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Energy acquisition and allocation to egg production in relation to fish reproductive strategies

Richard S McBride[1], Stylianos Somarakis[2], Gary R Fitzhugh[3], Anu Albert[4], Nathalia A Yaragina[5], Mark J Wuenschel[1], Alexandre Alonso-Fernández[6] & Gualtiero Basilone[7]

[1]National Marine Fisheries Service, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543, USA; [2]Hellenic Centre for Marine Research, PO Box 2214, Heraklion, 71003 Crete, Greece; [3]National Marine Fisheries Service, Southeast Fisheries Science Center, Panama City, FL 32408, USA; [4]Estonian Marine Institute, University of Tartu, Vanemuise 46, 51014 Tartu, Estonia; [5]Polar Research Institute of Marine Fisheries and Oceanography, 6 Knipovich St., Murmansk 183038, Russia; [6]Instituto de Investigaciones Marinas, Consejo Superior de Investigaciones Científicas, IIM-CSIC, c/Eduardo Cabello 6, 36208 Vigo (Pontevedra), Spain; [7]Consiglio Nazionale delle Ricerche Istituto Ambiente Marino Costiero UOS Mazara (CNR-IAMC), Via L. Vaccara, no. 61, 91026 Mazara del Vallo (Tp), Italy

Abstract

Oogenesis in fishes follows a universal plan; yet, due to differences in the synchrony and rate of egg development, spawning frequency varies from daily to once in a lifetime. Some species spawn and feed in separate areas, during different seasons, by storing energy and drawing on it later for reproduction (i.e. capital breeding). Other species spawn using energy acquired locally, throughout a prolonged spawning season, allocating energy directly to reproduction (i.e. income breeding). Capital breeders tend to ovulate all at once and are more likely to be distributed at boreal latitudes. Income breeding allows small fish to overcome allometric constraints on egg production. Income breeders can recover more quickly when good-feeding conditions are re-established, which is a benefit to adults regarding bet-hedging spawning strategies. Many species exhibit mixed capital- and income-breeding patterns. An individual's position along this capital–income continuum may shift with ontogeny or in relation to environmental conditions, so breeding patterns are a conditional reproductive strategy. Poor-feeding environments can lead to delayed maturation, skipped spawning, fewer spawning events per season or fewer eggs produced per event. In a few cases, variations in feeding environments appear to affect recruitment variability. These flexible processes of energy acquisition and allocation allow females to prioritize their own condition over their propagules' condition at any given spawning opportunity, thereby investing energy cautiously to maximize lifetime reproductive value. These findings have implications for temporal and spatial sampling designs, for measurement and interpretation of fecundity, and for interpreting fishery and ecosystem assessments.

Keywords Allocation of surplus energy, capital breeding, income breeding, lifetime fecundity, oogenesis, reproductive strategy, reproductive tactic

Correspondence:
Richard S McBride,
National Marine
Fisheries Service,
Northeast Fisheries
Science Center, 166
Water Street, Woods
Hole, MA 02543,
USA
Tel.: +508-495-2244
Fax: +508-495-2115
E-mail: richard.
mcbride@noaa.gov

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Introduction

Most female fishes, once mature, are capable of producing oocytes from mitotic oogonia throughout their lives (Nakamura *et al.* 2010), and many species are highly fecund (Tyler and Sumpter 1996). The fecundity of ocean sunfish (*Mola mola*, Molidae) is perhaps the most extreme with up to 300 million oocytes estimated for a single female at the time of examination (Pope *et al.* 2010). Equally impressive is the turnover rate of egg production. For example, a large dolphinfish (*Coryphaena hippurus*, Coryphaenidae; approximately 1 m) can produce more than 100 million eggs per year (McBride *et al.* 2012). Even much smaller species, such as medaka (*Oryzias latipes*, Adrianichthyidae; approximately 3 cm), produce 1000–2000 eggs in a lifetime (Yamamoto and Yoshioka 1964; Howard *et al.* 1998). Hence, the ovary is one of the most active organs of an adult fish (Hickling and Rutenberg 1936; Grier *et al.* 2009; Lubzens *et al.* 2010).

Spawning is the most metabolically demanding activity in the lives of fishes whether it occurs at a single spawning event or over multiple-spawning seasons (Glebe and Leggett 1981; Mustonen *et al.* 2002; Nielsen *et al.* 2012). Throughout a fish's life, the total energy available is allocated to basic maintenance, somatic growth, storage and reproduction (Fig. 1; Ware 1982; Bunnell and Marschall 2003; Jørgensen *et al.* 2006). During early life history, an individual's surplus energy is devoted primarily to somatic growth to reduce size-related mortality (Roff 1982; Thompson *et al.* 1991; Sogard 1997). Eventually, allocation of surplus energy towards somatic vs. reproductive growth can speed up or delay an individual's rate

