



## Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

### Food for thought

## BOFFFFs: on the importance of conserving old-growth age structure in fishery populations

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The value of big old fat fecund female fish (BOFFFFs) in fostering stock productivity and stability has long been underappreciated by conventional fisheries science and management, although [Hjort \(1914\)](#) indirectly alluded to the importance of maternal effects. Compared with smaller mature females, BOFFFFs in a broad variety of marine and freshwater teleosts produce far more and often larger eggs that may develop into larvae that grow faster and withstand starvation better. As (if not more) importantly, BOFFFFs in batch-spawning species tend to have earlier and longer spawning seasons and may spawn in different locations than smaller females. Such features indicate that BOFFFFs are major agents of bet-hedging strategies that help to ensure individual reproductive success in environments that vary tremendously in time and space. Even if all else were equal, BOFFFFs can outlive periods that are unfavourable for successful reproduction and be ready to spawn profusely and enhance recruitment when favourable conditions return (the storage effect). Fishing differentially removes BOFFFFs, typically resulting in severe truncation of the size and age structure of the population. In the worst cases, fishing mortality acts as a powerful selective agent that inhibits reversal of size and age truncation, even if fishing intensity is later reduced. Age truncation is now known to destabilize fished populations, increasing their susceptibility to collapse. Although some fisheries models are beginning to incorporate maternal and other old-growth effects, most continue to treat all spawning-stock biomass as identical: many small young females are assumed to contribute the same to stock productivity as an equivalent mass of BOFFFFs. A growing body of knowledge dictates that fisheries productivity and stability would be enhanced if management conserved old-growth age structure in fished stocks, be it by limiting exploitation rates, by implementing slot limits, or by establishing marine reserves, which are now known to seed surrounding fished areas via larval dispersal. Networks of marine reserves are likely to be the most effective means of ensuring that pockets of old-growth age structure survive throughout the geographic range of demersal species.

**Keywords:** age truncation, big old fat fecund female fish (BOFFFF), egg/offspring size/quality, maternal effects, recruitment, relative fecundity, stock productivity/stability, storage effect.

Logic surely demands that a fishery for a species having intermittent recruitment must somehow eschew the common practice of truncating the age structure.—Alan [Longhurst \(2002, p. 6\)](#)

Despite many models, truly understanding the mechanisms underlying the dynamics of exploited fish stocks remains elusive. [Hjort \(1914\)](#) was clearly prescient in his key assumption that the population dynamics of marine teleost fish are driven largely by variation in

larval survival. His two major hypotheses to explain variable larval mortality focused on, first, larvae finding sufficient food or not, and second, larvae drifting to or from suitable habitat ([Hjort, 1926](#)). Although it is clear that mortality during the larval phase is indeed the major source of density-independent mortality in marine fish ([Houde, 1987](#)), it has also been lamented that fisheries science has spent far too much time narrowly focused on these two particular hypotheses ([Houde, 2008](#)).

We believe that there are implications of Hjort's work that have not been fully embraced by fisheries science. In the chapter entitled "Fluctuations in Quality" of his classic treatise, Hjort (1914) explored variation in the condition of the parental stock, noting that large Atlantic cod (*Gadus morhua*) contain disproportionately more fat than smaller fish. In doing so, Hjort initiated the first excursion into what would eventually be called "maternal effects", the influence of the maternal phenotype on the phenotype of her offspring (Mousseau and Fox, 1998). Here, we expand this definition to include the effects of female age and size on the timing and location of spawning, which are also likely to affect offspring growth and survival. It is now known that maternal effects are evident in a broad diversity of fish and other organisms (reviews by Green, 2008; Marshall et al., 2008). However, fisheries models have historically assumed that many small, young, mature females are reproductively equivalent to fewer large, old females of the same total mass.

In this essay, we summarize the variety of ways that big old fat fecund female fish (hereafter, "BOFFFFs", Figure 1) contribute substantially to stock productivity and stability in ways considerably different from smaller females—i.e. all spawning-stock biomass (SSB) is not the same after all. Calling attention to the value of BOFFFFs matters because fisheries disproportionately remove BOFFFFs and typically truncate age and size distributions, leaving only younger, smaller spawners (Trippel, 1995; Levin et al., 2006; Sharpe and Hendry, 2009; Fisher et al., 2010; Stewart, 2011). Severe age truncation may thus lead to "longevity overfishing" (Beamish et al., 2006). Therefore, management is likely to enhance fisheries by conserving old-growth age structure and ensuring survival of a broad range of adult ages and sizes. Although such protection has only rarely been implemented in fisheries management, this thesis is not new and is shared by many (e.g. Longhurst, 2002; Francis, 2003; Berkeley et al., 2004a; Froese, 2004; Birkeland and Dayton, 2005; Berkeley, 2006; Hsieh et al., 2006, 2010; Francis et al., 2007; Froese et al., 2008; Rouyer et al., 2011, 2012).

Herein, we review the biological traits that vary with fish size and/or age and the implications of these traits for population resilience. We do not explicitly consider the economic benefits or costs of management strategies that preserve BOFFFFs. For many fisheries,



**Figure 1.** A big (1.1 m), old (ca.100 years), fat (27.2 kg), fecund female fish, in this case a shorttraker rockfish (*Sebastes borealis*) taken off Alaska (Karna McKinney, Alaska Fisheries Science Center, NOAA Fisheries Service).

