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Skipped Spawning in Fishes: More Common than You Might Think

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Abstract

The traditional view of iteroparity in fishes is one of an annual reproductive cycle that culminates each year in spawning. More recently, a more flexible view of fish reproduction has been adopted, including the potential for mature fish to skip spawning. Here, we review the abundance of recent research on skipped spawning, covering a broad range of fishes with diverse life history strategies. Evidence for skipped spawning has been collected by use of traditional histological techniques as well as modern technological advances, such as satellite tags and the ability to track fish movements based on elemental and isotope signatures. Skipped spawning is most commonly attributed to deficient diet and poor nutritional condition. Advances made in this field of study in recent years include descriptions of hormonal changes that precede and perhaps initiate skipped spawning, the development of life history models that incorporate the potential for skipped spawning, and estimates of the degree to which skipped spawning influences the reproductive potential of fish populations. In addition to summarizing this new research, we attempt to advance current knowledge by (1) providing the first review discussion of skipped spawning in males, (2) exploring skipped spawning in anadromous fishes by using the Atlantic salmon *Salmo salar* as an example, and (3) discussing the potential for and difficulties in identifying skipped spawning in species with indeterminate fecundity.

Surveys of fish populations are conducted to assess current population status as well as to collect biological information that might be used to make predictions about future population trends. An integral component of most fisheries surveys is to determine the reproductive status of a representative portion of individuals from that population (Tomkiewicz et al. 2003a). Such information can be used to understand aspects of the reproductive cycle, including where and when fish spawn and the size and age at which individuals become sexually mature, all of which are important to the reproductive potential of a population.

The reproductive status of individual fish as determined during research vessel surveys is generally based on the macroscopic appearance of the gonads. Although macroscopic maturity scales are seldom 100% accurate, they can be employed quickly and allow large numbers of fish to be processed. The goal of such monitoring research is to ascertain a population's "normal" or typical reproductive characteristics (rather than the entire scope of reproductive plasticity within the population) for application in fish stock assessment, and so the processing of large numbers of samples might effectively nullify infrequent errors in maturity classification.
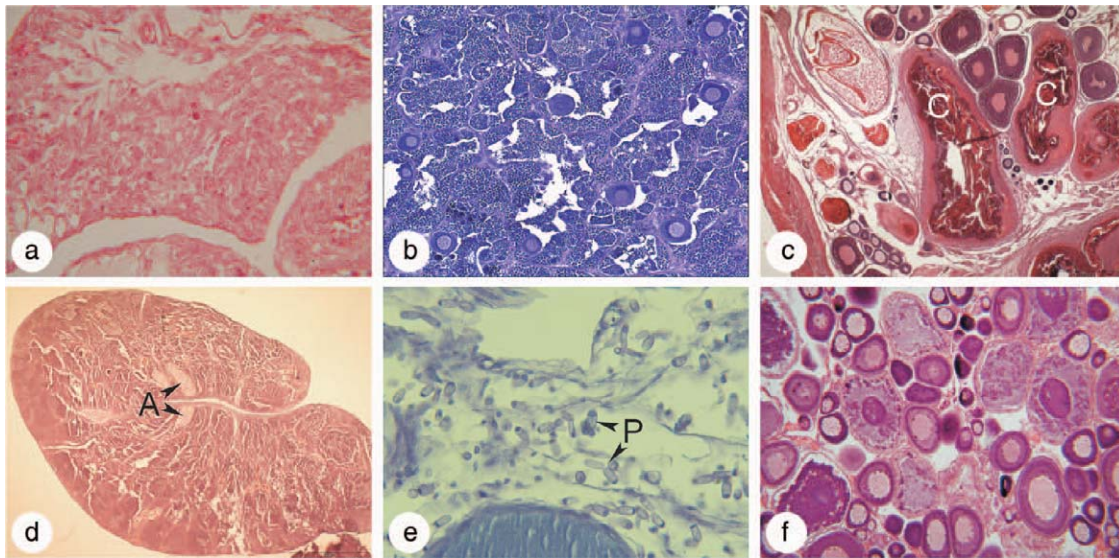
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FIGURE 1. Examples of "abnormal" histological observations on fish gonads: **(a)** sterile Atlantic cod *Gadus morhua* ovary with no oocytes; **(b)** intersex gonad of eelpout *Zoarces viviparus* with oocytes interspersed throughout spermatogenic cell stages; **(c)** Atlantic cod ovary with follicular cysts (C); **(d)** Atlantic herring *Clupea harengus* testis with adipose tissue (A); **(e)** ovary of a Greenland halibut *Reinhardtius hippoglossoides* with protozoan parasite (P) infection; and **(f)** ovary of an Atlantic cod that skipped spawning due to mass atresia of oocytes.

Needless to say, however, not all individuals within a population conform to the normal reproductive development schedule, and some may have gonads that would be considered abnormal in relation to other individuals or populations. Observations on fish gonads that have typically been considered abnormal (Figure 1) include sterility (Rideout and Burton 2000a), intersex (Schwindt et al. 2009), the presence of follicular cysts (Tomkiewicz et al. 2003b), development of adipose tissue within the testes (Tomkiewicz et al. 2002), parasitic infections that interfere with gamete production (Ruehl-Fehlert et al. 2005), and gonads of sexually mature fish that skip a spawning season (Rideout et al. 2005). Because most of these conditions are not specified in standard maturity scales or are only identifiable by histology, they tend to be overlooked. Hence, no consideration has been given to their true frequency, how they fit in with fish life history strategies, and how they affect individual and population reproductive capacity.

Egg production in fishes is an energetically demanding process that must be balanced with the energetic requirements of other life processes (growth, maintenance, etc.). It is very common for fish with determinate fecundity to be initially "optimistic" when it comes to egg production, recruiting more oocytes into vitellogenesis than will ultimately be spawned (Kjesbu 2009). This downregulation of fecundity occurs via the atretic breakdown of vitellogenic oocytes and allows fish to adjust the number of eggs produced in relation to the amount of available stored energy (Kennedy et al. 2008). Emerging research suggests that another potential plastic response of fishes to low levels of stored energy or unsuitable environmental conditions is to forego egg production until the subsequent year—commonly referred to as "skipped spawning." The objective of the current manuscript is to present skipped spawning as a widespread phenomenon among fishes and an adaptive trait that can lead to increased lifetime reproductive output rather than as an abnormal occurrence brought on only by extreme and unusual environmental and physiological conditions. Although skipped spawning is almost certainly a rarer means of regulating individual fish reproductive investment than is the downregulation of fecundity via atresia, it has nevertheless been demonstrated to be widespread among fishes (Rideout et al. 2005). We emphasize that our intent is not to thoroughly review all aspects of flexibility in reproductive investment and output in fishes but rather to concentrate on skipped spawning, as our understanding of this phenomenon is relatively poor but continually evolving.

The approach here is to build on a previous review of skipped spawning by Rideout et al. (2005), who summarized decades of sporadic evidence for skipped spawning and provided guidelines for identifying skipped spawning with the objective of better understanding its frequency in wild fish populations. Since that time, the concept of skipped spawning in fishes has become somewhat of a hot topic. Here, we extend the work of Rideout et al. (2005) to summarize this new research. We also expand on the 2005 review by looking at (1) evidence for skipped spawning among males and (2) the identification of skipped spawning via scale analysis in anadromous species, with the Atlantic salmon *Salmo salar* used as an example. In addition, because skipped spawning has been described as a phenomenon that primarily affects fishes with determinate fecundity, we also discuss the potential for skipped spawning among fishes with

indeterminate fecundity as well as the difficulties in identifying skipped spawning in fishes with this pattern of oocyte development. Taken together, the Rideout et al. (2005) paper and the present paper provide an in-depth summary of the history, evolution, and current state of knowledge pertaining to skipped spawning in fishes.

TERMINOLOGY

The terminology used here corresponds to that used by Rideout et al. (2005). Briefly, maturation is considered to occur only once in an individual's life such that immature fish have never spawned, whereas mature fish have spawned at least once previously. With respect to skipped spawning, a fish is considered immature until it actually spawns (i.e., a fish developing their gonads for the first time is considered to be maturing). When a mature fish fails to spawn in a given year, it is said to have skipped spawning. Other terminologies are per standard papers on reproductive development (Wallace and Selman 1981; Tyler and Sumpter 1996).