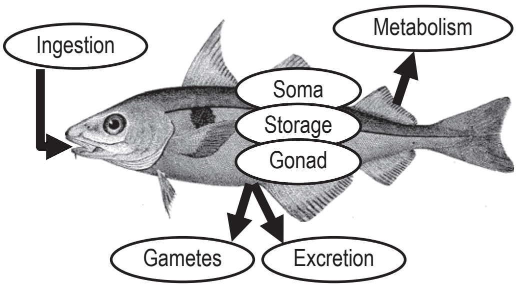

Figure 1 Acquired energy (ingestion) is allocated to basic metabolic maintenance (i.e. respiration, specific dynamic action, etc.), lost to excretion or available as surplus energy. Surplus energy is further allocated to direct growth (either somatic or reproductive) or storage (i.e. in muscle, liver or mesenteric fat). Fish image is of haddock (*Melanogrammus aeglefinus*), but these allocation pathways apply across the capital–income breeding continuum. These energetic components are shown for illustrative purposes and are not scaled in proportion to ingested energy.

of maturation (e.g. Marshall and Browman 2007; Jonsson *et al.* 2013). Once mature, surplus energy is needed to complete a clutch of eggs, as well as for accessory activities such as migration to spawning grounds, courtship and parental care.

The acquisition rate of energy often fluctuates temporally such as with seasonal cycles or interannual changes in productivity. Although similar external drivers may regulate surplus energy available in both immature and mature fishes, herein we focus on processes that affect the condition and behaviour of mature, reproductively active fish. For example, despite the need to acquire energy to reproduce, many fish species participate in costly migrations to spawning grounds, or stop feeding prior to or during spawning (Woodhead 1960; Pankhurst and Sorensen 1984; Jørgensen *et al.* 2008). To reduce the energetic conflict in such fishes, reproductive output comes either largely or entirely from surplus energy acquired and stored during an earlier period of food abundance (Fig. 1; Boulcott and Wright 2008; Moles *et al.* 2008; Palstra and van den Thillart 2010). This has been referred to, using economic terms, as ‘capital’ breeding (Henderson *et al.* 1996; Rijnsdorp *et al.* 2005; Kennedy *et al.* 2010). Alternatively, reproduction by ‘income’ breeders is ‘financed’ by energy acquired and mobilized rapidly during the breeding season (Stearns 1989; Wang and Houde 1994; Peebles *et al.* 1996).

The capital–income typology is appealing because it has the potential to integrate basic physiology and environmental drivers (i.e. ecophysiology), which may explain evolutionary processes operating at the individual level. It can also be scaled up to explore the effects of variations of ecosystem productivity on population- or community-level processes (Kjesbu and Witthames 2007; Jager *et al.* 2008; Stephens *et al.* 2009). For example, capital breeding allows feeding and spawning grounds to become disassociated in time and space whereby adults can store energy to use later, when it is more advantageous to spawn (MacKinnon 1972; Reznick and Braun 1987; Jönsson 1997). In such cases, the cost of reproduction becomes constrained by the actual physiological reserves that were stored, and the cues that stimulate egg production are independent of the environmental cues that the eggs and larvae will ultimately experience (Stearns 1989; Jørgensen *et al.* 2008). In contrast, income breeding imposes a closer spatial and temporal association between energy acquisition (feeding) and its use for spawning (Aristizabal 2007). It facilitates rapid transfer of ecosystem productivity to reproduction, which may allow constant adjustment of reproductive effort to food intake (Jönsson 1997). Spawning by income breeders may depend on factors such as daily foraging opportunities for adults. The cues that inform such adults about their environment may relate directly to egg production and the environment their propagules will experience (Peebles 2002).

Although examples of capital and income breeders have been identified among fishes (Stearns 1989), a comprehensive review of breeding patterns in fishes is unavailable (Stephens *et al.* 2009). An early generalization that ‘ectothermy preadapt(s) organisms to store energy for long periods prior to use (i.e. to rely on “capital” rather than “income”)’ focused on reptiles (Bonnet *et al.* 1998) and did not account for the taxonomic and life-history diversity of fishes. Early reviews of fish breeding patterns focused on boreal, commercially important species – largely capital breeders – unlikely to be representative of all fishes (Woodhead 1960; Iles 1974; Lambert *et al.* 2003). Capital and income breeding has been recognized within some taxa including Clupeiformes (Peebles *et al.* 1996), Pleuronectiformes (Rijnsdorp and Witthames 2005; Kjesbu and Witthames 2007) and viviparous fishes (Reznick and Braun 1987; Stearns 1989). Schultz *et al.* (1991) noted for the viviparous dwarf perch (*Micrometrus minimus*, Embiotocidae) that ‘females with large reserves are the capital breeders in the population, while females with smaller reserves draw more heavily on exogenous resources, closer to the income breeding strategy’. Therefore, in fishes, there are interspecific as well as intra-individual, ontogenetic variations in energy acquisition and allocation to reproduction.