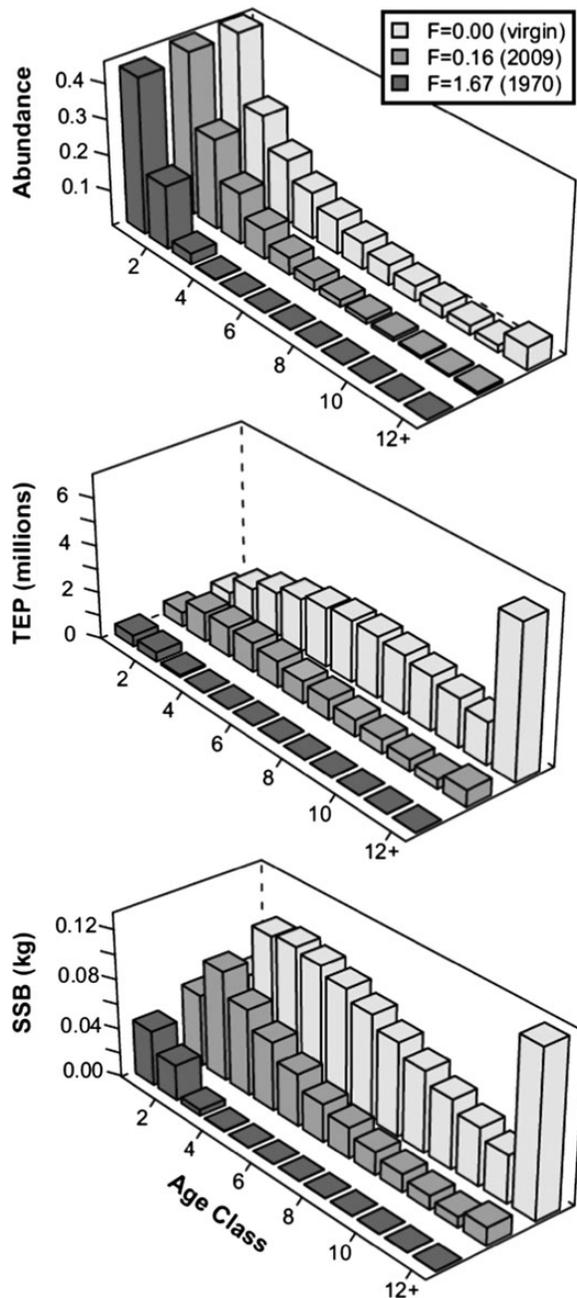
larger individuals are more valuable economically and there are potential financial trade-offs between harvesting these fish vs. implementing management measures to protect them. Mullan et al. (2012) address these trade-offs in a modelling framework comparing harvest scenarios with either a minimum size or a maximum size and varying size-based price differentials. They note that in some cases the two scenarios result in comparable economic gains but disparate success in matching conservation objectives. Our focus here is on the long-term biological goal of maintaining population stability.

We first summarize the reproductive biology of large old female fish, showing that BOFFFFs not only produce far more eggs than smaller females, even after accounting for body size, but also often produce larger or better provisioned eggs and larvae that grow faster and are better capable of withstanding starvation. Additionally, by spawning at different times or in different locations than smaller females, BOFFFFs extend the likelihood that at least some of a population's larvae will encounter favourable environments (a by-product of selection for individuals to maximize reproductive success). That is, the BOFFFFs that are characteristic of old-growth age structure contribute substantially to stock productivity. We then briefly review the fact that fishing typically causes extreme size and age truncation, i.e. severe declines in the abundance of BOFFFFs. Fishing thereby often becomes an agent of artificial selection causing both phenotypic and genetic shifts in fished populations in ways that not only inhibit fisheries productivity and stability, but also are difficult to reverse. In fact, size and age truncation destabilizes fish population dynamics, which renders fisheries less predictable and more subject to collapse. We conclude with a brief review of the policies by which BOFFFFs can be better conserved by fisheries management and explore why, despite Hjort's (1914) early explorations of parental effects, maintaining old-growth age structure by conserving BOFFFFs is still—a full century later—not yet standard practice.

### Relative fecundity of BOFFFFs

Fecundity generally increases with female age simply as a function of body size because a larger body cavity allows development of larger ovaries. In fisheries applications, the increase in fecundity with body size is accounted for by using the metric of SSB, which is an estimate of the total weight of mature fish in the population. Application of SSB in assessment models relies on the assumption that females of different sizes produce the same number and quality of offspring per unit of body weight. Here, we do not consider the increase in fecundity with body size to be a maternal effect unless there is a difference in weight-specific or relative fecundity, the number of eggs per gramme of female body weight. If relative fecundity differs with maternal traits, then SSB is not an adequate metric for the reproductive potential of populations with different maternal age/size compositions. Cooper et al. (2013) provide a clear example of the contrast between SSB and total egg production (TEP) with increasing age truncation (Figure 2).

Especially in long-lived species with low natural mortality, females devote increasingly more energy into reproduction than growth as they age (review by Roff, 1992). In fact, relative fecundity has been found to increase with maternal age or size in a wide range of species (Table 1). Stock assessments are increasingly incorporating such size- and age-dependent effects on fecundity. The degree to which older females produce disproportionate numbers of larvae varies greatly among species. In a review of 41 species of rockfish (genus *Sebastes*), Dick (2009) found that some of these differences could be explained by phylogeny. For example, species in the



**Figure 2.** Modelled abundance, TEP, and SSB at three fishing mortality rates ( $F$ ) per recruit of spotted seatrout (*Cynoscion nebulosus*). Note the extreme age truncation and decline in egg production caused by even moderate fishing (Cooper *et al.*, 2013).

subgenus *Acutomentum* showed limited evidence of size-related differences in relative fecundity. In contrast, species in the subgenera *Rosicola* and *Sebastomus* demonstrated strong increasing trends with female size.

For multiple-batch spawners (fish that spawn multiple times in a season), total annual egg production will of course depend on the number and size of batches released each season. In fisheries applications, the common assumption is that batch number does not vary with female size or age. A thorough review by Fitzhugh *et al.* (2012) reported 21 species in which the number of batches increases with female age or size, four species that show a decrease, and nine

**Table 1.** Representative teleost species with relative (weight-specific) fecundity documented to increase with female age and/or size.

Species	Reference
<i>Clupea harengus</i>	Oskarsson and Taggart (2006)
<i>Clupea pallasii</i>	Hay (1985)
<i>Coregonus pidschian</i>	Dupuis and Sutton (2011)
<i>Coregonus clupeaformis</i>	Johnston <i>et al.</i> (2012)
<i>Dicentrarchus labrax</i>	Mayer <i>et al.</i> (1990)
<i>Gadus morhua</i>	Marteinsdottir and Begg (2002)
<i>Melanogrammus aeglefinus</i>	Hislop (1988)
<i>Merluccius merluccius</i>	Mehault <i>et al.</i> (2010)
<i>Sebastes alutus</i>	Haldorson and Love (1991)
<i>Sebastes brevispinis</i>	Stanley and Kronlund (2005)
<i>Sebastes caurinus</i>	Dick (2009)
<i>Sebastes chlorostictus</i>	Haldorson and Love (1991)
<i>Sebastes crameri</i>	Dick (2009)
<i>Sebastes dalli</i>	Haldorson and Love (1991)
<i>Sebastes diploproa</i>	Dick (2009)
<i>Sebastes elongatus</i>	Haldorson and Love (1991)
<i>Sebastes entomelas</i>	Boehlert <i>et al.</i> (1982), Stafford (2012)
<i>Sebastes flavidus</i>	Sogard <i>et al.</i> (2008), Stafford (2012)
<i>Sebastes goodei</i>	Stafford (2012)
<i>Sebastes melanops</i>	Bobko and Berkeley (2004)
<i>Sebastes melanostomus</i>	Beyer <i>et al.</i> (in press)
<i>Sebastes miniatus</i>	Haldorson and Love (1991)
<i>Sebastes mystinus</i>	Sogard <i>et al.</i> (2008)
<i>Sebastes ovalis</i>	Beyer <i>et al.</i> (in press)
<i>Sebastes paucispinis</i>	Haldorson and Love (1991)
<i>Sebastes rosaceus</i>	Haldorson and Love (1991)
<i>Sebastes rosenblatti</i>	Haldorson and Love (1991)
<i>Sebastes rufus</i>	Haldorson and Love (1991)
<i>Sebastes saxicola</i>	Haldorson and Love (1991)
<i>Sebastes semicinctus</i>	Haldorson and Love (1991)
<i>Sebastes serranoides</i>	Haldorson and Love (1991)
<i>Seriphys politus</i>	DeMartini (1991)
<i>Tilapia zillii</i>	Coward and Bromage (1999)

