Review of size- and age-dependence in batch spawning: implications for stock assessment of fish species exhibiting indeterminate fecundity

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Abstract—Most assessments of fish stocks use some measure of the reproductive potential of a population, such as spawning biomass. However, the correlation between spawning biomass and reproductive potential is not always strong, and it likely is weakest in the tropics and subtropics, where species tend to exhibit indeterminate fecundity and release eggs in batches over a protracted spawning season. In such cases, computing annual reproductive output requires estimates of batch fecundity and the annual number of batches—the latter subject to spawning frequency and duration of spawning season. Batch fecundity is commonly measured by age (or size), but these other variables are not. Without the relevant data, the annual number of batches is assumed to be invariant across age. We reviewed the literature and found that this default assumption lacks empirical support because both spawning duration and spawning frequency generally increase with age or size. We demonstrate effects of this assumption on measures of reproductive value and spawning potential ratio, a metric commonly used to gauge stock status. Model applications showed substantial sensitivity to age dependence in the annual number of batches. If the annual number of batches increases with age but is incorrectly assumed to be constant, stock assessment models would tend to overestimate the biological reference points used for setting harvest rates. This study underscores the need to better understand the age- or size-dependent contrast in the annual number of batches, and we conclude that, for species without evidence to support invariance, the default assumption should be replaced with one that accounts for age- or size-dependence.

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The relationship between reproductive output and subsequent recruitment of new individuals is fundamental to population dynamics. In stock assessments, this relationship is typically quantified by using a spawner–recruit model. Such models were originally developed with population fecundity as the measure of spawners, but most current applications use spawning biomass, calculated as the total weight of mature females (Rothschild and Fogarty, 1989). A critical assumption with this approach is that spawning biomass accurately represents the reproductive potential of a stock. However, this assumption does not always hold (Trippel, 1999; Marshall et al., 2003, 2006) and, when violated, can inject error into assessment models and subsequent management advice (Rothschild and Fogarty, 1989; Murawski et al., 2001; Scott et al., 2006). Thus, recognition is growing for the need to integrate more reproductive biology into stock assessments by replacing spawning biomass with more accurate measures of reproductive potential (Trippel, 1999; Morgan, 2008; Witthames and Marshall, 2008).

Much of the work to date on reproductive potential and stock assessments comes from investigations on gadoids, pleuronectids, and other high-latitude species that typically have determinate fecundity patterns (Trippel, 1999; Murawski et al., 2001; Morgan, 2008; Witthames and Marshall, 2008; Morgan et al., 2009). Fewer studies have been conducted on fish species with indeterminate fecundity, in part because the data requirements can be more daunting (Lowerre-Barbieri et al., 2011a, 2011b). Many warm-water marine species from the subtropics (latitudes <40°) spawn multiple batches per year, usually over a protracted spawning season. For example, species off the southeastern United States typically spawn several times within a 3–4 month duration (Cuellar et al., 1996; McGovern et al., 1998; Waggy et al., 2006). Near the tropics, spawning seasons are even longer and often associated with peak (but variable) activity when local conditions favor transport and survival of offspring (Johannes, 1978; Thresher, 1984). Such extended patterns of spawning, or extended readiness to spawn, are typical of indeterminate spawners with asynchronous oocyte development patterns (Hunter et al., 1985; Murua et al., 2003). Although many species that exhibit determinate fecundity also spawn in batches, quantifying annual fecundity for indeterminate spawners requires estimates of batch fecundity (i.e., eggs per batch) and number of batches per year, each as a function of parental age or size (Murua et al., 2003). Estimating the number of batches per year requires knowledge about spawning season duration and spawning frequency within the season (or average time between batches), including any temporal patterns of that frequency (Murua et al., 2003). Then, annual fecundity of indeterminate species can be calculated as the product of the number of eggs per batch and the number of batches per year.

Estimation of batch fecundity by age is relatively straightforward (Porch et al., 2007). In fact, these estimates tend to relate linearly to body weight, and this relationship has been the rationale for the use of spawning biomass as a proxy for total egg production. However, estimation of spawning season duration and spawning frequency by size or age is much more difficult. Despite recognition from individual studies that frequency and duration of spawning may increase with age and size (Lowere-Barbieri et al., 2011a), much of this information is lacking for many species. Without information, the typical default assumption in stock assessment is that both spawning duration and frequency are invariant across age. Widespread application of this assumption of invariance raises 2 key questions. Is the assumption justified? If not, what are the consequences for stock assessment and resulting management advice? We address the first question through a review of the literature and the second one by modeling effects of age-dependent spawning activity (annual number of batches) on spawning potential ratio (Goodyear, 1993; Shertzer et al., 2008) and reproductive value (both of these metrics are defined in the next section).