Here, we explore the scope, complexity and advantages of patterns in energy use for reproduction by fishes, by reviewing the literature in general and examining case-studies for 39 species in 21 families and 12 orders (Table 1; see Supporting Information) in particular. Our focus is on comparisons between species, postulating that breeding patterns are not limited to extreme forms of capital or income types among species, but a range – perhaps a complete continuum – of intermediate types exists. Individuals may also be expected to adjust their reproductive investment to maximize their fitness (Williams 1966; Roff 2002), measured here as lifetime fecundity. Therefore, we also

Table 1 Tabulation of taxa used in this review, their characteristics, the effects of food on reproductive traits and important elements of the original studies. Species entries are sorted in phylogenetic order. Habitat is categorized by biogeographic zone (boreal, temperate, subtropical, tropical) and aquatic biome (marine, estuarine, freshwater). Breeder type is categorized within a continuum of capital to income breeders (see 'Species Selection'). Lifetime spawning frequency (Repeat) is categorized as either semelparous (single year of spawning) or iteroparous (multiple years of spawning) (see Fig. 2). Synchrony of development of secondary oocytes (Vitell.) is categorized as total synchrony, group synchrony or asynchrony (see Fig. 3, 'Oogenesis as the basis for reproductive strategies'). Synchrony of ovulation is categorized as either total spawner or batch spawner (Fig. 2). Fecundity is categorized as determinate or indeterminate (see 'Measuring fecundity'). Feeding effects on reproductive potential were listed as arising directly from either food amount (FA) or food type (FT) or indirectly from condition (K). Response variables were as follows: annual fecundity (AF), age at maturity (AM), batch fecundity (BF), decision to migrate (DM), egg size (ES), egg survival (ESR), gonadosomatic index (GSI), hepatosomatic index (HSI), condition factor (K), larval quality (LQ), lifetime fecundity (LF), spawning date (SD), spawning fraction (SF) or skipped spawning (SS). Increases in oocyte atresia with reduced consumption are also noted for some species. Study types were categorized as observational (O), experimental (E) or model-based (M). The level of resolution of the specific study was either individuals (I) or population mean (P). Maximum length (cm) and age (year) for each species were compiled from www.fishbase.org. See Supporting Information for original species synopses and cited references.

	Habitat		Breeder type		Synchrony				Maximum		Study type	
Species	Biogeo.	Biome	Energy	Repeat	Vitell.	Ovulat.	Fecund Type	Food effect	Size	Age	O, E, M	I, P
Petromyzontiformes, Petromyzontidae												
Sea lamprey (*Petromyzon marinus*)	Boreal	Mar.-Freshw.	Capital	Semel.	Total	Total	Determ.	FA, FT ~ LF	120	11	O	P
Anguilliformes, Anguillidae												
American and European eel (*Anguilla rostrata, Anguilla anguilla*)	Bor.-Temp.	Mar.-Freshw.	Capital	Semel.	Total	Total	Determ.	FA (K) ~ DM	133	88	O	P
Clupeiformes, Engraulidae												
Bay anchovy (*Anchoa mitchilli*)	Temp.-Subtrop.	Mar.-Estuar.	Income	Itero.	Asynch.	Batch	Indeterm.	FA ~ BF, SF (i.e. egg abundance in the field)	10	3	O	P
European anchovy (*Engraulis encrasicolus*)	Temp.	Marine	Inc.-Cap.	Itero.	Asynch.	Batch	Indeterm.	FA ~ BF (daily specific fecundity), K, GSI, SF	20	3	O	P
Japanese anchovy (*Engraulis japonicus*)	Temp.	Marine	Inc.-Cap.	Itero.	Asynch.	Batch	Indeterm.	FA ~ BF, ES, K, SF	18	4	E	P
Northern anchovy (*Engraulis mordax*)	Temp.	Marine	Cap.-Inc.	Itero.	Asynch.	Batch	Indeterm.	FA (actually starvation) ~ SF	25	7	E	P
Clupeiformes, Clupeidae												
Atlantic and Pacific herring (*Clupea harengus, C. pallasii*)	Boreal	Marine	Capital	Itero.	Group	Total	Determ.	FA ~ AF, K, SS	45	22	O, E	P
European sardine (*Sardina pilchardus*)	Temp.	Marine	Cap.-Inc.	Itero.	Asynch.	Batch	Indeterm.	FA ~ BF, SF	28	15	O	P
European sprat (*Sprattus sprattus*)	Temp.	Marine	Cap.-Inc.	Itero.	Asynch.	Batch	Indeterm.	FA (stock size) ~ BF	16	6	O	P
Cypriniformes, Cyprinidae												
Roach (*Rutilus rutilus*)	Boreal	Freshw.	Capital	Itero.	Group	Total	Determ.	FA, FT ~ AF, ES[1]	50	14	O, E, M	P
Zebrafish (*Danio rerio*)	Trop.	Freshw.	Income	Semel.	Asynch.	Batch	Indeterm.	FA ~ AM, GSI, ES[1], LQ[1], SF	4	1	E	I

Table 1 Continued.