Here, we consider skipped spawning to refer only to interruptions in the normal reproductive cycle that do not interfere with subsequent spawning. Skipped spawning has been studied in the most detail for coldwater fish species; most of these fishes have an annual reproductive cycle, so skipped spawning refers to a failure to spawn in a given year that does not interfere with the ability to spawn in subsequent years. Three general forms of skipped spawning have been described (Rideout et al. 2005): retaining, reabsorbing, and resting. Retaining nonreproductive fish are mature individuals that produce fully developed gametes that are never released. Reabsorbing nonreproductive fish are mature individuals in which oocyte development begins but is interrupted before vitellogenesis is complete, and all developing oocytes are subsequently reabsorbed via follicular atresia. Resting nonreproductive fish are mature fish (i.e., that have spawned previously) that do not produce secondary growth oocytes, instead maintaining all oocytes in various stages of primary growth throughout the year. This classification scheme has been useful in promoting the study of skipped spawning in various fishes but may not adequately encompass all scenarios of skipped spawning and all fecundity types. For example, under the current scheme, no distinction is made between fish with determinate fecundity that are reabsorbing endogenous vitellogenic oocytes (i.e., cortical alveoli oocytes) versus exogenous vitellogenic oocytes, despite the fact that these two stages of oocyte growth are under different regulatory control and indicate something quite different in terms of a fish's reproductive status. This shortcoming is reflected in the fact that Skjæraasen et al. (2009) observed Atlantic cod that were reabsorbing oocytes at the cortical alveoli stage of development and referred to these fish as "resting–early reabsorbing" since there was no clear fit within the current categories. However, the terminology suggested by Skjæraasen et al. (2009) might be considered somewhat ambiguous since it actually combines categories rather
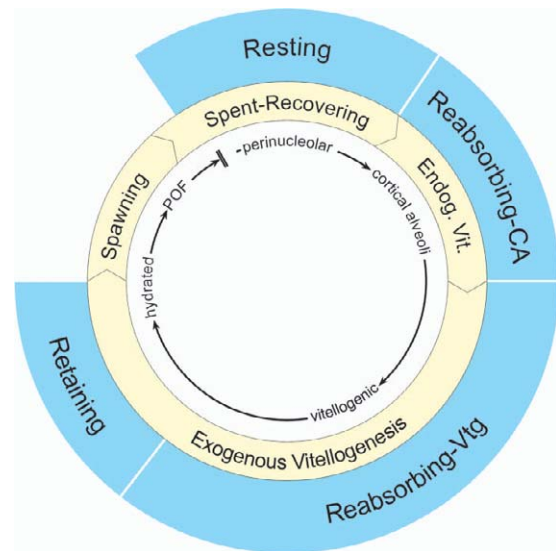

FIGURE 2. Schematic representation of various aspects of the reproductive cycle of a determinate-spawning fish, including (1) sequential stages of oocyte and follicular development (inner circle; POF = postovulatory follicle); (2) sequential stages of ovarian development (i.e., reproductive status; yellow circle; Endog. Vit. = endogenous vitellogenesis); and (3) forms of skipped spawning based on when oocyte or ovarian development is interrupted (outer circle; CA = cortical alveoli oocytes; Vtg = vitellogenic oocytes).

than establishing a new one. Here, we propose alternative terminology based on dividing reabsorbing into the resorption of cortical alveoli oocytes (reabsorbing-CA in Figure 2) and the resorption of true vitellogenic oocytes (reabsorbing-Vtg in Figure 2). Terminologies will probably continue to evolve as this area of research develops further. For example, formation of cortical alveoli is usually considered an indicator that fish are developing for the upcoming spawning season (Wallace and Selman 1981; Saborido-Rey 1997). However, there are also indications that oocytes can remain "inactive" at the cortical alveoli stage for an extended period of time, even years (e.g., Gunnarsson et al. 2006), perhaps suggesting that in some species "resting" can occur with oocytes that are more advanced than the perinucleolar stage.

Atretic follicles in fishes are thought to be short lived (Hunter and Macewicz 1985; Kjesbu et al. 1991; Kurita et al. 2003), and therefore the standing stock of atretic follicles in the ovary at any point in time may be small in comparison with the total number of follicles that are reabsorbed over an extended period. Due to the turnover rate, a relatively high intensity of atresia (rather than simultaneous atresia of all developing oocytes) may be sufficient to classify a female as exhibiting skipped spawning. For example, Hunter et al. (1992) considered Dover sole *Microstomus pacificus* with major atresia (>50%) to be reproductively "inactive" despite the fact that the ovaries still contained some advanced yolked oocytes. A note of caution should be exercised here since the cut-off criterion for classifying fish as demonstrating skipped spawning is somewhat subjective. Also,

a necessary assumption is that atresia will continue at a rate that will eventually lead to the resorption of all secondary growth oocytes.

At this point, it should be noted that the definitions presented here have been developed primarily for species with determinate fecundity and that high levels of atresia and perhaps other histological indicators of reproductive status can be interpreted quite differently for fishes with indeterminate fecundity (discussed in a later section). The distinction between determinate and indeterminate fecundity is based on whether or not the recruitment of oocytes to secondary growth stops prior to spawning (determinate) or continues even after spawning has commenced (indeterminate) and, hence, is based on whether or not a hiatus in the oocyte frequency distribution develops prior to spawning (Murua and Saborido-Rey 2003). Although the terms "determinate fecundity" and "indeterminate fecundity" are well entrenched in the fisheries literature, there is also a common perception that the term "indeterminate fecundity" is tautological in nature and that we should instead focus on oocyte development patterns, such as synchronous, group synchronous, and asynchronous, with the latter corresponding to what has commonly been called indeterminate. According to Murua and Saborido-Rey (2003), however, species with asynchronous oocyte development can also demonstrate determinate fecundity. Given that asynchronous oocyte development and indeterminate fecundity are not exactly equivalent and since our objective here is to distinguish between species with continuous versus discontinuous oocyte recruitment (Pavlov et al. 2009), we chose to stick with the traditional terms of determinate fecundity and indeterminate fecundity. A strong bias in the availability of skipped spawning data results in discussions being skewed toward determinate species, but in a later section we will also attempt to address questions relating to skipped spawning in species with indeterminate fecundity.

The ability to halt gamete development and undergo mass atresia is not exclusive to mature fish and has been noted previously in immature individuals (e.g., Ramsay and Witthames 1996). By strict definition (see above), this is not considered skipped spawning. Ramsay and Witthames (1996) referred to this as "abortive maturation." However, from a fisheries science perspective, this might be considered an artificial distinction since in both cases there is the potential for nonspawning individuals to be considered part of the spawning stock biomass (SSB; i.e., mistakenly identified as future spawners based on the fact that they started to develop). In accordance with this, Rideout and Rose (2006) did not distinguish between reabsorbing nonreproductive adults and immature individuals undergoing abortive maturation in their examination of how a failure to recognize mass oocyte atresia would affect the perceived population total egg production for an inshore group of Atlantic cod in the northwestern Atlantic Ocean. Such considerations led Secor (2008) to define skipped spawning in a more applied context as the investigators' misspecification of reproductive rates, a definition that would include abortive maturation and anything else that would cause nonspawners to be erroneously considered part of the SSB.

RECENT RESEARCH ON SKIPPED SPAWNING

Historic research (defined here as pre-2005) pertaining to skipped spawning in fishes has concentrated heavily on determining (1) whether or not individuals were skipping spawning and what proportion of the population was skipping and (2) what was causing individuals to skip spawning. "Who skips and why" continues to be a major emphasis of this line of research, and new techniques and technologies are being used to confirm skipped spawning in an ever-broadening range of fish species. With cumulative evidence suggesting that this is a widespread phenomenon in fishes (Rideout et al. 2005), recent research (2005 to present) has started to examine the underlying physiological mechanisms that control skipped spawning, the role that skipped spawning plays in life history models, and the significance of skipped spawning to fisheries science.

Who Skips and Why?

The majority of papers cited by Rideout et al. (2005) were of the variety that (1) identified large fish that were not developing secondary growth oocytes and (2) assumed or subsequently determined that these fish were skipping spawning. Such research continues to be important in terms of identifying the range of species that appear to have the reproductive flexibility to skip spawning as well as the extent of skipped spawning within a species. Recent research has produced evidence for skipped spawning in species with determinate and indeterminate fecundity and in sequential hermaphrodites. The species studied include the bluefin tuna *Thunnus thynnus* (Zupa et al. 2009), barramundi perch *Lates calcarifer* (Milton and Chenery 2005), black scabbardfish *Aphanopus carbo* (Neves et al. 2009), Pacific halibut *Hippoglossus stenolepis* (Loher and Seitz 2008), Atlantic herring *Clupea harengus* (Engelhard and Heino 2006; Kennedy et al. 2010), European horse mackerel *Trachurus trachurus* (Ndjaula et al. 2009), bull trout *Salvelinus confluentus* (Johnston and Post 2009), white crappie *Pomoxis annularis* (Bunnell et al. 2007), and redthroat emperor *Lethrinus miniatus* (Williams et al. 2006). There have also been additional reports of skipped spawning by species for which the phenomenon was previously documented, including Atlantic cod (Mukhin et al. 2006; Rideout and Rose 2006; Rideout et al. 2006; Skjæraasen et al. 2009), winter flounder *Pseudopleuronectes americanus* (Wuenschel et al. 2009), and striped bass *Morone saxatilis* (Secor and Piccoli 2007).

The shortage of historical data related to skipped spawning may be partially attributable to the difficulty in identifying the condition. Rideout et al. (2005) suggested methods for identifying skipped spawning, including the potential to track fish movements based on conventional tagging. Such an approach may work for anadromous species that can be corralled through

a single migration point but not for marine fish, which have migration routes that are not as well defined and cannot be controlled. However, advancements in tagging technology are overcoming the limitations of conventional tagging, and data are being obtained that support the idea of skipped spawning. For example, Loher and Seitz (2008) used pop-up archival transmitting tags to track the movements and reproductive activity of adult-sized Pacific halibut. Females that migrated to the continental slope and underwent abrupt midwater ascents were thought to be spawning. However, a number of mature fish did not take part in spawning—these fish either failed to make the offshore spawning migration (∼10%) or did migrate but did not exhibit the vertical movements (10–15%). Likewise, data storage tags have been used to show that some adult Atlantic cod in Baltic Sea populations skip spawning and do not migrate to the Bornholm Basin spawning area (Hüssy et al. 2009). Continued development and use of tagging technology could help to further increase our understanding of potential fish movements in relation to reproductive status.

