



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

Susan Lowerre-Barbieri^{1,2}, Greg DeCelles^{3,4}, Pierre Pepin⁵, Ignacio A Catalán⁶, Barbara Muhling^{7,8}, Brad Erisman⁹, Steven X Cadrin³, Josep Alós^{10,6}, Andres Ospina-Alvarez¹¹, Megan M Stachura^{12,13}, Michael D Tringali¹, Sarah Walters Burnsed¹ & Claire B Paris¹⁴

¹Florida Fish and Wildlife Conservation Commission, Florida Fish and Wildlife Research Institute, 100 Eighth Avenue S.E., St. Petersburg, FL 33701-5020, USA; ²Fisheries and Aquatic Science Program, School of Forest Resources and Conservation, University of Florida, 7922 North West 71st Street, Gainesville, FL 32653-3071, USA; ³School for Marine Science and Technology, University of Massachusetts Dartmouth, 200 Mill Rd., Fairhaven, MA 02719, USA; ⁴Massachusetts Division of Marine Fisheries, 1213 Purchase St., New Bedford, MA 02740, USA; ⁵Fisheries and Oceans Canada, Northwest Atlantic Fisheries Centre, 80 White Hills Road, PO Box 5667, St. John's, NL, Canada, A1C 5X1; ⁶Department of Ecology and Marine Resources, Mediterranean Institute for Advanced Studies (IMEDEA-CSIC/UIB), C/ Miquel Marqués 21, CP 07190 Esporles, Balearic Islands, Spain; ⁷Princeton University Program in Atmospheric and Oceanic Sciences, Forrestal Campus/Sayre Hall, Princeton, NJ 08544, USA; ⁸Geophysical Fluid Dynamics Laboratory, National Oceanic and Atmospheric Administration, 201 Forrestal Road, Princeton, NJ 08540, USA; ⁹Department of Marine Science, University of Texas at Austin, 750 Channel View Drive, Port Aransas, TX 78373-5015, USA; ¹⁰Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm, 310, 12587 Berlin, Germany; ¹¹Millennium Nucleus – Marine Conservation Center, Estación Costera de Investigaciones Marinas ECIM, Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 193, Correo 22, Santiago, C.P. 6513677, Chile; ¹²NOAA NMFS, Office of Sustainable Fisheries, 1315 East West Highway, Silver Spring, MD 20910, USA; ¹³Independent researcher, Seattle, WA 98103, USA; ¹⁴Department of Ocean Sciences, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149, USA

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

Correspondence:

Susan Lowerre-Barbieri, Florida Fish and Wildlife Conservation Commission, Florida Fish and Wildlife Research Institute, 100 8th Ave. SE St. Petersburg, FL 33701, USA
Tel.: (727) 502-4930
Fax: (727) 893-1374
E-mails: susan.barbieri@myfwc.com; slowerrebarbier@ufl.edu

Received 12 Mar 2016
Accepted 8 Aug 2016

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	1
Reproductive success and stock productivity	5
Productivity and scale	5
Commonality and diversity of reproductive strategies	7
Spawner-recruit systems	8
Modelling spawner-recruit systems	11
Stock assessments	11
Biophysical dispersal models	12
Spatially explicit integrated life cycle models	13
Fisheries management and reproductive resilience	13
Integrating spawner-recruit systems into the management framework	15
Measures of reproductive resilience and management applications	16
Reproductive resilience and climate change	17
Conclusions and recommendations	19
Acknowledgements	19

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 (Hedgcock 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 <i>et al.</i> 2013 Klaer <i>et al.</i> 2015
Stock productivity shift	Significant changes in any of the factors affecting stock productivity over time	Klaer <i>et al.</i> 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 <i>et al.</i> 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 <i>et al.</i> 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.

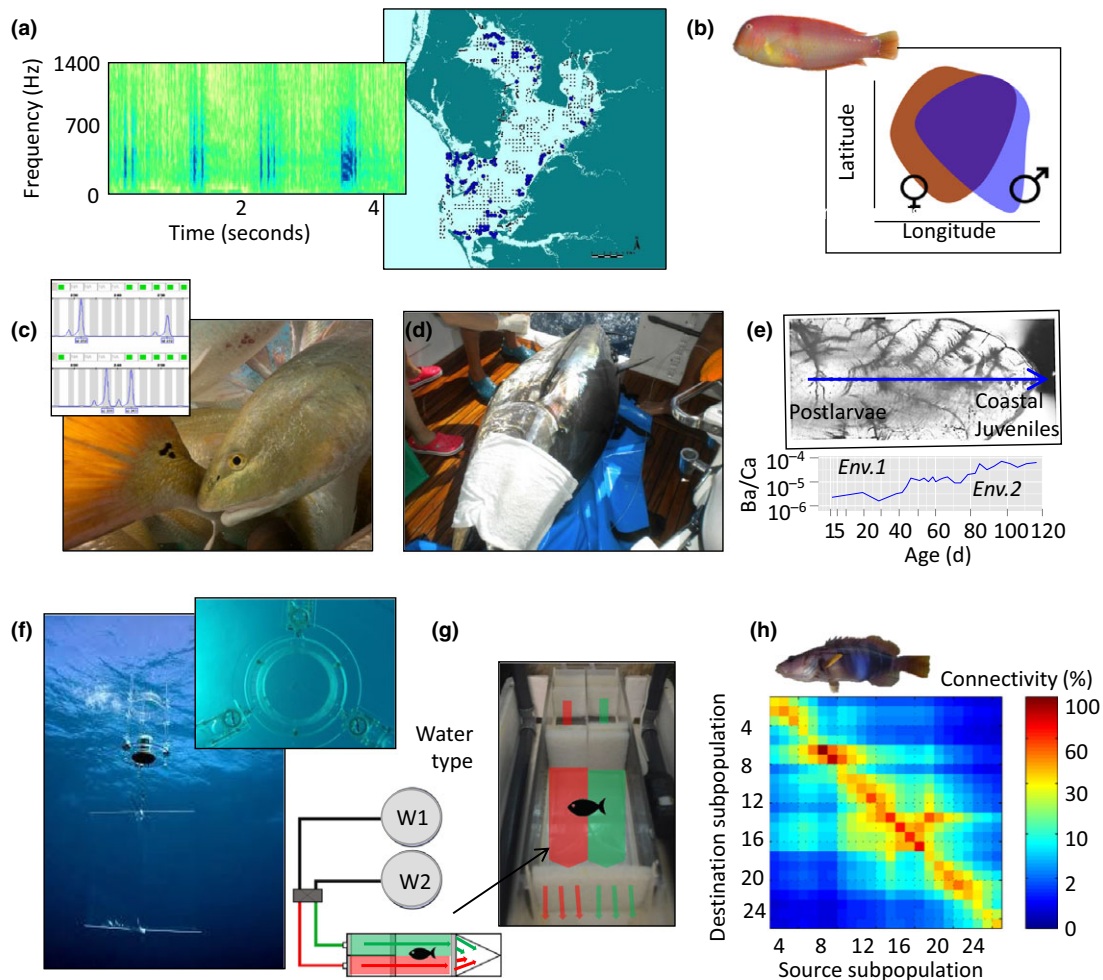


Figure 1 Examples of emerging methods to assess spawner-recruit processes: (a) passive acoustic surveys to map spawning sites based on species-specific courtship sounds (modified from Walters *et al.* 2009); (b) acoustic telemetry to assess sex-specific habitat use (Alós *et al.* 2012); (c) genetics, 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 (Cerreño *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

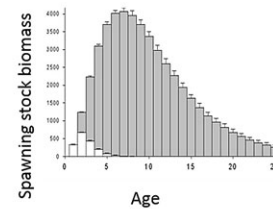
ability to harvest wild fish populations sustainably. The processes evaluated to understand stock productivity are commonly those occurring at the population scale as well as the lifetime, annual or seasonal temporal scales (Table 2). Recently, there has been increased interest in understanding ecological 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.