Species	Habitat		Breeder type		Synchrony				Maximum		Study type	
	Biogeo.	Biome	Energy	Repeat	Vitell.	Ovulat.	Fecund Type	Food effect	Size	Age	O, E, M	I, P
Salmoniformes, Salmonidae												
Arctic charr (*Salvelinus alpinus*)	Bor.-Temp.	Mar.-Freshw.	Capital	Itero.	Group	Total	Determ.	FA ~ AF, AM^2, DM, GSI, K	107	40	O	P
Atlantic salmon (*Salmo salar*)	Bor.-Temp.	Mar.-Freshw.	Capital	Itero.	Group	Total	Determ.	FA ~ AF, AM, DM, ES^1, GSI, K	150	13	O	P
Brown trout (*Salmo trutta*)	Bor.-Subtrop.	Mar.-Freshw.	Capital	Itero.	Group	Total	Determ.	FA ~ AF, AM, DM, ES^2, GSI, K	140	38	O, E	I, P
Gadiformes, Gadidae												
Atlantic cod (*Gadus morhua*)	Boreal	Marine	Capital	Itero.	Group	Batch	Determ.	FA, FT ~ AF, Atresia, BF, K, SS	200	25	O, E, M	I, P
Haddock (*Melanogrammus aeglefinus*)	Boreal	Marine	Capital	Itero.	Group	Batch	Determ.	FA, FT ~ K; HIS ~ AF, ES	112	20	O, E	I, P
Pouting (*Trisopterus luscus*)	Temp.	Marine	Cap.-Inc.	Itero.	Asynch.	Batch	Determ.	FA (K, HSI) ~ AF, ES, SD	46	4	O	P
Atheriniformes, Atherinopsidae												
Inland silverside (*Menidia beryllina*)	Temp.-Subtrop.	Marine-Freshw.	Income	Semel.	Asynch.	Batch	Indeterm.	FA ~ GSI, K	15	2	E	P
Beloniformes, Adrianichthyidae												
Medaka (*Oryzias latipes*)	Temp.	Freshw.	Inc.-Cap.	Semel.	Asynch.	Batch	Indeterm.	FA, K ~ BF, SF	3	1	E	P
Cyprinodontiformes, Fundulidae												
Mummichog (*Fundulus heteroclitus*)	Bor.-Subtrop.	Estuarine	Income	Itero.	Asynch.	Batch	Indeterm.	FA ~ SF	15	4	E	I
Gasterosteiformes, Gasterosteidae												
Threespine stickleback (*Gasterosteus aculeatus*)	Temp.	Mar.-Freshw.	Income	Itero.	Asynch.	Batch	Indeterm.	FA ~ AF, BF, K, SF	11	8	E	I
Perciformes, Moronidae												
European sea bass (*Dicentrarchus labrax*)	Temp.	Marine	Cap.-Inc.	Itero.	Group	Batch	Determ.	FA, FT ~ ES, ESR, K, LF, LQ	103	15	E	I
Perciformes, Centrarchidae												
Largemouth bass (*Micropterus salmoides*)	Temp.	Freshw.	Cap.-Inc.	Itero.	Asynch.	Batch	Indeterm.	FA, FT ~ AF, K, SD, SS	97	23	E, M	I, P
Pumpkinseed sunfish (*Lepomis gibbosus*)	Temp.	Freshw.	Income	Itero.	Asynch.	Batch	Indeterm.	FA ~ AF, ES, K, SD, SS	25	12	O	P
White crappie (*Pomoxis annularis*)	Temp.	Freshw.	Capital	Itero.	Group	Batch	Determ.	FA ~ AF, ES, GSI, K, SS	53	10	O, E, M	I, P
Perciformes, Percidae												
Eurasian and yellow perch (*Perca fluviatilis, P. flavescens*)	Bor.-Temp.	Freshw.	Capital	Itero.	Group	Total	Determ.	FA, FT ~ K ~ AF, SS	60	22	O	I, P
Walleye and pikeperch (*Sander vitreus, S. lucioperca*)	Bor.-Temp.	Freshw.	Capital	Itero.	Group	Total	Determ.	FA, K ~ AF, ES^1, SS	107	29	O	P

Table 1 Continued.

