FISH and FISHERIES

Reproductive resilience: a paradigm shift in understanding spawner-recruit systems in exploited marine fish

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Abstract

A close relationship between adult abundance and stock productivity may not exist for many marine fish stocks, resulting in concern that the management goal of maximum sustainable yield is either inefficient or risky. Although reproductive success is tightly coupled with adult abundance and fecundity in many terrestrial animals, in exploited marine fish where and when fish spawn and consequent dispersal dynamics may have a greater impact. Here, we propose an eco-evolutionary perspective, reproductive resilience, to understand connectivity and productivity in marine fish. Reproductive resilience is the capacity of a population to maintain the reproductive success needed to result in long-term population stability despite disturbances. A stock's reproductive resilience is driven by the underlying traits in its spawner-recruit system, selected for over evolutionary timescales, and the ecological context within which it is operating. Spawner-recruit systems are species specific, have both density-dependent and fitness feedback loops and are made up of fixed, behavioural and ecologically variable traits. They operate over multiple temporal, spatial and biological scales, with trait diversity affecting reproductive resilience at both the population and individual (i.e. portfolio) scales. Models of spawner-recruit systems fall within three categories: (i) two-dimensional models (i.e. spawner and

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recruit); (ii) process-based biophysical dispersal models which integrate physical and environmental processes into understanding recruitment; and (iii) complex spatially explicit integrated life cycle models. We review these models and their underlying assumptions about reproductive success vs. our emerging mechanistic understanding. We conclude with practical guidelines for integrating reproductive resilience into assessments of population connectivity and stock productivity.

Keywords Dispersal, fisheries management, productivity, reproductive potential, resilience, spawner-recruit

Introduction

The spawning stock-recruitment relationship is a fundamental and challenging problem in fisheries science and at the centre of a current debate on drivers of stock productivity and productivity regime shifts (Vert-pre *et al.* 2013; Klaer *et al.* 2015; Szuwalski *et al.* 2015; Porch and Lauretta 2016). Although there is increased emphasis on complex ecological processes and environmental forcing (Rice 2011), a growing body of literature demonstrating nonlinear relationships and tipping points (Glaser *et al.* 2014; Vasilakopoulos and Marshall 2015; Hunsicker *et al.* 2016) and increased recognition of the importance of resilience to natural resource management (Polasky *et al.* 2011; Brown and Williams 2015), we lack an eco-evolutionary framework to understand drivers of adult abundance in marine fish. As noted by Phil Levin in his 1989 Robert H. MacArthur award lecture (Levin 1992), ‘the chasm between evolutionary biology and ecosystems science is a wide one...yet neither discipline can afford to ignore the other: evolutionary changes take place within the context of ecosystems, and an evolutionary perspective is critical for understanding organisms’ behavioural and physiological responses to environmental change’. The concept of reproductive resilience can help fill this chasm.

In many animals, reproductive success (see definition in Table 1) is tightly coupled with adult abundance and fecundity (Stearns 1992). However, most exploited marine fish have evolved reproductive strategies, which differ from terrestrial animals, with effective breeding populations often orders of magnitude smaller than the mature census population (Hedgecock 1994; Christie *et al.* 2010), suggesting adult abundance is a poor predictor of recruitment and that we need to better understand the traits resulting in effective breeding. Recent meta-analyses of the RAM Legacy Stock Assessment Database also support the lack of a close relationship between adult abundance and stock productivity (Vert-pre *et al.* 2013; Szuwalski *et al.*

Table 1 Definitions of common terms used with processes discussed in this paper, including: reproductive success, productivity and resilience.

Term	Definition	References
Stock productivity	Net population increase in abundance and/or weight affected by natural mortality, growth, sexual maturation and recruitment	Vert-pre *et al.* 2013 Klaer *et al.* 2015
Stock productivity shift	Significant changes in any of the factors affecting stock productivity over time	Klaer *et al.* 2015
Stock reproductive potential	The annual variation in a stock's ability to produce viable eggs and larvae that may eventually recruit to the adult population or fishery	Trippel 1999
Reproductive success	The probability that offspring will survive to reproductive age based on reproductive output and the survival of that output	Stearns 1992
Ecological resilience	The magnitude of disturbance that a system can tolerate before it shifts into a different state (stability basin) with different controls on structure and function	Folke 2006 Scheffer *et al.* 2009
Reproductive resilience	The capacity of a population to maintain the level of reproductive success needed to result in long-term population stability despite disturbances such as environmental perturbations and fishing	Lowerre-Barbieri *et al.* 2015
Transgenerational inheritance	The ability of environmental factors to promote a phenotype not only in the exposed individual but also in subsequent progeny, potentially over multiple generations	Salinas and Munch 2012
Reproductive value	Weights the contributions of individuals of different ages to population growth and compares the sensitivity of fitness to events at different ages	Stearns 1992
Intrinsic rate of growth, *r*	The intrinsic rate of natural increase often used in theoretical work is the per capita instantaneous rate of increase in a population in a stable age distribution and calculated as $r \approx (\ln(\sum l_x m_x))/T$, where l_x = age-specific survivorship, m_x = age-specific fecundity and T = mean generation time (average age of mothers reproducing)	Stearns 1992
Life History Theory	Given a diversity of birth and death schedules and organismal designs, what kinds of life histories will evolution produce and why	Stearns 1992

2015). Less than 20% of the stocks evaluated in those papers showed a pattern of productivity consistently driven by adult abundance (Vert-pre *et al.* 2013), and only 39% showed a positive relationship between recruitment and spawning biomass (Szuwalski *et al.* 2015). However, fisheries management remains predicated on the concept that mature biomass drives long-term population productivity and yield (Vert-pre *et al.* 2013).

Efforts to improve our ability to predict marine fish stock productivity (i.e. future abundance) have fallen primarily within two approaches. The first uses the conceptual model of current stock-recruit relationships (SRRs) but replaces spawning stock biomass (SSB) with estimates of total egg production (TEP) based on age-based fecundity vectors (Marshall 2009; Saborido-Rey and Trippel 2013; Brodziak *et al.* 2015). The second approach draws from life history theory, either through the familiar r- and K- selection theory (Musick 1999) or by expanding this concept to categorize life history strategies based on the intrinsic rate of population growth (Winemiller and Rose 1992), as well as life tables and the Euler–Lotka equation (Kindsvater *et al.* 2016). Both approaches have improved our understanding of productivity in marine fish. However, these approaches remain heavily based on the assumption that fecundity drives reproductive success and do not include spatiotemporal reproductive behaviour, which is an important driver of offspring survival (Maunder and Deriso 2013; Donahue *et al.* 2015). The importance of where and when fish spawn and the conditions encountered at the time of first feeding was first proposed by Hjort (1914), extended to the member-vagrant hypothesis (Iles and Sinclair 1982), later integrated into the match/mismatch hypothesis (Cushing 1990) and more recently linked to oceanographic concentration mechanisms by Lasker (1978) and Bakun (1996). However, only through relatively new technological advances can we now test these hypotheses at the appropriate scales. For example, we can now track where and when individuals are spawning, as well as track eggs and larvae from a given spawning site.