species with no differences. Based on modelling studies of different hake (*Merluccius*) species, Field *et al.* (2008) estimated a dramatic increase in batch number with age, from one batch per year at age 2 to fourteen batches per year at age 15. As with other aspects of maternal influences on reproduction, there is a clear trend towards BOFFFFs contributing disproportionately to future cohorts, but sufficient variability to indicate that such reproductive parameters must be evaluated on a species-by-species basis. Such interspecific variability adds further complexity to the development of management approaches that incorporate maternal effects.

In addition to exhibiting lower relative fecundity, younger, smaller females have been observed to skip spawning altogether in some years. Evidence of this effect has been observed in Atlantic cod (Rideout and Rose, 2006), and the rockfish *Sebastes alutus* (Hannah and Parker, 2007) and *S. aurora* (Thompson and Hannah, 2010). Rideout *et al.* (2006) demonstrated a clear relationship of reduced energy stores in the liver associated with skipped spawning, harkening back to Hjort's (1914) prescient analysis of cod. Variation in the extent of skipped spawning among years may also be associated with differences in the quality of the larval environment (Rideout *et al.*, 2006; Hannah and Parker, 2007).

### Maternal effects on offspring size and quality

Intraspecific variability in offspring size or offspring quality has been widely observed in fish (Bagenal, 1971; Bernardo, 1996).

**Table 2.** Representative teleost species with offspring size and/or quality documented to increase with female age and/or size.

Species	Offspring trait	Maternal trait	Reference
<i>Clupea harengus</i>	Egg size	Length	Blaxter and Hempel (1963)
<i>Clupea pallasii</i>	Egg size	Length	Hay (1985)
<i>Coregonus clupeaformis</i>	Egg size	Age	Johnston et al. (2012)
<i>Cyprinus carpio</i>	Egg size	Age	Weber and Brown (2012)
<i>Engraulis anchoita</i>	Egg size	Length	de Ciechowski (1966)
<i>Gadus morhua</i>	Egg size	Length and age	Kjesbu (1989), Chambers and Waiwood (1996), Marteinsdottir and Steinarsson (1998), Vallin and Nissling (2000)
<i>Melanogrammus aeglefinus</i>	Egg size	Length	Hislop (1988), Trippel and Neil (2004)
<i>Merluccius hubbsi</i>	Egg size	Length	Macchi et al. (2006)
<i>Merluccius merluccius</i>	Egg size	Length	Mehault et al. (2010)
<i>Morone saxatilis</i>	Egg size	Weight	Zastrow et al. (1989)
<i>Oncorhynchus keta</i>	Egg size	–	Beacham and Murray (1985)
<i>Perca flavescens</i>	Egg size, larval quality	Length	Heyer et al. (2001), Lauer et al. (2005)
<i>Perca fluviatilis</i>	Egg size, larval quality	Length	Olin et al. (2012)
<i>Pleuronectes americanus</i>	Egg size	–	Buckley et al. (1991)
<i>Pleuronectes platessa</i>	Egg size	Weight	Kennedy et al. (2007)
<i>Pomoxis annularis</i>	Egg quality	Length	Bunnell et al. (2005)
<i>Pseudopleuronectes yokohamae</i>	Egg size	Length	Higashitani et al. (2007)
<i>Salmo salar</i>	Egg size	Length	Burton et al. (2013)
<i>Salmo trutta</i>	Egg size	Length	Ojanguren et al. (1996)
<i>Sander vitreus</i>	Egg size, egg quality	Length, age	Johnston and Leggett (2002), Wiegand et al. (2004), Johnston et al. (2007), Venturelli et al. (2010), Wang et al. (2012)
<i>Scophthalmus maximus</i>	Egg size	Weight	McEvoy and McEvoy (1991)
<i>Sebastes carnatus</i>	Larval quality	Age	Sogard et al. (2008)
<i>Sebastes flavidus</i>	Larval quality	Weight	Sogard et al. (2008)
<i>Sebastes maliger</i>	Larval quality	Weight	Rodgveller et al. (2012)
<i>Sebastes melanops</i>	Larval quality	Age	Berkeley et al. (2004b)
<i>Sebastes mystinus</i>	Larval quality	Length	Sogard et al. (2008)
<i>Seriphys politus</i>	Egg size	Weight	DeMartini (1991)
<i>Stegastes partitus</i>	Larval size, swimming performance	Length	Johnson et al. (2011)
<i>Xiphophorus birchmanni</i>	Larval size	Age	Kindsvater et al. (2012)

For studies where more than one maternal trait had a significant relationship with offspring traits, the maternal trait with the highest  $r^2$  is reported. Listing more than one maternal trait indicates different results among studies for that species. The review by Heath and Blouw (1998) provides additional examples.

There is a wealth of literature examining variation in egg size in oviparous teleosts, and differences in egg size among stocks can be extensive (Chambers and Leggett, 1996). For example, Johnston and Leggett (2002) noted widespread variation in egg size among walleye (*Stizostedion vitreum*) in different lakes, potentially a consequence of variation in productivity and the environment into which larvae hatch. Although the degree of variation in egg size among females within a local population is typically less than that among populations, significant maternal effects have been observed in a diverse range of species, generally indicating an increase in egg size with maternal age or size (Table 2). Kamler (2005) suggested that egg quality and size follow a parabolic trend with female age or size, increasing as fish reach intermediate ages/sizes then decreasing as females reach maximum ages/sizes. Such a pattern may reflect elevated maintenance metabolism costs of older fish, which limits energy for egg production (Kamler, 2005). The absence of such a decline for the species listed in Table 2 may reflect an absence of very old fish in the range of samples examined in these studies.