Temporal Scale	Spatial context	Biological scale relevant to reproductive success	
		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

Management context:

Harvest control rules=conserve some portion of mature females
(reproductive potential based on spawning stock biomass as a proxy)



Ecological context:

Reproductive success=an individual's offspring survive to reproductive age
(affected by genetics, habitat, environmental factors, predation, and food availability)

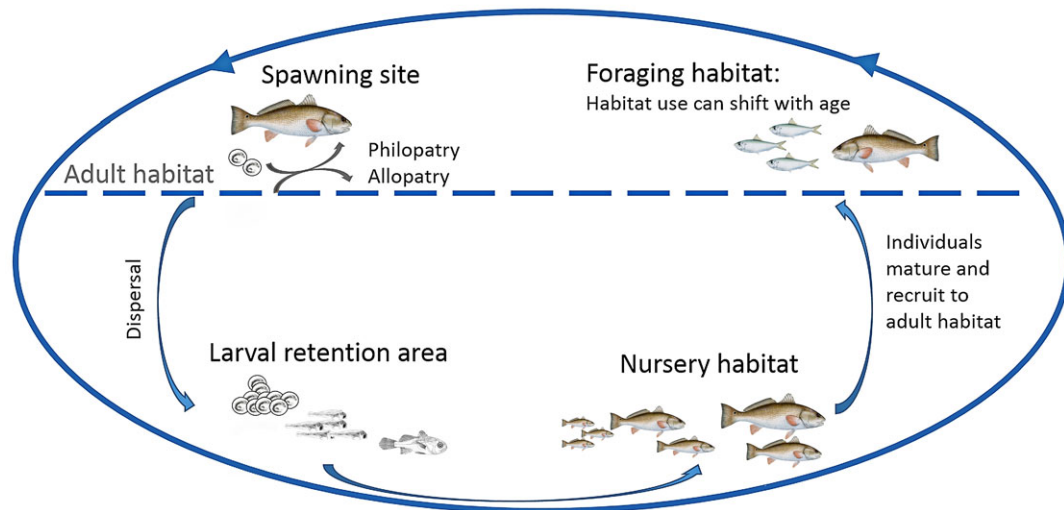


Figure 2 Reproductive potential is commonly based on spawning stock biomass, but in many marine species, spatial components of the life cycle may be more important to reproductive success.

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

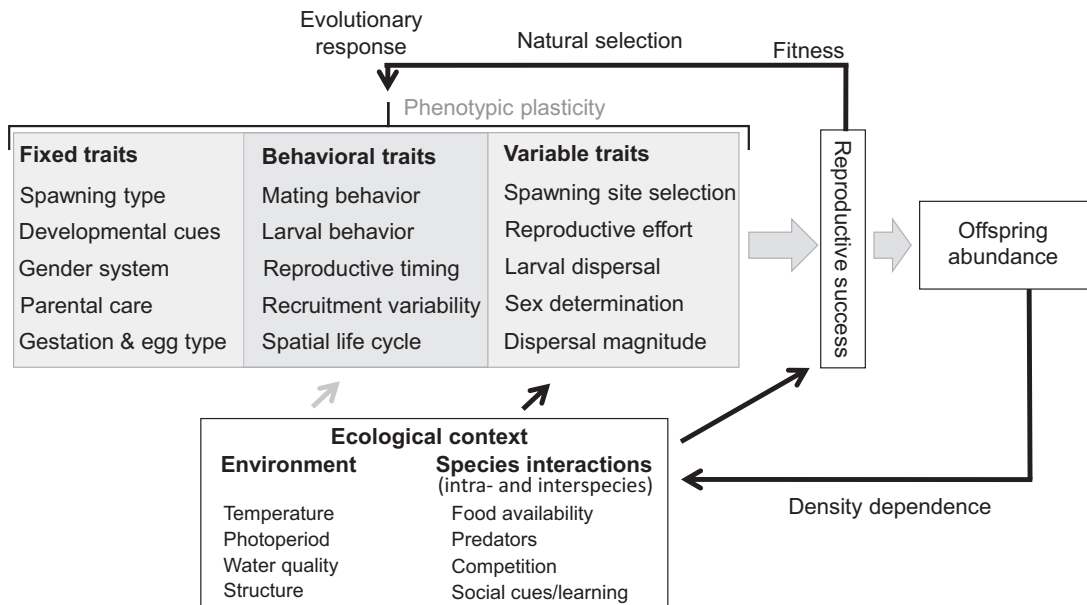


Figure 3 A stock's reproductive resilience is driven by its spawner-recruit system and the ecological context within which it is operating. Spawner-recruit systems are made up of three trait types with differing within-population variability, which ranges from: none (fixed traits) to extensive (variable 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 caprisus*, 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 rostrata*, 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

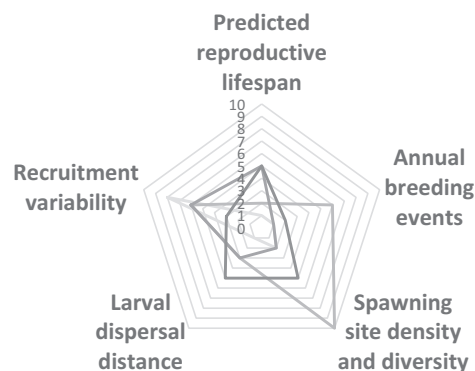
(b)

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 (Bergeius *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).

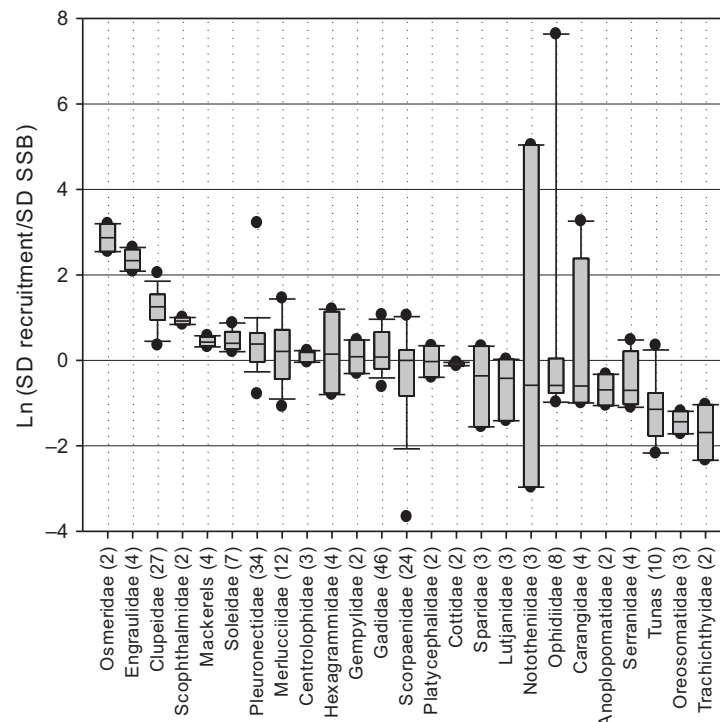


Figure 5 Box whisker plots of variability (SD) in recruitment relative to variability in spawner biomass (SSB) in relation to taxonomic family, with families ordered from highest to lowest median relative variability. Numbers indicate the number of stocks/management units in each family. Scombridae were 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 <i>et al.</i> 1989; Clark 1993; Goodyear 1993)
Full life cycle models	Dependent on spawning biomass	A density-dependent function of SSB or fecundity	(Beverton <i>et al.</i> 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 <i>et al.</i> 2005, 2013; Cowen <i>et al.</i> 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 <i>et al.</i> 2010; Rochette <i>et al.</i> 2013; Archambault <i>et al.</i> 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 time-scales (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).

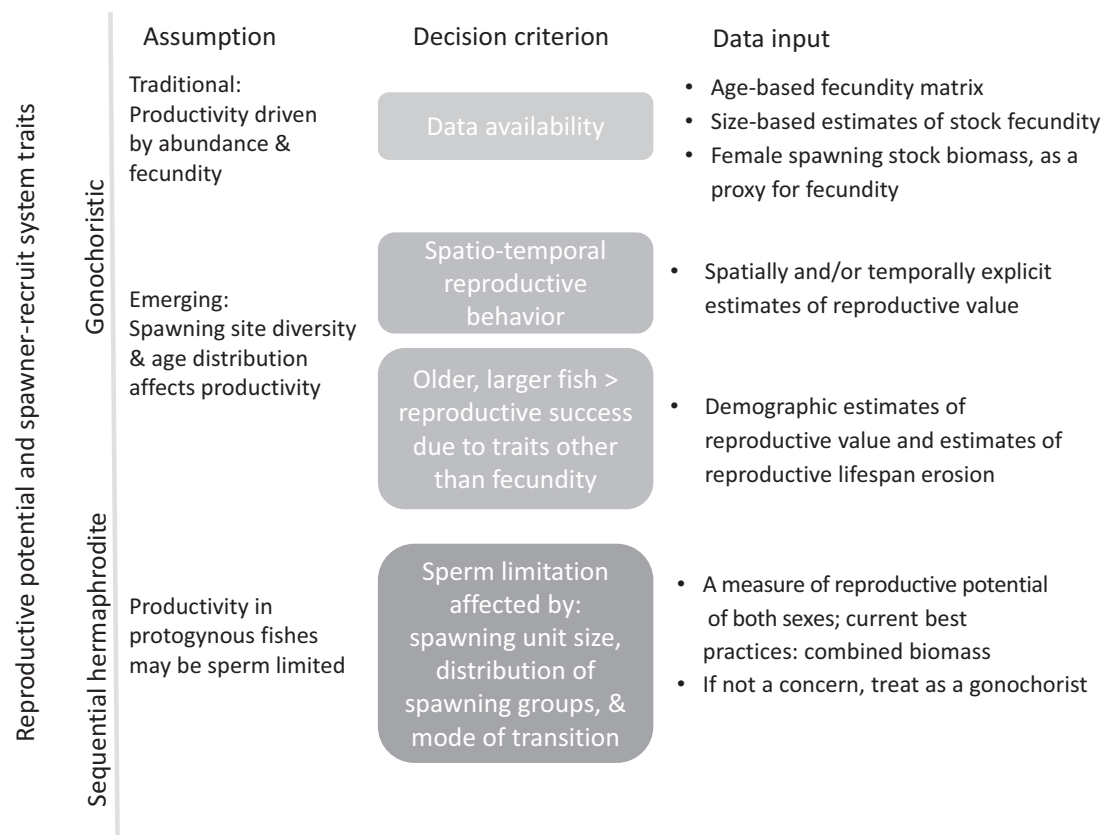


Figure 6 Reproductive potential and spawner-recruit systems: assumptions, decision criterion, and data needed for stock assessments.