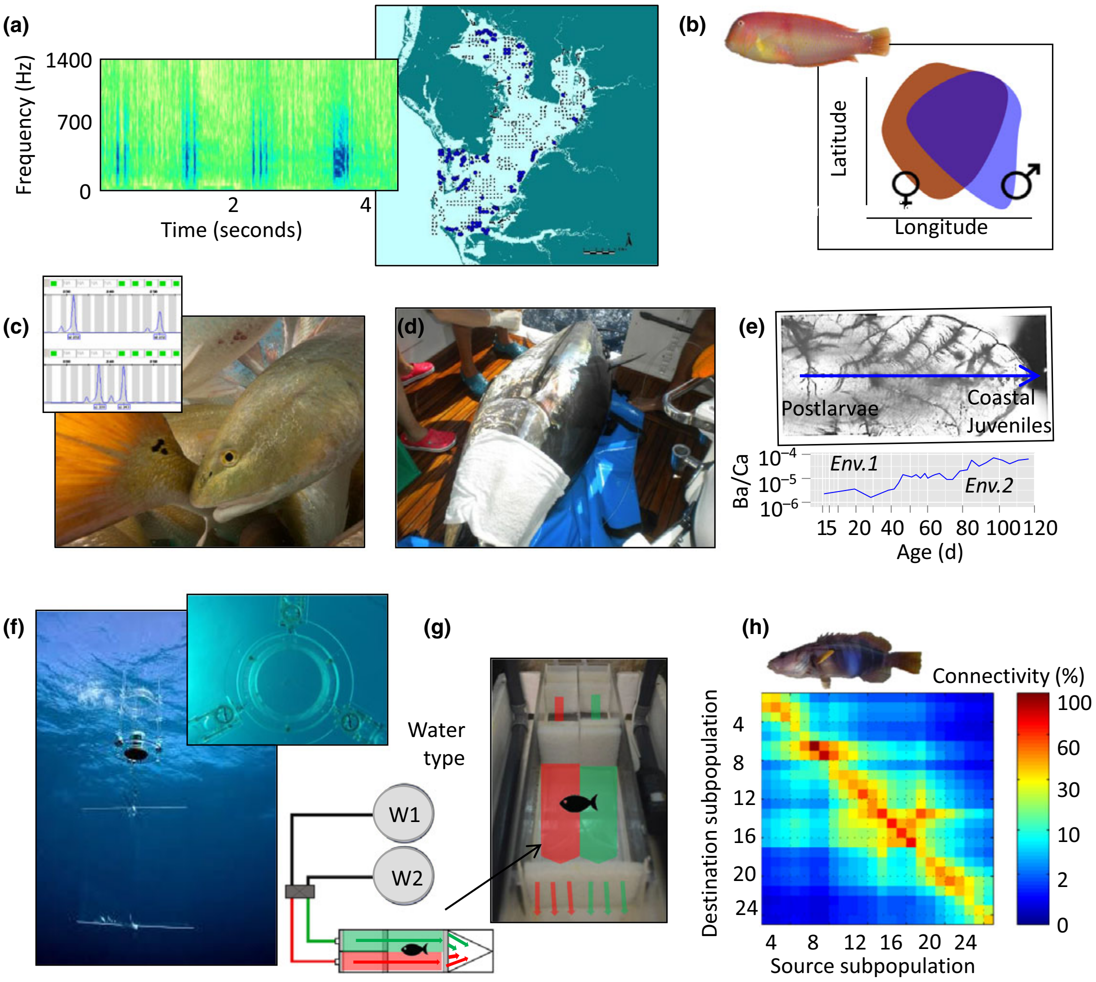

Figure 1 Examples of emerging methods to assess spawner-recruit processes: (a) passive acoustic surveys to map spawning sites based on species-specific courtship sounds (modified from Walters *et al.* 2009); (b) acoustic telemetry to assess sex-specific habitat use (Alós *et al.* 2012); (c) genetics, used as a tag to assess spawning population size and parentage analysis (S. Lowerre-Barbieri unpublished data); (d) pop up satellite tags used to understand spawning behaviour (Cermeño *et al.* 2015). (e) otolith microchemistry 'records' to evaluate individual habitat usage over time (I.A. Catalán, unpublished data); (f) the drifting in situ chamber (DISC) providing in situ evidence that pelagic reef fish larvae use reef odour as a navigational cue, changing their swimming speed and direction (modified from Paris *et al.* 2013); (g) choice chambers to provide empirical evidence of the use of odour cues in larval self-recruitment (modified from Gerlach *et al.* 2007); (h) biophysical modelling to study connectivity in meta-populations (modified from Alós *et al.* 2014).

We can also assess offspring fate (i.e. survivorship and settlement location) through transgenerational tagging, otolith microchemistry and genetic parentage analysis (Fig. 1). In addition, we now have the computing speed to develop spatially explicit individual-based models (IBMs) to evaluate factors affecting reproductive success (Mullon *et al.* 2002; Fiksen *et al.* 2007; Peck and Hufnagl 2012).

In this study, we bring together expertise in fisheries ecology, early life history and stock assessment to synthesize new understanding of reproductive potential in marine fish and its importance to fisheries management. We present an eco-evolutionary framework, reproductive resilience, to understand multidimensional 'spawner-recruit systems' and the role they play in stock productivity. To build the concept of multidimensional spawner-recruit systems, we review the commonality and diversity of traits addressed in fish reproductive strategies. We then show how additional traits associated with energetics, spatiotemporal behaviour and sensitivity to environmental forcing affect reproductive success. Reproductive resilience is defined as 'the capacity of a population to maintain the reproductive success needed to result in long-term population stability despite disturbances such as environmental perturbations and fishing' (Lowerre-Barbieri *et al.* 2015). Species-specific spawner-recruit system traits (and within-population diversity in these traits) and the ecological context within which a system is operating determine reproductive resilience. We review how spawner-recruit systems are modelled in traditional stock assessments as well as in recently developed dispersal and spatially explicit full life cycle models, comparing underlying assumptions about reproductive success with recent developments in mechanistic understanding. We conclude with guidelines for applying emerging understanding of reproductive resilience into marine fisheries management.

Reproductive success and stock productivity

Productivity and scale

In fisheries science, the term productivity is used to refer to factors affecting adult biomass and our ability to harvest wild fish populations sustainably. The processes evaluated to understand stock productivity are commonly those occurring at the population scale as well as the lifetime, annual or seasonal temporal scales (Table 2). Recently, there has been increased interest in understanding ecological and evolutionary factors affecting fish stock productivity (Kindsvater *et al.* 2016) and the concept of reproductive success can help move this effort forward (Fig. 2) Reproductive success is the ability of an individual to produce offspring that survive to reproductive age (Stearns 1992) and it drives population growth, allows species to persist, and varies amongst individuals with important consequences for population dynamics (Clutton-Brock and Sheldon 2010) and fisheries-induced evolution (Dunlop *et al.* 2015). Reproductive success is also the ecological process that defines the factors affecting reproductive potential, although we commonly associate this phrase with SSB or TEP. The temporal scale associated with reproductive success is transgenerational; that is, adults must successfully reproduce within their reproductive lifespan and offspring must survive to reproductive age. It is this component of stock productivity which we focus on in this paper,

Table 2 Factors affecting population productivity/reproductive success over multiple temporal, spatial and biological scales.

		Biological scale relevant to reproductive success	
Temporal Scale	Spatial context	Population	Individual/group
Evolutionary	Long-term mortality environment (rate and variability) associated with home range	Life history strategy Spawner-recruit system Larval navigation Pelagic larval duration	Fitness
Transgenerational			
Reproductive success	Population structure	Population persistence	Reproductive performance
Lifetime			
Maturity, growth, mortality, fecundity	Nursery, foraging, spawning habitats, Larval retention	Demographic trends in behaviour	Contingents
Annual			
Year-class strength	Spawning site selection & fidelity Dispersal Environment	Larval and juvenile survival	Not yet clear if strong year classes are associated with greater genetic diversity
Seasonal			
Spawning season Critical period Match/mismatch Birth date dynamics	Spawning site fidelity Predator hot spots Food and predator encounter rates	Trophic dynamics Larval/hydrography interactions Phenology	Egg quality Mating system Number of breeding events within the spawning period

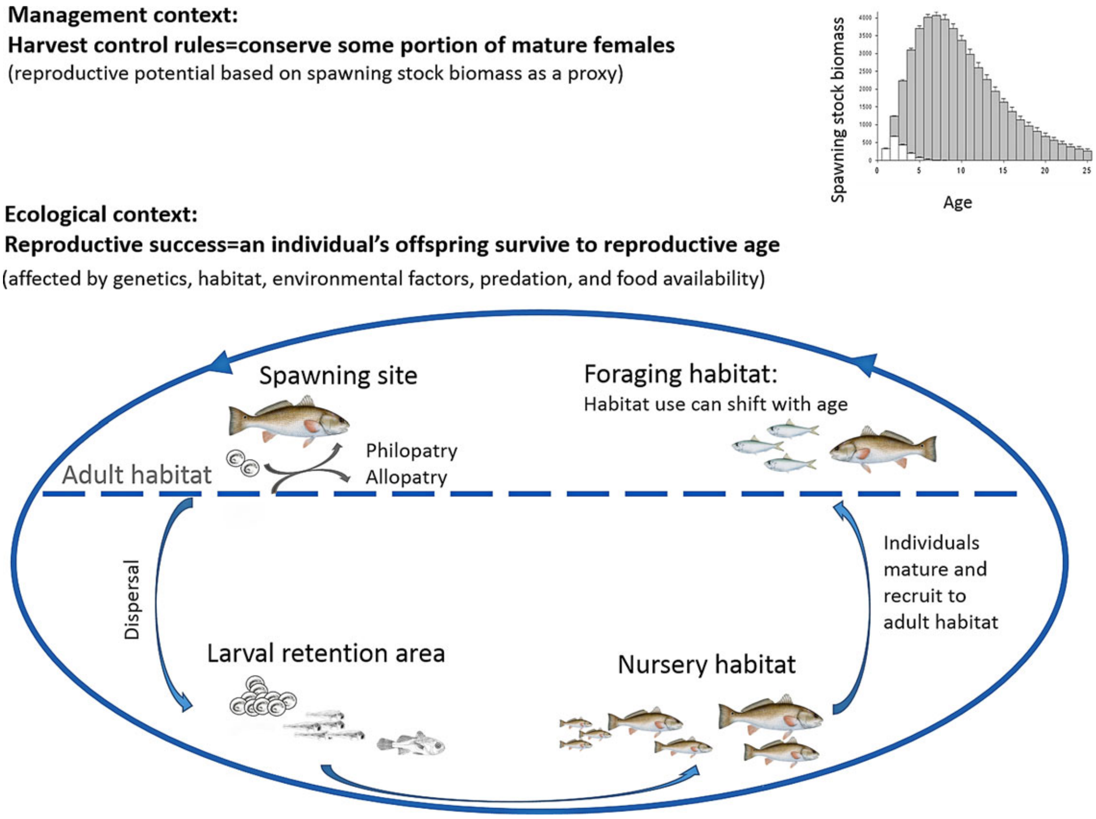

Figure 2 Reproductive potential is commonly based on spawning stock biomass, but in many marine species, spatial components of the life cycle may be more important to reproductive success.

using the terms 'transgenerational productivity' and 'productivity' interchangeably.

