B), although these structures can be difficult to distinguish from beta-stage atresia.

TABLE 3. Macroscopic and microscopic descriptions of the phases in the reproductive cycle of male fishes. Timing within each phase is species dependent. Some criteria listed for phases may vary depending on species, reproductive strategy, or water temperature. Subphases that apply to all fishes are listed; additional subphases can be defined by individual researchers (GE = germinal epithelium; Sc1 = primary spermatocyte; Sc2 = secondary spermatocyte; Sg1 = primary spermatogonia; Sg2 = secondary spermatogonia; St = spermatid; Sz = spermatozoa).

Phase	Previous terminology	Macroscopic and histological features
Immature (never spawned)	Immature, virgin	Small testes, often clear and threadlike. Only Sg1 present; no lumen in lobules.
Developing (testes beginning to grow and develop)	Maturing, early developing, early maturation, ripening	Small testes but easily identified. Spermatocysts evident along lobules. Sg2, Sc1, Sc2, St, and Sz can be present in spermatocysts. Sz not present in lumen of lobules or in sperm ducts. GE continuous throughout. *Early developing subphase*: Sg1, Sg2, and Sc1 only.
Spawning Capable (fish are developmentally and physiologically able to spawn in this cycle)	Late developing, mid-maturation, late maturation, late ripening, ripe, partially spent, running ripe, spawning	Large and firm testes. Sz in lumen of lobules and/or sperm ducts. All stages of spermatogenesis (Sg2, Sc, St, Sz) can be present. Spermatocysts throughout testis, active spermatogenesis. GE can be continuous or discontinuous. *Actively spawning subphase* (macroscopic): milt released with gentle pressure on abdomen. Histological subphases based on structure of GE. *Early GE*: continuous GE in all lobules throughout testes. *Mid-GE*: continuous GE in spermatocysts at testis periphery, discontinuous GE in lobules near ducts. *Late-GE*: discontinuous GE in all lobules throughout testes.
Regressing (cessation of spawning)	Spent, regression, postspawning, recovering	Small and flaccid testes, no milt release with pressure. Residual Sz present in lumen of lobules and in sperm ducts. Widely scattered spermatocysts near periphery containing Sc2, St, Sz. Little to no active spermatogenesis. Spermatogonial proliferation and regeneration of GE common in periphery of testes.
Regenerating (sexually mature, reproductively inactive)	Resting, regressed, recovering, inactive	Small testes, often threadlike. No spermatocysts. Lumen of lobule often nonexistent. Proliferation of spermatogonia throughout testes. GE continuous throughout. Small amount of residual Sz occasionally present in lumen of lobules and in sperm duct.

Male Reproductive Cycle

Morphological and histological criteria used to distinguish among reproductive phases for male teleost fishes are presented in Table 3. The table includes previously used terminology that is synonymous with the new phase terminology. Universal subphases (i.e., those that occur in all species) are included in Table 3.

Males in the immature phase (Figure 7A) are characterized by Sg1 in the germinal epithelium (GE) and by the early formation of testis lobules that contain only Sg (mostly Sg1, but some secondary spermatogonia [Sg2]). The lobules of immature males do not have a lumen (Figure 7A), and spermatogonial proliferation in the form of mitotic division is the only type of spermatogenic activity occurring.

As males move into the gonadotropin-stimulated developing phase, Sg2 within spermatocysts that line the lobules divide to form Sc1, which then enter meiosis, and active spermatogenesis occurs. The two most histologically distinct markers of the developing phase are the presence of a continuous GE with spermatocysts undergoing active spermatogenesis and the formation of a lumen in the lobule that is devoid of Sz (Figure 7B, C). The initiation of the reproductive season in males can be identified by the early developing subphase (Figure 7B), in which spermatocysts containing Sc1 and Sc2 first appear, although spermatocysts are dominated by Sg2 and Sc1 in males during this subphase. In contrast, spermatocysts containing all stages of spermatogenesis, including St and Sz (Figure 7C), are diagnostic of males in the developing phase. However, release

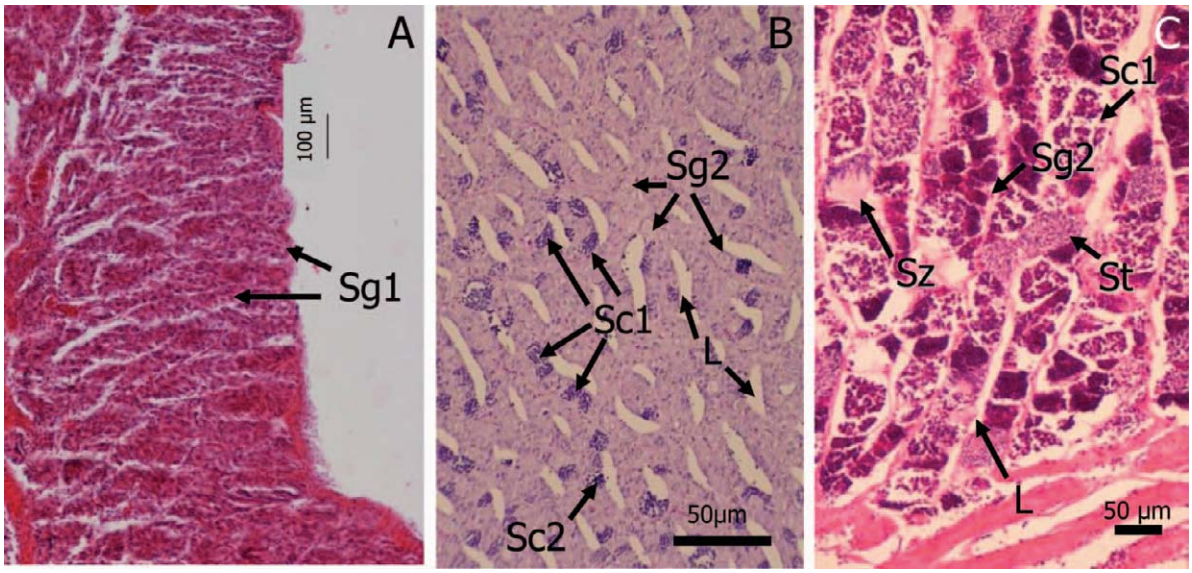

FIGURE 7. Photomicrographs of testicular histology, demonstrating reproductive phases of fishes: **(A)** red snapper in the immature reproductive phase (Sg1 = primary spermatogonia); **(B)** red snapper in the early developing subphase of the developing reproductive phase (L = lumen of lobule; Sc1 = primary spermatocyte; Sc2 = secondary spermatocyte; Sg2 = secondary spermatogonia); and **(C)** vermilion snapper in the developing phase (St = spermatid; Sz = spermatozoa).

of Sz from the spermatocysts into the lumen of the lobule does not occur in the developing phase.