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

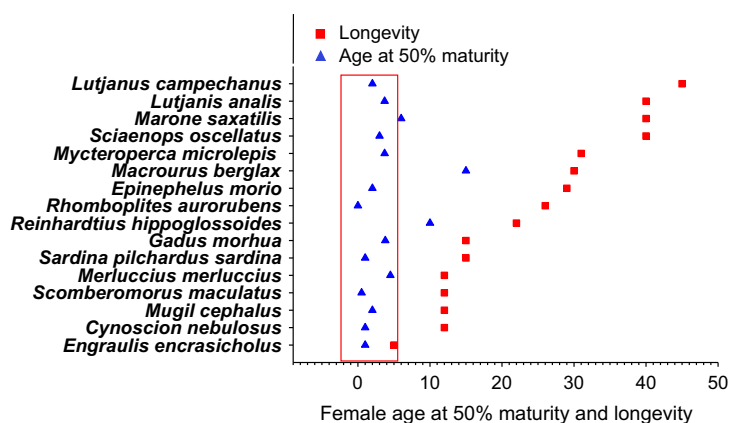


Figure 7 Estimated age at 50% maturity and maximum observed age in a range of exploited marine fishes.

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 nigrofusus*, 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

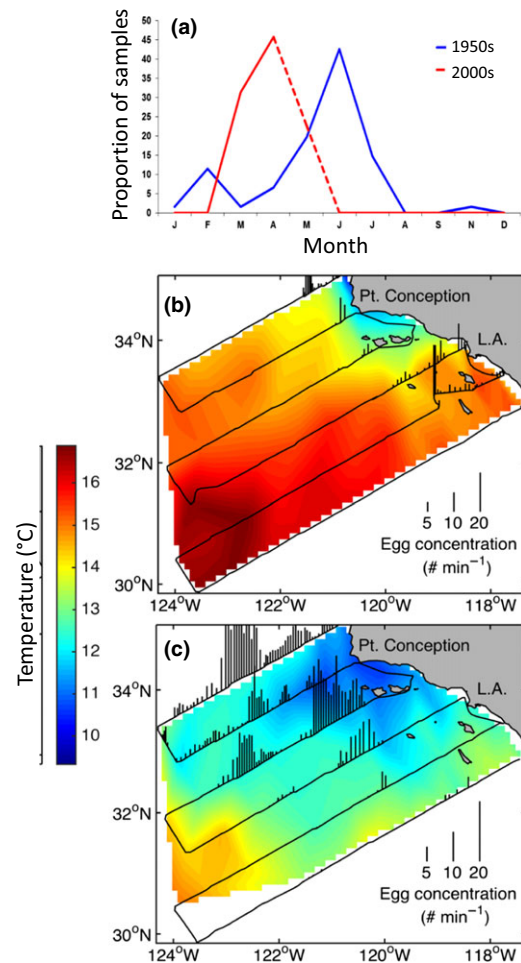


Figure 8 Influence of climate variations on the distribution and phenology of spawning in the Pacific Sardine (*Sardinops sagax*, Clupeidae) off the coast of Southern California, USA. Data modified from Asch (2013) and Asch and Checkley (2013). (a) Long-term changes in climatic conditions in California 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.

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

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.

Acknowledgements

We are grateful to PEW, SCRFA, ICES and the international AFS section for providing funding for international travel to attend the symposium, entitled, Reproductive Behavior and Recruitment in Marine Fish: Emerging Understanding and Future Needs, which was held at the American Fisheries Society meeting in Quebec, Canada, in 2014. We thank all participants in the symposium for helping to inform our understanding of spawner-recruit systems. In addition, we thank Luiz Barbieri, Jeff Leis, Mike Sinclair and two anonymous reviewers for sharing their expertise and providing helpful reviews, which improved this paper. We especially thank Reviewer #1 for making us clarify the dreaded 'take home message'. Lastly, we thank each of our institutions for their financial support throughout this collaborative project.

References

- Aiken, C.M. and Navarrete, S.A. (2011) Environmental fluctuations and asymmetrical dispersal: generalized stability theory for studying metapopulation persistence and marine protected areas. *Marine Ecology Progress Series* **428**, 77–88.
- Aiken, C.M., Navarrete, S.A. and Pelegrí, J.L. (2011) Potential changes in larval dispersal and alongshore connectivity on the central Chilean coast due to an

- altered wind climate. *Journal of Geophysical Research* **116**, G04026.
- Alós, J., Cabanellas-Reboredo, M. and Lowerre-Barbieri, S. (2012) Diel behaviour and habitat utilisation by the pearly razorfish during the spawning season. *Marine Ecology Progress Series* **460**, 207–220.
- Alós, J., Palmer, M., Catalán, I.A. et al. (2014) Selective exploitation of spatially structured coastal fish populations by recreational anglers may lead to evolutionary downsizing of adults. *Marine Ecology Progress Series* **503**, 219–233.
- Ames, E.P. (2004) Atlantic cod stock structure in the Gulf of Maine. *Fisheries* **29**, 10–28.
- Anderson, C.N.K., Hsieh, C.-H., Sandin, S.A. et al. (2008) Why fishing magnifies fluctuations in fish abundance. *Nature* **452**, 835–839.
- Anderson, S.C., Moore, J.W., McClure, M.M., Dulvy, N.K. and Cooper, A.B. (2015) Portfolio conservation of metapopulations under climate change. *Ecological Applications* **25**, 559–572.
- Archambault, B., Le Pape, O., Baulier, L., Vermard, Y., Véron, M. and Rivot, E. (2016) Adult-mediated connectivity affects inferences on population dynamics and stock assessment of nursery-dependent fish populations. *Fisheries Research* **181**, 198–213.
- Arnold, G.P., Walker, M.G., Emerson, L.S. and Holford, B.H. (1994) Movements of cod (*Gadus morhua* L.) in relation to the tidal streams in the southern North Sea. *ICES Journal of Marine Science* **51**, 207–232.
- Asch, R.G. (2013) *Interannual-to-decadal changes in phytoplankton phenology, fish spawning habitat, and larval fish phenology*. PhD thesis, University of California, 287 pages.
- Asch, R.G. (2015) Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. *Proceedings of the National Academy of Sciences of the United States of America* **112**, E4065–E4074.
- Asch, R.G. and Checkley, D.M. (2013) Dynamic height: a key variable for identifying the spawning habitat of small pelagic fishes. *Deep Sea Research Part I: Oceanographic Research Papers* **71**, 79–91.
- Audzijonyte, A., Kuparinen, A. and Fulton, E.A. (2013) How fast is fisheries-induced evolution? Quantitative analysis of modelling and empirical studies. *Evolutionary Applications* **6**, 585–595.
- Bailey, K.M., Abookire, A.A. and Duffy-Anderson, J.T. (2008) Ocean transport paths for the early life history stages of offshore-spawning flatfishes a case study in the Gulf of Alaska. *Fish and Fisheries* **9**, 44–66.
- Bakun, A. (1996) *Patterns in the Ocean: Ocean Processes and Marine Population Dynamics*. University of California Sea Grant, in cooperation with Centro de Investigaciones Biológicas de Noroeste, La Paz, Mexico.
- Baums, I.B., Paris, C.B. and Cherubin, L. (2006) A bio-oceanographic filter to larval dispersal in a reef-building coral. *Limnology and Oceanography* **51**(5), 1969–1981.
- Beaugrand, G., Brander, K.M., Alistair Lindley, J., Souissi, S. and Reid, P.C. (2003) Plankton effect on cod recruitment in the North Sea. *Nature* **426**, 661–664.
- Bergenius, M.A., Meekan, M.G., Robertson, R.D. and McCormick, M.I. (2002) Larval growth predicts the recruitment success of a coral reef fish. *Oecologia* **131**, 521–525.
- Berkeley, S.A., Hixon, M.A., Larson, R.J. and Love, M.S. (2004) Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries* **29**, 23–32.
- Bernal, M., Stratoudakis, Y., Wood, S.N., Ibaibarriaga, L., Valdes, L. and Borchers, D. (2011) A revision of daily egg production estimation methods, with application to Atlanto-Iberian sardine. 2. Spatially and environmentally explicit estimates of egg production. *ICES Journal of Marine Science* **68**, 528–536.
- Beverton, R.J.H. and Holt, S.J. (1957) *On the Dynamics of Exploited Fish Populations*, (Vol. 19). Great Britain, Ministry of Agriculture, Fisheries, and Food, London.
- Beverton, R.J.H., Cooke, J.G., Policansky, D.J. et al. (1984) Dynamics of Single Species. In: *Exploitation of Marine Communities: Report of the Dahlem Workshop on Exploitation of Marine Communities Berlin 1984, April 1–6*. (ed. R.M. May). Springer, Berlin, Heidelberg, pp. 13–58.
- Boehlert, G.W. and Mundy, B.C. (1988) Roles of behavioural and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. *American Fisheries Society Symposium* **3**, 51–67.
- Botsford, L.W., Hastings, A. and Gaines, S.D. (2001) Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecology Letters* **4**, 144–150.
- Botsford, L.W., White, J.W., Coffroth, M.A. et al. (2009) Connectivity and resilience of coral reef metapopulations in marine protected areas: matching empirical efforts to predictive needs. *Coral Reefs* **28**, 327–337.
- Brodziak, J., Mangel, M. and Sun, C.-L. (2015) Stock-recruitment resilience of North Pacific striped marlin based on reproductive ecology. *Fisheries Research* **166**, 140–150.
- Brown, E.D. and Williams, B.K. (2015) Resilience and resource management. *Environmental Management* **56**, 1416–1427.
- Caddy, J.F. and Agnew, D.J. (2004) An overview of recent global experience with recovery plans for depleted marine resources and suggested guidelines for recovery planning. *Reviews in Fish Biology and Fisheries* **14**, 43–112.
- Cadrin, S.X. and Dickey-Collas, M. (2015) Stock assessment methods for sustainable fisheries. *ICES Journal of Marine Science* **72**, 1–6.