Direct measurement of egg quality, usually in terms of lipid constituents, has been conducted less frequently, and egg size is often assumed to be a sufficient proxy for egg quality. Although there are notable exceptions, this assumption has support from a substantial number of experimental studies documenting a correlation of egg size with a variety of traits indicative of fitness during the egg stage, such as embryo growth rate, survival to hatch, and size at

hatch (Blaxter and Hempel, 1963; Knutsen and Tilseth, 1985; Hinckley, 1990; Bernardo, 1996; Chambers, 1997; Marteinsdottir and Steinarsson, 1998; Trippel, 1998; Einum and Fleming, 2000). Larger egg size and better condition of yolk-sac and feeding larval stages in turn generally confer advantages of better swimming capabilities, faster growth, better sensory detection of both predators and prey, and overall higher survival (Miller et al., 1988; Searcy and Sponaugle, 2001; Vigliola and Meekan, 2002; Fisher et al., 2007).

For the few studies that have measured offspring constituents, those detecting maternal effects have generally found that eggs or larvae from older or larger mothers contain more energy reserves. In an extensive review of primarily freshwater species, Kamler (2005) concluded that egg quality in terms of proximate composition often increases with female age but not female size. In many species, offspring with greater lipid content or other indices of energetic quality were not derived from larger eggs or larvae. In the primitively live-bearing rockfish species (Family Scorpaenidae), size of larvae at parturition appears to be a conservative trait with minimal intraspecific variation, although several species have demonstrated a maternal effect of increased lipid stores in larvae produced by older or larger mothers (Berkeley et al., 2004b; Sogard et al., 2008). The amount of triacylglycerol lipids in the oil globule at parturition determines a larva's ability to resist starvation (Fisher et al., 2007) and is also correlated with growth rates in the rockfish *S. melanops* (Berkeley et al., 2004b). Gagliano and

McCormick (2007) found that egg size was conserved but lipid stores varied in the damselfish *Pomacentrus amboinensis* when food availability varied. Kerrigan (1997) found that smaller mothers of the same damselfish produce longer larvae but with lower yolk reserves than offspring from larger mothers (see also Maddams and McCormick, 2012). In lab experiments, Uusi-Heikkilä *et al.* (2010) found that smaller female zebrafish (*Danio rerio*) produced larger eggs compared with larger females, but those eggs had higher mortality rates, again suggesting that size alone was not an accurate indicator of egg quality. Nonetheless, Cardinale and Arrhenius (2000) and Carr and Kaufman (2009) concluded that BOFFFFs and their eggs were the greatest contributor to recruitment success in Atlantic cod (but see Ottersen, 2008).

The underlying reason for the commonly observed increase in egg size or quality with maternal age or size is somewhat controversial. Is this pattern, an adaptation to the environment into which eggs will hatch, as suggested by Marshall *et al.* (2010), or a consequence of greater energy resources in larger females and a potential shift in the fecundity vs. egg size/quality trade-off as fish age (Roff, 1992)? Classic life-history theory suggests that this trade-off should be resolved around an optimal offspring size/quality for the expected environmental conditions encountered by early life stages (Smith and Fretwell, 1974). For a given offspring environment, mothers with more resources may maximize their fitness by simply producing more offspring. However, offspring environments may differ and environmental quality is thought to be inversely related to the degree to which investment in offspring results in greater offspring survival. Harsher environments should therefore select for larger offspring. There is extensive evidence suggesting that population level differences in egg size match the expectation of larger or higher quality eggs in lower quality larval environments (Johnston and Leggett, 2002; Castro *et al.*, 2009; Wang *et al.*, 2012).

Marshall *et al.* (2010) argue that one reason for observed maternal effects on offspring size may be a link between maternal phenotype and offspring environment. For example, in rockfish (genus *Sebastes*) younger mothers tend to produce lower quality larvae but release them later in the season (Sogard *et al.*, 2008), which may distribute their offspring into a more favourable environment than larvae produced earlier in the season by older mothers. Under this scenario, larvae would have equivalent fitness despite differences in energetic reserves provided by their mothers, and the expected survival of offspring would not differ with female size/age. This argument presumes that the number vs. quality trade-off does not differ with maternal resources. If, however, the shape of this trade-off varies with maternal resources, then younger or smaller females with low energetic reserves may shift allocation patterns and produce offspring of slightly lower quality while maintaining fecundity as high as possible. Evidence that this trade-off varies with female reproductive resources has been observed in three-spined stickleback (*Gasterosteus aculeatus*), where females with reduced energy reserves due to parasites had the same clutch biomass as unparasitized females, but shifted their allocation to produce larger numbers of smaller eggs (Heins, 2012). In this system, the larval stages would presumably encounter the same environmental conditions whether from parasitized or unparasitized mothers. Burton *et al.* (2013) similarly found that the fecundity/offspring size trade-off varied with maternal attributes in Atlantic salmon (*Salmo salar*).

The question of adaptive response vs. physiological constraints also pertains to changes in egg size for individual females within a

spawning season. Batch spawners often produce progressively smaller eggs as the spawning season continues (e.g. Hislop, 1975; Ware, 1977; Kjesbu *et al.*, 1991; Macchi *et al.*, 2006). This pattern may be due to seasonal changes in production cycles (Cushing, 1967), suggesting an adaptive strategy that balances egg fitness with fecundity over the spawning season (Ware, 1977), or depleted energy reserves, indicating that bioenergetic demands result in reduced egg fitness in successive batches. The anchoveta (*Engraulis ringens*) off the coast of Chile exhibits the latter pattern, with egg size and lipid content declining over the spawning season, resulting in a decreasing trend in hatching success (Castro *et al.*, 2009). The decline in egg size over a spawning season has been found primarily in winter/spring spawners. Fall spawning European pilchard (*Sardina pilchardus*), in contrast, showed increasing egg size as the spawning season progressed (Daoulas and Economou, 1986). These authors did not proscribe an adaptive explanation for this difference, but more proximally, suggested that decreasing temperatures caused this response in egg development.

Parker and Begon (1986) developed theory to explain increased egg size with increased maternal size, based on density-dependent sibling competition that might arise with increased fecundity. Such a mechanism may be a factor for teleosts that spawn demersal eggs in cohesive nests, but seems unlikely for the many pelagic spawners that exhibit maternal size effects. Indeed, the model of Kindsvater *et al.* (2011), relevant to highly fecund fish that are likely to experience survival costs associated with reproduction, suggests scenarios that depart from the Smith and Fretwell (1974) model summarized above. In this case, younger females are predicted to reduce offspring size, thereby maximizing survival until the next opportunity to reproduce.