The spawning capable phase is identified by the presence of Sz in the lumen of the lobules and in the sperm ducts. The actively spawning subphase for males can only be identified macroscopically and is defined as the release of milt when gentle pressure is placed on the abdomen (commonly referred to as "running ripe"). Males remain in the spawning capable phase during the majority of the reproductive season and undergo active spermatogenesis during which all stages of spermatogenesis are observed. However, changes in the GE as the reproductive season progresses (Grier and Taylor 1998; Parenti and Grier 2004) allow for differentiation among males that are in the early, middle, or late portion of the spawning season. Males in the early GE subphase of the spawning capable phase (Figure 8A) are distinguished by a continuous GE throughout the entire testis and the presence of Sg in the spermatocysts. During the mid-GE subphase of

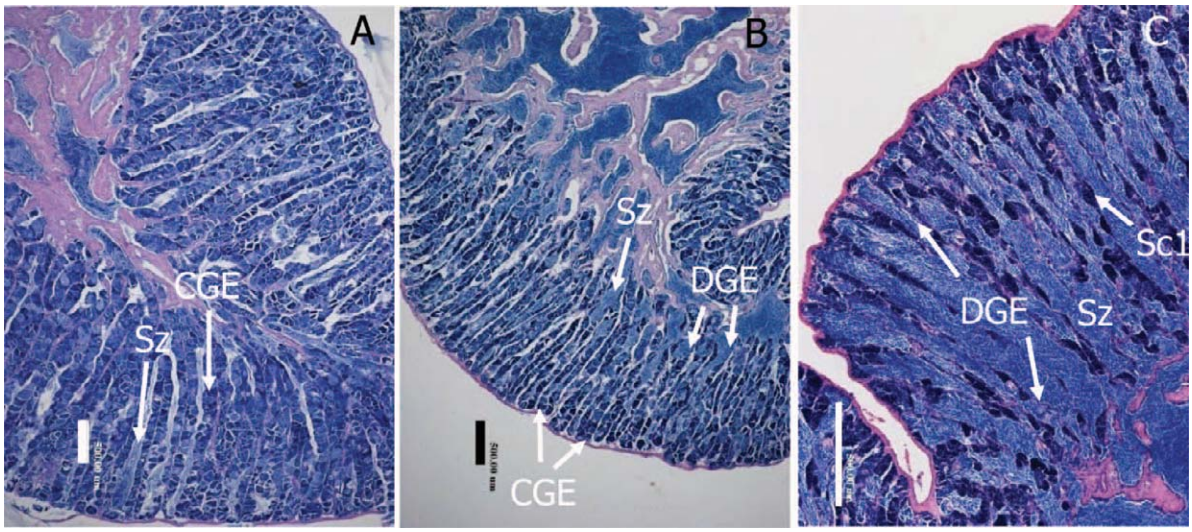

FIGURE 8. Photomicrographs of testicular histology, illustrating the spawning capable reproductive phase in vermilion snapper. Subphases are identified based on continuous germinal epithelium (CGE) or discontinuous germinal epithelium (DGE; scale bars = 500 µm): **(A)** early germinal epithelium (GE) subphase (Sz = spermatozoa); **(B)** mid-GE subphase; and **(C)** late-GE subphase (Sc1 = primary spermatocyte).

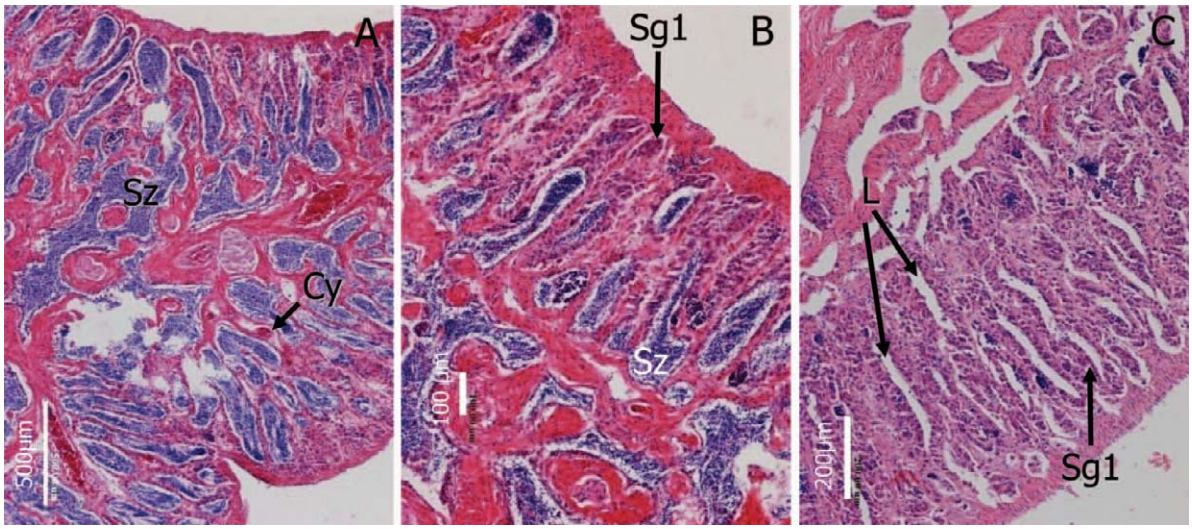

FIGURE 9. Photomicrographs of testicular histology, representing reproductive phases of fishes: **(A)** vermilion snapper in the regressing phase, showing reduced spermatogenesis and residual spermatozoa (Sz; Cy = spermatocyst); **(B)** vermilion snapper in the regressing phase, showing spermatogonial proliferation at the periphery of the testis (Sg1 = primary spermatogonia); and **(C)** red snapper in the regenerating phase (L = lumen of lobule).

spawning capable, spermatogenesis ceases in some spermatocysts in lobules near the sperm ducts (Figure 8B), resulting in a discontinuous GE near the ducts but a continuous GE at the periphery of the lobules. Spermatogonia are rarely seen in the mid-GE subphase, but Sc1 and Sc2 are common. By the end of the reproductive period, males are in the late-GE subphase of spawning capable (Figure 8C); this subphase is characterized by a discontinuous GE throughout the testis, an increasing prevalence of anastomosing lobules, and reduced spermatogenesis. All lobules have some spermatocysts undergoing spermatogenesis, but Sg are usually scarce during this subphase.

Males enter the regressing phase at the end of the spawning season. This phase is histologically characterized by depleted stores of Sz in the sperm ducts and in the lumen of lobules and by few lobules with spermatocysts present (Figure 9A). The amount of Sz present is noticeably reduced from that seen in the spawning capable phase. The GE is discontinuous throughout the testes, anastomosing lobules are common, and the few spermatocysts that are present contain only the late stages of spermatogenesis (Sc2, St, and Sz). Spermatogonial proliferation commonly occurs at the periphery of the testes in many species (Figure 9B).

The regenerating phase for males is characterized by spermatogonial proliferation in the lobules throughout the testes. In contrast to immature males, some residual Sz may remain in the sperm duct and in the lumen of the lobules of males in the regenerating phase, and a lumen is distinguishable in most lobules (Figure 9C). No spermatocysts are present in the lobules, and the only spermatogenic stages present, in addition to small amounts of residual Sz, are Sg1 and Sg2.