Recent debate about productivity drivers has coalesced around the importance of adult abundance (Vert-pre *et al.* 2013) vs. environmental impacts on recruitment (Szuwalski *et al.* 2015). Here, we use a reproductive resilience framework to integrate both of these factors into our understanding of spawner-recruit systems. Spawner-recruit system traits fall into three groups with differing phenotypic plasticity (Fig. 3, specific traits addressed in the next section). Fixed traits are constant amongst individuals within a species and invariant over ecological time. At the other end of the plasticity spectrum are ecologically variable traits. These traits are individually variable and affected by inter- and intraspecies (i.e. density dependent) interactions and environmental forcing. Behavioural traits exhibit phenotypic plasticity but often form a common pattern, or contingents, within a population.

The processes associated with spawner-recruit systems operate over multiple timescales (Table 2). Fixed and behavioural traits are critical biological determinants of reproductive success. These traits were selected for over evolutionary timescales to ensure population persistence in a given spatial context. Environmental forcing, operating at ecological timescales, inserts stochasticity into this system, functioning either as an on / off switch or as a modulator of the degree to which biological attributes can function. For example, recruitment occurs at the annual and population scales (Table 2) and strong year classes occur in years when either seasonal or episodic conditions result in physical processes favourable for larval and juvenile survival. These processes affect recruitment in many species and can include Ekman transport, storm-induced upwelling events and the occurrence of mesoscale eddies (Boehlert and Mundy 1988; Checkley *et al.* 1988; Rice *et al.* 1999; Sponaugle *et al.* 2005). Recently, Stachura *et al.* (2014) evaluated the potential for these physical processes to cause synchronized recruitment patterns across species within an ecosystem, with moderate coherence in exceptionally strong

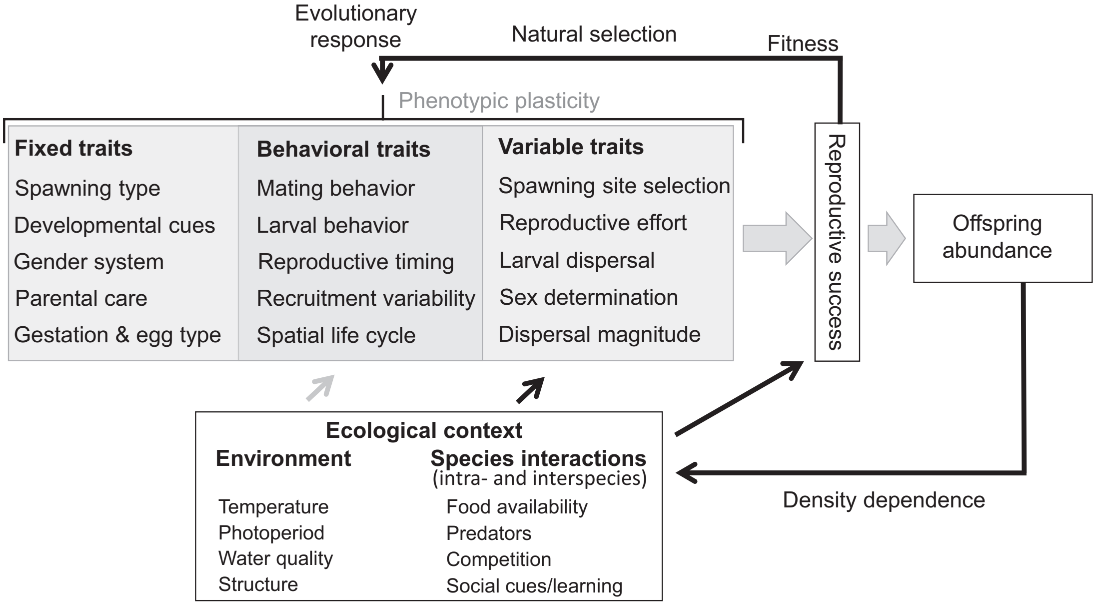

Figure 3 A stock's reproductive resilience is driven by its spawner-recruit system and the ecological context within which it is operating. Spawner-recruit systems are made up of three trait types with differing within-population variability, which ranges from: none (fixed traits) to extensive (variable traits), with behavioural traits exhibiting complex interactions between genotype and phenotype but typically a common pattern within a population. Inherent reproductive resilience depends on spawner-recruit traits selected over evolutionary time to overcome a given mortality regime. Current reproductive success occurs at the individual scale and results in both density-dependent and fitness feedback loops, which act to maintain population reproductive success over time and determine a stock's reproductive resilience to disturbance.

and weak year classes across 52 stocks in the Northeast Pacific.

However, at transgenerational timescales, weather and its effect on physical processes cannot be the sole driver of reproductive success, as natural selection acts on adult traits affecting offspring survival, resulting in species-specific reproductive resilience based on the selection pressures under which the species evolved (Garrod and Horwood 1984; Winemiller and Rose 1992; Lowerre-Barbieri 2009; Mangel *et al.* 2013). Mortality regimes (both intensity and variability of mortality) are spatially explicit and can vary over time. At the ecosystem scale, the marine environment differs in its selection pressures from terrestrial and freshwater systems due to size, oceanographic processes and trophic dynamics. The prevalence of high fecundity, pelagic larval stages and high offspring mortality in marine fish indicates a need to ensure adequate survival in a variable and unpredictable environment. The closest terrestrial comparison would be to plants which produce large numbers of seeds, dispersed with the wind. However, larval fish dispersal is often not passive, as a result of directed larval behaviour (Paris and Cowen 2004; Fiksen *et al.* 2007; Staaterman *et al.* 2012) and fish are not sessile, having the ability to select and move to their spawning sites (Leis 2015). Thus, drivers of reproductive success and resilience in the marine realm are expected to differ from terrestrial systems.

Commonality and diversity of reproductive strategies

Three drivers of transgenerational productivity, other than SSB, have been suggested for marine fish: increased reproductive value with age or the big old fat fecund female fish (BOFFFF) effect (Berkeley *et al.* 2004; Hixon *et al.* 2014), population structure (Frank and Brickman 2001; Fromentin *et al.* 2014) and diversity of spatiotemporal reproductive behaviour (Berkeley *et al.* 2004; Lowerre-Barbieri *et al.* 2015). Like natural mortality, the relative importance of these drivers can vary amongst species. Traits commonly considered in fish reproductive strategies are primarily fixed traits, including: (i) the number of breeding opportunities (iteroparous or semelparous); (ii) type of spawning (total vs. batch); (iii) mating system (promiscuous, polygamous, or pair spawners); (iv) gender system (gonochoristic or hermaphroditic); (v) secondary sex characteristics; (vi) spawning site preparation; (vii) place of fertilization; (viii) embryonic development; and (ix) degree of parental care (Murua and Saborido-Rey 2003; Wootton 2012). Most exploited marine fish (i.e. those which can sustain large increases in mortality and continue to have viable populations) exhibit either promiscuous or polygamous mating strategies with external fertilization, no parental care and no spawning site preparation. Of course, there are exceptions including the rockfishes (*Sebastes* spp.), which have internal fertilization and development but release pelagic larvae (Mangel *et al.* 2007), and grey triggerfish (*Balistes capriscus*, Balistidae) and lingcod (*Ophiodon elongates*, Hexagrammidae), which build nests and guard their eggs. Exploited species are somewhat more diverse in terms of the number of breeding opportunities, spawning type and gender system. Most species are iteroparous, but several semelparous species support extremely important fisheries, including the European and American eels (*Anguilla Anguilla* and *Anguilla rostrate*, Anguillidae), capelin (*Mallotus villosus*, Osmeridae), American shad (*Alosa sapidissima*, Clupeidae) and Pacific salmon (genus *Oncorhynchus*, Salmonidae). Similarly, at the annual scale, most species are batch spawners, spawning multiple times in a spawning season. Total spawners, those fish which spawn either in one event or over a short time period (Pavlov *et al.* 2009), occur less frequently and are typically diadromous, undertaking long spawning migrations (Jager *et al.* 2008). Total spawners, such as Atlantic salmon (*Salmo salmar*, Salmonidae), striped bass (*Morone saxatilis*, Moronidae), and grey and striped mullet (*Mugil liza, Mugil cephalus*, Mugilidae), support important fisheries. Similarly, the vast majority of exploited marine fish have a gonochoristic gender system. However, hermaphroditism is common in groupers (Epinephelidae), sea basses and combers (Serranidae), parrotfishes and wrasses (Labridae), and seabreams (Sparidae) and plays an important role in understanding transgenerational productivity in these fished species (Erisman *et al.* 2013). Sex determination, not to be confused with gender system, is an individual 'decision' to be one sex or the other and is an ecologically variable trait affected by temperature in some gonochorists and social cues in hermaphrodites (Mank and Avise 2009).