In addition to the use of man-made tags, advancements have also been made in our understanding of otolith and scale formation and the amount of information that can be extracted from those bony structures. For example, gonadal development in Atlantic herring is marked by reduced growth and thus the formation of very narrow circuli on scales. Engelhard and Heino (2005) used this information to determine that Atlantic herring that were about to spawn for the second time (i.e., in the year after maturation) were strongly underrepresented on the spawning grounds and were likely to have skipped spawning. The high incidence of skipped spawning was in particular related to the size and condition of Atlantic herring as first-time spawners and the time needed to recover energetically (Engelhard and Heino 2006). However, in experiments with Atlantic herring, Kennedy et al. (2010) found no evidence to support the idea that a high proportion of potential second-time spawners were skipping spawning. Kennedy et al. (2010) did observe skipped spawning in a small number of individuals characterized as being in very poor condition, but those authors suggested that such condition levels were seldom observed in the wild. Advances have also been made in our understanding of otolith chemistry and the ability to use elemental signatures as natural tags to understand fish movements and ecology. For example, $^{87}Sr{:}^{86}Sr$ and Sr:Ca ratios in the otoliths of catadromous barramundi perch in Papua New Guinea demonstrated that most adults do not migrate annually to spawn along the coast and that a large proportion of sampled fish had never migrated back to the coast (Milton and Chenery 2005). In fact, fish sampled on the spawning grounds were mostly marine residents, and some had spent only short periods in the rivers adjacent to the spawning grounds. Secor and Piccoli (2007) also used otolith Sr:Ca ratios to examine migration patterns of anadromous striped bass and concluded that while most fish spawned annually, a small proportion of individuals demonstrated evidence of skipped spawning.

Skipped spawning has primarily been linked with poor feeding conditions and insufficient energy accumulation (reviewed by Rideout et al. 2005). New research continues to support this generalization. For example, recent research on Atlantic cod indicates that skipped spawning is linked to poor condition (limited liver energy storage; Rideout and Rose 2006; Rideout et al. 2006; Skjæraasen et al. 2009). The same suggestion has been made for black scabbardfish (Neves et al. 2009). In a study by Bunnell et al. (2007), a small proportion of white crappie females that were starved or given intermediate rations failed to produce vitellogenic oocytes, whereas no females that were given the high rations failed to develop. Additional tools for examining diet and condition are now available for use in exploring aspects of reproductive biology. For example, Rideout and Rose (2006) demonstrated based on white muscle δC^{13} signatures that medium-sized Atlantic cod feeding on capelin *Mallotus villosus* were less likely to skip spawning than individuals that were feeding on shrimp. Despite the strong links with condition, there continue to be populations of fish that skip spawning due to unknown causes (e.g., Milton and Chenery 2005).

Underlying Physiological Mechanisms

The biochemical pathways controlling oocyte development have generally been well documented in fishes. For example, 17β-estradiol is known to control the hepatic synthesis of vitellogenin and its subsequent uptake by growing oocytes (Tyler and Sumpter 1996). With the realization that fish can halt and reverse oocyte development (i.e., atresia) and can thereby skip spawning, research effort is now being directed at understanding the pathways by which this is facilitated. For example, Skjæraasen et al. (2009) monitored the production of reproductive hormones in captive Atlantic cod (northeastern Arctic stock) and found that hormonal differences leading to skipped spawning were identifiable during the early stages of secondary oocyte growth (i.e., several months before spawning). Up until early November, oocyte development and hormone levels appeared to be similar for all females. In November, there was a clear increase in 17β-estradiol in fish that would later successfully spawn during the spawning season, whereas levels in females that ultimately skipped spawning in that season actually decreased. In fish with high hormone levels, oocytes proceeded normally through the cortical alveoli and vitellogenic stages of development; in contrast, fish with low or reduced hormone levels tended to halt development during the early cortical alveoli stage and to subsequently reabsorb those oocytes via follicular atresia.

Mukhin et al. (2006) compared ovarian protein levels and proteinase activity from resting and reabsorbing nonreproductive Atlantic cod with those of immature and developing Atlantic cod collected from the Barents Sea. Females with healthy vitellogenic oocytes had the highest levels of water-soluble proteins, which tended to be of high molecular mass (100–130 kDa). In contrast, ovaries undergoing mass atresia were clearly actively breaking down the oocyte cellular components, as evidenced by

(1) low levels of water-soluble proteins, which tended to be of low molecular mass (13–30 kDa), and (2) maximum activity of lysosomal and cytoplasmic proteolytic enzymes.

Life History Models

Although links have been made between skipped spawning and fish nutritional status and although some authors have speculated as to the role of skipped spawning in the life history of fishes, Jørgensen et al. (2006) were the first to incorporate the potential for skipped spawning into any sort of formal life history model. The Jørgensen et al. (2006) model was based on optimal allocation rules between growth and energy stores and included a consideration of fish age, amount of stored energy, fish length, and food availability. For each combination of age and state, the optimal strategy was one that used an allocation rule (including the decision of whether or not to spawn) that maximized future expected egg production discounted by survival probability. The model predicted that skipped spawning in Northeast Arctic (NEA) Atlantic cod was a regular phenomenon, exhibited by up to 30% of the sexually mature biomass. The model suggested that skipped spawning was most common early in life, particularly in the year after spawning for the first time. The Jørgensen et al. (2006) model also suggested that skipped spawning was common in years when natural mortality was low and when the energetic and mortality costs associated with migration and spawning were high. In line with empirical work, the model concluded that when food availability decreased, the occurrence of skipped spawning among NEA Atlantic cod increased due to insufficient energy to support gonad development. However, the model suggested that skipped spawning also becomes more common when food availability increases; this strategy would allow individuals to take advantage of opportunities for growth and the future impact that increased body size will have on gamete production. To our knowledge, there are no empirical data supporting the idea of an increase in skipped spawning with increased food availability.

An alternative life history model developed by Fischer et al. (2009) also predicts an increase in the probability of skipped spawning (reproductive investment = 0) as energy availability declines. However, this model suggests that at very low energy levels, all available resources would be invested in gamete production, which the authors referred to as "terminal investment." The Fischer et al. (2009) model lacks the realistic nature of the Jørgensen et al. (2006) model since it applies only to strict income breeders and does not account for growth or the tradeoff between growth and reproduction.

Significance to Fisheries Science

The degree of variability and plasticity in the reproductive biology of fishes is enormous and cannot—indeed, should not—be incorporated in its entirety into population models and resource assessments. However, the reproductive potential of a population is an important component of population productivity, so any variation in reproductive biology that is common enough to influence stock reproductive potential may have an influence on population dynamics and resource management. For example, the cumulative biomass of all sexually mature individuals within a population (i.e., SSB) has traditionally been used as an index of reproductive potential that is independent of fecundity type and for assessing population status relative to biological reference points. Failure to account for the proportion of these fish that are actually skipping spawning could result in an overestimation of SSB and ineffective management advice. Jager et al. (2008) suggested that including realistic estimates of spawning interval (i.e., number of years between spawnings)—rather than either assuming annual spawning or adopting the minimum interval that is physiologically possible—could help to reduce uncertainties in predictions of sustainable harvest or population recovery. On the other hand, when fish that skip spawning do not aggregate or migrate with reproductive individuals (e.g., Skjæraasen et al. 2009; Zupa et al. 2009), they may constitute a buffer against overfishing if the majority of fishing occurs in spawning areas (Sullivan and Cordue 1992).

Research summarized here and in the previous review (Rideout et al. 2005) suggests that skipped spawning exists among many species and populations of fish. However, understanding the population and management implications of skipped spawning will require time series data rather than the single-year and single-area studies that have been common to date. Multiyear data sets describing the proportion of fish that skip spawning have recently been produced for inshore (Rideout and Rose 2006) and offshore (Rideout et al. 2006) Atlantic cod in the Newfoundland and Labrador region. In both cases, extensive levels of skipped spawning were observed along with high degrees of spatial and temporal variability. The development of time series data on the proportion of fish that exhibit skipped spawning can then be used to adjust SSB accordingly. On the other hand, such adjustments would not be required if an estimate of the proportion of spawners derived from a spawning probability function (e.g., Bucholtz et al. 2008) is used in place of traditional SSB estimates.