Alternate Reproductive Strategies

Species with alternate reproductive strategies, such as hermaphrodites and livebearers, require a modification of the basic reproductive phase terminology presented here. Additional phases representing the sex transition in hermaphrodites and gestation in livebearers (Figure 10) can be added to accommodate the requirements of alterations in the reproductive

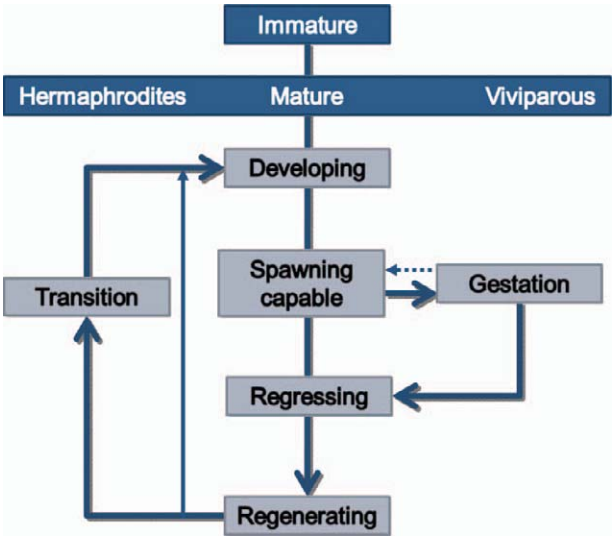

FIGURE 10. Modification of the reproductive phases of fishes to accommodate species with alternate reproductive strategies. The new transition phase applies to sequential hermaphrodites, and the new gestation phase applies to livebearers. Livebearers that produce more than one batch of embryos during the reproductive season cycle between the spawning capable phase as oocytes grow and the gestation phase as embryogenesis proceeds (dashed arrow).

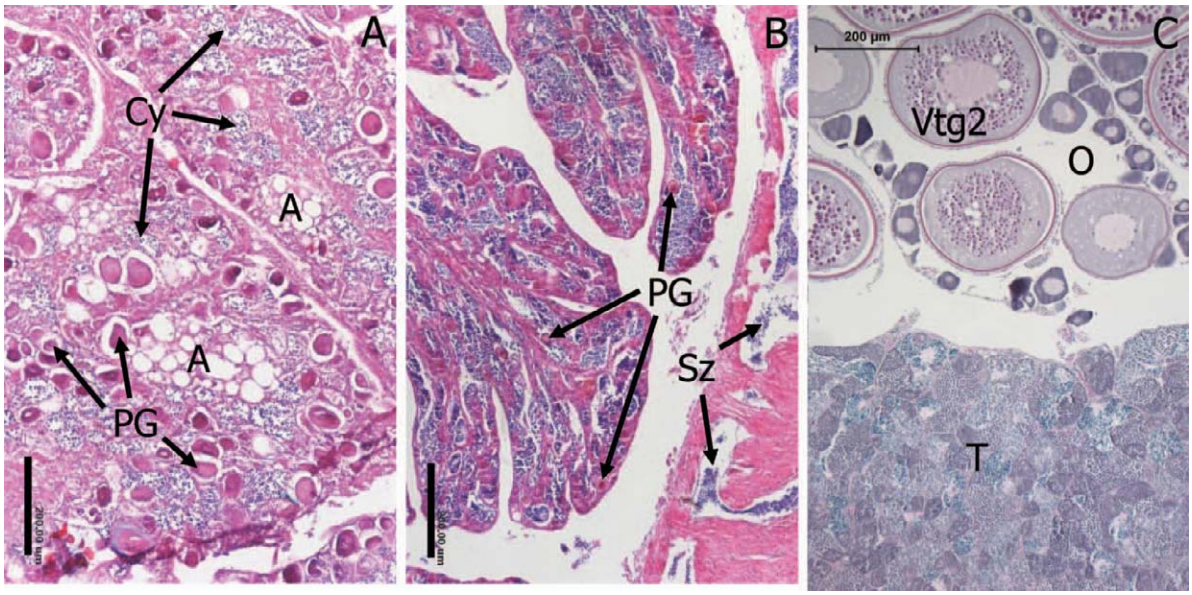

FIGURE 11. Photomicrographs of gonadal histology of hermaphroditic fishes (scale bars = 200 µm): **(A)** gag, a protogynous hermaphrodite, in the transition phase (note atresia of vitellogenic oocytes and development of spermatocysts [Cy]; PG = primary growth oocyte; A = atretic oocyte); **(B)** gag as a transitioned male in the spawning capable phase (note the presence of residual PG oocytes and spermatozoa [Sz] in the former ovarian wall); and **(C)** painted comber, a simultaneous hermaphrodite, in the developing phase based on ovarian tissue (O; T = testicular tissue; Vtg2 = secondary vitellogenic oocyte).

cycle demonstrated by these strategies. However, for both hermaphrodites and livebearers, the standard terminology continues to apply once the modifications have been made.

Hermaphrodites. Terminology for both protogynous and protandrous fishes in their initial female and male genders is identical to the standard terminology. At the time fish begin to change sex, they enter the transition phase (Figures 10, 11A), which occurs after they enter the regenerating phase in most species (Sadovy de Mitcheson and Liu 2008). However, for species that undergo transition after they enter the developing phase (e.g., yellowedge grouper *E. flavolimbatus*; Cook 2007), the transition phase would occur immediately after the developing phase and prior to the spawning capable phase. The transition phase is characterized by the presence of both oocytes and spermatogenic tissue as well as atresia of gametes from the initial gender (i.e., vitellogenic oocytes in protogynous hermaphrodites; Sz, St, and Sc2 in protandrous hermaphrodites) as described by Sadovy de Mitcheson and Liu (2008). The relative amount of each gamete type varies both during the transition phase and among individuals. After transition, terminology is again identical to the standard terminology as fish re-enter the reproductive cycle, usually at the developing phase, despite the remnants of either germ cells or gonadal structures from the previous gender (Figure 11B).

Simultaneous hermaphrodites, such as the painted comber, can show different reproductive phases in the ovarian and testicular portions of their gonadal tissue (Figure 11C). However, the reproductive phase of simultaneous hermaphrodites is assigned based on ovarian tissue, by following the standard terminology above, regardless of the phase of the testicular tissue. Thus, the gonad pictured in Figure 11C would be considered to represent a fish in the developing phase despite the presence of testicular tissue in the spawning capable phase.

Livebearing fishes. Terminology for the ovarian development of livebearing fishes (exclusive of individuals with embryos) is identical to the standard terminology described above prior to fertilization. Livebearing fishes depart from the standard reproductive cycle after ovulation, which occurs in the actively spawning subphase of the spawning capable phase. Livebearing fishes are characterized by internal fertilization; the eggs are retained while most or part of the embryonic development occurs within the female reproductive system during the gestation phase (Figure 10). Viviparity can be either lecithotrophic (embryos develop in the ovary in teleosts or the uterus in elasmobranchs without any specialized vascular exchange organ and rely solely on the yolk sac for nutrition) or matrotrophic (nutrients from the mother are transferred to the embryo directly; Wourms 1981, 2005). While these differences determine the terminology of the female reproductive system, embryogenesis basically does not differ among species; most of the differences are related to the degree of development of the embryos at the time of parturition. Embryos can be released in a very early stage (i.e., zygoparity; Wourms et al. 1988) as occurs in the blackbelly rosefish *Helicolenus dactylopterus* (White et al. 1998; Muñoz et al. 2002) and in wolffishes (Anarhichadidae; Pavlov 2005); the larval stage as occurs in rockfishes *Sebastes* spp. (Saborido-Rey 1994); or the juvenile stage as occurs in viviparous sharks (Wourms and Demski 1993).