- Cadrin, S.X. and Secor, D.H. (2009) Accounting for spatial population structure in stock assessment: past, present, and future. *Fish and Fisheries* **31**, 405–426.
- Cai, W., Borlace, S., Lengaigne, M. et al. (2014) Increasing frequency of extreme El Niño events due to greenhouse warming. *Nature Climate Change* **4**, 111–116.
- Carmichael, J. and Fenske, K. (eds) (2011) *Third National Meeting of the Regional Fisheries Management Councils' Scientific and Statistical Committees*. Report of a National SSC Workshop on ABC Control Rule Implementation and Peer Review Procedures. South Atlantic Fishery Management Council, Charleston, October 19–21, 2010.
- Carr, M.H. and Hixon, M.A. (1995) Predation effects on early post-settlement survivorship of coral-reef fishes. *Marine Ecology Progress Series* **124**, 31–42.
- Castonguay, M., Plourde, S., Robert, D., Runge, J.A. and Fortier, L. (2008) Copepod production drives recruitment in a marine fish. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 1528–1531.
- Cermeño, P., Quilez-Badía, G., Ospina-Alvarez, A. et al. (2015) Electronic tagging of Atlantic Bluefin tuna (*Thunnus thynnus*, L.) reveals habitat use and behaviors in the Mediterranean Sea. *PLoS One* **10**, e0116638.
- Checkley, D.M., Raman, S., Maillet, G.L. and Mason, K.M. (1988) Winter storm effects on the spawning and larval drift of a pelagic fish. *Nature* **335**, 346–348.
- Christie, M.R., Tissot, B.N., Albins, M.A. et al. (2010) Larval connectivity in an effective network of marine protected areas. *PLoS One* **5**, e15715.
- Ciannelli, L., Bailey, K. and Olsen, E.M. (2015) Evolutionary and ecological constraints of fish spawning habitats. *ICES Journal of Marine Science* **72**, 285–296.
- Clark, G.W. (1993) The effect of recruitment variability on the choice of a target level of spawning biomass per recruit. In: *Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations*. (eds G. Kruse, D.M. Engers, R.J. Marasco, C. Pautzke and T.J.I. Quinn). University of Alaska, Alaska Sea Grant Report No. 93-02, Fairbanks, Alaska, pp. 233–246.
- Clutton-Brock, T. and Sheldon, B.C. (2010) Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution* **25**, 562–573.
- Colin, P.L. (1996) Longevity of some coral reef fish spawning aggregations. *Copeia* **1996**, 189–192.
- Cooper, W.T., Barbieri, L.R., Murphy, M.D. and Lowerre-Barbieri, S.K. (2013) Assessing stock reproductive potential in species with indeterminate fecundity: effects of age truncation and size-dependent reproductive timing. *Fisheries Research* **138**, 31–41.
- Courchamp, F., Berec, L. and Gascoigne, J. (2008) Allee effects in ecology and conservation. *Environmental Conservation* **36**, 80–85.
- Cowen, R.K., Lwiza, K.M., Sponaugle, S., Paris, C.B. and Olson, D.B. (2000) Connectivity of marine populations: open or closed? *Science* **287**(5454), 857–859.
- Cowen, R.K., Paris, C.B. and Srinivasan, A. (2006) Scaling of connectivity in marine populations. *Science* **311**, 522–527.
- Crossin, G.T., Cooke, S.J., Goldbogen, J.A. and Phillips, R.A. (2014) Tracking fitness in marine vertebrates: current knowledge and opportunities for future research. *Marine Ecology Progress Series* **496**, 1–17.
- Cushing, D.H. (1975) *Marine Ecology and Fisheries*. Cambridge University Press, Cambridge.
- Cushing, D.H. (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology* **26**, 249–293.
- D'Aloia, C.C., Bogdanowicz, S.M., Francis, R.K., Majoris, J.E., Harrison, R.G. and Buston, P.M. (2015) Patterns, causes, and consequences of marine larval dispersal. *Proceedings of the National Academy of Sciences* **112**(45), 13940–13945.
- DeCelles, G. and Zemeckis, D. (2013) Acoustic and Radio Telemetry. In: *Stock Identification Methods: Applications in Fishery Science*. (eds S.X. Cadrin, L.A. Kerr and S. Mariani), 2nd edn. Elsevier, Amsterdam, pp. 397–428.
- Domeier, M.L. and Colin, P.L. (1997) Tropical reef fish spawning aggregations: defined and reviewed. *Bulletin of Marine Science* **60**, 698–726.
- Donahue, M.J., Karnauskas, M., Toews, C. and Paris, C.B. (2015) Location isn't everything: timing of spawning aggregations optimizes larval replenishment. *PLoS One* **10**, e0130694.
- Drouineau, H., Mahevas, S., Bertignac, M. and Duplisea, D. (2010) A length-structured spatially explicit model for estimating hake growth and migration rates. *ICES Journal of Marine Science* **67**, 1697–1709.
- Dunlop, E.S., Eikeset, A.M. and Stenseth, N.C. (2015) From genes to populations: how fisheries-induced evolution alters stock productivity. *Ecological Applications* **25**, 1860–1868.
- Erisman, B., Aburto-Oropeza, O., Gonzalez-Abraham, C., Mascareñas-Osorio, I., Moreno-Báez, M. and Hastings, P.A. (2012) Spatio-temporal dynamics of a fish spawning aggregation and its fishery in the Gulf of California. *Scientific Reports* **2**, 1–11.
- Erisman, B.E., Petersen, C.W., Hastings, P.A. and Warner, R.R. (2013) Phylogenetic perspectives on the evolution of functional hermaphroditism in teleost fishes. *Integrative and Comparative Biology* **53**, 736–754.
- Erisman, B., Heyman, W., Kobara, S. et al. (2015) Fish spawning aggregations: where well-placed management actions can yield big benefits for fisheries and conservation. *Fish and Fisheries* 1–17. doi: 10.1111-faf.12132.