	Habitat		Breeder type		Synchrony				Maximum		Study type	
Species	Biogeo.	Biome	Energy	Repeat	Vitell.	Ovulat.	Fecund Type	Food effect	Size	Age	O, E, M	I, P
Perciformes, Chaetodontidae												
Pebbled butterflyfish (*Chaetodon multicinctus*)	Trop.	Marine	Cap.-Inc.	Semel.	Asynch.	Batch	Indeterm.	FA ~ SD, SF	12	1	O	P
Perciformes, Pomacentridae												
Spiny chromis (*Acanthochromis polyacanthus*)	Trop.	Marine	Capital	Itero.	Group	Total	Indeterm.	FA ~ AF, ESR, LQ, SD	14	11	E	I
Perciformes, Ammodytidae												
Lesser sandeel *Ammodytes marinus*	Boreal	Marine	Capital	Itero.	Group	Total	Indeterm.	FA (K) ~ AM	25	10	E	I
Perciformes, Gobiidae												
Longjaw mudsucker (*Gillichthys mirabilis*)	Temp.	Estuarine	Cap.-Inc.	Itero.	Asynch.	Batch	Indeterm.	FA ~ GSI, SS	21	2	E	I
Pleuronectiformes, Scophthalmidae												
Turbot (*Scophthalmus maximus*)	Temp.	Marine	Capital	Itero.	Group	Batch	Determ.	FA ~ GSI, SS	100	25	E	I
Pleuronectiformes, Pleuronectidae												
Plaice (*Pleuronectes platessa*)	Temp.	Marine	Capital	Itero.	Group	Batch	Determ.	FA ~ AF, SS	100	50	O, E	I, P
Winter flounder (*Pseudopleuronectes americanus*)	Bor.-Temp.	Mar.-Estuarine	Capital	Itero.	Group	Total	Determ.	FA ~ AF, GSI, K, SS	64	14	O, E	I, P
Pleuronectiformes, Soleidae												
Sole (*Solea solea*)	Temp.	Marine	Cap.-Inc.	Itero.	Asynch.	Batch	Indeterm.	FA (K) ~ AF, Atresia	70	26	O	I

Effects are positive (e.g. more food reduced skip spawning or increased annual fecundity) unless indicated otherwise (i.e. [1]a negative response (e.g. smaller eggs); [2]both responses).

consider evidence for the flexibility of capital and income breeding tactics over an individual's lifetime, over long periods of multiple generations, or across broad geographic ranges constituting subpopulation structure.

In the next four background sections, we introduce terminology and concepts regarding: (i) reproductive traits, strategies and tactics; (ii) the diversity of female fish reproductive traits arising from the processes of oogenesis; (iii) the challenges to measuring female fecundity; and (iv) the depth and breadth of the literature regarding energy as the basis for egg production. In the central part of the study, we outline our methods to select a diverse array of species to review, and then discuss the major findings relative to capital breeding, income breeding and the evidence for mixed-breeding patterns; here, we also comment on the associated topics of viviparity and accessory reproductive activities. We conclude with a summary of the capital–income breeding continuum and consider the implications of this emerging conceptual framework, pointing out promising species models or approaches for further study.

Background

Strategies and tactics

A reproductive strategy is a suite of largely heritable traits, such as size and age at first reproduction, spawning seasonality and frequency and size-specific or age-specific fecundity (Glossary). These phenotypic traits are often correlated and presumably optimized by natural selection. The heritability of these traits, where measured, may be quite low (Ware 1984; Roff 2002; Brown *et al.* 2008; Charnov *et al.* 2013; McBride in press). Nonetheless, there are good examples where population-specific reproductive strategies are an adaptive response to energetic and environmental conditions (e.g. Leggett and Carscadden 1978; Conover 1992; Kinnison *et al.* 2001).

Non-genetic reproductive traits (i.e. tactics) can also emerge among phenotypes. Tactics are driven by an individuals' status – such as its size relative to other conspecifics, its internal energy level – or are driven by environment variations that benefit some segments of the population more than others. These drivers can affect an individual's fitness but do not induce selection (Wiegmann *et al.* 2004; Tomkins and Hazel 2007). Maternal effects' are prevalent in the fish literature (Green 2008). In the terminology of game theory, such tactics constitute 'conditional strategies.'

In a review of how biological properties, such as reproductive traits, are affected by the environment, such as feeding conditions, the terms 'strategies and tactics' may be confounded. We assume that there is some genetic component to the breeding types we will be categorizing that they are subjective to selection and are adaptive. Still, our review does not account for any specifics (e.g. additive genetic variance), emphasizing instead the variation in phenotypes as an expression of a conditional reproductive strategy.

Oogenesis as the basis for female reproductive strategies

Fishes employ many different reproductive strategies to produce offspring that will survive to reproduce themselves (Murua and Saborido-Rey 2003). A key proximate mechanism underlying these differences is the process of oogenesis (Marza 1938). Oogenesis follows a well-defined path from mitotic proliferation of oogonia, to meiotic development, and concluding with oocyte maturation and ovulation of an egg (Marza 1938; Harder 1975; Grier *et al.* 2009). A critical step in this process is the transition from primary to secondary oocytes, the latter of which are gonadotrophin dependent and are spawned in the upcoming season of spawning (Wallace and Selman 1981; Grier *et al.* 2009). For example, the initial provisioning of secondary oocytes with yolk (vitellogenesis) is a typical marker used to estimate size and age at maturity (McBride *et al.* 2012, 2013). Nucleus migration, a subsequent cellular marker indicating tertiary oocyte development, is also under hormonal control (Wallace and Selman 1980; Palstra *et al.* 2005; Grier *et al.* 2009). It initiates oocyte maturation, is associated with hydration of the oocyte and ends with ovulation, so that it is a typical marker used to estimate spawning seasonality (McBride *et al.* 2002, 2003).