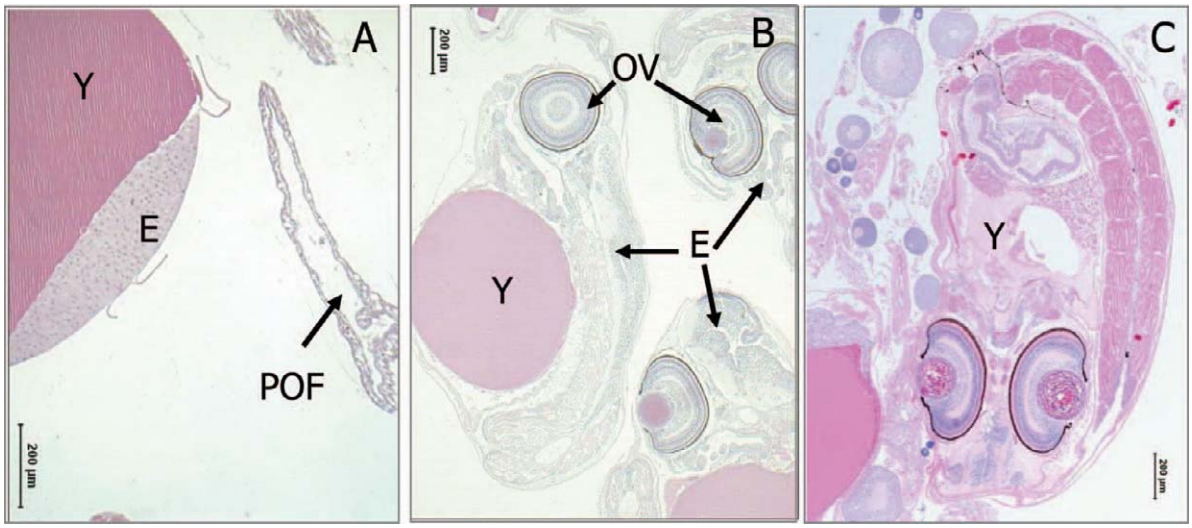

FIGURE 12. Photomicrographs of selected subphases of the gestation phase in the livebearing deepwater redfish (scale bars = 200 µm): **(A)** blastula subphase (Y = yolk; E = embryonic tissue; POF = postovulatory follicle complex); **(B)** retinal pigmentation subphase (OV = optic vesicle); and **(C)** yolk depletion subphase.

The six stages of embryonic development are defined as subphases of the gestation phase. The initial subphase of gestation is fertilization, which is initiated when the oocyte is ovulated into the lumen of the ovary or into the uterus and internal fertilization takes place. Intrafollicular fertilization occurs in some species, such as poeciliids and goodeids (Uribe-Aranzábal and Grier 2010); embryos that are fertilized in this manner are still considered to be in the fertilization subphase. Subsequent to the fertilization subphase are two subphases of organized but undifferentiated cells at the animal pole of the egg: the early celled embryo subphase and the blastula subphase (Figure 12A), which appear histologically similar. During the first three subphases of gestation, POFs can occur in the ovary (Figure 12A), although in coldwater species (i.e., Atlantic rockfishes *Sebastes* spp.) the POFs can be found even after parturition. Differentiation of the head, body, and tail and the beginning of organogenesis occur in the optic vesicle formation subphase. Continued organogenesis and the beginning of retinal pigmentation and embryo growth occur in the retinal pigmentation subphase (Figure 12B). While both the optic vesicle formation and retinal pigmentation subphases can be easily recognized by the presence of the eyes, the developing embryo appears larger than the yolk sac in the retinal pigmentation subphase. In the yolk depletion subphase (Figure 12C), the embryo is fully formed, organogenesis is complete, the mouth can be open, and little to no yolk is evident. In lecithotrophic species (e.g., *Sebastes* spp.), the occurrence of this subphase indicates immediate parturition (Bowers 1992; Saborido-Rey 1994); larval metamorphosis occurs outside the body of the mother. In matrotrophic species, however, the embryos may develop further due to nourishment taken through oophagy or adelphophagy or taken directly from the mother (Wourms et al. 1988; Wourms and Lombardi 1992); embryogenesis is completed during metamorphosis, and juvenile fish are released from the mother. In all cases, parturition is the final event of the gestation phase.

The reproductive phase of the livebearing female after fertilization is based on the subphase of embryonic development regardless of any development of subsequent oocyte batches in the ovaries. For total-spawning livebearers, such as *Sebastes* spp. (Saborido-Rey 1994), the female will move from the gestation phase to the regressing phase after parturition. However, for batch-spawning livebearers, such as the guppy *Poecilia reticulata*, western mosquitofish *Gambusia affinis*, and redtail splitfin *Xenotoca eiseni* (Grier et al. 2005), females return to the spawning capable phase as the next batch of oocytes matures (Figure 10, dashed arrow). Further complicating the terminology are livebearers, such as some poeciliid species (Reznick and Miles 1989), that exhibit superfetation, in which an individual female can have more than one batch of embryos in multiple stages of development (and thus multiple subphases) simultaneously. The specifics of the best way to define reproductive phase terminology for these complex situations (Koya and Muñoz 2006) in livebearers is best left to researchers working with these species.

DISCUSSION

The terminology described here is based on important developmental phases that all fish demonstrate within their reproductive cycles rather than on descriptions of gonadal development commonly used in other terminologies. Furthermore, temporal aspects (i.e., the amount of time spent in each phase) are species specific; thus, references to the "duration" of each phase are not appropriate for a universal terminology. These factors provide the advantage of introducing a terminology that is applicable to both sexes and all species of fish, regardless of reproductive

strategy or phylogeny. In addition, this terminology focuses on communication rather than on detailed staging criteria developed within a specific laboratory for the range of species studied. The literature has many examples of these classification schemes (see Table 1), which are appropriate for the given species but lead to confusion as one scientist's criteria will differ from another's. Recently, Núñez and Duponchelle (2009) introduced a classification system that required different numbers and descriptions for males and females as well as for differing female reproductive strategies, further adding to the confusion in reproductive terminology. In the present study, naming each of the phases for a clearly defined event within the reproductive cycle (i.e., developing, spawning capable, regressing, and regenerating) eliminates the vagueness of using a numbered system to describe gonadal development (e.g., Hjort 1914; Robb 1982; Tomkiewicz et al. 2003; Núñez and Duponchelle 2009), particularly when the same numbered stage is defined differently among scientists (Bromley 2003). While adoption of the proposed terminology may seem a radical change to some, in most cases it simply involves substituting a few new terms for previously used stages or classes since all fish have a similar reproductive cycle regardless of the terminology employed to describe it.

An additional source of confusion in the literature has been the use of the term "mature" or "maturation" to describe (1) the initial, one-time attainment of sexual maturity (Rideout et al. 2005); (2) a fish of any age that has already reached sexual maturity (Hilge 1977; Hunter et al. 1992; ICES 2007; Núñez and Duponchelle 2009); (3) an annual reproductive class in both males and females (Taylor et al. 1998; Brown-Peterson 2003; Murua et al. 2003); or (4) oocyte development (Patiño and Thomas 1990; Patiño and Sullivan 2002; Planas and Swanson 2008). Therefore, the terms "mature" or "maturation" are used to describe either sexual maturity or a stage of oocyte development in a specific phase or subphase of the current terminology. These terms should not be used to name phases, as suggested by Grier and Uribe-Aranzábal (2009).