In summary, although there is substantial evidence that, all else being equal, offspring of BOFFFFs typically perform better than those of smaller females, additional studies are needed to determine whether the larger or better provisioned offspring produced by BOFFFFs have a higher probability of survival than offspring of younger and/or smaller females spawned at different times or places. New genetic approaches for matching parents and offspring hold much promise for such studies (e.g. Christie, 2010). For example, Beldade *et al.* (2012) found that larger female orange-fin anemonefish (*Amphiprion chrysopterus*) were more likely than smaller females to produce successful recruits and that fecundity alone was insufficient to account for the success of BOFFFFs, suggesting maternal effects on larval quality. In any case, we do not assert that maternal effects on offspring size or quality are universal in teleost fish. Rather, we believe that, because maternal effects have evolved in a diverse taxonomic range of species, removing older, larger fish from a population may have deleterious consequences for fisheries productivity. In years or locations with high-quality, food-rich larval habitats, larval fitness may be equivalent among individuals with varying levels of maternal provisioning. Likewise, in some environments, larger offspring or those with more energy reserves may potentially have lower fitness than smaller, less well provisioned eggs. Over the long term, however, we believe that continual contribution of higher quality offspring from older females provides one of the mechanisms that buffer survival of a larval cohort.

### Benefits of maternal effects and old-growth age structure to fisheries productivity

Temporal variability in the conditions experienced by larvae is a basic characteristic of many aquatic ecosystems and a presumed

**Table 3.** Representative teleost species with the timing of annual spawning or parturition documented to be earlier and/or longer with increasing female age and/or size.

Species	Reference
<i>Clupea harengus</i>	Lambert (1987)
<i>Engraulis encrasicolus</i>	Millan (1999)
<i>Gadus morhua</i>	Hutchings and Myers (1993)
<i>Hemiramphus balao</i>	Berkeley and Houde (1978)
<i>Hemiramphus brasiliensis</i>	Berkeley and Houde (1978)
<i>Melanogrammus aeglefinus</i>	Wright and Gibb (2005)
<i>Morone saxatilis</i>	Cowan et al. (1993)
<i>Pleuronectes platessa</i>	Rijnsdorp (1994)
<i>Sebastes crameri</i>	Nichol and Pikitch (1994)
<i>Sebastes entomelas</i>	Stafford (2012)
<i>Sebastes flavidus</i>	Sogard et al. (2008)
<i>Sebastes atrovirens</i>	Sogard et al. (2008)
<i>Sebastes melanops</i>	Bobko and Berkeley (2004) and Sogard et al. (2008)
<i>Sebastes mystinus</i>	Sogard et al. (2008)
<i>Trisopterus luscus</i>	Alonso-Fernandez and Saborido-Rey (2011)

Reviews by Miranda and Muncy (1987), Trippel et al. (1997), and Wright and Trippel (2009) provide additional examples.

driver of the evolution of the long lifespans that produce old-growth age structure (Murphy, 1968; Longhurst, 2002). BOFFFFs often have earlier and/or longer spawning seasons than smaller, younger female fish, as documented in a variety of species (Table 3). Additionally, in multiple-batch spawners, older fish may produce more batches of eggs over a longer period each season, as documented in drum (DeMartini and Fountain, 1981), anchovy (Parrish et al., 1986), striped bass (Secor, 2000a), haddock (Wright and Gibb, 2005), and sardine (Claramunt et al., 2007), among others. For example, individual Atlantic cod can spawn over a range of 2–7 weeks, and by individuals spawning at different times, a population may spawn over a range of 4–15 weeks (Marteinsdóttir and Björnsson, 1999).

This temporal spread of reproductive effort provides a bet-hedging life-history strategy helping to ensure that some larvae are spawned at times of favourable environmental conditions, including high food availability (Cushing, 1990, as foreshadowed by Hjort, 1914) and/or low predation intensity (Bailey and Houde, 1989). Additionally, BOFFFFs may spawn in different locations than younger, smaller fish (reviews by Wright and Trippel, 2009; Hsieh et al., 2010), providing spatial as well as temporal bet-hedging. Empirical evidence for bet-hedging includes settlement of plaice (*Pleuronectes platessa*) occurring over several weeks despite spawning occurring over several months (Hovenkamp, 1991). Likewise, the extensive occurrence of “sweepstakes reproductive success” (Hedgecock and Pudovkin, 2011) demonstrates the rarity of each individual contributing to recruitment in any given year. Evidence for the importance of BOFFFFs in bet-hedging includes the fact that first-time, late-spawning female haddock (*Melanogrammus aeglefinus*) contribute little to recruitment (Wright and Gibb, 2005; see also the state-based model of Wright and Trippel, 2009). The fact that young, late-spawning female black rockfish (*Sebastes melanops*) contribute substantially to recruitment some years yet not others is indicative of the hit-or-miss nature of recruitment in age-truncated stocks (Bobko, 2002, cited in Bobko and Berkeley, 2004). More directly, positive relationships are evident between the age diversity of spawners and subsequent recruitment success

(Lambert, 1990; Marteinsdóttir and Thorarinsson, 1998; O’Brien et al., 2003). Other empirical examples are provided in Secor’s (2007) review. Thus, there is increasing evidence that old-growth age structure is a better index of the reproductive potential of a stock than simply SSB alone (Marshall et al., 2003; Lambert, 2008). Overall, age truncation due to fishing may alter the timing and duration of annual reproduction by delaying and shortening the spawning season (Scott et al., 2006), contributing to the observed increase in recruitment variability for stocks comprised of only younger spawners (Marteinsdóttir and Thorarinsson, 1998; Secor, 2000b; Wieland et al., 2000; Hsieh et al., 2006).

Effects of maternal age/size on both offspring size/quality and relative fecundity may reflect higher body condition as females age. Many of the studies reporting significant effects in Tables 1 and 2 did not measure body condition, but we suspect that often energy reserves increase with female age and size, as first noted by Hjort (1914). Thus, BOFFFFs have more resources to apply to reproduction compared to younger/smaller females. The importance of energy accumulation by mature females was aptly demonstrated in Atlantic salmon by Reid and Chaput (2012), who found that females spawning in consecutive years had smaller eggs than females that skipped spawning for a year, presumably allowing the latter to acquire more resources for the years in which they did eventually spawn. In any case, recent explorations suggest that incorporating maternal effects into fisheries models are likely to be more useful than continuing to assume that all SSB is equivalent (e.g. Scott et al., 1999; Berkeley, 2006; Lucero, 2008, 2009; O’Farrell and Botsford, 2006; Shelton et al., 2012). In a modelling exercise, O’Farrell and Botsford (2006) found that, for typical long-lived fish, maternal effects result in large errors in estimates of lifetime reproductive success when there is a large difference in the mortality rate of larvae produced by young vs. old females. However, examining empirical data for black rockfish (*S. melanops*) from Berkeley et al. (2004b), they concluded that such errors in traditional management would be small for this species (O’Farrell and Botsford, 2006).