Spawner-recruit systems

To understand spawner-recruit systems, we need to expand beyond traditional reproductive strategy traits to include energetics, spatiotemporal behaviour, sensitivity to environmental forcing, and demographic trends in traits affecting reproductive success (Fig. 4a). There is growing awareness that energetics and spatiotemporal reproductive behaviour affect productivity. Reproductive effort is an ecologically variable trait and refers to the proportion of the total energy budget an individual devotes to reproductive processes. It will be affected by both ecological context (food availability) and internal state and affects spawning migrations, egg quality, skip spawning and annual fecundity (McBride *et al.* 2013). Reproductive timing, or the temporal pattern of reproduction over a fish's lifetime can act as both a behavioural trait (i.e. spawning seasonality) and an ecologically variable trait (i.e. individual spawn times) and plays an important role in reproductive success, determining the first environment offspring encounter (Ims 1990; Yamahira 2004; Lowerre-Barbieri *et al.* 2011) and the number of breeding events and thus the probability of releasing offspring during the window associated with favourable survival conditions. Reproductive timing also determines reproductive lifespan and generation time and thus expected recovery times following over-exploitation. Spawning site selection is also both a behavioural (spawning habitat) and ecologically variable trait (individual site choice). Spawning site selection determines the starting point of larval dispersal and affects fisheries selectivity, and potentially all spatial components later in the life cycle (Bailey *et al.* 2008; Maunder and Piner 2014; Ciannelli *et al.* 2015). Availability of spawning habitat affects population viability (Valavanis *et al.* 2008) and consistent spawning site selection over time, or spawning site fidelity, affects population structure. If spawning site selection is driven by returning to an individual's birthplace, this is considered natal homing or philopatry.

For offspring to survive and recruit to a fishery, larvae must find food, avoid predation and reach suitable nursery habitat, which often differs from

(a) **Important spawner-recruit system traits**

Reproductive effort: energy devoted to reproductive processes affecting skip spawning, migrations and egg quality

Demographic trends in behavior affecting reproductive success

Reproductive timing: Sexual maturity, Reproductive lifespan, Generation time, Spawning seasonality, Annual breeding events (spawning frequency), Diel periodicity

Spawning site selection: Distribution of life cycle (distance between spawning, nursery, and adult foraging habitats), Spawning site density and diversity, Spawning site fidelity

Larval dispersal potential: Gestation type, Egg type (benthic or pelagic) and size, Larval behavior related to self-recruitment

Recruitment variability: Relationship to SSB, Variability, after standardized for SSB,over generational time periods

(b)

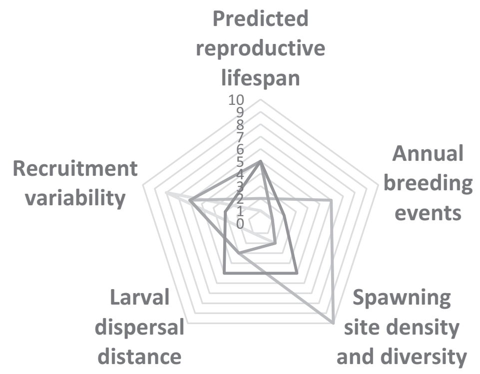

Figure 4 Important traits in spawner-recruit systems (a) and graphic representation of how these traits are species specific, resulting in differing reproductive resilience (b). Although the graphs are hypothetical, they represent how known variability in the selected traits in exploited marine fishes could be categorized from 1 (least resilient) to 10 (most resilient). Categories are based primarily on diversity, with greater diversity assumed to correlate with greater resilience.

spawning habitat. In addition, juveniles need to avoid predation, eat, grow and, in many species, move to adult habitat. Drivers of larval survivorship are also species specific, because each species has evolved unique behaviours and physiological characteristics to survive in a given habitat. For example, late-stage larvae of coral reef fish typically need a suitable reef habitat on which to settle at the end of their pelagic larval phase. Many of these species therefore have physiological traits which aid in their abilities to locate this habitat, such as strong swimming abilities, advanced sensory perception and navigation capabilities (Kingsford *et al.* 2002; Leis 2007). In contrast, many pelagic species do not rely on a particular benthic habitat for settlement, completing their life cycle in the pelagic environment. For example, most species of tuna spawn in oligotrophic subtropical environments (Reglero *et al.* 2014). These environments may be food-limited and these species have evolved specialized feeding behaviours, including piscivory and cannibalism from very small sizes (Llopiz and Hobday 2015). Like adult survivorship, there is no universal process or temporal predictor of offspring survival. For pelagic species, it may be determined more in the egg (Richardson *et al.* 2011) or larval stages (Bergenius *et al.* 2002; Sætre *et al.* 2002; Beaugrand *et al.* 2003; Castonguay *et al.* 2008). In demersal and reef species, juvenile mortality may play a more important role (Shulman 1985; Gibson 1994; Carr and Hixon 1995), although it often simply dampens year-class variability, rather than driving year-class strength (Myers and Cadigan 1993; Leggett and DeBlois 1994). Similarly, processes affecting offspring survivorship will differ with latitude. For example, the close relationship between high chlorophyll events and larval feeding success observed in temperate species (Platt *et al.* 2003) may not be an appropriate model for species adapted to tropical environments (Leis *et al.* 2013).

Spawner-recruit systems differ in their sensitivity to environmental effects and the temporal pattern of strong year classes over the expected reproductive lifespan. Both have important implications to management as they will affect recovery potential and vulnerability to climate change. For example, wind has a strong effect on the retention or dispersal of the eggs of spring-spawning cod (Hinrichsen *et al.* 2003; Pacariz *et al.* 2014), whereas for menhaden, spawning in the winter offshore, it is the large-scale atmospheric drivers that have the greatest effect on across-shelf transport and reproductive success (Rice *et al.* 1999). Short-term, episodic events also affect survival as seen in increased survivorship of striped bass eggs in estuaries when spawning follows a pulse of freshwater discharge (North *et al.* 2005), but decreased survival associated with storm events that affect water temperature (Rutherford and Houde 1985; Secor and Houde 1995). The temporal patterns of strong year classes are also species specific (Pineda *et al.* 2007; Morgan 2014). Assessing the data reported by Pepin (2015), we show that commercially exploited stocks from primarily temperate habitats had recruitment variability patterns that differed amongst families (Fig. 5). Forage fish and two families of Pleuronectiformes had greater recruitment variability relative to variability in spawner biomass, whereas tunas (Scombridae), sablefish (Anoplopomatidae), sea basses (Serranidae) and roughies (Trachichthyidae) had lower relative levels of recruitment variability. However, spawner-recruit systems are species specific and vary considerably within a family, and the limited differences in median relative recruitment variability amongst many of the families (from Pleuronectidae to Carangidae) may point to a need for finer taxonomic resolution and/or greater consideration of the ecological context (i.e. expected environmental variability) associated with a species' home range.

A species' reproductive resilience depends on its fixed, behavioural and ecologically variable traits and the within-population diversity in these traits. At the population scale, spawner-recruit systems differ amongst species in their trait diversity (Fig. 4). For example, reproductive lifespan in semelparous species is one year, whereas it is more than 70 years for Pacific ocean perch (*Sebastes alutus*, Sebastidae). Similarly, the number of annual breeding events can vary from one in striped bass to 54 in the bay anchovy (*Anchoa mitchilli*, Engraulidae). High spawning site density and low diversity is seen in species like Nassau grouper (*Epinephelus striatus*, Serranidae) (Erisman *et al.* 2015) and the reverse is seen in the red snapper (*Lutjanus campechanus*, Lutjanidae) (Lowerre-Barbieri *et al.* 2015). Larval dispersal and recruitment variability also differ, presumably associated with the distance between spawning and nursery sites, which can be widely separated in species such as in gag grouper (*Mycteroperca microlepis*, Serranidae) (Fitzhugh *et al.* 2005) or overlapping in estuarine fish such as the spotted sea trout (*Cynoscion nebulosus*, Sciaenidae) (Walters *et al.* 2009).