Historically, most research on fish reproduction has focused on females; thus, gonadal classification terminology is often based on either ovarian or oocyte development (West 1990; ICES 2007; Núñez and Duponchelle 2009), and the most advanced oocyte stage is used to determine the overall classification (e.g., Hilge 1977; Wallace and Selman 1981; Morrison 1990; Hunter et al. 1992; Tomkiewicz et al. 2003). However, basing an overall classification on ovarian development will result either in (1) the necessity of creating a separate classification for males (e.g., Grier and Taylor 1998; Núñez and Duponchelle 2009) or (2) the often awkward application of the same classification terminology to both males and females (Taylor et al. 1998; Brown-Peterson 2003; Burgos et al. 2007). Furthermore, certain terms typically used to classify the level of ovarian development (e.g., "spawning") are often based on a specific event occurring during the reproductive season, such as the release of ova, rather than on defined histological and physiological criteria that are common to all species.

For the reproductive phase terminology presented here to be a truly universal terminology, it needs to be flexible enough to accommodate the wide variety of reproductive strategies that are reported to occur among species (see Balon 1975; Murua and Saborido-Rey 2003). For example, reproductive cycles may not be annual. Species living in cold, deep water, such as the Dover sole and Greenland halibut *Reinhardtius hippoglossoides*, may encompass a reproductive cycle exceeding 12 months between the first appearance of CA oocytes during the developing phase and entry into the regenerating phase (Hunter et al. 1992; Simonsen and Gundersen 2005; Gundersen et al. 2010). However, such species still move through each of the phases in consecutive order. These species may be in the developing phase (including the early developing subphase with the appearance of CA oocytes but no vitellogenic oocytes) for 6 months or longer as they acquire the energetic resources necessary to initiate and complete vitellogenesis (Stenberg 2007). This variation in the reproductive cycle should be taken into account when estimating maturity ogives. In contrast, the amarillo snapper *L. argentiventris* may complete two reproductive cycles within a 12-month period as females in the regenerating phase were found during spring and autumn and spawning females were found during summer and winter (Piñon et al. 2007). Indeed, the amount of time any species spends in a specific phase is dependent on both abiotic (e.g., water temperature, depth, day length, and moon phase) and biotic (e.g., food resources, competition, mate availability, and habitat structure) factors and can vary both among and within species based on the availability of suitable factors. This temporal component of phase duration is also illustrated in batch spawners, not only as variations in spawning frequencies among individuals (Kjesbu 2009; Lowerre-Barbieri et al. 2011b, this special section) but also as individual differences in the amount of time that is spent in the spawning capable phase before entering the regressing phase. The importance of understanding spatiotemporal aspects of the reproductive biology of fishes has been addressed by Rowe and Hutchings (2003), and the actively spawning subphase defined here has applications for assessing these aspects (Lowerre-Barbieri et al. 2009). A detailed discussion of temporal components of the reproductive cycle as they relate to phase duration is provided by Lowerre-Barbieri et al. (2011b).

Another variation in the reproductive cycle occurs in spawn-skipping individuals—fish that have reached sexual maturity but do not enter the spawning capable phase during the current reproductive cycle (Rideout et al. 2005). Skipped spawning has been recognized as being a more frequent occurrence than originally thought (Rideout and Tomkiewicz 2011, this special section), but definitive histological markers to specifically identify this phenomenon are lacking, as fish can either fail to develop oocytes or resorb developed oocytes prior to spawning. Thus, fish that skip spawning would be placed either in the

regenerating phase (i.e., no gonadal recrudescence; Rideout et al. 2005) or in the regressing phase (i.e., undergoing atresia of secondary growth oocytes without releasing any gametes; Saborido-Rey et al. 2010).

Although the reproductive phase terminology was developed by using oviparous marine teleosts as a model, the terminology is flexible enough to include other groups of fishes. For instance, anadromous, semelparous species, such as Pacific salmon *Oncorhynchus* spp. and anguillid eels *Anguilla* spp., do not have a complete reproductive cycle since they die prior to entering the regenerating phase. However, these species do proceed from the immature phase through the developing, spawning capable, and regressing phases, thus following an orderly progression of the cycle until death. Additionally, some iteroparous species may simply skip one or more phases in the reproductive cycle. For example, females of an oviparous elasmobranch, the thornback ray *Raja clavata*, may progress directly from the regressing phase to the developing phase, whereas the males do not appear to enter either the regressing phase or the regenerating phase (Serra-Pereira et al. 2011, this special section); in this species, gamete proliferation occurs in the developing phase, spawning capable phase, or both. The reproductive phase terminology is likely to require some adjustments and development of additional subphases as it is applied to other elasmobranch species, both oviparous and viviparous. However, the ability of Serra-Pereira et al. (2011) to use a terminology developed for marine teleosts and apply it to elasmobranchs suggests that this terminology has universal application in fishes.

In conclusion, the reproductive phase terminology as presented here has great promise for eliminating the rampant confusion that is evident in the literature regarding the reproductive classification of fishes. A similar step has been taken by parasitologists to standardize the terminology used to describe the ecology of parasites (Bush et al. 1997). The proposed reproductive terminology appears to be applicable to all fishes, from primitive to more evolved, regardless of reproductive strategy or gender. Indeed, this terminology has recently been used to describe the reproductive cycle of an elasmobranch (thornback ray: Serra-Pereira et al. 2011), a freshwater teleost (threespine stickleback *Gasterosteus aculeatus*: Brown-Peterson and Heins 2009), and several marine teleosts (e.g., silver perch *Bairdiella chrysoura*: Grammer et al. 2009; spotted seatrout: Lowerre-Barbieri et al. 2009; red snapper: Brown-Peterson et al. 2009 and Brulé et al. 2010; beardfish *Polymixia lowei*: Baumberger et al. 2010). It is our strong hope that researchers studying fish reproduction will adopt this terminology for the purpose of improving communication among those in fish-related disciplines.

ACKNOWLEDGMENTS

We are grateful to all participants attending the Third and Fourth Workshops on Gonadal Histology of Fishes (Third Workshop in New Orleans, Louisiana, 2006; Fourth Workshop in Cadiz, Spain, 2009) for their input and insights as this terminology was being developed. In particular, discussions with J. Tomkiewicz were invaluable during the development of the terminology, and we are very appreciative of the time she devoted to this project. Additionally, H. Grier, H. Murua, D. Nieland, and R. Rideout were helpful in refining specific aspects of the terminology. All Atlantic herring photographs in the manuscript were graciously provided by J. Tomkiewicz, and R. Hagstrom assisted with the photography. We also thank each of our institutions for their financial support throughout this collaborative project. Fish Reproduction and Fisheries (FRESH; European Cooperation in Science and Technology Action FA0601) and the West Palm Beach Fishing Club (Florida) provided funding for the gonadal histology workshops where this terminology was developed and refined. Additionally, we thank FRESH for travel and publication funds. This is Contribution Number 678 of the South Carolina Marine Resources Center.