Materials and methods

Review of scientific literature—spawning frequency and duration

To examine whether or not age and size effects on spawning duration and frequency were common, we reviewed scientific literature on fishes, including aquaculture studies that investigated natural spawning (nonhormonally induced), as well as field studies. Although most of these studies were of marine species, freshwater species were not excluded from this review. In addition, our search included species not necessarily classified as indeterminate spawners because relatively few studies distinguish fecundity pattern (Murua et al., 2003). Our review proceeded in 2 stages. First, we selected articles in which batch spawning frequency was examined, either as spawning fraction (proportion of mature fish actively spawning), number of batches within a fixed time period, or average time interval between batches. From these articles, we further narrowed the list to those that reported the relationship (or lack thereof) between spawning frequency and age or size. Second, we selected articles in which spawning duration was examined by age or size. Numerous articles reported the season or duration of spawning, but duration by age or size was examined in relatively few of them. Thus, in this second review, we did not restrict our search to batch spawners; instead, we noted any study that reported spawning duration by age or size.

Implications for stock assessment and management

To examine how the age-dependent annual number of batches affects stock assessment results and management advice, we used classical per-recruit analyses (Shertzer et al., 2008) of spawning potential ratio and reproductive value. Standard fishery equations described equilibrium abundance of females at age (N_a), weight at age (W_a), maturity at age (m_a), fecundity at age of mature fish (f_a), and selectivity of fishing gear (s_a) (Table 1). These analyses are "per recruit" by virtue of scaling to an initial abundance of one (N_1=1). To populate our model with parameter values representing warm-water marine fishes, we used average life-history characteristics reported for the Gulf of Mexico (Table 2). Fishes of this region tend to be characterized by indeterminate fecundity and batch spawning, in contrast to fishes from higher latitudes where determinate fecundity is more common.

Annual fecundity at age was determined as the product of eggs produced per batch (assumed to be proportional to body weight) and the annual number of batches, which implicitly accounted for joint effects of spawning frequency and spawning duration. The annual number of batches at age followed 1 of 4 qualitative patterns: constant, increasing, decreasing, or dome shaped (Fig. 1A). To create these patterns, we first set the constant pattern to a value of 1, and then we scaled the remaining patterns such that the 4 patterns had equal integration (i.e., area under the curve). Although not all these patterns were prevalent in the literature review, we included all for completeness and comparison. In this article, we report spawning potential ratio and reproductive value across these 4 patterns.

Spawning potential ratio Spawning potential ratio (Goodyear, 1993; Shertzer et al., 2008) was computed by using standard fishery equations (Table 1):

$$\Psi_F = \phi_F / \phi_0 . \tag{1}$$

The numerator (ϕ_F) of this ratio quantified expected reproductive output (e.g., fecundity) per recruit under fishing rate F,

$$\phi_F = \sum_{a=1}^{A_{\max}} f_a m_a N_a , \tag{2}$$

Table 1

Model equations used in our per-recruit analysis of spawning potential ratio and reproductive value.

Equation	Description
$N_1 = 1$ $N_{a+1} = N_a e^{-(s_a F + M)}$	Equilibrium number of females (N_a) per recruit at age a—a function of selectivity at age (s_a), fishing mortality rate (F), and natural mortality rate (M)
$s_a = \frac{1}{1+e^{-(\rho_s(a-A_s))}}$	Selectivity at age—a logistic function characterized by a slope parameter (ρ_s) and age of 50% selectivity (A_s)
$m_a = \frac{1}{1+e^{-(\rho_m(a-A_m))}}$	Maturity at age (m_a)—a logistic function characterized by a slope parameter (ρ_m) and age of 50% maturity (A_m)
$W_a = \left[L_\infty\left(1-e^{-Ka}\right)\right]^\tau$	Weight at age (W_a)(von Bertalanffy, 1938)—a function of asymptotic length (L_∞), somatic growth parameter (K), and an exponent (τ) relating length to weight
$b_a^i = c_i\left(\frac{1}{1+e^{-\left(\rho_1(a-A_b)+\rho_2(a-A_b)^2\right)}}\right)$	Annual number of batches spawned at age (b_a) per mature female—a function of 3 parameters (ρ_1, ρ_2, A_b), scaled by a constant c_i so that the area under the curve is the same for each spawning pattern i (Fig. 1)
$f_a^i = b_a^i W_a$	Annual fecundity at age (f_a) per mature female of spawning pattern i. Batch fecundity was assumed to be proportional to body weight

Table 2

Model parameters used in the per-recruit analysis of spawning potential ratio and reproductive value. Means of values reported for Gulf of Mexico reef fishes are taken from Table 1 of Farmer et al.[1], excluding sand perch (*Diplectrum formosum*) because of an apparent error and deepwater tilefishes and groupers because they inhabit waters typically colder than the waters of tropical and subtropical species.