- Figge, F. (2004) Bio-folio: applying portfolio theory to biodiversity. *Biodiversity and Conservation* **13**, 827–849.
- Fiksen, Ø., Jørgensen, C., Kristiansen, T., Vikebø, F. and Huse, G. (2007) Linking behavioural ecology and oceanography: larval behaviour determines growth, mortality and dispersal. *Marine Ecology Progress Series* **347**, 195–205.
- Fitzhugh, G., Koenig, C., Coleman, F., Grimes, C. and Wilton Sturges, L.I. (2005) Spatial and temporal patterns in fertilization and settlement of young gag (*Mycteroperca microlepis*) along the west Florida shelf. *Bulletin of Marine Science* **77**, 377–396.
- Fitzhugh, G.R., Shertzer, K.W., Kellison, G.T. and Wyanski, D.M. (2012) Review of size- and age-dependence in batch spawning: implications for stock assessment of fish species exhibiting indeterminate fecundity. *Fishery Bulletin* **110**, 413–425.
- Folke, C. (2006) Resilience: the emergence of a perspective for social-ecological systems analyses. *Global Environmental Change* **16**, 253–267.
- Fortin, N.L., Pekins, P.J. and Gustafson, K.A. (2015) Productivity measures of white-tailed deer in New Hampshire: assessing reduced recruitment. *Wildlife Society Bulletin* **39**, 56–64.
- Francis, R.C., Hixon, M.A., Clarke, M.E., Murawski, S.A. and Ralston, S. (2007) Ten commandments for Ecosystem-Based Fisheries scientists. *Fisheries* **32**, 217–233.
- Frank, K.T. and Brickman, D. (2001) Contemporary management issues confronting fisheries science. *Journal of Sea Research* **45**, 173–187.
- Frisk, M.G., Jordaan, A. and Miller, T.J. (2014) Moving beyond the current paradigm in marine population connectivity: are adults the missing link? *Fish and Fisheries* **15**, 242–254.
- Fromentin, J.-M., Bonhommeau, S., Arrizabalaga, H. and Kell, L.T. (2014) The spectre of uncertainty in management of exploited fish stocks: the illustrative case of Atlantic bluefin tuna. *Marine Policy* **47**, 8–14.
- Fuiman, L.A., Connelly, T.L., Lowerre-Barbieri, S.K. and McClelland, J.W. (2015) Egg boons: central components of marine fatty acid food webs. *Ecology* **96**, 362–372.
- Gabriel, W.L., Sissenwine, M.P. and Overholtz, W.J. (1989) Analysis of spawning stock biomass per recruit: an example for Georges Bank haddock. *North American Journal of Fisheries Management* **9**, 383–391.
- Garcia-Gonzalez, F., Yasui, Y. and Evans, J.P. (2015) Mating portfolios: bet-hedging, sexual selection and female multiple mating. *Proceedings of the Royal Society of London B: Biological Sciences* **282**, 20141525.
- Garrod, D.J. and Horwood, J.W. (1984) Reproductive Strategies and the Response to Exploitation. In: *Fish Reproduction: Strategies and Tactics*. (eds G.W. Potts and R.J. Wootton). Academic Press, New York, pp. 367–384.
- Gerber, L.R., Mancha-Cisneros, M. and O'Connor, M.I. (2014) Climate change impacts on connectivity in the ocean: implications for conservation. *Ecosphere* **5**, 1–18.
- Gerlach, G., Atema, J., Kingsford, M.J., Black, K.P. and Miller-Sims, V. (2007) Smelling home can prevent dispersal of reef fish larvae. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 858–863.
- Giacomini, H.C., Shuter, B.J. and Lester, N.P. (2013) Predator bioenergetics and the prey size spectrum: do foraging costs determine fish production? *Journal of Theoretical Biology* **332**, 249–260.
- Gibson, R.N. (1994) Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. *Netherlands Journal of Sea Research* **32**, 191–206.
- Glaser, S.M., Fogarty, M.J., Liu, H. et al. (2014) Complex dynamics may limit prediction in marine fisheries. *Fish and Fisheries* **15**, 616–633.
- Goodyear, C.P. (1993) Spawning stock biomass per recruit in fisheries management: foundation and current use. *Canadian Special Publication of Fisheries and Aquatic Sciences* **120**, 67–82.
- Gwinn, D.C., Allen, M.S., Johnston, F.D., Brown, P., Todd, C.R. and Arlinghaus, R. (2015) Rethinking length-based fisheries regulations: the value of protecting old and large fish with harvest slots. *Fish and Fisheries* **16**, 259–281.
- Hamilton, S.L., Regetz, J. and Warner, R.R. (2008) Post-settlement survival linked to larval life in a marine fish. *Proceedings of the National Academy of Sciences* **105** (5), 1561–1566.
- Hare, J.A., Morrison, W.E., Nelson, M.W. et al. (2016) A vulnerability assessment of fish and invertebrates to climate change on the northeast U.S. continental shelf. *PLoS One* **11**, e0146756.
- Harrison, H.B., Williamson, D.H., Evans, R.D. et al. (2012) Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Current Biology* **22**, 1023–1028.
- Hastings, A. and Botsford, L.W. (1999) Equivalence in yield from marine reserves and traditional fisheries management. *Science* **284**, 1537–1538.
- Hastings, A. and Botsford, L.W. (2006) Persistence of spatial populations depends on returning home. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 6067–6072.
- Hedgecock, D. (1994) Temporal and spatial genetic structure of marine animal populations in the California Current. *California Cooperative Oceanic Fisheries* **35**, 73–81.
- Heino, M., Baulier, L., Boukal, D.S. et al. (2013) Can fisheries-induced evolution shift reference points for fisheries management? *ICES Journal of Marine Science* **70**, 707–721.
- Hilborn, R. and Walters, C.J. (1992) *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty*. Chapman and Hall, London.
- Hilborn, R., Quinn, T.P., Schindler, D.E. and Rogers, D.E. (2003) Biocomplexity and fisheries sustainability.

- Proceedings of the National Academy of Sciences of the United States of America* **100**, 6564–6568.
- Hinrichsen, H., Lehmann, A., Mollmann, C. and Schmidt, J.O. (2003) Dependency of larval fish survival on retention/dispersion in food limited environments: the Baltic Sea as a case study. *Fisheries Oceanography* **12**, 425–433.
- Hixon, M.A., Johnson, D.W. and Sogard, S.M. (2014) BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science* **71**, 2171–2185.
- Hjort, J. (1914) Fluctuations in the great fisheries of northern Europe, viewed in the light of biological research. *Rapports et proces-verbaux, Conseil permanent international pour l'ex-ploration de la mer Cooperative Research Report* **20**, 1–228.
- Hogan, J.D., Thiessen, R.J., Sale, P.F. and Heath, D.D. (2012) Local retention, dispersal and fluctuating connectivity among populations of a coral reef fish. *Oecologia* **168**, 61–71.
- Hsieh, C.-H., Reiss, C.S., Hewitt, R.P. and Sugihara, G. (2008) Spatial analysis shows that fishing enhances the climatic sensitivity of marine fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 947–961.
- Hunsicker, M.E., Kappel, C.V., Selkoe, K.A. et al. (2016) Characterizing driver–response relationships in marine pelagic ecosystems for improved ocean management. *Ecological Applications* **26**, 651–663.
- Iacchei, M., Ben-Horin, T., Selkoe, K.A., Bird, C.E., García-Rodríguez, F.J. and Toonen, R.J. (2013) Combined analyses of kinship and FST suggest potential drivers of chaotic genetic patchiness in high gene-flow populations. *Molecular Ecology* **22**, 3476–3494.
- ICES. (2015) *Report of the Fifth Workshop on the Development of Quantitative Assessment Methodologies based on Life-history Traits, Exploitation Characteristics and other Relevant Parameters for Data-limited Stocks (WKLIFE V)*, 5–9 October 2015, Lisbon, Portugal. ICES CM 2015/ACOM:56. 157 pp.
- Iles, T.D. and Sinclair, M. (1982) Atlantic herring: stock discreteness and abundance. *Science* **215**, 627–633.
- Ims, R.A. (1990) On the adaptive value of reproductive synchrony as a predator-swamping strategy. *The American Naturalist* **136**, 485–498.
- Iwasa, Y. and Roughgarden, J. (1986) Interspecific competition among metapopulations with space-limited subpopulations. *Theoretical Population Biology* **30**, 194–214.
- Jager, H.I., Rose, K.A. and Vila-Gispert, A. (2008) Life history correlates and extinction risk of capital-breeding fishes. *Hydrobiologia* **602**, 15–25.
- Jørgensen, C., Ernande, B., Fiksen, Ø. and Dieckmann, U. (2006) The logic of skipped spawning in fish. *Canadian Journal of Fisheries and Aquatic Sciences* **63**, 200–211.
- Jørgensen, C., Enberg, K., Dunlop, E.S. et al. (2007) Managing evolving fish stocks. *Science* **318**, 1247–1248.
- Kamler, E. (2005) Parent–egg–progeny relationships in teleost fishes: an energetics perspective. *Reviews in Fish Biology and Fisheries* **15**, 399–421.
- Karnauskas, M., Paris, C.B., Zapfe, G., Grüss, A., Walter, J.F. and Schirripa, M.J. (2013) *Use of the Connectivity Modeling System to Estimate Movements of Gag Grouper (Mycteroperca microlepis) Recruits in the Northern Gulf of Mexico*. SEDAR33-DW18. SEDAR, North Charleston, South Carolina.
- Kell, L.T., Nash, R.D.M., Dickey-Collas, M., Mosqueira, I. and Szuwalski, C. (2015) Is spawning stock biomass a robust proxy for reproductive potential? *Fish and Fisheries* **55**, 1766–1783.
- Kindsvater, H.K., Mangel, M., Reynolds, J.D. and Dulvy, N.K. (2016) Ten principles from evolutionary ecology essential for effective marine conservation. *Ecology and Evolution* **6**, 2125–2138.
- Kingsford, M.J., Leis, J.M., Shanks, A., Lindeman, K.C., Morgan, S.G. and Pineda, J. (2002) Sensory environments, larval abilities and local self-recruitment. *Bulletin of Marine Science* **70**, 309–340.
- Klaer, N.L., O'Boyle, R.N., Deroba, J.J. et al. (2015) How much evidence is required for acceptance of productivity regime shifts in fish stock assessments: are we letting managers off the hook? *Fisheries Research* **168**, 49–55.
- Kooijman, S.A.L.M. (2010) *Dynamic Energy Budget Theory for Metabolic Organisation*, 3rd edn. Cambridge University Press, Great Britain.
- Kough, A.S. and Paris, C.B. (2015) The influence of spawning periodicity on population connectivity. *Coral Reefs* **34**, 753–757.
- Kough, A.S., Paris, C.B. and Butler, M.J. IV (2013) Larval connectivity and the international management of fisheries. *PLoS One* **8**, e64970.
- Kraak, S. (2007) Does the probabilistic maturation reaction norm approach disentangle phenotypic plasticity from genetic change? *Marine Ecology Progress Series* **335**, 295–300.
- Lasker, R. (1978) The relation between oceanographic conditions and larval anchovy food in the California current: identification of factors contributing to recruitment failure. *Rapports et proces-verbaux, Conseil permanent international pour l'ex-ploration de la mer* **173**, 212–230.
- Law, R. and Grey, D.R. (1989) Evolution of yields from populations with age-specific cropping. *Evolutionary Ecology* **3**, 343–359.
- Leggett, W.C. and DeBlois, E. (1994) Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? *Netherlands Journal of Sea Research* **32**, 119–134.
- Leibold, M., Holyoak, M., Mouquet, N. et al. (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* **7**, 601–613.