The recruitment of secondary oocytes is known to occur in three general patterns: synchronous, group synchronous and asynchronous (Marza 1938; Harder 1975; Wallace and Selman 1981). A synchronous pattern is evident in fish that spawn once then die; only a single cohort of oocytes progresses from primary to secondary to tertiary status during the fish's life (Figs 2a and

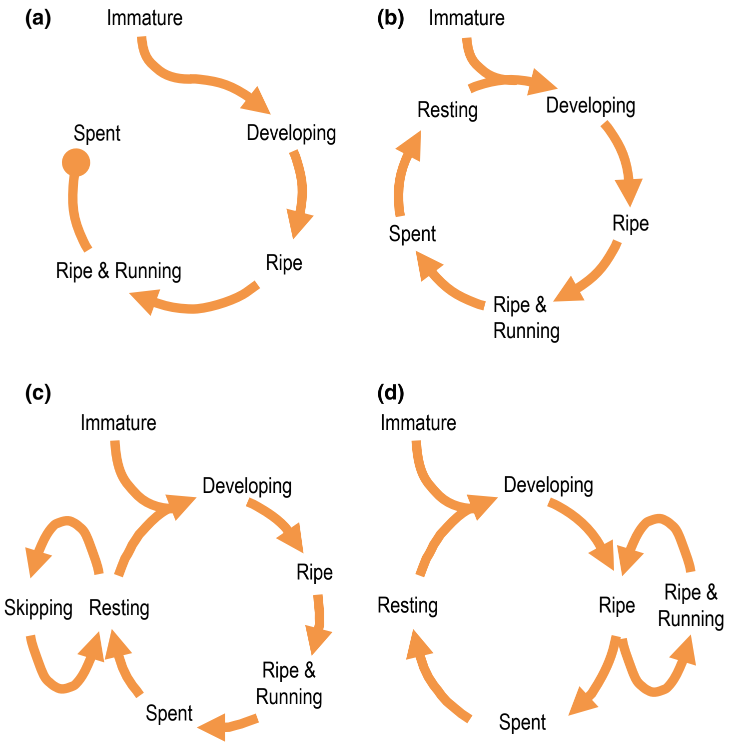

Figure 2 Four samples of female fish reproductive histories, following from the immature to mature phase and around the spawning cycle. (a) Semelparity, where a fish matures and breeds as a total spawner. (b) Iteroparity, for a total spawner that ovulates and spawns eggs in a single wave. (c) Iteroparity, for a total spawner that skips spawning in some years. (d) Iteroparity, for a batch spawner that ovulates and spawns eggs in discrete intervals. Maturity classes follow the terminology of Burnett *et al.* (1989).

3a–f). In many mature, iteroparous fishes, a reserve of primary growth oocytes persists from year to year, from which secondary oocytes develop and mature on a seasonal basis. When a discrete cohort of secondary oocytes advances, resulting in a size hiatus between primary and secondary oocytes, this pattern is referred to as group synchronism (Fig. 3g–l). When overlapping size cohorts of primary and secondary oocytes arise and persist throughout the spawning season, this pattern is referred to as asynchronism (Fig. 3m–r). Semelparous fishes that have synchronous oocyte development are rare (Finch 1994). Group synchronism is more common at higher latitudes, and asynchronism is more common at lower latitudes (Qasim 1956; Yamamoto and Yamazaki 1961; Houde 1989).

Independent of synchrony of secondary oocyte development, synchrony also occurs with respect to ovulation. When the available secondary oocytes undergo tertiary development, mature and ovulate in a single, uninterrupted event, this pattern is referred to as 'total spawning' (Figs 2b and 3a–f, g–l). Total spawning is an expected extension of synchronous oocyte development with respect to vitellogenesis, but it also occurs in some species with group-synchronous oocyte development (Murua and Saborido-Rey 2003). Although few species put all their annual reproductive effort into a single event, some do, in relation to some measure of predictability of reproductive success associated with a discrete spawning event or predictably high adult mortality (Charnov and Schaffer 1973; Bell 1980; Crespi and Teo 2002).