Parameter	Value	Description	Source
A_{max}	22	Maximum age; ages modeled are 1, 2,…, A_{max}	Farmer et al.[1]
M	$M = 4.22/A_{max} = 0.19$	Natural mortality rate	Hewitt and Hoenig, 2005
F	Range [0.0, 0.6]	Fishing mortality rate	Independent variable
L_∞	1.0	Asymptotic length	Assumed
K	0.19	Somatic growth parameter	Farmer et al.[1]
τ	3.0	Exponent relating body length to weight	Assumed
A_m	3.16	Age of 50% maturity	Farmer et al.[1]
A_s	$A_S = A_{max}/4 = 5.5$	Age of 50% selectivity	Assumed
ρ_m, ρ_s	1.0	Slope of logistic maturity or selectivity, respectively	Assumed
ρ_1, ρ_2, A_b for $i = 1$	∞, ∞, 0.0	Spawning frequency constant with age	Control variables
ρ_1, ρ_2, A_b for $i = 2$	0.5, 0.0, $A_{max}/2$	Spawning frequency increases with age	Control variables
ρ_1, ρ_2, A_b for $i = 3$	–0.5, 0.0, $A_{max}/2$	Spawning frequency decreases with age	Control variables
ρ_1, ρ_2, A_b for $i = 4$	0.5, –0.05, $A_{max}/4$	Spawning frequency dome-shaped with age	Control variables

[1] Farmer, N. A., R. P. Malinowski, and M. F. McGovern. 2010. Species groupings for management of the Gulf of Mexico reef fish fishery. NOAA, NMFS, SERO-LAPP-2010-03 Rep., 32 p.

where f_a = annual fecundity at age a (the product of batch fecundity and number of batches per year);
m_a = maturity at age; and
N_a = relative abundance at age, discounted through time by natural mortality and fishing rates (Table 1).

The denominator (ϕ_0) of this ratio was similarly computed, but with N_a discounted only by natural mortality. Thus, Ψ_F measured effects of fishing on the expected reproductive output per recruit relative to the output under no fishing. It decreased with increased fishing rate.

Spawning potential ratio was suggested conceptually by Goodyear (1977), and its use remains widely

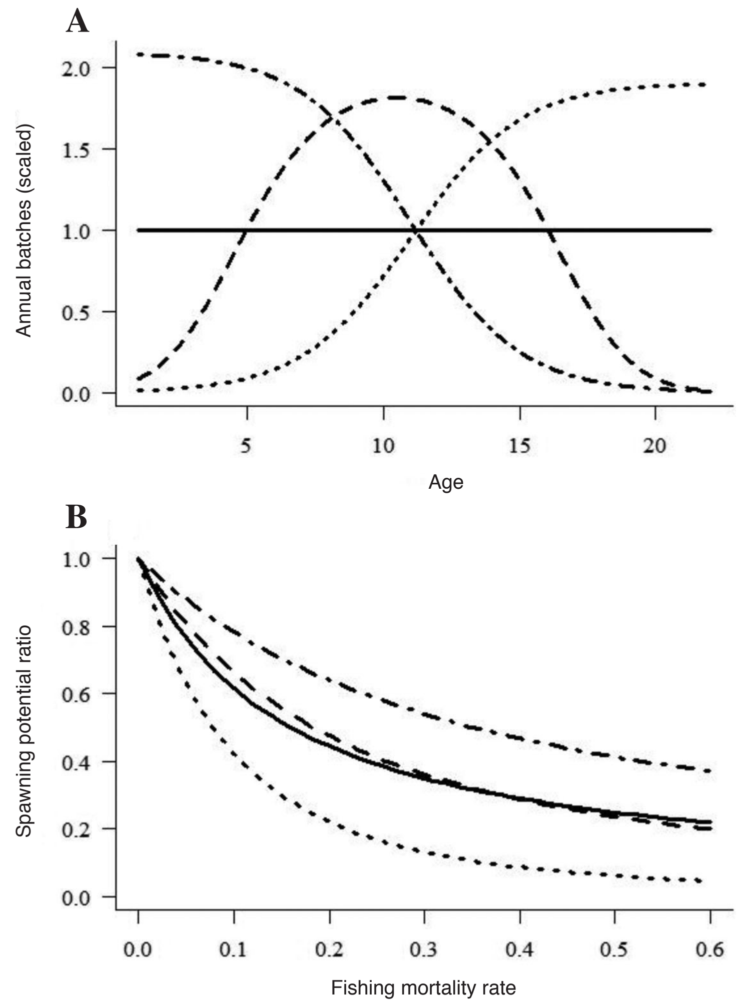

Figure 1

(**A**) Annual number of batches spawned per mature female, based on 4 qualitative patterns used in our per-recruit analysis of spawning potential and reproductive value: constant (i=1, solid line), increasing (i=2, dotted line), decreasing (i=3, dash-dot line), and dome-shaped (i=4, dashed line). (**B**) Spawning potential ratio as a function of fishing mortality rate. Model equations and parameters are given in Tables 1 and 2 respectively.