There is an obvious negative influence on the reproductive potential of a population when in any given year a proportion of the adult fish do not spawn. However, the impact of skipped spawning on reproductive potential has rarely been quantified. Rideout and Rose (2006) examined skipped spawning in Smith Sound Atlantic cod and determined that failure to recognize the occurrence of skipped spawning in this population (i.e., including nonreproductive fish as part of the SSB) would result in an overestimation of total population egg production by 8–41% annually (Figure 3). Morgan and Rideout (2005) estimated based on fish condition that the number of Atlantic cod that skipped spawning in Northwest Atlantic Fisheries Organization subdivision 3Ps was 8–30% annually, but they found that adjusting SSB accordingly did not improve the stock–recruit relationship. Likewise, the modeling of a range of skipped spawning scenarios for striped bass (Secor 2008) and Atlantic bluefin tuna (Secor 2007) suggested that skipped spawning had only a minor
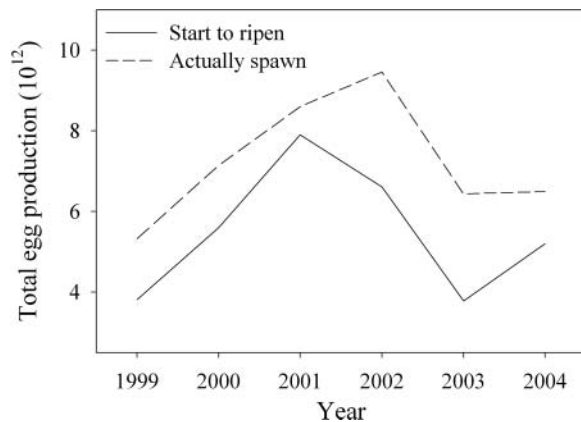
FIGURE 3. Comparison of estimated total egg production for the Smith Sound spawning aggregation of Atlantic cod based on the total number of fish in the spawning aggregation (dashed line) versus the number of fish adjusted for the proportion that would skip spawning (solid line). Data are from Rideout and Rose (2006).

impact on the biological reference point of egg production per recruit. In contrast, Rideout et al. (2005) examined varying levels of fishing mortality, spawning mortality, and other natural mortality and demonstrated that skipped spawning could have a major impact on egg production per recruit when spawning mortality is expected to be high.

SKIPPED SPAWNING IN MALES

As is often the case with fish reproductive biology, less is known about the potential for skipped spawning in males than in females. In fact, Rideout et al.'s (2005) review of skipped spawning in fishes dealt exclusively with females. The sex bias may reflect the general perception that egg production is more critical to population sustainability than sperm production, but this bias could also result from the fact that egg production requires a greater energetic and nutrient investment than the production of sperm, making females a better model for understanding energy allocation in fishes. Such reasoning is supported by studies that have found no evidence for skipped spawning among males of certain species. For example, nutritional deprivation in the period prior to spawning did not influence reproductive development in male white crappies, whereas females either showed reduced egg size or skipped spawning altogether (Bunnell et al. 2007). Likewise, skipped spawning was observed in female Eurasian perch *Perca fluviatilis* but not in males (Holmgren 2003). The shortage of data describing skipped spawning in males might also reflect difficulties in identifying this phenomenon in males due to the small size of spermatogenic cell stages. Here, we summarize the available data on skipped spawning in male fish based on the premise that a lack of attention to skipped spawning among males is not equivalent to saying that skipped spawning does not occur in males.

As is the case for females, maturity data for males are routinely collected during regular fisheries assessment surveys via macroscopic inspection of the gonads and are used to estimate SSB. Classification schemes for male gonad development typically do not account for the possibility of skipped spawning (for notable exceptions, see Tomkiewicz et al. 2002 and Bucholtz et al. 2008), so clear data regarding the degree of skipped spawning among males are rare. However, maturity data can be used to make inferences about skipped spawning. Perhaps the crudest way of identifying skipped spawning is to assume that (1) all fish above a certain size are mature and (2) individuals above the size threshold that are not developing are actually skipping spawning (Rideout et al. 2005). For example, Pulliainen and Korhonen (1990) reported that nearly 30% of burbot *Lota lota* from Bothnian Bay, Finland, were larger than 40 cm but were not developing and therefore were considered to be skipping spawning (referred to therein as a "rest year"). This group included both males and females. The presence of such large, nondeveloping individuals is suggestive of skipped spawning but should be confirmed histologically given the plastic nature of fish size and age at maturity. In another approach, Shirokova (1969) tracked cohorts of fish across multiple years, and the fact that the proportion of mature fish fluctuated substantially for the same cohort across years was used as evidence for skipped spawning. For example, the percentage of males that were "mature" among the 1958 cohort was 98% in 1961, 87% in 1962, and 97% in 1963. The decrease in maturity percentage in 1962 was interpreted as evidence for skipped spawning. M. Storr-Paulsen and J. Tomkiewicz (Technical University of Denmark, unpublished data) performed similar analyses for Atlantic cod in the Baltic Sea, but only those males that were clearly developing were considered to be potential spawners. They found that male spawning probability ogives leveled off at considerably less than 1.00: in fact, 0.75 for the western Baltic stock of Atlantic cod and 0.83 for the eastern Baltic stock. This suggests that spawning omission in certain years can be observed in males of all size-classes.

Numerous studies have demonstrated skipped spawning in both wild and experimental male winter flounder (Burton and Idler 1984, 1987a, 1987b; Burton 1991; Maddock and Burton 1994). These fish were reported to have a gonadosomatic index similar to that of recently spent fish (Burton and Idler 1987b). Macroscopically, the testes are distinguishable from developing testes by the smaller size and grayish color. Histologically, the testes of males that skip spawning are distinguished from immature testes by a thickened wall and are different from the testes of developing males in that they show sparse lobule contents with no evidence of spermatogenesis (Burton and Idler 1987b). While the overall morphology of Atlantic cod testes is much different than that of winter flounder testes, the histological description of skipped spawning appeared to be quite similar: male Atlantic cod that skipped spawning also had a very low gonadosomatic index, a thick testicular wall, and no sign of active spermatogenesis (Burton et al. 1997). Residual sperm in the sperm ducts can also sometimes be used to distinguish between mature and immature individuals (Rideout et al. 2000).

Because less work has been done with respect to the timing and energy requirements of gametogenesis in males than in females, there has been some hesitation to classify males as skipping spawning. For example, Rideout et al. (2000) observed male Atlantic cod with evidence of previous spawning (i.e., residual sperm) that were showing no spermatogenic development several months after the end of the spawning season. Although Rideout et al. (2000) acknowledged that these fish were far behind in the normal development cycle for Atlantic cod in this area (Burton et al. 1997; Rideout and Burton 2000b), they labeled the fish as "delayed" rather than skipped spawners, but did acknowledge that the latter was probably true. The reason for hesitation was based on the fact that although spermatogenesis is typically completed many months prior to spawning, the time required to develop sperm from spermatogonia was not well known and thus the authors were reluctant to say that these fish could not develop in time to spawn. Similarly, Burton et al. (1997) observed Atlantic cod testes in November that were only in the very early stages of spermatogenesis (i.e., no flagellated sperm), while other males demonstrated the species-typical pattern of having fully developed testes by this time. Burton et al. (1997) categorized these fish as delayed, although they questioned whether or not such a delay in development might be the first step towards skipped spawning.

As has been observed in females, skipped spawning in males is linked primarily with poor nutritional status. For example, an extended period of starvation resulted in skipped spawning for male winter flounder, and feeding these fish at an adequate level in the subsequent feeding period allowed them to become reproductive again for the next year (Burton 1991; Maddock and Burton 1994). The energetic requirements of reproduction may not be limited strictly to gamete development. Males, for example, may have energetic costs associated with reproductive displays and competition for mates. Energetic investment into gonad development and migration is approximately equal among male and female salmonids, but males are less likely to survive the breeding season and are less likely to exhibit repeat spawning (Hutchings 1993; Fleming 1996). The higher mortality is thought to be associated with male competition costs. Such costs may also play a role in skipped spawning by males.

SKIPPED SPAWNING IN ATLANTIC SALMON

In their attempt to summarize evidence for skipped spawning in female iteroparous fishes, Rideout et al. (2005) focused primarily on marine and freshwater species and, with the exception of citing Schaffer and Elson (1975), almost entirely overlooked anadromous species, including Atlantic salmon. This omission is significant since there may be more data available on skipped spawning for this species than for any other species. It is also significant because skipped spawning in Atlantic salmon is identified based on scale analysis rather than on the gonadal histology methods described by Rideout et al. (2005). Here, we attempt to summarize these data, and in doing so we emphasize the

reproductive plasticity of salmonids. We also briefly introduce the unique terminology and nomenclature system for classifying various salmon life history stages and reproductive patterns, including skipped spawning.

Allan and Ritter (1977) provided standard terminologies for the various life history stages of salmonids. Here, we concentrate only on those stages that are related to spawning. Salmon of any age-class that are developing to spawn for the first time (i.e., maturing) are described as "maiden spawners" or "virgin spawners," while those that are developing for a second (or subsequent) time are referred to as "previous spawners." A spent salmon is typically referred to as a "kelt," although there are differing interpretations as to how long after spawning this terminology applies. Although variations in timing do exist, most kelts overwinter in freshwater before descending to the ocean in spring (Bardonnet and Baglinière 2000). Fish that return to spawn in the same year after a short ocean residence are referred to as "consecutive spawners." Other fish may not return to spawn until the next year, electing to overwinter at sea, and these are referred to as "alternate spawners." Alternate spawning in this case is equivalent to skipped spawning since the fish in question "takes a year off" between spawnings.