REFERENCES

Acuña, A., F. Viana, D. Vizziano, and E. Danualt. 2000. Reproductive cycle of female Brazilian codling, *Urophycis brasiliensis* (Kaup 1858) caught off the Uruguayan coast. Journal of Applied Ichthyology 16:48–55.

Alekseyev, F. Y., Y. I. Alekseyeva, and A. N. Zakharov. 1991. Vitellogenesis, nature of spawning, fecundity, and gonad maturity stages of the roundnose grenadier, *Coryphaenoides rupestris*, in the north Atlantic. Voprosy Ikhtiologii 31:917–927.

Balon, E. K. 1975. Reproductive guilds of fishes: a proposal and definition. Journal of the Fisheries Research Board of Canada 32:821–864.

Barbieri, L. R., M. E. Chittenden Jr., and S. K. Lowerre-Barbieri. 1994. Maturity, spawning and ovarian cycle of Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay and adjacent coastal waters. U.S. National Marine Fisheries Service Fishery Bulletin 92:671–685.

Baumberger, R. E., N. J. Brown-Peterson, J. K. Reed, and R. G. Gilmore. 2010. Spawning aggregation of *Polymixia lowei* in a deep-water sinkhole off the Florida Keys. Copeia 2010:41–46.

Bowers, M. J. 1992. Annual reproductive cycle of oocytes and embryos of yellowtail rockfish *Sebastes flavidus* (Family Scorpaenidae). U.S. National Marine Fisheries Service Fishery Bulletin 90: 231–242.

Bromley, P. J. 2003. Progress towards a common gonad grading key for estimating the maturity of North Sea plaice. Pages 19–24 *in* O. S. Kjesbu, J. R. Hunter, and P. R. Witthames, editors. Modern approaches to assess maturity and fecundity of warm- and cold-water fish and squids. Institute of Marine Research, Bergen, Norway.

Brown-Peterson, N. J. 2003. The reproductive biology of spotted seatrout. Pages 99–133 *in* S. A. Bortone, editor. Biology of the spotted seatrout. CRC Press, Boca Raton, Florida.

Brown-Peterson, N. J., K. M. Burns, and R. M. Overstreet. 2009. Regional differences in Florida red snapper reproduction. Proceedings of the Gulf and Caribbean Fisheries Institute 61:149–155.

Brown-Peterson, N. J., H. J. Grier, and R. M. Overstreet. 2002. Annual changes in germinal epithelium determine male reproductive classes of the cobia. Journal of Fish Biology 60:178–202.

Brown-Peterson, N. J., and D. C. Heins. 2009. Interspawning interval of wild female three-spined stickleback *Gasterosteus aculeatus* in Alaska. Journal of Fish Biology 74:2299–2312.

Brulé, T., T. Colás-Marrufo, E. Pérez-Díaz, and J. C. Sámano-Zapata. 2010. Red snapper reproductive biology in the southern Gulf of Mexico. Transactions of the American Fisheries Society 139:957–968.

Burgos, J. M., G. R. Sedberry, D. M. Wyanski, and P. J. Harris. 2007. Life history of red grouper (*Epinephelus morio*) off the coasts of North Carolina and South Carolina. Bulletin of Marine Science 80:45–65.

Bush, A. O., K. D. Lafferty, J. M. Lotz, and A. W. Shostak. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. Journal of Parasitology 83:575–583.

Bye, V. J. 1984. The role of environmental factors in the timing of reproductive cycles. Pages 187–205 *in* G. W. Potts and R. J. Wootton, editors. Fish reproduction: strategies and tactics. Academic Press, New York.

Calvo, J., E. Morriconi, and G. A. Rae. 1999. Reproductive biology of the icefish *Champsocephalus esox* (Gunther, 1961) (Channichthyidae). Antarctic Science 11:140–149.

Cook, M. 2007. Population dynamics, structure, and per-recruit analyses of yellowedge grouper, *Epinephelus flavolimbatus*, from the northern Gulf of Mexico. Doctoral dissertation. University of Southern Mississippi, Hattiesburg.

Dodd, J. M. 1986. The ovary. Pages 351–397 *in* P. K. T. Pang and M. P. Shcreibman, editors. Vertebrate endocrinology: fundamentals and biomedical implications. Academic Press, San Diego, California.

Forberg, K. C. 1983. Maturity classification and growth of capelin, *Mallotus villosus villosus* (M), oocytes. Journal of Fish Biology 22:485–496.

Foucher, R. P., and R. J. Beamish. 1977. A review of oocyte development in fishes with special reference to Pacific hake (*Merluccius productus*). Canadian Fisheries Marine Service Technical Report 755.

Ganias, K., S. Somarakis, A. Machias, and A. Theodorou. 2004. Pattern of oocyte development and batch fecundity in the Mediterranean sardine. Fisheries Research 67:13–23.

Grammer, G. L., N. J. Brown-Peterson, M. S. Peterson, and B. H. Comyns. 2009. Life history of silver perch *Bairdiella chrysoura* (Lacepède 1803) in north-central Gulf of Mexico estuaries. Gulf of Mexico Science 27:62–73.

Grier, H. J., and R. G. Taylor. 1998. Testicular maturation and regression in the common snook. Journal of Fish Biology 53:521–542.

Grier, H. J., M. C. Uribe, L. R. Parenti, and G. Rosa-Cruz. 2005. Fecundity, the germinal epithelium and folliculogenesis in viviparous fishes. Pages 191–216 *in* M. C. Uribe and H. J. Grier, editors. Viviparous fishes. New Life Publications, Homestead, Florida.

Grier, H. J., and M. C. Uribe-Aranzábal. 2009. The testis and spermatogenesis in teleosts. Pages 119–142 *in* B. G. M. Jameson, editor. Reproductive biology and phylogeny of fishes (agnathans and bony fishes), volume 8A. Science Publishers, Enfield, New Hampshire.

Grier, H. J., M. C. Uribe-Aranzábal, and R. Patiño. 2009. The ovary, folliculogenesis, and oogenesis in teleosts. Pages 25–84 *in* B. G. M. Jamieson, editor. Reproductive biology and phylogeny of fishes (agnathans and bony fishes), volume 8A. Science Publishers, Enfield, New Hampshire.

Gundersen, A. C., J. Kennedy, A. S. Hrines, and O. S. Kjesbu. 2010. Ovarian development and the assessment of maturity stage in Greenland halibut. Pages 33–36 *in* D. M. Wyanski and N. J. Brown-Peterson, editors. Proceedings of the Fourth Workshop on Gonadal Histology of Fishes, El Puerto de Santa Maria, Spain. Available: hdl.handle.net/10261/24937. (August 2010).

Hay, D. E. 1985. Reproductive biology of Pacific herring (*Clupea harengus pallasii*). Canadian Journal of Fisheries and Aquatic Sciences 42:111–126.

Heins, D. C., and J. A. Baker. 1993. Reproductive biology of the brighteye darter, *Etheostoma lynceum* (Teleostei: Percidae), from the Homochitto River, Mississippi. Ichthyological Explorations of Freshwaters 4:11–20.