popular in stock assessments for 2 reasons. First, data requirements are low relative to other age-structured assessment approaches; for example, computation does not depend on a spawner–recruit relationship. Second, the spawning potential ratio can provide biological reference points for fishery management (Caddy and Mahon, 1995), in particular for a target fishing rate $F_{X\%}$. The fishing rate $F_{X\%}$ is defined as the F that provides $X\%$ of reproductive output per recruit relative to the unfished output level (i.e., spawning potential ratio expressed as a percentage). In many cases, $F_{X\%}$ is used as a proxy for the F associated with maximum sustainable yield (F_{MSY}). Mace (1994) suggested a default proxy of $F_{40\%}$ when the spawner–recruit relationship is unknown; however, the appropriate level of $X\%$ will depend on life-history and fishery characteristics (Clark, 2002; Williams and Shertzer, 2003; Brooks et al., 2009).

Reproductive value Reproductive value (V_a) measures the age-dependent contribution to population growth by combining survivorship and fecundity, the 2 life-history elements crucial to fitness. The concept of reproductive value has been applied most commonly to examine life-history evolution (Goodman, 1982; Stearns, 1992), but it also has been suggested as useful in the context of fishery management (MacArthur, 1960; Ware, 1985; Xu et al., 2012). For example, MacArthur (1960) argued that the highest harvest rates can be achieved by removing first those ages with the lowest reproductive value. For our purposes, we use reproductive value to demonstrate the importance of older fish toward population growth and to quantify how that importance depends on the pattern of annual number of batches.

We computed reproductive value of a stationary population as the expected number of offspring produced by an individual from age a until the end of the lifespan ($A_{\max}$):

$$V_a = \sum_{x=a}^{A_{\max}} \frac{l_x}{l_a} g_x, \tag{3}$$

where l_x = the probability that an individual survives to age x; and
g_x = the mean number of offspring produced by an individual of age x (Stearns, 1992), here the product of annual fecundity and maturity.

Because this analysis was conducted on a per-recruit basis, l_x was equivalent to N_a of Table 1. The term l_x/l_a was the probability of surviving to age x conditional on having survived to age a. To examine implications for optimal management strategies, we computed V_a across a range of fishing rates. For each of the 4 qualitative patterns in annual spawning frequency, we report V_a in the absence of fishing in addition to the age for which V_a was maximized as a function of fishing rate.

Results

Review of the literature—spawning frequency and duration

In our review of spawning frequency, we found 208 articles that reported multiple batches and indicated some information about the frequency or number of batches occurring within a specified time period. Only 20% (41 articles, 34 species) presented findings about spawning frequency related to age or size (Table 3). Of this subset, most (28 articles, 21 species) reported increases of spawning frequency with age or size. Some (9 articles, 9 species) reported no effect, but several of these articles cautioned about lack of power. Only 4 articles (4 species) indicated a decrease in spawning frequency with age or size.

We found that if we tried to restrict our review of spawning frequency to stocks or species that exhibit indeterminate fecundity, we would have had a challenging task. Of the articles (n=208) reporting some information about spawning frequency, only 52 were explicit about fecundity type or oocyte development pattern, and most (38) of them indicated an indeterminate type. Of the 41 articles reporting a spawning frequency trend by size or age, 10 indicated a fecundity type and 7 reported an indeterminate type.

In our review of spawning duration, we found 33 articles (28 species) that reported results related to age or size (Table 4). Of these articles, most (28 articles, 23 species) of them reported increased spawning duration with age or size. Several articles noted no change (5 articles, 5 species). None of them mentioned a decreased duration with age or size.

Implications for stock assessment and management

Across all levels of fishing, spawning potential ratio was highest when batch production decreased with age and lowest when it increased with age (Fig. 1B). Therefore, an incorrect assumption about annual batch production could lead to substantial bias in biological reference points and consequently in resulting management advice. For example, in this model, $F_{40\%}$ equals 0.24 for age-invariant batch production, $F_{40\%}$ equals 0.11 for increasing production, $F_{40\%}$ equals 0.53 for decreasing production, and $F_{40\%}$ equals 0.26 for dome-shaped production. If the actual pattern was that of increasing batch production but was incorrectly assumed to be age invariant, the estimated $F_{40\%}$ would be biased high by 118%.

As with spawning potential ratio, reproductive value was sensitive to the spawning pattern. In the absence of fishing, older females were considerably more important to population growth in cases of constant or increasing batch production than in cases of decreasing or dome-shaped batch production (Fig. 2A). For example, with the increasing pattern, reproductive value exceeded a value of 5 and was maximized near age 14, indicating that a fish of that age can produce more than 5 times the number of offspring throughout its remaining lifespan than can a fish of age 1. With the decreasing pattern, the maximum reproductive value was less than twice the value of fish at age 1 and occurred near age 6. As the rate of fishing increased, the age of maximum reproductive value shifted toward older fishes in each case but did so more quickly and to much older ages in cases of constant or increasing batch production (Fig. 2B). This result highlights the importance of older individuals for population growth.