There are two aspects of working with anadromous salmon that contribute to the thorough documentation of alternate spawning. The first is the fact that all migrating (i.e., reproductive) individuals can be monitored and sampled by corralling individuals through a single point in the river (e.g., counting fence) or at a hydroelectric dam bypass that is equipped with some form of live trap. The second is that a huge amount of information, including reproductive history, can be interpreted from salmon scales. Scales show seasonal differences in formation of circuli (reflective of fast growth in summer and slow growth in winter), which allow fish to be aged. In addition, growth is much higher at sea, resulting in more widely spaced annuli and the ability to determine the number of years spent in the river prior to smoltification (Figure 4). Also, salmon do not feed during their upstream spawning migration, instead relying on stored energy reserves. The lack of feeding results in some degree of scale resorption, which leaves a distinct spawning mark (Figure 4). These spawning marks can then be used to determine the reproductive history of the fish. Spawning episodes separated by one or more years at sea would suggest alternate spawning, whereas the absence of an extended marine period between spawning episodes would indicate consecutive spawning (Figure 4).

The information garnered from salmon scales is organized into a unique life history nomenclature. The actual nomenclature may vary somewhat between countries but generally follows a format similar to "$Y_R.Y_S.RH$," where Y_R represents the number of years spent in the river before smoltification and migration to the sea, Y_S represents the number of years spent at sea before returning to the river to spawn, and RH indicates the reproductive history of the fish. The nomenclature is perhaps best explained
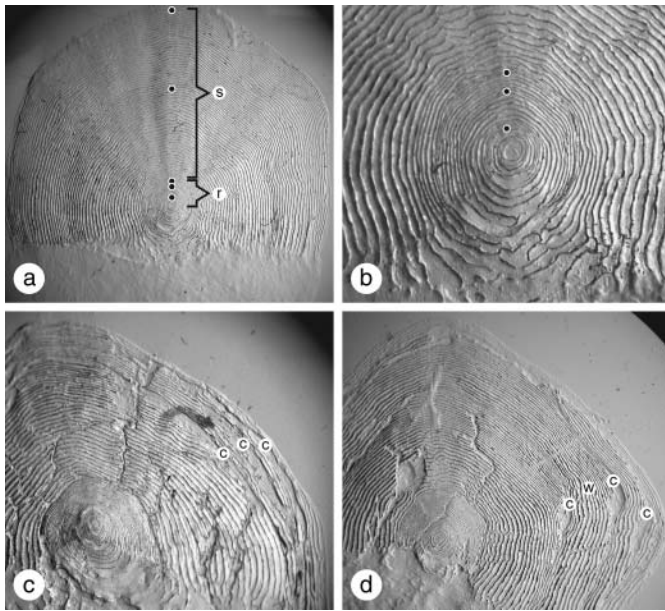
FIGURE 4.   Examples of life history information recorded in Atlantic salmon scales: **(a)** a fish that spent 3 years in the river before spending 2 years at sea (r = riverine growth; s = sea growth; distance between black dots represents 1 year of growth); **(b)** the same scale but with a higher-magnification view of riverine growth; **(c)** a fish that spawned in three consecutive years (c = spawning check); and **(d)** a fish that spent a complete year at sea between spawning for the first and second times but then spawned in consecutive years (w = winter spent at sea). Photos were provided by M. Bloom (Fisheries and Oceans Canada).

with a few examples as given below. It is important to remember that these fish are sampled during their reproductive migration, so it is assumed that they are about to spawn (i.e., are potential spawners). All of the examples listed below demonstrate different reproductive histories for fish that spent 3 years in the river followed by 1 year at sea:

3.1 = a maiden spawner;

3.1.SM = a second-time spawner, as indicated by the presence of a previous spawning mark (SM) on the scale (i.e., consecutive spawner);

3.1.SM.1 = a second-time spawner, as indicated by the presence of a previous SM on the scale, but the fish spent an additional full year at sea before returning to spawn for the second time (i.e., alternate spawner);

3.1.SM.SM = a third-time spawner, as indicated by the presence of two previous SMs in consecutive years (i.e., consecutive spawner).

The proportion of anadromous salmon that survive to spawn a second time is typically low but can be highly variable across stocks (Allan and Ritter 1977). For example, Hubley et al. (2008) reported Atlantic salmon kelt survival rates of less than 10%, Chaput and Jones (2006) reported a return rate of less than 5% for the Saint John River, and Niemela et al. (2006) reported that the proportion of repeat spawners in the River Teno was approximately 5%. In contrast, a 20–60% return rate has been reported

for some year-classes from the Miramichi River (Chaput and Jones 2006), and repeat spawners have occasionally been reported to constitute 50% or more of the fish in a river (Schaffer and Elson 1975; Moore et al. 1995) or in one or more tributaries (Niemela et al. 2006).

The amount of time required between spawning episodes (i.e., consecutive versus alternate) and the time required at sea before becoming sexually mature (i.e., the sea age) are no doubt related to the time required to attain sufficient condition to support reproduction. In Norway, reproductive costs have been reported to be greater for large Atlantic salmon than for their smaller counterparts (Jonsson et al. 1997); thus, large Atlantic salmon tend to need one full year at sea to recondition, whereas small fish may spawn annually (Jonsson et al. 1991). Of course, part of the energetic cost associated with reproduction for anadromous fish is the migration cost; therefore, aspects of a particular river system may affect a fish's reproductive strategy. Schaffer and Elson (1975) reported a link between river "harshness" (of which a major component was river size) and the interval between spawning episodes such that fish from particularly harsh rivers tended to adopt an alternate-year spawning strategy. Such is the case for the large Miramichi River, in which alternate-spawning Atlantic salmon are very common (Moore et al. 1995). On the other hand, consecutive spawning is especially common in stocks that generally spend a single winter at sea before returning to spawn, like those in Newfoundland (Klemetsen et al. 2003).

Atlantic salmon are clearly capable of a high degree of reproductive plasticity, including the ability to spawn annually or on an alternate-year schedule. Such plasticity may also be characteristic of other salmonids and not just those groups that have an anadromous life history. For example, spawning on a 2-year cycle may be the norm for northern populations of anadromous Arctic char *Salvelinus alpinus* (Dutil 1986) and for lake trout *Salvelinus namaycush* living in northern lakes (Kennedy 1954). Given the long history of studying this reproductive plasticity in Atlantic salmon, we are not suggesting a need to change terminology, but it is important to point out that "alternate spawning" and "skipped spawning" are in fact referring to the same thing. The possibility should be raised, however, that the terms "consecutive spawning" and "alternate spawning" might be mistaken as indicating fixed life history strategies, whereas it is known that salmon may switch from a strategy of spawning every 2 years to spawning every year and vice versa (Klemetsen et al. 2003; see also Figure 4d). The "skipped spawning" terminology may better reflect this degree of reproductive plasticity. Also, the term "alternate spawning" comes from the notion that fish can spawn in alternate years (i.e., 2-year interval). However, in rare cases, salmon may actually spend multiple years at sea between spawnings (E. Niemelä, Finnish Game and Fisheries Research Institute, Helsinki, personal communication), which might also question the appropriateness of the current terminology. On the other hand, it could perhaps be said that using the term "skipped spawning" implicitly suggests that individual fish should spawn

every year (or season) and that the phenomenon of not spawning every year (or season) is rare. There is no such apparent connotation with the use of the term "alternate spawning."

SKIPPED SPAWNING IN FISHES WITH INDETERMINATE FECUNDITY

A strong seasonal element exists with respect to the normal pattern of oocyte development in fishes with determinate fecundity (Murua and Saborido-Rey 2003). The reproductive period is generally limited to specific times of the year (e.g., an annual spawning season in spring), and the development of oocytes is slow such that vitellogenesis must begin several months prior to the spawning season in order to be completed in time for spawning. The time constraints on vitellogenesis mean that females without healthy secondary growth oocytes within the couple of months prior to the start of the spawning season will not be able to complete gamete development in time to spawn during the current year (or season). Such fish can be reliably categorized as skipped spawners when histological indicators of maturity status (i.e., postovulatory follicles [POFs] and a thick tunica albuginea [ovary wall]) are present.

Oocyte development in fishes with indeterminate fecundity is less temporally constrained. Such fishes tend to be characterized by a very lengthy reproductive period, sometimes with a period of major reproductive activity but also with a small proportion of spawners being observed throughout much of the remainder of the year. Extended spawning in these species is linked with the ability to continually recruit oocytes into vitellogenesis even after spawning has commenced. This oocyte development pattern and its reduced dependence on seasonality have strong implications for the fish's propensity to skip spawning and our ability to detect skipped spawning. For example, fishes with determinate fecundity have no capacity for de novo vitellogenesis once a hiatus has formed between primary growth and secondary growth oocytes in the oocyte size frequency distribution; hence, when an entire cohort of developing oocytes becomes atretic (i.e., mass atresia), there is no potential for that individual to recruit additional oocytes in order to spawn in the given year. Interpreting mass atresia and its consequences in fishes with indeterminate fecundity is much more problematic. In some cases, mass atresia of secondary growth oocytes is indicative of the cessation of spawning (Lowerre-Barbieri 1996; Torres-Villegas et al. 2007). In other cases, mass atresia might suggest a "skipped batch" of oocytes (Lowerre-Barbieri 1996). However, because of the ability of these fish to continually recruit oocytes into vitellogenesis, it is difficult to say with certainty that no more oocyte recruitment will occur (even if developing oocytes are not currently present) and, hence, that some degree of spawning will not occur (i.e., it is difficult to conclude that the fish will skip an entire reproductive cycle or season).