- Leis, J.M. (2007) Behaviour as input for modelling dispersal of fish larvae: behaviour, biogeography, hydrodynamics, ontogeny, physiology and phylogeny meet hydrography. *Marine Ecology Progress Series* **347**, 185–193.
- Leis, J.M. (2015) Is Dispersal of Larval Reef Fishes Passive? In: *Ecology of Fishes on Coral Reefs*. (ed. C. Mora). Cambridge University Press, Cambridge, U.K., pp. 223–226.
- Leis, J.M., Caselle, J.E., Bradbury, I.R. et al. (2013) Does fish larval dispersal differ between high and low latitudes? *Proceedings of the Royal Society of London B: Biological Sciences* **280**, 1–9.
- Lett, C., Ayata, S.-D., Huret, M. and Irsson, J.-O. (2010) Biophysical modelling to investigate the effects of climate change on marine population dispersal and connectivity. *Progress in Oceanography* **87**, 106–113.
- Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology* **73**, 1943–1967.
- Levin, L.A. (2006) Recent progress in understanding larval dispersal: new directions and digressions. *Integrative and Comparative Biology* **46**, 282–297.
- Llopiz, J.K. and Hobday, A.J. (2015) A global comparative analysis of the feeding dynamics and environmental conditions of larval tunas, mackerels, and billfishes. *Deep Sea Research Part II: Topical Studies in Oceanography* **113**, 113–124.
- Lowerre-Barbieri, S.K. (2009) Reproduction in Relation to Conservation and Exploitation of Marine Fishes. In: *Reproductive Biology and Phylogeny of Fishes (Agnathans and Bony Fishes)*. (ed. B.G.M. Jamieson). Science Publishers, Enfield, New, Hampshire, pp. 371–394.
- Lowerre-Barbieri, S.K., Ganiyas, K., Saborido-Rey, F., Murua, H. and Hunter, J.R. (2011) Reproductive timing in marine fishes: variability, temporal scales, and methods. *Marine and Coastal Fisheries* **3**, 71–91.
- Lowerre-Barbieri, S.K., Walters, S. and Bickford, J. (2013) Site fidelity and reproductive timing at a spotted seatrout spawning aggregation site: individual versus population scale behavior. *Marine Ecology Progress Series* **481**, 181–197.
- Lowerre-Barbieri, S.K., Villegas-Ríos, D., Walters, S. et al. (2014) Spawning site selection and contingent behavior in Common Snook, *Centropomus undecimalis*. *PLoS One* **9**, e101809.
- Lowerre-Barbieri, S., Crabtree, L., Switzer, T., Walters Burnsed, S. and Guenther, C. (2015) Assessing reproductive resilience: an example with South Atlantic red snapper *Lutjanus campechanus*. *Marine Ecology Progress Series* **526**, 125–141.
- Lowerre-Barbieri, S.K., Walters Burnsed, S.L. and Bickford, J.W. (2016) Assessing reproductive behavior important to fisheries management: a case study with red drum, *Sciaenops ocellatus*. *Ecological Applications* **26**, 979–995.
- Manel, S., Gaggiotti, O.E. and Waples, R.S. (2005) Assignment methods: matching biological questions with appropriate techniques. *Trends in Ecology and Evolution* **20**, 136–142.
- Mangel, M., Kindsvater, H.K. and Bonsall, M.B. (2007) Evolutionary analysis of life span, competition, and adaptive radiation, motivated by the Pacific rockfishes (*Sebastes*). *Evolution* **61**, 1208–1224.
- Mangel, M., MacCall, A.D., Brodziak, J. et al. (2013) A perspective on steepness, reference points, and stock assessment. *Canadian Journal of Fisheries and Aquatic Sciences* **70**, 930–940.
- Mank, J.E. and Avise, J.C. (2009) Evolutionary diversity and turn-over of sex determination in teleost fishes. *Sexual Development* **3**(2–3), 60–67.
- Marshall, C.T. (2009) Implementing Information on Stock Reproductive Potential in Fisheries Management: the Motivation, Challenges and Opportunities. In: *Fish Reproductive Biology: Implications for Assessment and Management*. (eds T. Jakobsen, M.J. Fogarty, B.A. Megrey and E. Moksness). Wiley-Blackwell, West Sussex, pp. 395–420.
- Marshall, C.T., O'Brien, L., Tomkiewicz, J. et al. (2003) Incorporating alternative indices of reproductive potential into fisheries management: case studies for stocks spanning an information gradient. *Journal of Northwest Atlantic Fishery Science* **33**, 161–190.
- Marty, L., Rochet, M.J. and Ernande, B. (2014) Temporal trends in age and size at maturation of four North Sea gadid species: cod, haddock, whiting and Norway pout. *Marine Ecology Progress Series* **497**, 179–197.
- Maunder, M.N. and Deriso, R.B. (2013) A stock-recruitment model for highly fecund species based on temporal and spatial extent of spawning. *Fisheries Research* **146**, 96–101.
- Maunder, M.N. and Piner, K.R. (2014) Contemporary fisheries stock assessment: many issues still remain. *ICES Journal of Marine Science* **72**, 7–18.
- Mazeroll, A.I. and Montgomery, W.L. (1998) Daily migrations of a coral reef fish in the Red Sea (Gulf of Aqaba, Israel): initiation and orientation. *Copeia* **1998**, 893.
- McBride, R.S., Somarakis, S., Fitzhugh, G.R. et al. (2013) Energy acquisition and allocation to egg production in relation to fish reproductive strategies. *Fish and Fisheries* **16**, 23–57.
- Meehl, G.A., Washington, W.M., Collins, W.D. et al. (2005) How much more global warming and sea level rise? *Science* **307**, 1769–1772.
- Miller, T.J. (2007) Contribution of individual-based coupled physical–biological models to understanding recruitment in marine fish populations. *Marine Ecology Progress Series* **347**, 127–138.
- Morgan, S.G. (2014) Behaviorally mediated larval transport in upwelling systems. *Advances in Oceanography* **2014**, 1–17.