Discussion

Our review of literature on batch spawning revealed that most studies have not examined, or at least have not reported, size- or age-dependent effects. In those studies where spawning frequency was examined, the majority of species (62%) were found to spawn more often with increasing age or size. Similarly, in those studies where spawning duration was examined, the majority of species (82%) were found to spawn over a longer duration with increasing age or size. These patterns of increasing spawning frequency and duration were common but not universal. Several studies found no discernible change with age or size, and patterns of decreases with age or size appeared to be rare. Although 1 of 2 articles on Atlantic cod (*Gadus morhua*) found spawning frequency to decrease with age (Kjesbu et al., 1996), that article

Table 3

Patterns of spawning frequency by age or size based on a review of spawning frequency within the scientific literature on fish reproduction.

Spawning frequency	Species	Reference(s)
Increases with size or age	*Atherina boyeri* (sand smelt, Atherinidae)	Tomasini et al., 1996
	Cynoscion nebulosus (spotted seatrout, Sciaenidae)	Crabtree and Adams[1]; Roumillat and Brouwer, 2004; Brown-Peterson, 2003; Lowerre-Barbieri et al., 2009
	Danio rerio (zebra danio, Cyprinidae)	Uusi-Heikkilä et al., 2010
	Engraulis mordax (northern anchovy, Engraulidae)	Parrish et al., 1986
	Engraulis ringens (Peruvian anchoveta, Engraulidae)	Claramunt et al., 2004, 2007
	Gasterosteus aculeatus (threespine stickleback, Gasterosteidae)	Wootton, 1973
	Hemiramphus brasiliensis (ballyhoo, Hemiramphidae)	McBride and Thurman, 2003
	Limanda aspera (yellowfin sole, Pleuronectidae)	Nichol and Acuna, 2001
	Lutjanus campechanus (red snapper, Lutjanidae)	Collins et al., 2001
	Melanogrammus aeglefinus (haddock, Gadidae)	Trippel and Neil, 2004
	Merluccius hubbsi (Argentine hake, Merlucciidae)	Macchi et al., 2004
	Mycteroperca microlepis (gag, Serranidae)	Collins et al., 1998
	Ocyurus chrysurus (yellowtail snapper, Lutjanidae)	Trejo-Martinez et al., 2011
	Sardinops ocellatus (southern African pilchard, Clupeidae)	LeClus, 1989
	Sardina pilchardus (true sardine, Clupeidae)	Perez et al.[2]; Garcia et al., 1992; Quintanilla and Perez, 2000; Ganias et al., 2003a
	Sciaenops ocellatus (red drum, Sciaenidae)	Roberts et al., 1978
	Scomber japonicus (Pacific chub mackerel, Scombridae)	Dickerson et al., 1992
	Solea solea (sole, Soleidae)	Witthames[3]
	Sprattus sprattus balticus (Baltic sprat, Clupeidae)	Kraus and Koster, 2004
	Tautoga onitis (tautog, Labridae)	LaPlante and Schultz, 2007
	Thunnus albacares (yellowfin tuna, Scombridae)	McPherson, 1991
Decreases with size or age	*Clupea bentincki* (Chilean herring, Clupeidae)_	Cubillos et al., 2007
	Engraulis australis (Australian anchovy, Engraulidae)	Dimmlich et al., 2009
	Engraulis ringens (Peruvian anchoveta, Engraulidae)	Cubillos et al., 2007
	Gadus morhua (Atlantic cod, Gadidae)	Kjesbu et al., 1996
No change with size or age	*Decapterus punctatus* (round scad, Carangidae)	McBride et al., 2002
	Engraulis mordax (northern anchovy, Engraulidae)	Hunter and Macewicz, 1980
	Gadus morhua (Atlantic cod, Gadidae)	Kjesbu, 1989
	Hyphessobrycon pulchripinnis (lemon tetra, Characidae)	Burt et al., 1988
	Lepomis gibbosus (pumpkinseed, Centrarchidae)	Fox and Crivelli, 1998
	Pogonias cromis (black drum, Sciaenidae)	Nieland and Wilson, 1993
	Seriphus politus (queenfish, Sciaenidae)	DeMartini and Fountain, 1981
	Stegastes partitus (bicolor damselfish, Pomacentridae)	Cole and Sadovy, 1995
	Tilapia zillii (redbelly tilapia, Cichlidae)	Coward and Bromage, 1999

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[1] Crabtree, R. E., and D. H. Adams. 1998. Spawning and fecundity of spotted seatrout, *Cynoscion nebulosus*, in the Indian River Lagoon, Florida. *In* Investigations into nearshore and estuarine gamefish abundance, ecology, and life history in Florida, p. 526–566. Technical Report for Federal Aid in Sportfish Restoration Act Project F-59. Florida Dept. Environmental Protection, Florida Mar. Res. Inst., St. Petersburg, FL.