Identifying skipped spawning in fishes with indeterminate fecundity is complicated not only by the inability to determine whether additional oocytes will become vitellogenic and eventu-ally be spawned but also by the potential difficulty in determining the reproductive history of the fish. In coldwater fish with determinate fecundity, POFs are slow to reabsorb, sometimes persisting for many months and remaining identifiable well into the next reproductive cycle (e.g., Witthames et al. 2010). In such cases, the presence of POFs can be used not only to determine whether a fish has started spawning in the current season but also to determine whether a fish in the early to middle stages of development spawned in the previous year—something that has proven quite valuable in identifying skipped spawning (Rideout et al. 2005). In warmwater species with indeterminate fecundity, however, the POFs are highly transitory structures that disappear after only a few days (Hunter and Macewicz 1985) and are therefore only indicative of very recent spawning activity and hold no potential for determining distant (i.e., previous year) reproductive history. Figures presented by Lowerre-Barbieri et al. (2011, this special section) suggest that a thickened tunica albuginea could potentially be used to distinguish mature and immature spotted seatrout *Cynoscion nebulosus*. Likewise, Coleman et al. (1996) reported that a thick tunica albuginea could be used to suggest prior spawning activity for three shallow-water grouper species, although those authors were careful to point out that such observations were not a true confirmation of previous spawning. It is unclear whether the difference in tunica albuginea thickness between immature and mature fish increases with the number of spawning years, but the suggestion that tunica albuginea thickness increases with fish size (Holdway and Beamish 1985) is a complicating factor that should be considered.

The aforementioned difficulties in identification make the notion of skipped spawning in fishes with indeterminate fecundity a fascinating yet problematic topic. There are two primary pieces of evidence that have been used to suggest skipped spawning in indeterminate spawners. The first type of evidence is the identification of large fish with ovaries still in the regenerating stage from collections made during the major part of the spawning season. Such observations have been discussed in relation to potential skipped spawning for the wahoo *Acanthocybium solandri* (Brown-Peterson et al. 2000; Jenkins and McBride 2009), red grouper *Epinephelus morio* (Collins et al. 2002), gag *Mycteroperca microlepis* (Fitzhugh et al. 2006), and blue marlin *Makaira nigricans* (Brown-Peterson et al. 2006). Labeling such fish as potential skipped spawners is based on the premise that they should be demonstrating at least some secondary oocyte growth during the spawning season if they are going to spawn. There are two complications to this approach, however. First, as was pointed out by Lowerre-Barbieri et al. (2009), to consider such fish as having skipped spawning, the recrudescence and resorption times of yolked oocytes and spawning indicators would have to be greater than the spawning season. Lowerre-Barbieri et al. (2009) also noted that this is not the case for most warmwater species (i.e., even fish without vitellogenic oocytes could conceivably advance through vitellogenesis quickly enough to still take part in the current year's

spawning). The second complication is that although fishes with indeterminate fecundity usually demonstrate a "peak spawning season," it is often possible to observe lower levels of spawning at other times of the year. Hence, fish that exhibit regenerating ovaries when collected during the peak spawning season may have simply spawned earlier than most other fish (Collins et al. 2002).

The second type of evidence that has been used to suggest potential skipped spawning in fishes with indeterminate fecundity is the presence of large (presumably mature) individuals outside of the spawning area during the spawning season. For example, the western Atlantic population of bluefin tuna is thought to spawn in the Gulf of Mexico and the Straits of Florida from April to July, but adult-sized individuals have been reported to occur in the central Atlantic Ocean and elsewhere during this period (Lutcavage et al. 1999; Block et al. 2005). Such data might suggest skipped spawning (Lutcavage et al. 1999). Histologically, only a very small number of postmature, nonreproductive bluefin tuna have been reported (Zupa et al. 2009). However, based on a regression relationship between skipped spawning proportion and longevity for a variety of fishes, Secor (2007) predicted that 44% of bluefin tuna may skip spawning. Unfortunately, such observations of large fish outside of the spawning area during the reproductive period do not represent irrefutable evidence of skipped spawning. Perhaps these observations simply suggest the existence of previously unknown spawning areas. For example, early indications of potential skipped spawning among bluefin tuna in the Mediterranean Sea (Corriero et al. 2003) were later reconsidered with the discovery of fish spawning earlier in the year in the Levantine Sea. Lowerre-Barbieri et al. (2009) warned that to designate fish found outside the spawning area during the spawning season as skipped spawners, the time it takes the fish to migrate between these habitats must be greater than the duration of the spawning season.

The propensity for skipped spawning in fishes may also be linked with energy allocation strategies. Fishes with determinate fecundity generally use stored energy reserves to support gamete development and therefore must reduce fecundity or abandon reproductive investment completely (i.e., must skip spawning) when energy reserves become too limited to support reproduction without unduly compromising other necessary life processes. This strategy of energy allocation, in combination with slow oocyte development rates, requires reproductive decisions to be made far in advance of spawning and therefore, not surprisingly, results in skipped spawning being common among fishes with determinate fecundity (Rideout et al. 2005). Fishes with indeterminate fecundity, on the other hand, tend to be income breeders, supporting oocyte production by continual feeding. Such a strategy, along with asynchronous oocyte development, is likely to reduce the probability of skipped spawning (of an entire reproductive year), whereas "skipped batches" (along with a reduced number of batches and batch size) are more likely. These fish can abandon the most advanced oocytes during periods of poor feeding and still have smaller developing oocytes

that can be spawned if conditions improve. For example, final oocyte maturation was halted in mummichogs *Fundulus heteroclitus* that were starved for 3 d but resumed in subsequent oocyte size-classes upon resumption of feeding (Wallace and Selman 1978). For this same reason, Jenkins and McBride (2009) were careful to refer to nonspawning adult wahoos observed during the spawning season as "mature-inactive" rather than skipped spawners.

Although details of oogenesis and the pattern of energy allocation suggest that skipped spawning is less likely in fishes with indeterminate fecundity than in fishes with determinate fecundity, there is nevertheless at least some empirical evidence to support the idea that fish with indeterminate fecundity will skip spawning if conditions are not suitable. For example, Ndjaula et al. (2009) reported that European horse mackerel held in captivity completed vitellogenesis but failed to undergo oocyte maturation and spawning. This result conforms to the "retaining" form of skipped spawning, and although results from tank experiments are not always transferable to wild populations, the Ndjaula et al. (2009) study suggests that proper environmental stimuli are required for spawning to occur. Retention of vitellogenic oocytes (i.e., failure to spawn) was also noted in wild gags (Coleman et al. 1996).

OVERVIEW OF SKIPPED SPAWNING RESEARCH

The main objectives of this paper were to (1) summarize research on skipped spawning since the review by Rideout et al. (2005) was published; (2) address some of the shortcomings and oversights of that previous paper, including the potential for skipped spawning among males, fishes with indeterminate fecundity, and anadromous Atlantic salmon; and (3) address the notion that skipped spawning is an abnormal phenomenon among fishes. For this last point, we take a quick look at the publication record with respect to skipped spawning research. Bull and Shine (1979) reviewed missed reproduction opportunities among vertebrates and included data for four fish species. The Rideout et al. (2005) paper cited evidence for skipped spawning in 22 species of fish (although it has since become clear that several citations were overlooked). Since that time, data have been published with respect to skipped spawning in 13 species, 9 of which were not previously documented. When the total body of literature pertaining to skipped spawning in fishes is taken together, there is evidence for skipped spawning in at least 31 species. The list of species includes important commercial marine groundfishes (Skjæraasen et al. 2009), small pelagic fishes (Kennedy et al. 2010), large pelagic fishes (Zupa et al. 2009), deepwater species (Neves et al. 2009), freshwater species (Holmgren 2003), anadromous fishes (Schaffer and Elson 1975), and catadromous fishes (Milton and Chenery 2005). Skipped spawning is clearly a mechanism that is integrated in the reproductive strategy of a broad range of fishes.

Guidelines for identifying skipped spawning were provided by Rideout et al. (2005) in an attempt to increase interest in skipped spawning, thus prompting work to address how

common this phenomenon is among various fish species. Based on the number of papers cited by Rideout et al. (2005) and the years in which those papers were published, we estimate that the pre-2005 publication rate of papers pertaining to skipped spawning was approximately two per year. Since that time (and based on the papers cited here), papers pertaining to skipped spawning have been published at a rate of five per year. This suggests an increase in skipped spawning research since 2005. Only time will tell whether research in this area will continue to grow and what contributions will be made to our understanding of fish reproductive biology and fisheries ecology.

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REFERENCES

Allan, I. R. H., and J. A. Ritter. 1977. Salmonid terminology. Journal du Conseil International pour L'Exploration de la Mer 37:293–299.

Bardonnet, A., and J.-L. Baglinière. 2000. Freshwater habitat of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 57:497–506.