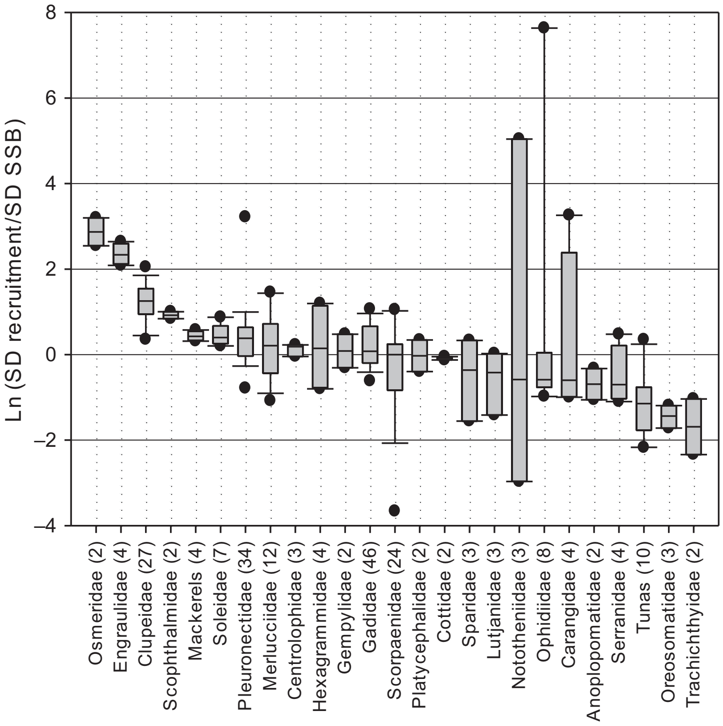

Figure 5 Box whisker plots of variability (SD) in recruitment relative to variability in spawner biomass (SSB) in relation to taxonomic family, with families ordered from highest to lowest median relative variability. Numbers indicate the number of stocks/management units in each family. Scombridae were separated into mackerels and tunas because of clear distinctions in the patterns of relative variability. Grey bars represent the 25th, median and 75th percentiles; error bars represent 5th and 95th percentiles; closed circles represent outliers. Data on fish populations from analytical population assessments collated in the Ransom Myers Legacy database.

Reproductive resilience is also driven by individual diversity in behavioural and ecologically variable traits, often called the 'the portfolio effect' (Figge 2004). The underlying concept is to maximize population fitness through spreading the risk (Garcia-Gonzalez *et al.* 2015), resulting in increased population reproductive success in an unpredictable environment (Secor 1999). For example, Bristol Bay salmon stock exhibit spatiotemporal spawning diversity, which increases the resilience of the regional stock, and reduces variability in fishery yields (Hilborn *et al.* 2003; Schindler *et al.* 2010), with similar patterns observed in a range of species (Secor 2007). The portfolio effect has been studied primarily in terms of the spatiotemporal behaviour of diadromous species. But portfolio theory can be used to estimate components of a stock's reproductive resilience by assessing spawner-recruit traits along axes of conservation risk and return (Anderson *et al.* 2015).

Modelling spawner-recruit systems

Stock assessments

Given increased awareness that adult abundance and TEP are poor predictors of future productivity in many marine fish (Kell *et al.* 2015), we need to develop alternative ways to assess spawner-recruit systems and their productivity. Conventional fisheries management attempts to control fishing mortality on a given stock in a way that produces near-maximum sustainable yields (O'Farrell and Botsford 2006) and prevents recruitment overfishing, even if a direct link between spawning stock size and subsequent recruitment cannot be established statistically, which is commonly the case (Rosenberg and Restrepo 1994). By necessity, all stock assessment models simplify ecological processes (Cadrin and Dickey-Collas 2015), but they differ in their complexity and their assumptions regarding reproductive success and productivity (Table 3). The simplest stock assessment models assume constant recruitment and that productivity is driven by density dependence and the mature census population (i.e. SSB). Traditional self-regenerating models (Beverton *et al.* 1984) combine yield and SSB per recruit with a stock-recruitment relationship (SRR), which relates the abundance of spawners with subsequent recruitment (Ricker 1954; Beverton and Holt 1957; Cushing 1975; Shepherd 1982). Two SRR models are the most commonly used: the Beverton–Holt model, where recruitment increases asymptotically, and the

Table 3 Models used to assess spawner-recruit systems and their productivity and recruitment assumptions.

Model type	Productivity assumption	Recruitment assumption	References
Biomass dynamics models	Density dependent	Implicitly assumes recruitment is a function of stock size	(Schaefer 1957; Pella and Tomlinson 1969)
Yield per recruit	Density independent	Constant	(Thompson and Bell 1934; Beverton and Holt 1957)
Spawner-per-recruit	Dependent on spawning biomass	Constant	(Gabriel *et al.* 1989; Clark 1993; Goodyear 1993)
Full life cycle models	Dependent on spawning biomass	A density-dependent function of SSB or fecundity	(Beverton *et al.* 1984)
		Ricker: Over compensatory at high stock levels	(Ricker 1954)
		Beverton–Holt: asymptotic at high stock levels	(Beverton and Holt 1957)
Biophysical dispersal models	Dependent on resolved oceanographic processes and available spatio-temporal reproductive data	Affected by larval dispersal dynamics and settlement habitat and cues	(Paris *et al.* 2005, 2013; Cowen *et al.* 2006)
Integrated life cycle models	In addition to the factors above, dependent on juvenile habitat and survival, as well as adult survival and increasingly, adult population structure	The same as above	(Drouineau *et al.* 2010; Rochette *et al.* 2013; Archambault *et al.* 2016)

Ricker model, where recruitment declines at high spawning stock abundance. However, both predict recruitment produced by a given spawning biomass based on the product of maximum productivity per unit spawning biomass and the degree of density dependence (Mangel *et al.* 2013). A parameter used in conjunction with SRRs is steepness or the fraction of recruitment from an unfished population when the SSB declines to 20% of its unfished level (Hilborn and Walters 1992). Brodziak *et al.* (2015) state that 'steepness determines the expected resilience of a fish stock to harvest and is fundamentally important for the estimation of biological reference points such as maximum sustainable yield'.

However, population growth rates and equilibrium abundance are affected by multiple complex processes not integrated into stock assessments (Watson *et al.* 2012; Snyder *et al.* 2014). Stock assessment models are predicated on the concept that population growth can be explained by birth and death rates and density dependence, independent of how behaviour impacts reproductive success (i.e. behavioural ecology). Similar to models used to estimate maximum sustainable yield for hunted wildlife, such as deer (Fortin *et al.* 2015), these models assume all births are created equal and that birth rate is the main driver of reproductive success. However, most exploited marine fish are pelagic spawners with high fecundity and high offspring mortality. In these spawner-recruit systems, the dispersal pathways of propagules (eggs and larvae) will determine source–sink dynamics (Iwasa and Roughgarden 1986; Leibold *et al.* 2004; Kough *et al.* 2013), population persistence (Hastings and Botsford 2006; Aiken and Navarrete 2011), rates of population replenishment (Hastings and Botsford 1999; Botsford *et al.* 2001; Cowen *et al.* 2006) and spatial overlap with competitors, predators and prey (Salomon *et al.* 2010; White and Samhouri 2011). This suggests that where and when 'birth' occurs may be as, or more important, than birth rates (Hamilton *et al.* 2008).

Biophysical dispersal models

Over the past decade, our understanding of spawner-recruit systems has been greatly improved by modelling efforts linking reproductive and dispersal processes (Rose *et al.* 1999; Werner *et al.* 2001; Cowen *et al.* 2006; Peck and Hufnagl 2012). The spatial scale of traditional stock assessments is that of the unit stock, with the biological definition based on reproductive isolation. Marine fish populations are typically assumed to be relatively open, with high levels of gene flow and stocks consequently defined based on geographical features and managed at large spatial scales. In addition, it is assumed that within a stock there is complete mixing of individuals and that the population exhibits homogeneous vital rates (Cadrin and Secor 2009). However, recent studies suggest spatial structuring occurs at much smaller scales and that this population structure can play an important role in productivity (Levin 2006; Stanley *et al.* 2013; Teacher *et al.* 2013; D'Aloia *et al.* 2015). Dispersal models are allowing us to test hypotheses about connectivity processes at these more realistic time–space scales (Paris *et al.* 2002, 2005; Miller 2007; Werner *et al.* 2007; Peck and Hufnagl 2012; Karnauskas *et al.* 2013; Ospina-Alvarez *et al.* 2015), resulting in dynamics and stability properties unsuspected from models which assume homogeneous spawning populations (Hastings and Botsford 1999; Botsford *et al.* 2009; Alós *et al.* 2014; Ospina-Alvarez *et al.* 2015).

Coupled biophysical IBMs, used to simulate egg and larval dispersal and survivorship, combine a stochastic biological model with ocean circulation models (Cowen *et al.* 2000). Typically, they use a Lagrangian particle-tracking framework to address individual variability, and information on currents and environmental conditions from ocean circulation models to track large numbers of individuals through space and time (Paris *et al.* 2007). An example is the Connectivity Modeling System (CMS), which is a probabilistic, multiscale model (Paris *et al.* 2013) with open-source code (https://github.com/beatrixparis/connectivity-modeling-system). The CMS couples an offline nested-grid technique to a stochastic Lagrangian framework where individual variability is introduced by drawing the biological attributes of individual larvae at random from a specified probability distribution of traits. The model generates an ensemble forecast or hindcast of the larvae's three-dimensional trajectories, dispersal kernels and transition probability matrices used for connectivity estimates.