[2] Perez, N., A. Garcia, N. C. H. Lo, and C. Franco. 1989. The egg production method applied to the spawning biomass estimation of sardine (*S. pilchardus*, Walb.) in the North-Atlantic Spanish coast. ICES Council Meeting (CM) Doc.1989/H:23, p. 1–20.

[3] Witthames, P. R. 2003. Methods to assess maturity and realized fecundity illustrated by studies on Dover sole *Solea solea*. *In* Report of the Working group of modern approaches to assess maturity and fecundity of warm- and cold-water fish and squids; 4–7 September 2001, Bergen, Norway (O. S. Kjesbu, J. R. Hunter and P. R. Witthames, eds.), Fisken og havet. no. 12-2003, p. 125–138. Inst. Mar. Res., Bergen, Norway.

Table 4

Patterns of spawning duration by age or size based on a review of spawning season duration within the scientific literature on fish reproduction.

Spawning Duration	Species	Reference(s)
Increases with size or age	*Atherina boyeri* (sand smelt, Atherinidae)	Tomasini et al., 1996; Tomasini and Laugier, 2002
	Clupea bentincki (Chilean herring, Clupeidae)	Cubillos and Claramunt, 2009
	Cynoscion nebulosus (spotted seatrout, Sciaenidae)	Lowerre-Barbieri et al., 2009
	Engraulis encrasicolus (European anchovy, Engraulidae)	Millan, 1999
	Engraulis mordax (northern anchovy, Engraulidae)	Parrish et al., 1986
	Engraulis ringens (Peruvian anchoveta, Engraulidae)	Claramunt et al., 2007; Cubillos and Claramunt, 2009
	Gadus morhua (Atlantic cod, Gadidae)	Kjesbu et al., 1996; Lawson and Rose, 2000
	Genyonemus lineatus (white croaker, Sciaenidae)	Love et al., 1984
	Hemiramphus brasiliensis (ballyhoo, Hemiramphidae)	McBride and Thurman, 2003
	Lepomis gibbosus (pumpkinseed, Centrarchidae)	Fox and Crivelli, 1998
	Leuresthes tenuis (California grunion, Atherinidae)	Clark, 1925
	Lutjanus carponotatus (stripey sea perch, Lutjanidae)	Kritzer, 2004
	Melanogrammus aeglefinus (haddock, Gadidae)	Trippel and Neil, 2004
	Merluccius hubbsi (Argentine hake, Merlucciidae)	Macchi et al., 2004
	Sardina caerulea (Califorinia sardine, Clupeidae)	Clark, 1934
	Sardina pilchardus (true sardine, Clupeidae)	Zwolinski et al., 2001
	Sardina pilchardus sardina (Mediterranean sardine, Clupeidae)	Ganias et al., 2003b
	Sardinops ocellatus (southern African pilchard, Clupeidae)	LeClus, 1989
	Sardinops sagax (Pacific sardine, Clupeidae)	Claramunt and Herrera, 1994
	Scomber japonicus (Pacific chub mackerel, Scombridae)	Dickerson et al., 1992; Knaggs and Parrish[1]; MacCall et al., 1980
	Seriphus politus (queenfish, Sciaenidae)	DeMartini and Fountain, 1981
	Solea solea (sole, Soleidae)	Witthames[2]
	Trachurus symmetricus (jack mackerel, Carangidae)	Wine and Knaggs[3]
No change noted overall, but larger fish develop eggs and/or spawn earlier	*Clupea harengus* (Atlantic herring, Clupeidae	Lambert, 1987
	Clupea pallasi (Pacific herring, Clupeidae)	Ware and Tanasichuk, 1989
	Cynoscion regalis (weakfish, Sciaenidae)	Lowerre-Barbieri et al., 1996
	Scomber scombrus (Atlantic mackerel, Scombridae)	Priede and Watson, 1993
	Trachurus trachurus (horse mackerel, Carangidae)	Abaunza et al., 2003

[1] Knaggs, E. H., and R. H. Parrish. 1973. Maturation and growth of Pacific mackerel *Scomber japonicus* Houttuyn. Marine Resources Tech. Rept. 3, 19 p. Calif. Dept. Fish and Game, Long Beach, CA.

[2] Witthames, P. R. 2003. Methods to assess maturity and realized fecundity illustrated by studies on Dover sole *Solea solea*. *In* Report of the working group of modern approaches to assess maturity and fecundity of warm- and cold-water fish and squids; 4–7 September 2001, Bergen, Norway (O. S. Kjesbu, J. R. Hunter and P. R. Witthames, eds.), Fisken og havet. no. 12-2003, p. 125–138. Inst. Mar Res., Bergen, Norway.