When secondary oocytes undergo tertiary development, mature and ovulate in multiple, discontinuous events, this pattern is referred to as 'batch spawning' (Figs 2d and 3m–r). Iteroparity and batch spawning overcome the physical constraint of body size on egg production (Smith and Fretwell 1974; Bromage *et al.* 1990; Kamler 2005) and promote a 'bet-hedging' strategy of spawning events (Olofsson *et al.* 2009; Wright and Trippel 2009; Nakayama *et al.* 2011; Morrongiello *et al.*

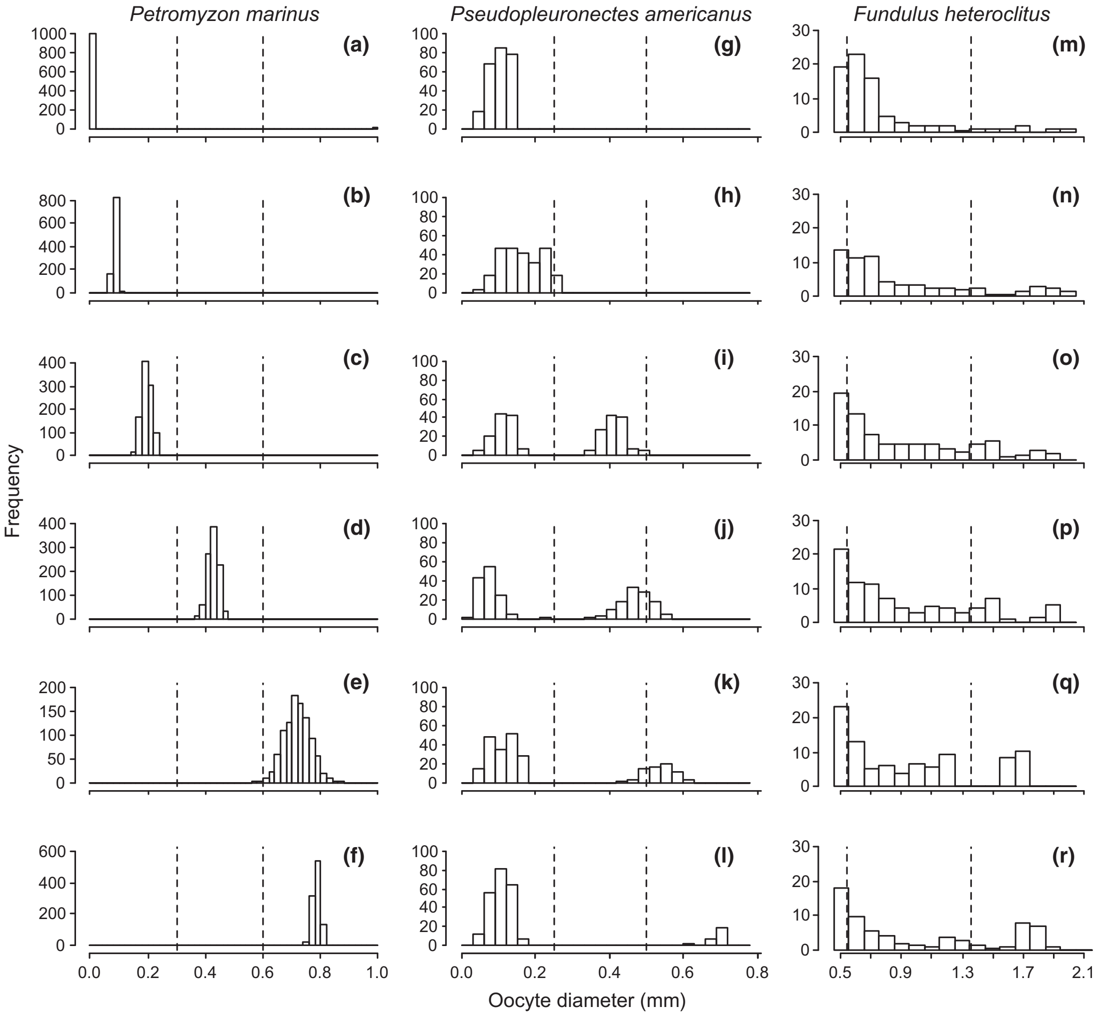

Figure 3 Three examples of oocyte development: total synchrony (left), group synchrony (centre) and asynchrony (right). Example 1. Sea lamprey, *Petromyzon marinus*, a semelparous fish with synchronous oocyte development. (a) Immature (undifferentiated gonad, age 1), (b) immature (metamorphosis, age 5), (c) immature (subadult) (d) developing (a few months before spawning), (e) developing (early spawning), (f) ripe (late spawning period). Oocyte sizes are simulated as normal distributions using mean values (±SD) measured from histology sections (Lewis and McMillan 1965). Example 2. Winter flounder, *Pseudopleuronectes americanus*, an iteroparous fish with group-synchronous oocyte development. (g) Resting (or immature), only primary growth oocytes present (August), (h) developing, a clutch of secondary oocytes developing (October), (i) developing, distinct modes of primary and secondary growth oocytes (November), (j) ripe, an advanced clutch of secondary growth and mature oocytes (December), (k) ripe, oocytes in advanced clutch are nearly all mature but remain in the follicle (March), (l) spent, some residual, mature oocytes remain after spawning is complete (April). Oocyte sizes are direct measurements from gonad histology sections of fish collected from the Gulf of Maine in 2010–11 (Y. Press and R. McBride, Northeast Fisheries Science Center, unpublished data). Example 3. Mummichog, *Fundulus heteroclitus*, an iteroparous fish with asynchronous oocyte development. All fish are running ripe, with ovulated eggs (size approximately 2 mm, not shown) collected during a protracted spawning season (February–September): (m–n) mature oocyte clutches overlapping by size early in the spawning season (February–March), (o–p) mature oocyte clutches also polymodal during the middle of the spawning season (May–June), (q–r) mature oocyte clutches with a distinct size hiatus relative to smaller secondary oocytes found at the end of the spawning season (August–September). Mummichog oocytes sizes are direct measures of fresh whole oocytes flushed from fish collected in Florida (Hsiao *et al.* 1994). In all three examples, the vertical, dashed lines indicate transition points from primary to secondary oocytes (left line) and from secondary to mature oocytes (right line): sea lamprey (0.3, 0.6 mm), winter flounder (0.25, 0.5 mm), mummichog (0.55, 1.35 mm).

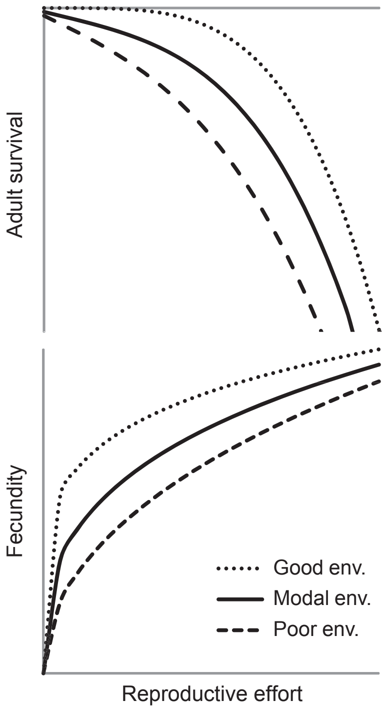