One of the greatest remaining challenges for biophysical models is the need for data at the appropriate spatial and temporal scales. These data include the following: spatiotemporal distributions of spawning activity, egg and larval buoyancy, larval behaviour, stage durations, validated hydrodynamic models at biologically meaningful resolutions (Munguia-Vega *et al.* 2014), and better data on ecological context (e.g. prey and predator abundance). High-resolution data on spatiotemporal reproductive behaviour and how it may vary over time is often unavailable (Kough and Paris 2015), necessitating the assumption that reproductive behaviour is static. This can lead to spurious results, given that circulation patterns and current regimes can differ on relatively short timescales (Vikebø *et al.* 2005). However, the need for these data are increasingly recognized (Erisman *et al.* 2012). Emerging methods to collect data on spawning include the following: passive acoustic surveys to map spawning sites of soniferous species (Walters *et al.* 2009) and acoustic telemetry to track fine-scale reproductive behaviour (DeCelles and Zemeckis 2013; Lowerre-Barbieri *et al.* 2016). High-resolution data on spawning activity can also be gleaned from species for which the Daily Egg Production Method has been applied, predominantly small pelagics (Ospina-Alvarez *et al.* 2013). It is also increasingly available from fisheries-independent surveys (Lowerre-Barbieri *et al.* 2014) and can be augmented by examining available fisheries-dependent data (i.e. looking at peaks in catch per unit effort with spawning season for aggregating species) or drawing on the local ecological knowledge of fishermen (Ames 2004; Murray *et al.* 2008).

Spatially explicit integrated life cycle models

Although dispersal and settlement drive the fitness landscape in sedentary marine species, fish have the ability to select and move to a given spawning site (Paris *et al.* 2005; Fiksen *et al.* 2007) leading to the need to integrate spatial components over the full life cycle (Ciannelli *et al.* 2015). Key spatial elements of an individual's life cycle (Fig. 2) include where an individual is spawned (i.e. the spawning site used by its parents), larval retention area, juvenile nursery habitat, adult foraging habitat, and where that individual spawns, which closes the life cycle and results in either philopatry or allopatry (Smedbol and Stephenson 2001). To assess population connectivity and its effect on reproductive resilience, it is necessary to assess dispersal throughout the life cycle (Frisk *et al.* 2014). To do so necessitates combining submodels into a single modelling framework (Plagányi and Butterworth 2004) to address environmental effects on larval drift, development and mortality rates, density-dependent effects in juveniles, and the population dynamics of the fished portion of the stock (Rochette *et al.* 2013). Such spatially explicit end-to-end modelling frameworks have focused primarily on trophic dynamics (e.g. Atlantis, OSMOSE and Ecospace). However, there is growing awareness that linkages between energetics and reproductive success at the individual and population scales affect stock productivity (Giacomini *et al.* 2013; Politikos *et al.* 2015; Rose *et al.* 2015). For example, full life cycle models have been developed to assess spatial and environmental drivers of productivity but applied primarily to small pelagics (Bernal *et al.* 2011). This is because these species often have the needed data, as the daily egg production method is used to estimate SSB. However, the differing spawning site selection processes in small pelagics with many other exploited marine species highlight the need to build these models for a wider range of species.

As with biophysical models, the greatest bottleneck is often data collected at the necessary spatial and temporal scales and the need to ground-truth model predictions and develop outputs applicable to management decision rules (White *et al.* 2011). An additional challenge is field-testing results through individual-based studies of spatial ecology and fitness. To test the efficacy of marine protected areas (MPAs), there is the added need to evaluate larval connectivity amongst MPAs (White *et al.* 2014). However, with recent empirical gains in molecular assays and statistical analytics for parentage and other first-order (i.e. full- and half-sibling) genetic assignments, there has been great improvement to our ability to ground-truth dispersal models (Baums *et al.* 2006). These genetic techniques provide a direct means to quantify individual reproductive success, identify sources of recruits, and ground-truth larval dispersal trajectories and dynamics (Manel *et al.* 2005; Harrison *et al.* 2012; Iacchei *et al.* 2013; Crossin *et al.* 2014).

Fisheries management and reproductive resilience

Fisheries management uses harvest control rules and measures (e.g. minimum size limits, closed seasons, closed areas, catch limits) based on biological reference points associated with the level of fishing at which there would be negative consequences (Marshall *et al.* 2003). Stock assessment models typically assume adult abundance drives recruitment, with density-dependent feedback loops driving productivity. However, our understanding is rapidly changing with the recognition that productivity is affected by more than density-dependent compensation (Walters and Martell 2004; Francis *et al.* 2007), SSB and TEP are relatively insensitive measures of stock reproductive potential (Kell *et al.* 2015) and effective breeding populations are significantly smaller than adult populations (Christie *et al.* 2010; Hogan *et al.* 2012). At the same time, there is increased awareness of the role environment plays in annual recruitment (Szuwalski *et al.* 2015). If there is not a close relationship between adult abundance and recruitment for a given species, then the assumption that larger SSB results in greater sustainable yield is invalid and consequently, the single management target of maximum sustainable yield, predicated on this concept, is either inefficient or risky (Vert-pre *et al.* 2013).

In this review, we develop the concept of multi-dimensional spawner-recruit systems to better understand productivity and reproductive resilience in marine fish. Resilience refers to a system's ability to withstand disturbance while maintaining its essential functionality, structure and feedback loops (Walker *et al.* 2004). Here, we propose the term reproductive resilience to refer to the capacity of a spawner-recruit system to adapt to changing conditions while maintaining long-term stability in abundance but not changing its key traits, such as reproductive timing or spawning site selection. Reproductive resilience is not limited to reproductive processes but rather encompasses all processes affecting offspring survival to reproductive age. As such, it is an expansion on the concept of compensatory reserve, the suite of density-dependent processes resulting in slowed population growth at high population densities and faster population growth at low densities (Rose *et al.* 2001). Reproductive resilience is driven by a stock's spawner-recruit system and is the capacity of a population to maintain the level of reproductive success needed to result in long-term population stability despite disturbances. In this system, reproductive success is affected by both density-dependent and fitness feedback loops, and ecological context (Fig. 3). Evolutionary processes determine a stock's inherent reproductive resilience, but ecological conditions determine the reproductive success of an individual. When the mortality environment of a stock significantly changes from that under which the species evolved, outcomes range along a continuum from easily reversed density-dependent adaptation to extinction of population components, or whole species. In the middle of this continuum are adaptations to alternate states (productivity regime shifts), resulting from either the fitness feedback loop (e.g. selection for earlier maturation), or changes in the ecological context affecting reproductive success. Depensation occurs when density-dependent effects (in this case low density) cause changes in the ecological context, decreasing reproductive success. This negative feedback can be due to a number of processes, such as increased predation or decreased food availability, potentially associated with complex multilevel trophic dynamics dependent on large egg boons (Fuiman *et al.* 2015), loss of population connectivity or decreased fertilization (Courchamp *et al.* 2008). Thus, reproductive resilience of a stock will be dependent on the stock's sensitivity to disturbance and its adaptive capacity within a given ecological context.

In the United States, the Magnuson-Stevens Fishery Conservation and Management Act and the associated National Standard Guidelines require fishery management councils to avoid overfishing by specifying 'acceptable biological catch' (ABC), which is typically based on an estimated over-fishing limit from the stock assessment (usually maximum sustainable yield or its proxy) and a 'buffer' adjustment to decrease the probability of over-fishing given scientific uncertainty (Prager and Shertzer 2010). Spawner-recruit systems consist of multiple interacting traits which occur over varying demographic, spatial and temporal scales, with greater resilience associated with greater diversity or redundancies within traits. Because spawner-recruit systems evolved to ensure population persistence in an environment with variable mortality, unfished populations possess inherent buffers to disturbance. However, because they are fundamentally based on the concept of compensatory capacity, SRRs have traditionally only looked at one element of a spawner-recruit system, that is adult abundance, and thus may not capture the system's built-in buffers nor how fishing may erode them or affect the fitness feedback loop. This conceptual model of spawner-recruit systems brings us closer to representing ecological processes than what has commonly been used in fisheries science and we believe can be used to better inform the development of reference points, as well as highlight the need for protection of non-traditional reproductive potential components.

Integrating spawner-recruit systems into the management framework

So what are the steps needed to take this conceptual model and apply it to the assessment and management of marine fish stocks? First, we need greater scientific dialogue amongst fisheries ecologists, geneticists, early life history scientists and stock assessment scientists. Each of these subgroups work somewhat independently from the others and often speak a different language, or at least a different dialect. We also need to address the differing scales associated with ecological and management processes. For reproductive resilience, the generational timescale (i.e. reproductive lifespan) is what is important, but operational management advice is usually provided at a shorter timescale, typically within a one- to three-year time horizon. Fluctuations in year-class strength (i.e. the production of strong or weak year classes) take on differing importance at these temporal scales. Ecologically, they may simply be part of a spawner-recruit system's ability to maintain a stable population over the species' reproductive lifespan, but from a management perspective they affect short-term yield and stakeholder's perception of abundance. Similarly, protection of key traits affecting reproductive resilience may not be possible with the use of only traditional fisheries management measures such as annual catch limits. Spawner-recruit systems are species specific with traits occurring over spatial, temporal and demographic scales. Fortunately, there is growing awareness of this (SEDAR, 2015) and the need for incorporating non-traditional measures of reproductive potential in the stock assessment and fisheries management processes (Fig. 6).