[3] Wine, V. L., and E. H. Knaggs. 1975. Maturation and growth of jack mackerel, *Trachurus symmetricus*. Mar. Resources Tech. Rept 32, p. 1–25. Calif. Dept. Fish and Game, Long Beach, CA,

also found that older fish had greater annual fecundity, and less frequent spawning over a longer season. In other cases, mediating factors, such as temperature or productivity, may have explained an anomalous size-based trend. Two articles on anchovies and a sardine reported lower spawning frequency among larger-size fish of stocks in shelf waters that were geographically separated from smaller fish in warmer coastal waters (Cubillos et al., 2007; Dimlich et al., 2009). Elsewhere, one of the anchovy species, Peruvian anchoveta (*Engraulis ringens*), was noted to have a positive relationship of size with both spawning frequency (Claramunt et al., 2004, 2007) and duration (Claramunt et al., 2007; Cubillos and Claramunt, 2009). From life-history theory, we would expect older fishes to invest relatively more energy into reproduction (Stearns, 1992); however, increased investment could manifest in various ways (e.g., egg quality rather than quantity; Berkeley et al., 2004a, 2004b). Empirical observations, as reviewed here, were necessary to elucidate patterns in the annual number of batches. The common assumption of age or size invariance would appear to be generally wrong.

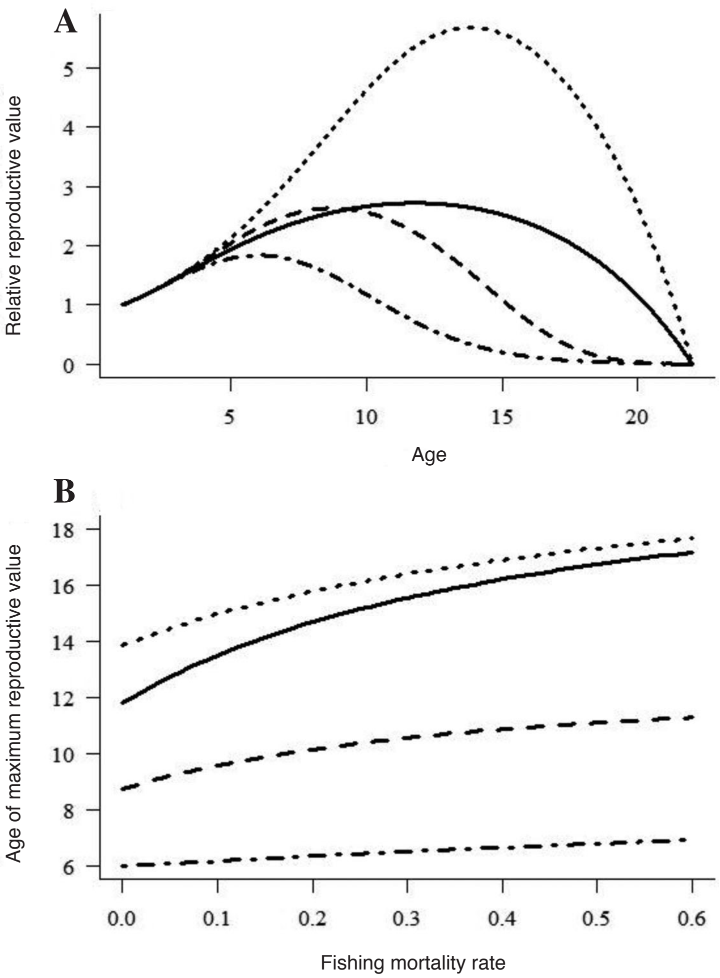

Figure 2

(**A**) Reproductive value incorporating survival, maturity, batch fecundity, and 4 qualitative patterns of annual number of batches. Results are based upon these qualitative patterns are shown in relation to the value at age 1, computed as a function of age under natural mortality only. (**B**) Age of maximum reproductive value as a function of fishing-induced mortality rate. In both panels, annual number of batches spawned (shown in Fig. 1A) per mature female are constant (i=1, solid line), increasing (i=2, dotted line), decreasing (i=3, dash-dot line), and dome-shaped (i=4, dashed line).

Measures of mean spawning frequency and duration are commonly applied to derive estimates of spawning stock biomass through the daily egg production method (DEPM) in species with indeterminate fecundity (Stratoudakis et al., 2006). Although this method is difficult to apply with precision, the DEPM has been used most often in assessments of short-lived clupeoid species for which direct methods of estimating spawning biomass are preferred (Stratoudakis et al., 2006). Because this approach is not explicitly dependent on age structure, the implications of size and age variation should be minimal. However, Priede and Watson (1993) provide an example of the difficulties in applying the DEPM to a longer-lived species, including the case when older Atlantic mackerel (*Scomber scombrus*) begin spawning earlier than younger mature females. The knowledge that older adults may spawn earlier, over a longer season, or more often to produce more batches may help guide sampling designs. Sampling of adults should be representative of a population or enough information on stock structure should be gathered to properly weight the adult data used for DEPM (Stratoudakis et al., 2006).