### Age truncation and artificial selection caused by fishing

Because old-growth age structure can provide the benefits of maternal effects and other bet-hedging strategies reviewed above, it follows that BOFFFFs are a valuable component of stock productivity. However, fishing tends to differentially remove BOFFFFs because fishing both elevates mortality and changes the age/size-selective pattern of mortality within fished populations. Commercial fisheries tend to target phenotypes that are the most valuable or marketable (e.g. large fish). This focus, in turn, influences how and where fish are caught, which can lead to selective removal of certain phenotypes. An obvious example of how fishing may be selective is through net mesh size: a given mesh size will catch larger fish while allowing many smaller fish to escape. Gear types can also be selective in other ways. In addition to selecting on body size, passive gear types such as driftnets or longlines also tend to remove bolder individuals from the population (Biro et al., 2004; Biro and Post, 2008). Even bait type and hook size will generate some degree of selection because the fish that are caught by these methods are fish that are both drawn to the bait and large enough to bite the baited hook (e.g. Millar, 1992; Myers and Hoenig, 1997). Other mechanisms of fishery selection may be less intuitive, but also very important (Millar and Fryer, 1999).

For example, larvae of many demersal species settle in shallow coastal regions, then slowly move offshore as they age and grow (e.g. North Pacific rockfish, Love *et al.*, 1991). Given such ontogenetic habitat shifts, concentrating fishing effort by depth or location can cause artificial selection on age and size.

In addition to the direct effects of fishing practices causing selective mortality, fishing of course elevates mortality rates overall, often to high levels. Even if fishing mortality is constant with respect to age and body size, increasing the overall mortality rate can still result in selection favouring smaller size and earlier age at maturation (Stearns and Koella, 1986).

Although fishing can be strongly size selective, it is more informative to consider the selective effects that fishing can have on a suite of related life-history traits (e.g. growth rate, maximum size, life-span, boldness, etc.). In this regard, it is useful to view fishery selection through the lens of life-history theory, which provides a framework for combining the selectivity of fishing practices with the effects of overall increases in mortality rates. Importantly, life-history theory allows one to evaluate how fishery selection interacts with natural patterns of selection. Life-history characteristics such as growth form and size/age at maturation evolve towards maximizing individual fitness, given the abiotic and biotic constraints a population experiences (Roff, 1992; Stearns, 1992). For example, patterns of natural (unfished) selection on body size at maturation are often stabilizing, such that size-related reproductive advantages (including maternal effects on offspring quality) are balanced by size-related delays in maturation that result in lower average survival to adulthood (Roff *et al.*, 2006; Johnson and Hixon, 2011). In other words, there may be a trade-off between being large at maturation (which allows the production of more and better provisioned offspring) and the time it takes to attain a large size (greater development time results in a greater risk of dying before reproducing at all). By both increasing total mortality and changing patterns of size-dependent mortality, fishing can upset such balances and shift patterns of selection such that smaller fish are favoured (Allendorf and Hard, 2009). In essence, fishing mortality can alter the selective regime that a population experiences.

Whenever a population is fished, there is the potential for substantial changes in the phenotypic composition of the population. In the short term, fishing mortality tends to remove larger and older individuals (BOFFFFs) from the population. This removal often leads to strong truncation of age and size distributions within fished populations (Trippel, 1995; Levin *et al.*, 2006; Sharpe and Hendry, 2009; Fisher *et al.*, 2010; Stewart, 2011). Over longer periods (i.e. across generations), the distribution of phenotypes may change due to phenotypic plasticity and/or evolution. It is quite clear that over generations, life-history characteristics can change substantially within fished populations (e.g. Ricker, 1981; Jorgensen, 1990; Rijnsdorp, 1993; Trippel *et al.*, 1997; Olsen *et al.*, 2004; Rijnsdorp *et al.*, 2005; Swain *et al.*, 2007). However, it is often difficult to discern how much of the observed phenotypic changes are due to an underlying genetic response vs. a sustained, plastic response of phenotypes (Kuparinen and Merila, 2007). Long-term studies of wild populations tend to be observational. However, there is solid evidence from laboratory experiments that changes in mortality patterns can lead to evolved responses (Conover and Munch, 2002; Reznick and Ghalambor, 2005; van Wijk *et al.*, 2013), and recent field studies have demonstrated changes in gene frequencies for a wild, fished population (Arnason *et al.*, 2009; Jakobsdottir *et al.*, 2011). In light of this evidence, it seems likely that at least some of the observed phenotypic

changes in fished populations are due to an evolved response. Based on these conclusions, one would expect that fisheries-induced changes in phenotypes may not be easily reversible (Law, 2000, 2007; Conover *et al.*, 2009; Heino *et al.*, 2013).

When populations evolve in response to fishing and maternal effects are present, there may be long-term consequences for both the characteristics and the demography of offspring. Maternal effects may result in complex evolutionary responses of offspring characteristics, including time-lags, and responses that carry on after selection ceases (Kirkpatrick and Lande, 1989). Characteristics of offspring may also affect demographic rates. For example, sizes of larval and juvenile fish often strongly affect their survival rates (reviewed by Sogard, 1997; Perez and Munch, 2010). Fishery selection that changes the characteristics of adults may, through maternal effects, also change the characteristics of offspring. In turn, changes in offspring characteristics may strongly affect offspring survival and population replenishment. For example, Johnson *et al.* (2011) calculated that, over a single generation, a reasonable amount of fishery selection on adult size could lower larval size at hatching and reduce larval survival (over 90 d) by a factor of 0.86 (95% CI: 0.77–0.96). Although the rate of change in offspring characteristics is expected to slow over multiple generations (Kirkpatrick and Lande, 1989), these results suggest that, through correlated responses of larvae, fishery selection can result in a persistent reduction of larval survival. Maternal effects should therefore be considered when evaluating the long-term consequences that fishery selection will have for the dynamics of populations.