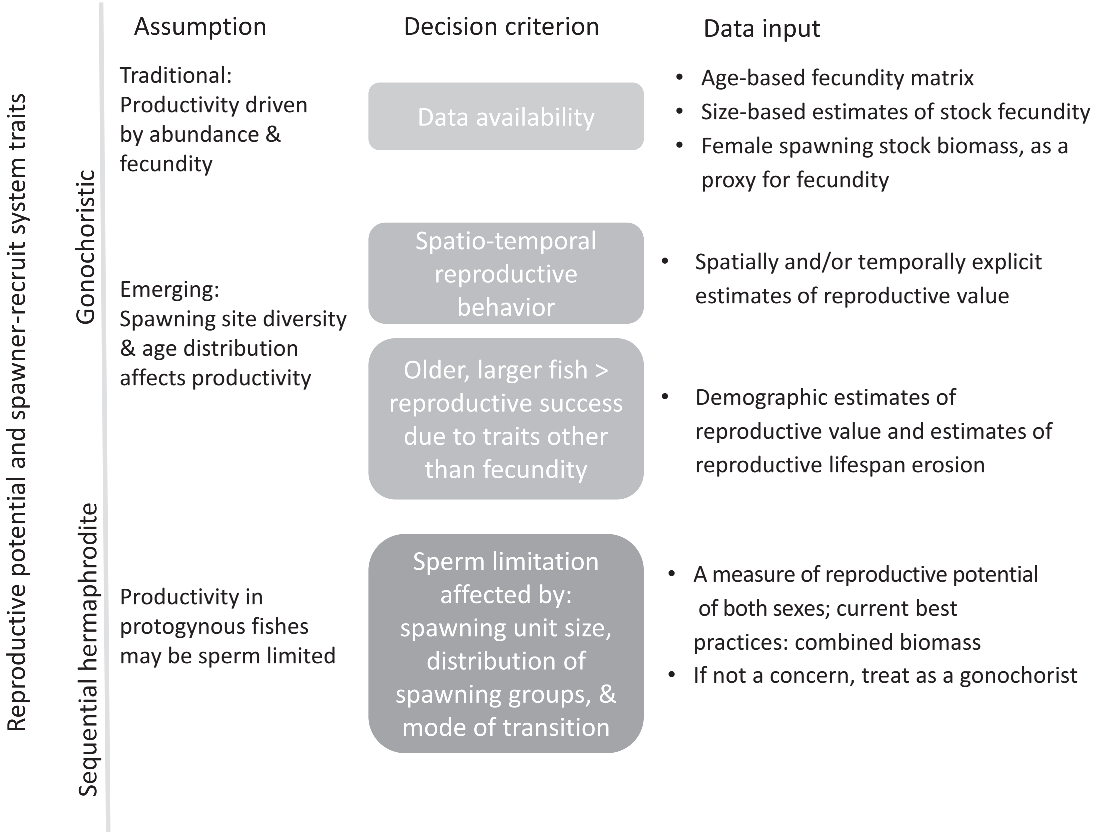

Figure 6 Reproductive potential and spawner-recruit systems: assumptions, decision criterion, and data needed for stock assessments.

Although aligning fishery management systems to better protect reproductive resilience seems daunting, it is already occurring. There is growing awareness that fishing is a selective force, stocks are not in equilibrium and both longevity and maturity schedules may be impacted, potentially changing a spawner-recruit system's structure and feedback loops. Because data-poor stocks do not have estimates of SSB, methods developed to assess them, such as the productivity and susceptibility analysis (PSA) and evaluation of life history traits (ICES WKLIFE working group, ICES 2015), are paving the way for better integrating reproductive resilience into assessments. The PSA approach evaluates how stocks will be impacted by fishing with the assumption that the risk to a species depends on two characteristics: (i) the productivity of the unit, which will determine the rate at which the unit can sustain fishing pressure or recover from depletion or other impacts due to the fishery; and (ii) the susceptibility of the unit to fishing activities (Patrick *et al.* 2010). This approach can easily be extended to include traits important to reproductive resilience, which will affect both productivity and susceptibility as well as to develop a reproductive resilience index which can be used as a post-assessment scaler to help inform ABC harvest control rules. Such consideration of reproductive resilience in ABC determination broadens the current practice of considering PSA vulnerability scores (Carmichael and Fenske 2011). At the mechanistic level, technological advances are allowing us to assess reproductive resilience in ways which were not previously possible. However, our modelling and simulation capability is greatly outpacing our available data, leading to a need for increased research on spawner-recruit systems and especially how they will function in this time of multiple disturbances, including climate change.

Measures of reproductive resilience with management applications

There is growing evidence that long-term high exploitation rates truncate age distributions, with feedback loops affecting other life history traits, especially maturation schedules (Jørgensen *et al.* 2007; Heino *et al.* 2013). The long-term effect of these changes is a potential decrease in a stock's resilience to other disturbances (Hsieh *et al.* 2008). Reproductive value is hypothesized to increase with size and age in exploited marine fish (Hixon *et al.* 2014) due to increased annual fecundity, increased spawning events in multiple batch spawners (Fitzhugh *et al.* 2012; Cooper *et al.* 2013), differing spatiotemporal reproductive behaviour (Scott *et al.* 2006; Anderson *et al.* 2008; Wright and Trippel 2009) and differing energy reserves (Jørgensen *et al.* 2006; Rideout and Tomkiewicz 2011), which impact egg and larval quality (Kamler 2005). The result is that a stock's age distribution plays an important role in sustainability and recovery, with 'fishing down of age classes' and loss of spawning potential due to excess fleet capacity probably the main cause of many stock collapses' (Caddy and Agnew 2004).

Fisheries selection often contradicts natural selection, with the prevalence of length-based fisheries management creating trade-offs between conservation and maximizing yield (Gwinn *et al.* 2015). This could be improved by integrating into our stock assessment process a way to quantify erosion of reproductive lifespan to better inform the development of limit and target reference points needed for setting short- and long-term management goals (i.e. evaluating the trade-offs between the long-term goal of protecting generations vs. maximizing short-term yield from strong year classes). Reproductive lifespan is an important component of reproductive resilience, as it determines the time frame over which an individual fish can potentially spawn. It is calculated based on age at maturity and maximum observed age, and point estimates can be used to assess reproductive resilience erosion based on parameters already collected for stock assessments (Lowerre-Barbieri *et al.* 2015; Secor *et al.* 2015). For example, by calculating the ratio of current to potential reproductive lifespan, as well as the effective reproductive lifespan based on the 90th percentile of the sampled age distribution (Lowerre-Barbieri *et al.* 2015). This ratio reflects the proportion of a species' reproductive lifespan lost due to fishing and can be used to identify the age distribution supporting a given spawning potential ratio. This is especially important for both short-lived opportunistic fish and long-lived episodic species (Kindsvater *et al.* 2016), as they are the most vulnerable to reproductive lifespan erosion, although for different reasons. In short-lived species, fishing has the potential to virtually wipe out the reproductive lifespan, while long-lived species evolved to have many years to reproduce successfully.

Changes in reproductive lifespan will affect other traits in a spawner-recruit system, the most documented of these being maturity. However, for many exploited species we do not yet track changes in maturity schedules to assess whether overfishing is causing earlier maturation (Fig. 7), as reported for multiple species (Jørgensen *et al.* 2007; Audzijonyte *et al.* 2013; Marty *et al.* 2014). Traditionally, maturity has been assumed to be invariant, and stocks with earlier maturation assumed to be more resilient to fishing. However, earlier maturation due to adaptive change rather than as an inherent spawner-recruit trait is expected to in turn affect other life history traits, especially growth. Decreased growth with earlier maturation can be due to individual physiological trade-offs; that is, energy allocated earlier to reproduction would mean less energy left over for growth (Stearns 1992; see also the Dynamic Energy Budget framework, Kooijman 2010). Or decreased growth could be selected for due to the fitness feedback loop (Alós *et al.* 2014). If slower growth is selected for, this change in productivity would not be easily reversed (Law and Grey 1989; Kraak 2007; Thorpe 2007).

By developing a reproductive resilience index, we can begin to move from two-dimensional to multidimensional spawner-recruit systems and more fully assess a stock's sensitivity and adaptive capacity to a given disturbance. A first simplistic step is to build on the PSA approach and categorize a stock's spawner-recruit system traits in terms of diversity and/or relationship to resilience. For highly fecund species with no parental care, we can identify key demographic, spatial and temporal spawner-recruit traits such as potential reproductive lifespan, annual breeding events, spawning density and diversity, larval dispersal distance and recruitment variability. Radar graphs can be used to map the system's resilience based on its traits, with larger areas conveying greater resilience (Fig. 4). In this example, greater resilience (10 being the highest score) is associated with greater diversity in the system and intermediate reproductive lifespans are considered the most resilient (Winemiller and Rose 1992). Although fully operationalizing how to integrate reproductive resilience into stock assessments is beyond the scope of this paper, we present this simplistic example to: (i) demonstrate the variability in species' reproductive resilience; (ii) highlight non-traditional components of reproductive potential; and (iii) identify data gaps which will need to be filled before we can fully assess a species' reproductive resilience and how it drives susceptibility to fishing and other disturbances.