In contrast to application of egg production methods to short-lived species, our results may be most informative for estimates of reproductive potential used in age-structured assessments of relatively long-lived species that have been shown or must be assumed to be indeterminate spawners. When information is lacking to make a distinction about fecundity type, the recommendation is to follow an indeterminate approach that, in theory, will give accurate estimates of annual fecundity regardless of fecundity type (Lowerre-Barbieri et al., 2011b).

Applications of our model showed substantial sensitivity to age dependence in the annual number of batches. If the annual number of batches increased with age but was incorrectly assumed constant, stock assessment models tended to overestimate the biological reference points used for setting harvest rates. We found this result to be true for rates based on spawning potential ratio (Fig. 1B), as well as for those rates based on maximum sustainable yield.

This source of error in the determination of harvest rate may be of particular concern when management is based on output controls, such as annual catch limits, where the estimation of absolute scale of a population matters. However, it is not straightforward to predict a priori the consequences of all the interactions within an assessment model. For example, age dependence of spawning may not affect the estimated number of recruits (Morgan et al., 2007) but could affect the estimated spawning biomass and, therefore, the estimated spawner–recruit curve. As a result, the erroneous assumption of age invariance may be a common source of the error-in-variables problem identified in spawner–recruit estimation (Walters and Ludwig, 1981). Whether through error-in-variables or other latent assumptions, inadequately accounting for the effects of age structure on reproductive potential can result in poor prediction of stock status (Witthames and Marshall, 2008; Murua et al., 2010).

Our study adds to a growing list of age-dependent characteristics shown to influence reproductive success, including skipped spawning (Jørgensen et al., 2006; Secor, 2008; Rideout and Tomkiewicz, 2011), egg or larval quality (O'Farrell and Botsford, 2006; Spencer et al., 2007), and senescence (Woodhead, 1979; Porch et al., 2007). The first 2 characteristics likely would (although not necessarily) increase the value of older fishes beyond that considered by our models, and senescence would likely decrease the value of older fishes for population growth. Another consideration more difficult to ascertain is the influence of males on reproductive success (Van Doornik et al., 2008). Although our models predicted recruitment through the conventional use of only females, some other assessments model stock productivity as a function of both sexes (Brooks et al., 2008). Sperm limitation may be important in population dynamics if sex ratio fluctuates with changes in population structure, as it does, for example, in hermaphroditic fishes, particularly if the sperm quality, production, or allocation depends on age or size (Brooks et al., 2008; Uusi-Heikkilä et al., 2012).

In many assessments, spawning biomass is used in place of total egg production, either for simplicity or because no reliable information on batch fecundity exists. Because batch fecundity typically scales with body weight (Hunter et al., 1985; Porch et al., 2007; but see Dick, 2009), the use of spawning biomass may serve as a first-order approximation, particularly when no other measure of reproductive potential is available. To additionally account for increased number of batches, the age-based vector of body weight can be multiplied by an age-based vector ($\boldsymbol{b}$) of annual number of batches. In essence, this technique generalizes the usual approach, where $\boldsymbol{b}=\mathbf{1}$ is assumed. An increasing vector would seem more credible and, in data-limited cases, could be obtained by borrowing data from similar species or from meta-analysis.

Indeed, we initially considered a meta-analysis of the studies from our literature review. However, after examining the data as reported, we did not think we could provide meaningful, quantitative analyses. In aggregate, those studies were more useful in the qualitative sense of identifying patterns of increase, decrease, or no change in the number of batch spawnings. We anticipate that quantitative meta-analysis will become possible as more detailed data on batch spawning are collected. Lowerre-Barbieri et al. (2011a) provide guidance on the standardized information and approaches needed for estimating spawning frequency and duration.

We also desired to categorize the results of our literature review by fecundity type, but we could identify only a trend for indeterminate type among studies reporting multiple spawning. Most studies did not explicitly indicate either fecundity type or oocyte recruitment pattern. For warm-water species, indeterminate fecundity type is often assumed but not proven, and, as mentioned earlier, this assumption can be a robust one for estimating annual fecundity (Lowerre-Barbieri et al., 2011b). Careful review within the literature by species may yield more insight, but fecundity type often may defy easy categorization because the synchrony of oogenesis and resulting fecundity type may vary even within a species. Different stocks, especially those separated by latitudinal zones, may exhibit different fecundity types (Abaunza et al., 2003). Therefore, multiple criteria are recommended for defining fecundity type (Murua and Saborido-Rey, 2003; Lowerre-Barbieri et al., 2011b) and, accordingly, some corrections have been made to previous classifications (Arocha, 2002).

Conclusions

The 2 principal findings of this study are that, for fishes with indeterminate or uncertain fecundity type, age (size) dependence in the annual number of batches is more common than age invariance and that this dependence merits consideration in population models. For many species, stock assessments could be improved by collecting age-specific information on spawning frequency and duration. Without such information, or unless data indicate otherwise, the assumption that annual spawning increases with age may be more plausible than the currently common assumption of age invariance.

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