Block, B. A., L. L. H. Teo, A. Walli, A. Boustany, M. J. W. Sokesbury, C. J. Farewell, K. C. Weng, H. Dewar, and T. D. Williams. 2005. Electronic tagging and population structure of Atlantic bluefin tuna. Nature (London) 434:1121–1127.

Brown-Peterson, N. J., J. S. Franks, and A. M. Burke. 2000. Preliminary observation on the reproductive biology of wahoo, *Acanthocybium solandri*, from the Northern Gulf of Mexico and Bimini, Bahamas. Proceedings of the Gulf and Caribbean Fisheries Institute 51:414–427.

Brown-Peterson, N. J., J. S. Franks, B. H. Comyns, and J. R. McDowell. 2006. Do blue marlin spawn in the northern Gulf of Mexico? Proceedings of the Gulf and Caribbean Fisheries Institute 60:372–378.

Bucholtz, R. H., J. Tomkiewicz, and J. Dalskov. 2008. Manual to determine gonadal maturity of herring (*Clupea harengus* L.). Technical University of Denmark, National Institute of Aquatic Resources, Aqua Report 197–2008, Charlottenlund.

Bull, J. J., and R. Shine. 1979. Iteroparous animals that skip opportunities for reproduction. American Naturalist 114:296–303.

Bunnell, D. B., S. E. Thomas, and R. A. Stein. 2007. Prey resources before spawning influence gonadal investment of female, but not male, white crappie. Journal of Fish Biology 70:1838–1854.

Burton, M. P., and D. R. Idler. 1984. The reproductive cycle in winter flounder, *Pseudopleuronectes americanus* (Walbaum). Canadian Journal of Zoology 62:2563–2567.

Burton, M. P., and D. R. Idler. 1987a. An experimental investigation of the non-reproductive, post-mature state in winter flounder. Journal of Fish Biology 30:643–650.

Burton, M. P., and D. R. Idler. 1987b. Variability of reproductive status in a population of *Pseudopleuronectes americanus*. Pages 207–212 *in* S. O. Kullander and B. Fernaholm, editors. Proceedings of the 5th Congress of European ichthyologists. Swedish Museum of Natural History, Stockholm.

Burton, M. P. M. 1991. Induction and reversal of the non-reproductive state in winter flounder, *Pseudopleuronectes americanus* Walbaum, by manipulating food availability. Journal of Fish Biology 39:909–910.

Burton, M. P. M., R. M. Penney, and S. Biddiscombe. 1997. Time course of gametogenesis in northwest Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 54(Supplement 1):122–131.

Chaput, G., and R. Jones. 2006. Reproductive rates and rebuilding potential for two multi-sea-winter Atlantic salmon (*Salmo salar* L.) stocks of the Maritime Provinces. Canadian Science Advisory Secretariat (CSAS) Research Document, 2006/027, Ottawa.

Coleman, F. C., C. C. Koenig, and L. A. Collins. 1996. Reproductive styles of shallow-water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. Environmental Biology of Fishes 47:129–141.

Collins, L. A., G. R. Fitzhugh, L. A. Lombardi-Carlson, H. M. Lyon, W. T. Walling, and D. W. Oliver. 2002. Characterization of red grouper (Serranidae: *Epinephelus morio*) reproduction from the eastern Gulf of Mexico. NOAA Fisheries, Panama City Laboratory Contribution Series 2002-07 Available: www.sefsc.noaa.gov/sedar/. (February 2011).

Corriero, A., S. Desantis, M. Deflorio, F. Acone, C. R. Bridges, J. M. de la Serna, P. Megalofonou, and G. De Metrio. 2003. Histological investigation on the ovarian cycle of the eastern Atlantic bluefin tuna (*Thunnus thynnus* L.). Journal of Fish Biology 63:108–119.

Dutil, J. D. 1986. Energetic constraints and spawning interval in the anadromous Arctic charr (*Salvelinus alpinus*). Copeia 1986:945–955.

Engelhard, G. H., and M. Heino. 2005. Scale analysis suggests frequent skipping of the second reproductive season in Atlantic herring. Biology Letters 1:172–175.

Engelhard, G. H., and M. Heino. 2006. Climate change and condition of herring (*Clupea harengus*) explain long-term trends in extent of skipped reproduction. Oecologia 149:593–603.

Fischer, B., B. Taborsky, and U. Dieckmann. 2009. Unexpected patterns of plastic energy allocation in stochastic environments. American Naturalist 173:108–120.

Fitzhugh, G. R., H. M. Lyon, L. A. Collins, W. T. Walling, and L. A. Lombardi-Carlson. 2006. Update of gag (*Mycteroperca microlepis*) reproductive parameters: eastern Gulf of Mexico, SEDAR 10 data workshop. NOAA Fisheries, Panama City Laboratory Contribution Series 05-06. Available: www.sefsc.noaa.gov/sedar/. (February 2011).

Fleming, I. A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. Reviews in Fish Biology and Fisheries 6:379–416.

Gunnarsson, Á., E. Hjörleifsson, K. Thórarinsson, and G. Marteinsdottir. 2006. Growth, maturity and fecundity of wolffish *Anarhichas lupus* L. in Icelandic waters. Journal of Fish Biology 68:1158–1176.

Holdway, D. A., and F. W. H. Beamish. 1985. The effect of growth rate, size, and season on oocyte development and maturity of Atlantic cod (*Gadus morhua* L.). Experimental Marine Biology and Ecology 85:3–19.

Holmgren, K. 2003. Omitted spawning in compensatory-growing perch. Journal of Fish Biology 62:918–927.

Hubley, P. B., P. G. Amiro, A. J. F. Gibson, G. L. Lacroix, and A. M. Redden. 2008. Survival and behaviour of migrating Atlantic salmon (*Salmo salar* L.) kelts in river, estuarine, and coastal habitat. ICES (International Council for the Exploration of the Sea) Journal of Marine Science 65:1626–1634.

Hunter, J. R., and B. J. Macewicz. 1985. 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, N. 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.

Hüssy, K., B. Nielsen, H. Mosegaard, and L. W. Clausen. 2009. Using data storage tags to link otolith macrostructure in Baltic cod *Gadus morhua* with environmental conditions. Marine Ecology Progress Series 378:161–170.

Hutchings, J. A. 1993. Adaptive life histories effected by age-specific survival and growth rate. Ecology 74:673–684.

Jager, H. I., K. A. Rose, and A. Vila-Gispert. 2008. Life history correlates and extinction risk of capital-breeding fishes. Hydrobiologia (Heidelberg) 602:15–25.

Jenkins, K. L. M., and R. S. McBride. 2009. Reproductive biology of wahoo, *Acanthocybium solandri*, from the Atlantic coast of Florida and the Bahamas. Marine and Freshwater Research 60:893–897.

Johnston, F. D., and J. R. Post. 2009. Density-dependent life-history compensation of an iteroparous salmonid. Ecological Applications 19:449–467.

Jonsson, N., L. P. Hansen, and B. Jonsson. 1991. Variation in age, size and repeat spawning of adult Atlantic salmon in relation to river discharge. Journal of Animal Ecology 60:937–947.

Jonsson, N., B. Jonsson, and L. P. Hansen. 1997. Changes in proximate composition and estimates of energetic costs during upstream migration and spawning in Atlantic salmon *Salmo salar*. Journal of Animal Ecology 66:425–436.

Jørgensen, C., B. Ernande, Ø. Fiksen, and U. Dieckmann. 2006. The logic of skipped spawning in fish. Canadian Journal of Fisheries and Aquatic Sciences 63:200–211.

Kennedy, J., J. E. Skjæraasen, R. D. M. Nash, A. Thorsen, A. Slotte, T. Hansen, and O. S. Kjesbu. 2010. Do capital breeders like Atlantic herring (*Clupea harengus* L.) exhibit sensitive periods of nutritional control on ovary development and fecundity regulation? Canadian Journal of Fisheries and Aquatic Sciences 67:16–27.

Kennedy, J., P. R. Witthames, R. D. M. Nash, and C. J. Fox. 2008. Is fecundity in plaice (*Pleuronectes platessa* L.) down-regulated in response to reduced food intake during autumn? Journal of Fish Biology 72:78–92.

Kennedy, W. A. 1954. Growth, maturity and mortality in the relatively unexploited lake trout, *Cristivomer namaycush*, of Great Slave Lake. Journal of the Fisheries Research Board of Canada 11:827–852.

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. Blackwell Scientific Publications, Oxford, UK.

Kjesbu, O. S., J. Klungsøyr, H. Kryvi, P. R. Witthames, and M. Greer Walker. 1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. Canadian Journal of Fisheries and Aquatic Sciences 48:2333–2343.

Klemetsen, A., P.-A. Amundsen, J. B. Dempson, B. Jonsson, N. Jonsson, M. F. O'Connell, and E. Mortensen. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish 12:1–59.

Kurita, Y., S. Meier, and O. S. Kjesbu. 2003. Oocyte growth and fecundity regulation by atresia of Atlantic herring (*Clupea harengus*) in relation to body condition throughout the maturation cycle. Journal of Sea Research 49:203–219.

Loher, T., and A. C. Seitz. 2008. Characterization of active spawning season and depth for eastern Pacific halibut (*Hippoglossus stenolepis*) and evidence of probable skipped spawning. Journal of Northwest Atlantic Fishery Science 41:23–36.