Reproductive resilience and climate change

Many may say that consideration of broader spawner-recruit systems is unnecessary, because the traditional system has worked relatively well for the past 50 years. But the next 50 years are expected to be quite different, as climate change profoundly affects marine ecosystems (Sydeman *et al.* 2015) and stock productivity (Hare *et al.* 2016). Coastal oceanography is predicted to change in the coming decades in terms of sea level rise, storm regimes, temperature and pH (Meehl *et al.* 2005), which may impact productivity and reproductive resilience. Life cycle habitat connectivity will also be impacted by these changes and

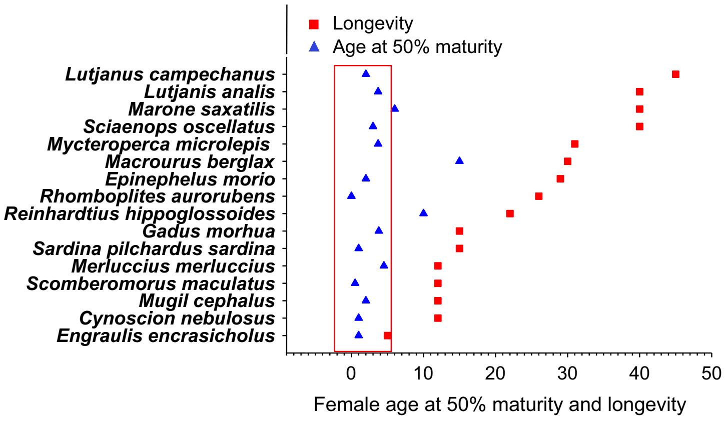

Figure 7 Estimated age at 50% maturity and maximum observed age in a range of exploited marine fishes.

consequently affect the ability of individuals to mature at the appropriate time and return to spawning grounds to reproduce successfully (Sinclair and Iles 1988; Rijnsdorp *et al.* 2009). The projected increase in both equator-ward transport and coastal upwelling along the coast of South America from Peru to Chile (Aiken *et al.* 2011), and an increase in the frequency of extreme Eastern Pacific El Niño-Southern Oscillation events (Cai *et al.* 2014) are expected to modify dispersal pathways and resulting survivorship (Aiken *et al.* 2011). Similarly, increases in water temperature will impact dispersal and connectivity via changes in reproductive phenology (Fig. 8), faster developmental rates, changes in larval swimming speeds and changes in predator and prey encounter rates (Lett *et al.* 2010; Pörtner and Peck 2010; Asch 2015). For example, O'Connor *et al.* (2007) demonstrated a negative relationship between temperature and pelagic larval duration across 69 marine species, with the expectation this will lead to changes in population spatial connectivity (Munday *et al.* 2009; Gerber *et al.* 2014).

It is unknown how climate change will affect species with high spawning site fidelity, where individuals return each year to spawn at the same sites. Natal homing allows fish to release offspring in the same location and presumed set of environmental conditions as those of the parent, resulting in a spatial component of fitness (Ciannelli *et al.* 2015). Spawning can persist at the same sites for many years, even decades (Colin 1996; Domeier and Colin 1997) and there is also good evidence in several species that social learning and tradition play a role in the repeated use of the same sites for spawning, with younger fish learning to use and find sites from older, experienced fish (e.g. bluehead wrasse (*Thalassoma bifasciatum*, Labridae) Warner 1988, 1990; Atlantic cod (*Gadus morhua*, Gadidae) Rose 1993; European plaice (*Pleuronectes platessa*, Pleuronectidae) Arnold *et al.* 1994; brown surgeonfish (*Acanthurus nigrofuscus*, Acanthuridae) Mazeroll and Montgomery 1998). Although the fitness benefits in spawning site fidelity not connected with natal homing are less clear, birth site may still influence spawning site selection in less direct ways and thus confer increased fitness. A disruption of factors associated with spawning site selection and fidelity will clearly affect future productivity. However, we do not yet have a mechanistic understanding of these processes, highlighting the need for additional research on spawning site selection and fidelity at both the population and individual scales (Lowerre-Barbieri *et al.* 2013; Donahue *et al.* 2015). We also need greater application of genetic analyses, given that

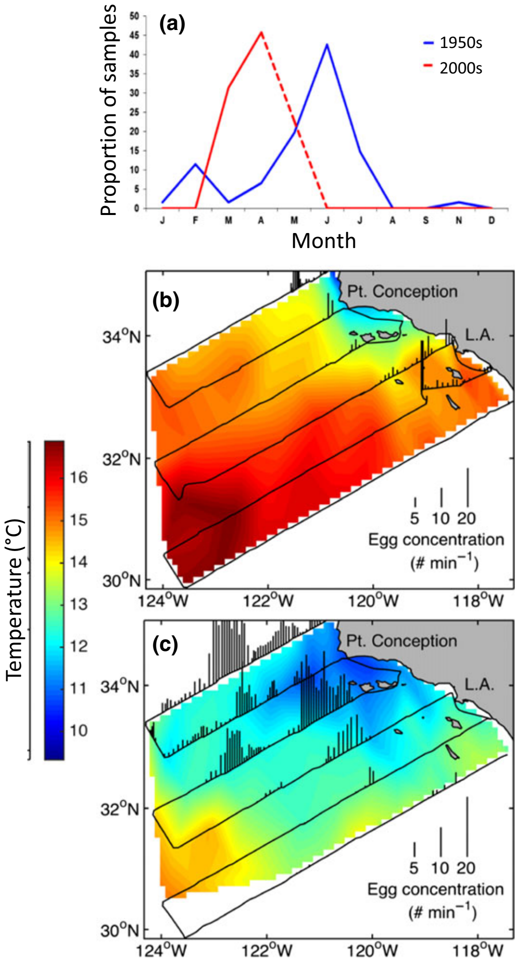

Figure 8 Influence of climate variations on the distribution and phenology of spawning in the Pacific Sardine (*Sardinops sagax*, Clupeidae) off the coast of Southern California, USA. Data modified from Asch (2013) and Asch and Checkley (2013). (a) Long-term changes in climatic conditions in California waters, including the timing and magnitude of seasonal water temperatures, are associated with marked shifts in the reproductive phenology of sardine, with peaks in monthly larval abundance occurring 2 months earlier in the 2000s than in the 1950s. (b) During El Niño years associated with warm sea surface temperatures, sardine spawning activity and egg production are low and restricted to a small range close to shore where thermal refuges remain. (c) Conversely, during La Niña years associated with cooler sea surface temperatures, spawning activity and egg production are high and widely distributed in both nearshore and offshore waters.

estimates of effective breeding population size show potential as proxies for delineating neighbourhood sizes (i.e. mean single-generation dispersal distances) and spatially explicit breeding densities (Neel *et al.* 2013) and thus the ability to track effects of climate change on phenology and reproductive success over time.

Conclusions and recommendations

Factors affecting reproductive success and resilience in marine exploited fish are extremely complex, poorly understood and not all can be managed. Assessment practices based on SSB to recruitment relationships and steepness are strongly based on the assumption of density-dependent population growth, that is compensatory capacity, and do not capture important traits impacting reproductive resilience. But does this matter, that is do the benefits of a better understanding of reproductive resilience and its integration into the stock assessment process outweigh the costs and competition with other areas of emerging fisheries science? We think so, particularly in the light of the uncertainty in how climate change may affect productivity. Similar to the push to move beyond the von Bertalanffy growth equation to understand trophic dynamics, we need to move beyond the intrinsic population growth equation to understand drivers of transgenerational productivity.

We recognize there are limited resources and many stock assessment demands and so organize our recommendations along a continuum from using existing data in new ways to improving our mechanistic understanding of reproductive resilience. Because maturity and maximum age are part of many highly developed stock assessment processes, estimating reproductive lifespan erosion and evaluating whether maturity schedules change over time should be relatively easy. In addition, many reproductive studies have the data needed to begin to quantify spawning site diversity and density (Lowerre-Barbieri *et al.* 2015), but these data often go unreported. Comparative and meta-analytical studies of large databases (e.g. Ricard *et al.* 2012) can be used to assess recruitment variability for a wide range of species, by calculating an index based on the variability seen in annual recruitment per unit of SSB over the potential reproductive lifespan. Through this, we can assess the similarities and differences in patterns of recruitment variability across species, highlighting those most sensitive to environmental conditions. In addition, we can then evaluate whether there are specific spawner-recruit traits which result in greater recruitment variability. These combined analyses should help provide the data needed to calculate reproductive resilience indices. To improve our mechanistic understanding of spawner-recruit systems and reproductive resilience, we need to fund field work applying novel approaches to track processes over multiple generations and to evaluate whether early life history conditions can have transgenerational inheritance effects, as seen in other species (Naguib and Gil 2005). Lastly, simulation modelling or management strategy evaluations with operating models which integrate more ecologically realistic reproductive success processes will greatly improve our understanding of species-specific reproductive resilience in this time of climate change.

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