### Deleterious consequences of age truncation for fisheries stability

Boom-and-bust cycles in exploited populations can lead to economic collapse and local extinction (Lande *et al.*, 2003). Importantly, such erratic population fluctuations may be indicative of deleterious fishing effects well before obvious signs of stock collapse occur (Hsieh *et al.*, 2006). It is increasingly well-documented that age-truncated fish stocks are more variable through time, and thus more susceptible to collapse, than populations with more intact age structure. This pattern is especially but not exclusively true for “periodic species” (*sensu* Winemiller and Rose, 1992) that exhibit relatively low early survival, late maturation, and high individual fecundity (such as cods and rockfish). In short, old-growth age structure fosters population stability, whereas age truncation often destabilizes population dynamics (Rouyer *et al.*, 2012).

In the most comprehensive reviews to date, Hsieh *et al.* (2006, 2008) and Anderson *et al.* (2008) analysed the 50-year California Cooperative Oceanic Fisheries Investigations (CalCOFI) time-series (13 exploited and 16 unexploited species) and found that fishing significantly increased fluctuations of stocks in the southern California Current ecosystem. Anderson *et al.* (2008) tested three likely and non-mutually exclusive mechanisms proposed to explain this pattern. First, variable fishing intensity may directly cause population variability independent of any age-truncation effects (Jonzen *et al.*, 2002). This hypothesis was falsified. Second, unlike BOFFFFs, small, young fish in age-truncated populations may not buffer environmental variability by “bet-hedging” reproductive output via a protracted spawning season (Murphy, 1968; Leaman and Beamish, 1984; Longhurst, 2002; Berkeley *et al.*, 2004a; Hutchings and Reynolds, 2004; Hsieh *et al.*, 2005, 2006). Third, the demographic characteristics of age-truncated populations (in particular, the per capita population growth rate) may be prone to unstable dynamics (Dixon *et al.*, 1999;

Hsieh *et al.*, 2005). Although both the second and third hypotheses are due to age truncation, they generate subtly different predictions: the loss-of-bet-hedging hypothesis predicts that a population will more linearly track environmental variation, whereas the demographic-alteration hypothesis predicts clearly non-linear responses. For the CalCOFI data, the demographic-alteration hypothesis provided the better fit, although there was also evidence for the loss-of-bet-hedging hypothesis (Anderson *et al.*, 2008).

Modelling the dynamics of cod and herring populations, Rouyer *et al.* (2011) found that age truncation simultaneously increases the sensitivity of stocks to environmental fluctuations and lessens their response to variation in fishing intensity, resulting in “the paradox that heavily exploited, age-truncated populations are those most in need of careful management, but also are those least responsive to the effects of such management” (p. 3056). Murawski *et al.* (2001) reported similar results in modelling the collapse of Atlantic cod. In general, regardless of the specific causative mechanisms involved, age-truncated populations more closely track environmental fluctuations (Lambert, 1987; Marteinsdóttir and Steinarsson, 1998; Hutchings and Myers, 1993; Ottersen *et al.*, 2006; Hidalgo *et al.*, 2011, 2012), with associated destabilizing consequences for the fishery (Wright and Trippel, 2009). Additionally, a model and meta-analysis by Venturelli *et al.* (2009) of 25 exploited temperate and Arctic fish species subjected to age truncation indicated that old-growth age structure enhances population growth and thus supports higher exploitation rates. They concluded that severe age truncation is analogous to “forcing an iteroparous species to spawn as if it was semelparous [and] is unsustainable” (p. 923).

Age truncation also inhibits stock resilience over time-scales longer than annual production. The extremely high fecundity of teleost fish, the commonality of relatively long lifespans, and the high variability of recruitment in annual cohorts all suggest that individual reproductive success is rare and episodic. Recent technological advances in genetics have allowed quantification of effective population size ( $N_e$ ) and estimations of the proportion of adults that successfully contribute to subsequent generations. Hauser and Carvalho (2008) report surprisingly low  $N_e$  in a taxonomically diverse range of marine species, suggesting that a large proportion of mature adults are unsuccessful at producing surviving progeny. Based on the evidence of maternal effects outlined above, they suggest that only older spawners ready in years of excellent recruitment may have a chance to become rare “sweepstake winners”. For a 28-year time-series of pelagic juvenile rockfish surveys, Ralston *et al.* (2013) found a striking pattern of increased individual size, coherent among the ten most common *Sebastes* species, in years of high abundance. This result suggests that, in environmentally favourable years, larvae released earlier in the reproductive season had particularly high survival. Because older, larger rockfish females tend to release larvae earlier than younger, smaller females (Nichol and Pikitch, 1994; Bobko and Berkeley, 2004; Sogard *et al.*, 2008), it is likely that much of the production in high-recruitment years came from BOFFFFs. In contrast, when environmental conditions were not favourable for early spawners, much of the production was likely derived from younger females, with reduced offspring abundance despite the presumably greater amount of SSB compared with older females.

Repeated spawning over many years increases the likelihood that an individual's offspring will encounter a favourable environment in at least one of those years. For species with highly sporadic recruitment success, the long-term survival of older females provides a

“storage effect” of reproductive potential whereby elder and overlapping age classes of the population can out-live extended periods of poor recruitment, ready to take advantage of favourable conditions when they return, thereby fostering population persistence (Warner and Chesson, 1985). This phenomenon was implicit in Hjort's (1914) recognition that unusually strong year classes of herring sustained recruitment over subsequent years. Indeed, there is a well-documented positive relationship in a broad variety of exploited fish (excluding flatfish) between recruitment uncertainty and longevity (reviews by Secor, 2007, and Longhurst, 2002, 2010). However, it is only recently that managing for storage effects in fished populations by maintaining old-growth age structure has been seen as important for fisheries stability (Frank and Brickman, 2001; Berkeley *et al.*, 2004a; Field and Francis, 2006; Secor, 2007; Longhurst, 2010). The storage effect is likely to be particularly important at the margins of species geographical ranges, where successful recruitment is often rare (MacCall, 1990).