- Mullon, C., Cury, P. and Penven, P. (2002) Evolutionary individual-based model for the recruitment of anchovy (*Engraulis capensis*) in the southern Benguela. *Canadian Journal of Fisheries and Aquatic Sciences* **59**, 910–922.
- Munday, P.L., Leis, J.M., Lough, J.M. et al. (2009) Climate change and coral reef connectivity. *Coral Reefs* **28**, 379–395.
- Munguia-Vega, A., Jackson, A., Marinone, S.G. et al. (2014) Asymmetric connectivity of spawning aggregations of a commercially important marine fish using a multidisciplinary approach. *PeerJ* **2**, e511.
- Murray, G., Neis, B., Palmer, C.T. and Schneider, D.C. (2008) Mapping cod: fisheries science, fish harvesters' ecological knowledge and cod migrations in the Northern Gulf of St. Lawrence. *Human Ecology* **36**, 581–598.
- Murua, H. and Saborido-Rey, F. (2003) Female reproductive strategies of marine fish species of the North Atlantic. *Journal of Northwest Atlantic Fishery Science* **33**, 23–31.
- Musick, J.A. (1999) Ecology and Conservation of Long Lived Marine Animals. In: *Life in the Slow Lane: Ecology and Conservation of Long-Lived Marine Animals*. (ed. J.A. Musick). American Fisheries Society Symposium 23. American Fisheries Society, Bethesda, Maryland, USA, pp. 1–7.
- Myers, R.A. and Cadigan, N.G. (1993) Density-dependent juvenile mortality in marine demersal fish. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 1576–1590.
- Naguib, M. and Gil, D. (2005) Transgenerational effects on body size caused by early developmental stress in zebra finches. *Biology Letters* **1**, 95–97.
- Neel, M.C., McKelvey, K., Ryman, N. et al. (2013) Estimation of effective population size in continuously distributed populations: there goes the neighborhood. *Heredity* **111**, 189–199.
- North, E.W., Hood, R.R., Chao, S.Y. and Sanford, L.P. (2005) The influence of episodic events on transport of striped bass eggs to the estuarine turbidity maximum nursery area. *Estuaries* **28**, 108–123.
- O'Connor, M.I., Bruno, J.F., Gaines, S.D. et al. (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 1266–1271.
- O'Farrell, M.R. and Botsford, L.W. (2006) The fisheries management implications of maternal-age-dependent larval survival. *Canadian Journal of Fisheries and Aquatic Sciences* **63**, 2249–2258.
- Ospina-Alvarez, A., Bernal, M., Catalán, I.A., Roos, D., Bigot, J.-L. and Palomera, I. (2013) Modeling fish egg production and spatial distribution from acoustic data: a step forward into the analysis of recruitment. *PLoS One* **8**, e73687.
- Ospina-Alvarez, A., Catalán, I.A., Bernal, M., Roos, D. and Palomera, I. (2015) From egg production to recruits: connectivity and inter-annual variability in the recruitment patterns of European anchovy in the northwestern Mediterranean. *Progress in Oceanography* **138**, 431–447.
- Pacariz, S., Björk, G. and Svedäng, H. (2014) Interannual variability in the transport of fish eggs in the Kattegat and Öresund. *ICES Journal of Marine Science* **71**, 1706–1716.
- Paris, C.B. and Cowen, R.K. (2004) Direct evidence of a biophysical retention mechanism for coral reef fish larvae. *Limnology and Oceanography* **49**, 1964–1979.
- Paris, C.B., Cowen, R.K., Lwiza, K.M.M., Wang, D.P. and Olson, D.B. (2002) Objective analysis of three-dimensional circulation in the vicinity of Barbados, West Indies: implication for larval transport. *Deep Sea Research* **49**, 1363–1386.
- Paris, C.B., Cowen, R.K., Claro, R. and Lindeman, K.C. (2005) Larval transport pathways from Cuban snapper (Lutjanidae) spawning aggregations based on biophysical modeling. *Marine Ecology Progress Series* **296**, 93–106.
- Paris, C.B., Chérubin, L.M. and Cowen, R.K. (2007) Surfing, spinning, or diving from reef to reef: effects on population connectivity. *Marine Ecology Progress Series* **347**, 285–300.
- Paris, C.B., Helgers, J., van Sebille, E. and Srinivasan, A. (2013) Connectivity Modeling System: A probabilistic modeling tool for the multi-scale tracking of biotic and abiotic variability in the ocean. *Environmental Modelling and Software* **42**, 47–54.
- Patrick, W.S., Spencer, P., Link, J. et al. (2010) Using productivity and susceptibility indices to assess the vulnerability of United States fish stocks to overfishing. *Fishery Bulletin* **108**, 305–322.
- Pavlov, D.A., Emel'yanova, N.G. and Novikov, G.G. (2009) Fish Reproductive Biology. In: *Reproductive Dynamics*. (eds T. Jakobsen, M.J. Fogarty, B.A. Megrey and E. Moksness). Wiley-Blackwell Scientific Publications, Chichester, UK, pp. 48–90.
- Peck, M.A. and Hufnagel, M. (2012) Can IBMs tell us why most larvae die in the sea? Model sensitivities and scenarios reveal research needs. *Journal of Marine Systems* **93**, 77–93.
- Pella, J.J. and Tomlinson, P.K. (1969) A generalized stock production model. *Inter-American Tropical Tuna Commission Bulletin* **13**, 419–496.
- Pepin, P. (2015) Reconsidering the impossible — linking environmental drivers to growth, mortality, and recruitment of fish. *Canadian Journal of Fisheries and Aquatic Sciences* **73**, 205–215.
- Pineda, J., Hare, J.A. and Sponaugle, S. (2007) Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography* **20**, 22–39.
- Plagányi, É.E. and Butterworth, D.S. (2004) A critical look at the potential of Ecopath with ecosim to assist

- in practical fisheries management. *African Journal of Marine Science* **26**, 261–287.
- Platt, T., Fuentes-Yaco, C. and Frank, K.T. (2003) Marine ecology: Spring algal bloom and larval fish survival. *Nature* **423**, 398–399.
- Polasky, S., de Zeeuw, A. and Wagener, F. (2011) Optimal management with potential regime shifts. *Journal of Environmental Economics and Management* **62**, 229–240.
- Politikos, D.V., Huret, M. and Petitgas, P. (2015) A coupled movement and bioenergetics model to explore the spawning migration of anchovy in the Bay of Biscay. *Ecological Modelling* **313**, 212–222.
- Porch, C.E. and Lauretta, M.V. (2016) On making statistical inferences regarding the relationship between Spawners and Recruits and the irresolute case of Western Atlantic Bluefin Tuna (*Thunnus thynnus*). *PLoS One* **11**, e0156767.
- Pörtner, H.O. and Peck, M.A. (2010) Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Journal of Fish Biology* **77**, 1745–1779.
- Prager, M.H. and Shertzer, K.W. (2010) Deriving acceptable biological catch from the overfishing limit: Implications for assessment models. *North American Journal of Fisheries Management* **30**, 289–294.
- Reglero, P., Tittensor, D.P., Alvarez-Berastegui, D., Aparicio-Gonzalez, A. and Worm, B. (2014) Worldwide distributions of tuna larvae: revisiting hypotheses on environmental requirements for spawning habitats. *Marine Ecology Progress Series* **501**, 207–224.
- Ricard, D., Minto, C., Jensen, O.P. and Baum, J.K. (2012) Examining the knowledge base and status of commercially exploited marine species with the RAM Legacy Stock Assessment Database. *Fish and Fisheries* **13**, 380–398.
- Rice, J. (2011) Managing fisheries well: delivering the promises of an ecosystem approach. *Fish and Fisheries* **12**, 209–231.
- Rice, J.A., Quinlan, J.A., Nixon, S.W., Hettler, W.F.J., Warlen, S.M. and Stegmann, P.M. (1999) Spawning and transport dynamics of Atlantic menhaden: inferences from characteristics of immigrating larvae and predictions of a hydrodynamic model. *Fisheries Oceanography* **8**, 93–110.
- Richardson, D.E., Hare, J.A., Fogarty, M.J. and Link, J.S. (2011) Role of egg predation by haddock in the decline of an Atlantic herring population. *Proceedings of the National Academy of Sciences of the United States of America* **108**, 13606–13611.
- Ricker, W.E. (1954) Stock and recruitment. *Journal of the Fisheries Research Board of Canada* **11**, 559–623.
- Rideout, R.M. and Tomkiewicz, J. (2011) Skipped spawning in fishes: More common than you might think. *Marine and Coastal Fisheries* **3**, 176–189.
- Rijnsdorp, A.D., Peck, M.A., Engelhard, G.H., Möllmann, C. and Pinnegar, J.K. (2009) Resolving the effect of climate change on fish populations. *ICES Journal of Marine Science* **66**, 1570–1583.
- Rochette, S., Le Pape, O., Vigneau, J. and Rivot, E. (2013) A hierarchical Bayesian model for embedding larval drift and habitat models in integrated life cycles for exploited fish. *Ecological Applications* **23**, 1659–1676.
- Rose, G.A. (1993) Cod spawning on a migration highway in the north-west Atlantic. *Nature* **366**, 458–461.
- Rose, K.A., Cowan, J.H., Clark, M.E., Houde, E.D. and Wang, S.-B. (1999) An individual-based model of bay anchovy population dynamics in the mesohaline region of Chesapeake Bay. *Marine Ecology Progress Series* **185**, 113–132.
- Rose, K.A., Cowan, J.H., Winemiller, K.O., Myers, R.A. and Hilborn, R. (2001) Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries* **2**, 293–327.
- Rose, K.A., Fiechter, J., Curchitser, E.N. et al. (2015) Demonstration of a fully-coupled end-to-end model for small pelagic fish using sardine and anchovy in the California Current. *Progress in Oceanography* **138**, 348–380.
- Rosenberg, A.A. and Restrepo, V.R. (1994) Uncertainty and risk evaluation in stock assessment advice for U.S. marine fisheries. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 2715–2720.
- Rutherford, E.S. and Houde, E.D. (1985) The influence of temperature on cohort-specific growth, survival, and recruitment of striped bass, *Morone saxatilis*, larvae in Chesapeake Bay. *Fishery Bulletin* **93**, 315–332.
- Saborido-Rey, F. and Trippel, E.A. (2013) Fish reproduction and fisheries. *Fisheries Research* **138**, 1–4.
- Sætre, R., Toresen, R. and Anker-Nilssen, T. (2002) Factors affecting the recruitment variability of the Norwegian spring-spawning herring (*Clupea harengus* L.). *ICES Journal of Marine Science* **59**, 725–736.
- Salinas, S. and Munch, S.B. (2012) Thermal legacies: transgenerational effects of temperature on growth in a vertebrate. *Ecology Letters* **15**, 159–163.
- Salomon, Y., Connolly, S.R. and Bode, L. (2010) Effects of asymmetric dispersal on the coexistence of competing species. *Ecology Letters* **13**, 432–441.
- Schaefer, M.B. (1957) Some considerations of population dynamics and economics in relation to the management of the commercial marine fisheries. *Journal of the Fisheries Research Board of Canada* **14**, 669–681.
- Scheffer, M., Bascompte, J., Brock, W.A. et al. (2009) Early-warning signals for critical transitions. *Nature* **461**, 53–59.
- Schindler, D.E., Hilborn, R., Chasco, B. et al. (2010) Population diversity and the portfolio effect in an exploited species. *Nature* **465**, 609–612.
- Scott, B.E., Marteinsdottir, G., Begg, G.A., Wright, P.J. and Kjesbu, O.S. (2006) Effects of population size/age