Hilge, V. 1977. On the determination of the gonad ripeness in female bony fishes. Meeresforschung 25:149–155.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Journal du Conseil Permanent International pour L'Exploration de la Mer 20:1–228.

Hunter, J. R., and B. J. Macewicz. 1985a. Measurement of spawning frequency in multiple spawning fishes. NOAA Technical Report NMFS 36:79–94.

Hunter, J. R. and B. J. Macewicz. 1985b. Rates of atresia in the ovary of captive and wild northern anchovy, *Engraulis mordax*. U.S. National Marine Fisheries Service Fishery Bulletin 83:119–136.

Hunter, J. R., B. J. Macewicz, C. H. Lo, and C. A. Kimbrell. 1992. Fecundity, spawning, and maturity of female Dover sole, *Microstomus pacificus*, with an evaluation of assumptions and precision. U.S. National Marine Fisheries Service Fishery Bulletin 90:101–128.

Hunter, J. R., B. J. Macewicz, and J. R. Sibert. 1986. The spawning frequency of skipjack tuna, *Katsuwonus pelamis*, from the south Pacific. U.S. National Marine Fisheries Service Fishery Bulletin 84:895–903.

ICES (International Council for the Exploration of the Sea). 2007. Report of the workshop on sexual maturity sampling (WKMAT). ICES, CM 2007/Advisory Committee for Fishery Management 03, Copenhagen.

Jackson, M. W., D. L. Nieland, and J. H. Cowan Jr. 2006. Diel spawning periodicity of red snapper *Lutjanus campechanus* in the northern Gulf of Mexico. Journal of Fish Biology 68:695–706.

Jalabert, B. 2005. Particularities of reproduction and oogenesis in teleost fish compared to mammals. Reproduction, Nutrition and Development 45:261–279.

Junquera, S., E. Roman, J. Morgan, M. Sainze, and G. Ramilo. 2003. Time scale of ovarian maturation in Greenland halibut (*Reinhardtius hippoglossoides*, Walbaum). ICES (International Council for the Exploration of the Sea) Journal of Marine Science 60:767–773.

Kjesbu, O. S. 2009. Applied fish reproductive biology: contribution of individual reproductive potential to recruitment and fisheries management. Pages 293–332 *in* T. Jakobsen, M. J. Fogarty, B. A. Megrey, and E. Moksness, editors. Fish reproductive biology: implications for assessment and management. Wiley-Blackwell Scientific Publications, Oxford, UK.

Koya, Y., and M. Muñoz. 2006. Comparative study on ovarian structures in scorpaenids: possible evolutional process of reproductive mode. Ichthyological Research 54:221–230.

Lowerre-Barbieri, S. K. 2009. Reproduction in relation to conservation and exploitation of marine fishes. Pages 371–394 *in* B. G. M. Jameson, editor. Reproductive biology and phylogeny of fishes (agnathans and bony fishes), volume 8B. Science Publishers, Enfield, New Hampshire.

Lowerre-Barbieri, S. K., N. J. Brown-Peterson, H. Murua, J. Tomkiewicz, D. Wyanski, and F. Saborido-Rey. 2011a. Emerging issues and methodological advances in fisheries reproductive biology. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 3:32–51.

Lowerre-Barbieri, S. K., M. E. Chittenden Jr., and L. R. Barbieri. 1996. The multiple spawning pattern of weakfish in the Chesapeake Bay and Middle Atlantic Bight. Journal of Fish Biology 48:1139–1163.

Lowerre-Barbieri, S. K., K. Ganias, F. Saborido-Rey, H. Murua, and J. R. Hunter. 2011b. Reproductive timing in marine fishes: variability, temporal scales, and methods. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 3:71–91.

Lowerre-Barbieri, S., N. Henderson, J. Llopiz, S. Walters, J. Bickford, and R. Muller. 2009. Defining a spawning population (*Cynoscion nebulosus*) over temporal, spatial, and demographic scales. Marine Ecology Progress Series 394:231–245.

Lubzens, E., G. Young, J. Bobe, and J. Cerda. 2010. Oogenesis in teleosts: how fish eggs are formed. General and Comparative Endocrinology 165:367–389.

Luckenbach, J. A., D. B. Iliev, F. W. Goetz, and P. Swanson. 2008. Identification of differentially expressed ovarian genes during primary and early secondary oocyte growth in coho salmon, *Oncorhynchus kisutch*. Reproductive Biology and Endocrinology [online serial] 6:2. DOI: 10.1186/1477-7827-6-2.

Macer, C. T. 1974. The reproductive biology of the horse mackerel *Trachurus trachurus* (L.) in the North Sea and English Channel. Journal of Fish Biology 6:415–438.

Mackie, M., and P. Lewis. 2001. Assessment of gonad staging systems and other methods used in the study of the reproductive biology of the narrow-barred Spanish mackerel, *Scomberomorus commerson*, in western Australia. Fisheries Research Reports of Western Australia 136:1–32.

Matsuyama, M., S. Adachi, Y. Nagahama, K. Maruyama, and S. Mansura. 1990. Diurnal rhythm of steroid hormone levels in the Japanese whiting, *Sillago japonica*, a daily-spawning teleost. Fish Physiology and Biochemistry 8:329–338.

Morrison, C. M. 1990. Histology of cod reproductive tract. Canada Special Publication of Fisheries and Aquatic Sciences 110.

Muñoz, M., M. Casadevall, and S. Bonet. 2002. Gametogenesis of *Helicolenus dactylopterus dactylopterus* (Teleostei: Scorpaeniformes). Sarsia 87:119–127.

Murphy, M. D., and R. G. Taylor. 1990. Reproduction, growth, and mortality of red drum *Sciaenops ocellatus* in Florida waters. U.S. National Marine Fisheries Service Fishery Bulletin 88:531–542.

Murua, H., G. Krous, F. Saborido-Rey, P. R. Whittames, A. Thorsen, and S. Junquera. 2003. Procedures to estimate fecundity in marine fish species in relation to their reproductive strategy. Journal of Northwest Atlantic Fisheries Science 33:33–54.

Murua, H., L. Motos, and P. Lucio. 1998. Reproductive modality and batch fecundity of the European hake, *Merluccius merluccius*, in the Bay of Biscay. California Cooperative Oceanic Fisheries Investigations Report 39:196–204.

Murua, H., and F. Saborido-Rey. 2003. Female reproductive strategies of marine fish species of the north Atlantic. Journal of Northwest Atlantic Fisheries Science 33:23–31.

Núñez, J., and F. Duponchelle. 2009. Towards a universal scale to assess sexual maturation and related life history traits in oviparous teleost fishes. Fish Physiology and Biochemistry 35:167–180.

Parenti, L. R., and H. J. Grier. 2004. Evolution and phylogeny of gonad morphology in bony fishes. Integrative and Comparative Biology 44:333–348.

Patiño, R., and C. V. Sullivan. 2002. Ovarian follicle growth, maturation, and ovulation in teleost fish. Fish Physiology and Biochemistry 26:57–70.

Patiño, R., and P. Thomas. 1990. Induction of maturation of Atlantic croaker oocytes by 17α, 20ß, 21-trihydroxy-4-pregnen-3-one in vitro: consideration of some biological and experimental variables. Journal of Experimental Zoology 255:97–109.