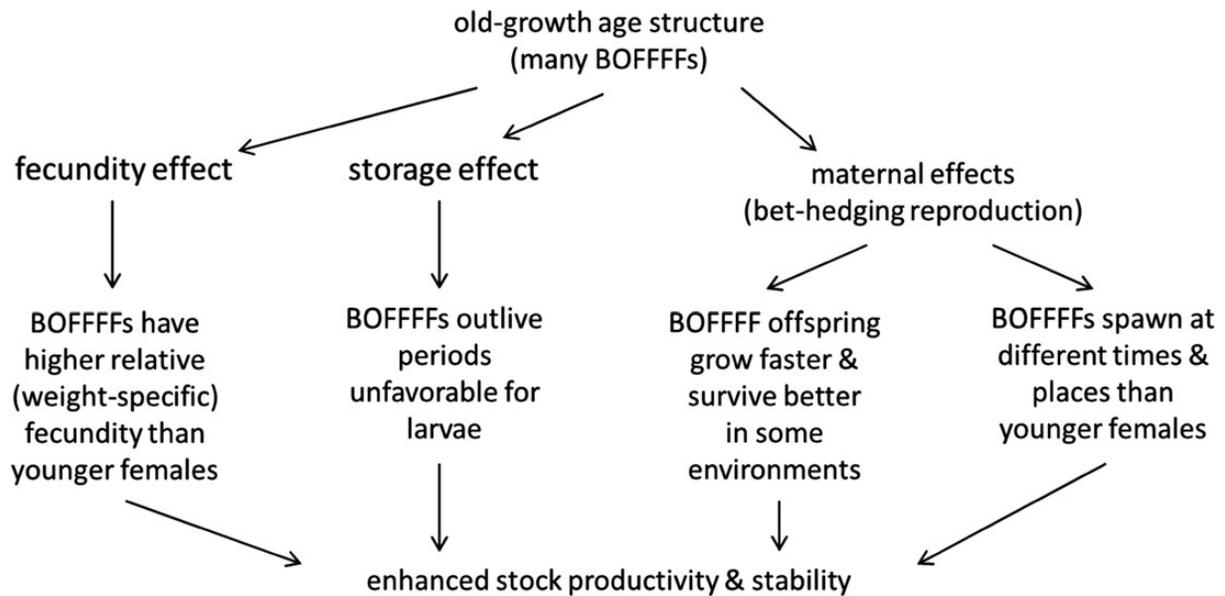
### Approaches and challenges of managing for old-growth age structure

The empirical evidence summarized here indicates that, for a broad diversity of exploited marine fish, populations characterized by old-growth age structure with a substantial abundance of BOFFFFs are more stable, more predictable, and less prone to overfishing collapse than age-truncated stocks (Figure 3). Given that at least 30% of the world's fisheries stocks are overexploited (FAO, 2012), the onus is on fisheries scientists and managers to better conserve BOFFFFs than we have in the past. How can this goal be accomplished and why have we not yet done so already?

The pattern of selective fishing has profound effects on the age structure, productivity, and stability of an exploited stock (Brunel and Piet, 2013). Berkeley *et al.* (2004a) reviewed three management approaches that can help to conserve BOFFFFs in an exploited population: (i) very low rates of fishing mortality, (ii) slot size limits in which there is both a minimum and maximum size for retention, and (iii) marine reserves, where old-growth age structure can develop, spawn, and seed nearby fished areas unhindered. In the first approach, reduced exploitation will allow more fish to reach old age. However, to be effective this strategy may require fishing mortality to be reduced to prohibitively low and economically unfeasible levels. This approach successfully rebuilt populations and restored old-growth age structure in Atlantic striped bass (*Morone saxatilis*), yet involved severe fishing restrictions, including a virtual moratorium lasting 5 years (Richards and Rago, 1999; Secor, 2000b).

The second option—a slot size limit—is feasible only for species that can be released unharmed after capture, typically recreational fish (e.g. Arlinghaus *et al.*, 2010). Many deepwater fish typically do not survive post-capture release due to the internal trauma of expansion and rupture of the swimbladder during capture. Swimbladder or not, the condition of many fish after capture, especially in commercial fisheries, is typically too poor to ensure subsequent survival.

The final option to conserve BOFFFFs and prevent age truncation—marine reserves—has the greatest potential to allow at least a segment of a population of a demersal species to age naturally and export larvae produced by a broad age and size range of spawners (Murray *et al.*, 1999; Berkeley *et al.*, 2004a; Berkeley, 2006; Edwards and Plaganyi, 2011). Importantly, the “seeding effect” of marine reserves in a fisheries context—larvae being



**Figure 3.** Summary of the benefits to stock productivity and stability provided by old-growth age structure, which includes many BOFFFFs. These benefits are negated by severe size and age truncation (removal of BOFFFFs) caused by fishing, which can further result in fisheries-induced evolution that is difficult to reverse once a stock has collapsed.

spawned inside reserves, dispersing and replenishing fished populations outside—has now been demonstrated using novel genetic methods (Christie *et al.*, 2010; Harrison *et al.*, 2012; Almany *et al.*, 2013), so the value of BOFFFFs in the context of marine reserves is now clear. However, the marine reserve approach is viable only for species whose post-settlement home ranges remain largely within the boundaries of the reserve, which fortunately includes a broad variety of demersal species (reviews by Halpern and Warner, 2002; Halpern, 2003; Gaylord *et al.*, 2005; Claudet *et al.*, 2008; Lester *et al.*, 2009). Given that recruitment may come from restricted temporal and spatial oceanographic windows that change from year to year (review by Berkeley *et al.*, 2004a), such management should include efforts to preserve minimal spawning stock sizes over the entire geographic range of the stock (e.g. Larson and Julian, 1999). Networks of marine reserves, where replicate sites include a variety of seabed habitats in each biogeographic region, therefore offer the greatest potential to conserve old-growth age structure in a multispecies assemblage of exploited demersal species.

Why—100 years after Hjort (1914) first inferred indirectly that parental effects may be important in replenishing fishery stocks—have there been no widespread efforts to conserve old-growth age structure and the increasingly obvious fishery benefits provided by BOFFFFs? Perhaps the answer lies in the real and perceived difficulties of implementing the above management approaches. Uniformly low exploitation levels are seldom if ever implemented until reactive, emergency stock-rebuilding measures are in place following stock collapse. Slot limits are typically difficult to implement, especially in commercial fisheries. Marine reserves worldwide are increasingly well documented to provide fisheries benefits from at least a biological perspective (Halpern and Warner, 2002; Halpern, 2003; Gaylord *et al.*, 2005; Claudet *et al.*, 2008; Lester *et al.*, 2009; Christie *et al.*, 2010; Harrison *et al.*, 2012), yet the collective psyche of the combined fishing/fisheries science/fisheries management community has historically been unwilling to consider proactive, permanent, spatial closures to ensure

that fisheries benefit from the reproductive capacity of old-growth age structure. Fortunately, change is in the air. For example, recent stock assessments of 12 of 19 rockfish species (genus *Sebastes*) incorporate age or size-dependent relationships with relative fecundity, thus accounting for some documented BOFFFF effects (<http://www.pcouncil.org/groundfish/stock-assessments/by-species/>). Overall, following many authors cited here, we believe that it is time for a sea change in worldview regarding the value of old-growth age structure.

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