- structure, condition and temporal dynamics of spawning on reproductive output in Atlantic cod (*Gadus morhua*). *Ecological Modelling* **191**, 383–415.
- Secor, D. (1999) Specifying divergent migrations in the concept of stock: the contingent hypothesis. *Fisheries Research* **43**, 13–34.
- Secor, D.H. (2007) The year-class phenomenon and the storage effect in marine fishes. *Journal of Sea Research* **57**, 91–103.
- Secor, D.H. and Houde, E.D. (1995) Temperature effects on the timing of striped bass egg production, larval viability, and recruitment potential in the Patuxent River (Chesapeake Bay). *Estuaries* **18**, 527–544.
- Secor, D.H., Rooker, J.R., Gahagan, B.I., Siskey, M.R. and Wingate, R.W. (2015) Depressed resilience of bluefin tuna in the western Atlantic and age truncation. *Conservation Biology* **29**, 400–408.
- SEDAR (2015) SEDAR Procedural Workshop 7: Data Best Practices, 151.
- Shepherd, J.G. (1982) A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. *Journal du Conseil* **40**, 67–75.
- Shulman, M.J. (1985) Recruitment of coral reef fishes: effects of distribution of predators and shelter. *Ecology* **66**, 1056–1066.
- Sinclair, M. and Iles, D.T. (1988) Population richness of marine fish species. *Aquatic Living Resources* **1**, 71–83.
- Smedbol, R.K. and Stephenson, R. (2001) The importance of managing within-species diversity in cod and herring fisheries of the north-western Atlantic. *Journal of Fish Biology* **59**, 109–128.
- Snyder, R.E., Paris, C.B., Vaz, A.C., Mangel, M. and Bronstein, E.J.L. (2014) How much do marine connectivity fluctuations matter? *The American Naturalist* **184**, 523–530.
- Sponaugle, S., Lee, T.N., Kourafalou, V. and Pinkard, D. (2005) Florida current frontal eddies and the settlement of coral reef fishes. *Limnology and Oceanography* **50**, 1033–1048.
- Stachura, M.M., Essington, T.E., Mantua, N.J. et al. (2014) Linking Northeast Pacific recruitment synchrony to environmental variability. *Fisheries Oceanography* **23**, 389–408.
- Stanley, R.R.E., deYoung, B., Snelgrove, P.V.R. and Gregory, R.S. (2013) Factors regulating early life history dispersal of Atlantic cod (*Gadus morhua*) from coastal Newfoundland. *PLoS One* **8**, e75889.
- Staaterman, E., Paris, C.B. and Helgers, J. (2012) Orientation behavior in fish larvae: a missing piece to Hjort's critical period hypothesis. *Journal of Theoretical Biology* **304**, 188–196.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Sydeman, W.J., Poloczanska, E., Reed, T.E. and Thompson, S.A. (2015) Climate change and marine vertebrates. *Science* **350**, 772–777.
- Szuwalski, C.S., Vert-pre, K.A., Punt, A.E., Branch, T.A. and Hilborn, R. (2015) Examining common assumptions about recruitment: a meta-analysis of recruitment dynamics for worldwide marine fisheries. *Fish and Fisheries* **16**, 633–648.
- Teacher, A.G., Andre, C., Jonsson, P.R. and Merilä, J. (2013) Oceanographic connectivity and environmental correlates of genetic structuring in Atlantic herring in the Baltic Sea. *Evolutionary Applications* **6**, 549–567.
- Thompson, W.F. and Bell, F.H. (1934) *Biological Statistics of the Pacific Halibut Fishery: (2) Effect of Changes in Intensity Upon Total Yield and Yield Per Unit of Gear*. International Fisheries Commission No. 8, 47 pp.
- Thorpe, J.E. (2007) Maturation responses of salmonids to changing developmental opportunities. *Marine Ecology Progress Series* **335**, 285–288.
- Trippel, E. (1999) Estimation of stock reproductive potential: history and challenges for Canadian Atlantic gadoid stock assessments. *Journal of Northwest Atlantic Fishery Science* **25**, 61–82.
- Valavanis, V.D., Pierce, G.J., Zuur, A.F. et al. (2008) Modelling of essential fish habitat based on remote sensing, spatial analysis and GIS. *Hydrobiologia* **612**, 5–20.
- Vasilakopoulos, P. and Marshall, C.T. (2015) Resilience and tipping points of an exploited fish population over six decades. *Global Change Biology* **21**, 1834–1847.
- Vert-pre, K.A., Amoroso, R.O., Jensen, O.P. and Hilborn, R. (2013) Frequency and intensity of productivity regime shifts in marine fish stocks. *Proceedings of the National Academy of Sciences of the United States of America* **110**, 1779–1784.
- Vikebø, F., Sundby, S., Ådlandsvik, B. and Fiksen, Ø. (2005) The combined effect of transport and temperature on distribution and growth of larvae and pelagic juveniles of Arcto-Norwegian cod. *ICES Journal of Marine Science* **62**, 1375–1386.
- Walker, B., Holling, C.S., Carpenter, S.R. and Kinzig, A. (2004) Resilience, adaptability and transformability in social-ecological systems. *Ecology and Society* **9**, 5. (online).
- Walters, C.J. and Martell, S. (2004) *Fisheries Ecology and Management*. Princeton University Press, Princeton and Oxford.
- Walters, S., Lowerre-Barbieri, S., Bickford, J. and Mann, D. (2009) Using a passive acoustic survey to identify spotted seatrout spawning sites and associated habitat in Tampa Bay, Florida. *Transactions of the American Fisheries Society* **138**, 88–98.
- Warner, R.R. (1988) Traditionality of mating-site preferences in a coral reef fish. *Nature* **335**, 719–721.
- Warner, R.R. (1990) Male versus female influences on mating-site determination in a coral reef fish. *Animal Behaviour* **39**, 540–548.
- Watson, J.R., Kendall, B.E., Siegel, D.A. and Mitarai, S. (2012) Changing seascapes, stochastic connectivity,

- and marine metapopulation dynamics. *The American Naturalist* **180**, 99–112.
- Werner, F.E., Quinlan, J.A., Lough, R.G. and Lynch, D.R. (2001) Spatially-explicit individual based modeling of marine populations: a review of the advances in the 1990s. *Sarsia* **86**, 411–421.
- Werner, F.E., Cowen, R.K. and Paris, C.B. (2007) Coupled biological and physical models: present capabilities and necessary developments for future studies of population connectivity. *Oceanography* **20**, 54–69.
- White, J.W. and Samhouri, J.F. (2011) Oceanographic coupling across three trophic levels shapes source–sink dynamics in marine meta-communities. *Oikos* **120**, 1151–1164.
- White, J.W., Botsford, L.W., Baskett, M.L., Barnett, L.A.K., Barr, R.J. and Hastings, A. (2011) Socioeconomics and bioeconomics in MPA network planning: a comparison of approaches used in California's MLPA initiative process. *Ocean and Coastal Management* **74**, 77–89.
- White, J.W., Schroeger, J., Drake, P.T. and Edwards, C.A. (2014) The value of larval connectivity information in the static optimization of marine reserve design. *Conservation Letters* **7**(6), 533–544.
- Winemiller, K.O. and Rose, K.A. (1992) Patterns of life-history diversification in North American fishes: Implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 2196–2218.
- Wootton, R. (2012) *Ecology of Teleost Fishes*. Chapman and Hall, London.
- Wright, P.J. and Trippel, E.A. (2009) Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. *Fish and Fisheries* **10**, 283–304.
- Yamahira, K. (2004) How do multiple environmental cycles in combination determine reproductive timing in marine organisms? A model and test. *Functional Ecology* **18**, 4–15.