Pavlov, D. 2005. Reproductive biology of wolffishes (Anarhichidaeidae) and transition from oviparity to viviparity in the suborder Zoarcoidei. Pages 89–103 *in* M. C. Uribe and H. J. Grier, editors. Viviparous fishes. New Life Publications, Homestead, Florida.

Pavlov, D. A., N. G. Emel'yanova, and G. G. Novikov. 2009. Reproductive dynamics. Pages 48–69 *in* T. Jakobsen, M. J. Fogarty, B. A. Megrey, and E. Moksness, editors. Fish reproductive biology. Wiley-Blackwell Scientific Publications, Oxford, UK.

Piñon, A., F. Amezcua, and N. Duncan. 2007. Reproductive cycle of female yellow snapper *Lutjanus argentiventris* (Pisces, Actinopterygii, Lutjanidae) in the SW Gulf of California: gonadic stages, spawning seasonality and length at sexual maturity. Journal of Applied Ichthyology 25:18–25.

Planas, J. V., and P. Swanson. 2008. Physiological function of gonadotropins in fish. Pages 37–66 *in* M. J. Rocha, A. Arukwe, and B. G. Kapoor, editors. Fish reproduction. Science Publishers, Enfield, New Hampshire.

Reznick, D. N., and D. B. Miles. 1989. Review of life history patterns in poeciliid fishes. Pages 125–148 *in* G. K. Meffe and F. F. Snelson Jr., editors. Ecology and evolution of livebearing fishes (Poeciliidae). Prentice Hall, Englewood Cliffs, New Jersey.

Rideout, R. M., G. A. Rose, and M. P. M. Burton. 2005. Skipped spawning in female iteroparous fishes. Fish and Fisheries 6:50–72.

Rideout, R. M., and J. Tomkiewicz. 2011. Skipped spawning in fishes: more common than you might think. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 3:176–189.

Robb, A. P. 1982. Histological observations on the reproductive biology of the haddock, *Melanogrammus aeglefinus* (L.). Journal of Fish Biology 20:397–408.

Rowe, S., and J. A. Hutchings. 2003. Mating systems and the conservation of commercially exploited marine fish. Trends in Ecology and Evolution 19:567–572.

Saborido-Rey, F. 1994. The genus *Sebastes* Cuvier, 1829 (Pisces: Scorpaenidae) in the North Atlantic: species and population identification using morphometric techniques— growth and reproduction of the Flemish Cap populations. Doctoral dissertation. Universidad Autónoma, Madrid. (In Spanish.)

Saborido-Rey, F., D. Garabana, A. Alonso-Fernandez, R. Dominguez-Petit, and T. Sigurdsson. 2010. Impact of mass atresia in reproductive ecology, maturity ogive, spawning migration and population dynamics on *S. mentella* in Icelandic waters. Pages 99–102 *in* D. M. Wyanski and N. J. Brown-Peterson, editors. Proceedings of the Fourth Workshop on Gonadal Histology of Fishes, El Puerto de Santa Maria, Spain. Available: hdl.handle.net/10261/24937. (August 2010).

Sadovy de Mitcheson, Y., and M. Liu. 2008. Functional hermaphroditism in teleosts. Fish and Fisheries 9:1–43.

Serra-Pereira, B., I. Figueiredo, and L. S. Gordo. 2011. Maturation of the gonads and reproductive tracts of the thornback ray *Raja clavata*, with comments on the development of a standardized reproductive terminology for oviparous elasmobranchs. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 3:160–175.

Shapiro, D. Y., Y. Sadovy, and M. A. McGehee. 1993. Periodicity of sex change and reproduction in the red hind, *Epinephelus guttatus*, a protogynous grouper. Bulletin of Marine Science 53:1151–1162.

Simonsen, C. S., and A. C. Gundersen. 2005. Ovary development in Greenland halibut *Reinhardtius hippoglossoides* in west Greenland waters. Journal of Fish Biology 67:1299–1317.

Stenberg, C. 2007. Recruitment processes in west Greenland waters with special focus on Greenland halibut (*Reinhardtius hippoglossoides*, W.). Doctoral dissertation. University of Bergen, Bergen, Norway.

Taylor, R. G., H. J. Grier, and J. A. Wittington. 1998. Spawning rhythms of common snook in Florida. Journal of Fish Biology 53:502–520.

Tomkiewicz, J., L. Tybjerg, and Å. Jesperson. 2003. Micro- and macroscopic characteristics to stage gonadal maturation of female Baltic cod. Journal of Fish Biology 62:253–275.

Treasurer, J. W., and F. G. T. Holliday. 1981. Some aspects of the reproductive biology of perch *Perca fluviatilis* L.: a histological description of the reproductive cycle. Journal of Fish Biology 18:359–376.

Uriarte, A., A. Alday, and M. Santos. 2010. Estimation of spawning frequency for the Bay of Biscay anchovy (*Engraulis encrasicolus*, L.). Pages 173–176 *in* D. M. Wyanski and N. J. Brown-Peterson, editors. Proceedings of the Fourth Workshop on Gonadal Histology of Fishes. El Puerto de Santa Maria, Spain. Available: hdl.handle.net/10261.24937. (February 2011).

Uribe-Aranzábal, M. C., and H. Grier. 2010. Ovarian structure and oogenesis in viviparous teleosts: poeciliids and goodeids. Pages 40–44 *in* D. M. Wyanski and N. J. Brown-Peterson, editors. Proceedings of the Fourth Workshop on Gonadal Histology of Fishes, El Puerto-de Santa Maria, Spain. Available: hdl.handle.net/10261/24937. (August 2010).

Wallace, R. A., and K. Selman. 1981. Cellular and dynamic aspects of oocyte growth in teleosts. American Zoologist 21:325–343.

West, G. 1990. Methods of assessing ovarian development in fishes: a review. Australian Journal of Marine and Freshwater Research 41:199–222.

White, D. B., D. M. Wyanski, and G. R. Sedberry. 1998. Age, growth, and reproductive biology of the blackbelly rosefish from the Carolinas, USA. Journal of Fish Biology 53:1274–1291.

Wourms, J. P. 1981. Viviparity: the maternal-fetal relationship in fishes. American Zoologist 21:473–515.

Wourms, J. P. 2005. Functional morphology, development and evolution of trophotaeniae. Pages 237–262 *in* M. C. Uribe and H. J. Grier, editors. Viviparous fishes. New Life Publications, Homestead, Florida.

Wourms, J. P., and L. S. Demski. 1993. The reproduction and development of sharks, rays and ratfishes: introduction, history, overview and future prospects. Environmental Biology of Fish 38:7–21.

Wourms, J. P., B. D. Grove, and J. Lombardi. 1988. The maternal embryonic relationship in viviparous fishes. Pages 1–134 *in* W. S. Hoar and D. J. Randall, editors. Fish physiology, volume XIB. Academic Press, San Diego, California.

Wourms, J. P., and J. Lombardi. 1992. Reflections on the evolution of piscine viviparity. American Zoologist 32:276–293.

Yamamoto, K., and F. Yamazaki. 1961. Rhythm of development in the oocyte of the gold-fish, *Carassius auratus*. Bulletin of the Faculty of Fisheries, Hokkaido University 12:93–115.