Lowerre-Barbieri, S. K. 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. 2011. 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. K., N. Henderson, J. Llopiz, S. Walters, J. Bickford, and R. Muller. 2009. Defining a spawning population (spotted seatrout *Cynoscion nebulosus*) over temporal, spatial, and demographic scales. Marine Ecology Progress Series 394:231–245.

Lutcavage, M., R. Brill, G. Skomal, B. Chase, and P. Howey. 1999. Results of pop-up satellite tagging on spawning size class fish in the Gulf of Maine. Do North Atlantic bluefin tuna spawn in the mid-Atlantic? Canadian Journal of Fisheries and Aquatic Sciences 56:173–177.

Maddock, D. M., and M. P. M. Burton. 1994. Some effects of starvation on the lipid and skeletal muscle layers of the winter flounder, *Pleuronectes americanus*. Canadian Journal of Zoology 72:1672–1679.

Milton, D. A., and S. R. Chenery. 2005. Movement patterns of barramundi *Lates calcarifer*, inferred from ^{87}Sr/^{86}Sr and Sr/Ca ratios in otoliths, indicate non-participation in spawning. Marine Ecology Progress Series 301:279–291.

Moore, D. S., G. J. Chaput, and P. R. Pickard. 1995. The effects of fisheries on the biological characteristics and survival of mature Atlantic salmon (*Salmo salar*) from the Miramichi River. Canadian Special Publication of Fisheries and Aquatic Sciences 123:229–247.

Morgan, M. J., and R. M. Rideout. 2005. A preliminary examination of spawning suppression in relation to recruitment in NAFO subdivision 3Ps cod (*Gadus morhua*). Canadian Science Advisory Secretariat (CSAS) Research Document, 2005/085, Ottawa.

Mukhin, V. A., E. A. Filina, Y. A. Serba, and I. N. Mukhina. 2006. Physiological-biochemical aspects of omission of the spawning period in the Barents Sea cod *Gadus morhua*. Journal of Evolutionary Biochemistry and Physiology 42:292–298.

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

Ndjaula, H. O. N., T. Hansen, M. Krüger-Johnsen, and O. S. Kjesbu. 2009. Oocyte development in captive Atlantic horse mackerel *Trachurus trachurus*. ICES (International Council for the Exploration of the Sea) Journal of Marine Science 66:623–630.

Neves, A., A. R. Vieira, I. Farias, I. Figueiredo, V. Sequeira, and L. S. Gordo. 2009. Reproductive strategies in black scabbardfish, *Aphanopus carbo* (Teleostei: Trichiuridae). Scientia Marina 73(Supplement 2):19–31.

Niemela, E., J. Erkinaro, M. Julkunen, E. Hassinen, M. Länsman, and S. Brørs. 2006. Temporal variation in abundance, return rate and life histories of previously spawned Atlantic salmon in a large subarctic river. Journal of Fish Biology 68:1222–1240.

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.

Pulliainen, E., and K. Korhonen. 1990. Seasonal changes in condition indices in adult mature and non-maturing burbot, *Lota lota* (L.), in the northeastern Bothnian Bay, northern Finland. Journal of Fish Biology 36:251–259.

Ramsay, K., and P. Witthames. 1996. Using oocyte size to assess seasonal ovarian development in *Solea solea* (L.). Journal of Sea Research 36:275–283.

Rideout, R. M., and M. P. M. Burton. 2000a. Peculiarities in ovarian structure leading to multiple-year delays in oogenesis and possible senescence in Atlantic cod, *Gadus morhua* L. Canadian Journal of Zoology 78:1840–1844.

Rideout, R. M., and M. P. M. Burton. 2000b. The reproductive cycle of male Atlantic cod (*Gadus morhua* L.) from Placentia Bay, Newfoundland. Canadian Journal of Zoology 78:1017–1025.

Rideout, R. M., M. P. M. Burton, and G. A. Rose. 2000. Observations on mass atresia and skipped spawning in northern Atlantic cod, from Smith Sound, Newfoundland. Journal of Fish Biology 57:1429–1440.

Rideout, R. M., M. J. Morgan, and G. R. Lilly. 2006. Variation in the frequency of skipped spawning in Atlantic cod (*Gadus morhua*) off Newfoundland and

Labrador. ICES (International Council for the Exploration of the Sea) Journal of Marine Science 63:1101–1110.

Rideout, R. M., and G. A. Rose. 2006. Suppression of reproduction in Atlantic cod (*Gadus morhua* L.). Marine Ecology Progress Series 320:267–277.

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

Ruehl-Fehlert, C., C. Bomke, M. Dorgerloh, X. Palazzi, and M. Rosenbruch. 2005. Pleistophora infestation in fathead minnows, *Pimephales promelas* (Rafinesque). Journal of Fish Diseases 28:629–637.

Saborido-Rey, F. 1997. Sexual maturity and spawning biomass of the cod stock on Flemish Cap (Division 3M). Northwest Atlantic Fisheries Organization, Scientific Council Research Document 97/18, Dartmouth, Canada.

Schaffer, W. M., and P. F. Elson. 1975. The adaptive significance of variations in life history among local populations of Atlantic salmon in North America. Ecology 56:577–590.

Schwindt, A. R., M. L. Kent, L. K. Ackerman, S. L. M. Simonich, D. H. Landers, T. Blett, and C. B. Schreck. 2009. Reproductive abnormalities in trout from western U.S. national parks. Transactions of the American Fisheries Society 138:522–531.

Secor, D. H. 2007. Do some Atlantic bluefin tuna skip spawning? ICCAT (International Commission for the Conservation of Atlantic Tunas) Collective Volume of Scientific Papers 60:1141–1153 (Madrid.)

Secor, D. H. 2008. Influence of skipped spawning and misspecified reproductive schedules on biological reference points in sustainable fisheries. Transactions of the American Fisheries Society 137:782–789.

Secor, D. H., and P. M. Piccoli. 2007. Oceanic migration rates of upper Chesapeake Bay striped bass (*Morone saxatilis*), determined by otolith microchemical analysis. U.S. National Marine Fisheries Service Fishery Bulletin 105: 62–73.

Shirokova, M. Y. 1969. The sexual maturation rate of the generations of Baltic cod taken from 1961–63. Atlanticeskii Nauchno-Issledovatel'skii Institut Rybnogo Khoziaistva i Okeanografii Trudy Kaliningrad 21:37–44.

Skjæraasen, J. E., J. Kennedy, A. Thorsen, M. Fonn, B. N. Strand, I. Mayer, and O. S. Kjesbu. 2009. Mechanisms regulating oocyte recruitment and skipped spawning in Northeast Arctic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 66:1582–1596.

Sullivan, K. J., and P. L. Cordue. 1992. Stock assessment of hoki for the 1992–93 fishing year. New Zealand Fisheries Assessment, Research Document 92/12.

Tomkiewicz, J., M. J. Morgan, J. Burnett, and F. Saborido-Rey. 2003a. Available information for estimating reproductive potential of Northwest Atlantic groundfish stocks. Journal of Northwest Atlantic Fishery Science 33:1–21.

Tomkiewicz, J., L. Tybjerg, N. Holm, A. Hansen, C. Broberg, and E. Hansen. 2002. Manual to determine gonadal maturity of Baltic cod. Danish Institute for Fisheries Research, DFU-116-02, Charlottenlund.

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

Torres-Villegas, J. R., R. I. Ocha-Baez, L. Perezgomez, and G. Garcia-Melgar. 2007. Major atresia assessment in the Pacific sardine (*Sardinops sagax*) in the 1999–2000 reproductive season, off Bahia Magdalena, Mexico. Revista de Biologia Marina y Oceanografia 42:299–310.

Tyler, C. R., and J. P. Sumpter. 1996. Oocyte growth and development in teleosts. Reviews in Fish Biology and Fisheries 6:287–318.

Wallace, R., and K. Selman. 1978. Oogenesis in *Fundulus heteroclitus*. 1. Preliminary observations on oocyte maturation in vivo and in vitro. Developmental Biology 62:354–369.

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

Williams, A. J., C. R. Davies, and B. D. Mapstone. 2006. Regional patterns in reproductive biology of *Lethrinus miniatus* on the Great Barrier Reef. Marine and Freshwater Research 57:403–414.

Witthames, P. R., A. Thorsen, and O. S. Kjesbu. 2010. The fate of vitellogenic follicles in experimentally monitored Atlantic cod *Gadus morhua* (L.): application to stock assessment. Fisheries Research 104:24–37.

Wuenschel, M. J., K. W. Able, and D. Byrne. 2009. Seasonal patterns of winter flounder *Pseudopleuronectes americanus* abundance and reproductive condition on the New York Bight continental shelf. Journal of Fish Biology 74:1508–1524.

Zupa, R., A. Corriero, M. Deflorio, N. Santamaria, D. Spedicato, C. Marano, M. Losurdo, C. R. Bridges, and G. D. Metrio. 2009. A histological investigation of the occurrence of non-reproductive female bluefin tuna *Thunnus thynnus* in the Mediterranean Sea. Journal of Fish Biology 75:1221–1229.