Figure 4 Theoretical trade-offs between energy allocated to reproductive effort and the effect on survival (top) and fecundity (bottom). Shown here are annual rates for a hypothetical iteroparous species, as mediated by good, typical (or modal) and poor conditions of environmental productivity. Reproductive effort equals the amount of energy assimilated and allocated to reproduction, as opposed to somatic growth, storage of surplus energy or metabolic maintenance.

2012). Iteroparity and batch spawning are also advantageous to the adult because they reduce mortality associated with very high, short-term levels of reproductive effort necessary for semelparity or total spawning (Fig. 4; Gunderson and Dygert 1988; Stearns 1992; Gunderson 1997), and they decrease the negative fitness effect from high-mortality events of offspring (Cushing 1972, 1990; Mertz and Myers 1994).

In sum, from the basic sequence of oogenesis, where the synchrony and rate of oocyte cohorts vary, a variety of reproductive traits emerge, including size and age at maturity, reproductive seasonality, spawning frequency and the number of eggs produced per spawning event.

Measuring fecundity

Estimation of lifetime fecundity integrates the individual traits of a reproductive strategy (Roff 2002; Jørgensen *et al.* 2008; Morgan 2008). Hunter *et al.* (1992) predicted that 'Inevitably, [fecundity] will be estimated for every species of economic consequence because of [its] importance in the dynamics of the population'. Yet Trippel (1999) later pointed out that fecundity had been estimated for only about 600 individual Atlantic cod (*Gadus morhua*, Gadidae) in the north-west Atlantic Ocean, and Tomkiewicz *et al.* (2003) noted that fecundity was the most poorly measured metric among 42 marine groundfish stocks assessed in the same region. Fecundity information is similarly lacking for many economically important freshwater fishes such as bloater (*Coregonus hoyi*; Salmonidae), for which fecundity is based on measurements of <150 individuals (Emery and Brown 1978; Bunnell *et al.* 2009). Lambert (2008) presents a few case-studies to show how repeated measurements of fecundity permit a better understanding of observed fluctuations in reproductive output and enhance our ability to estimate recruitment and population growth rate. Despite this evidence that 'counting eggs' matters, the paucity of data contributes to a poor understanding of how fish maximize lifetime fecundity and the role of fecundity in multistage population dynamics (e.g. Paulik 1973).

Although estimating fecundity can be relatively straightforward for some species and there is a long history of such measurements (Hickling 1940; Vladykov and Legendre 1940; Crim and Glebe 1990), for other species it can be quite difficult (Murua *et al.* 2003), and for still others the basic biology is insufficiently known to allow estimation (Gonçalves *et al.* 2009). It is relatively easy to measure fecundity of fishes with synchronous or group-synchronous oocyte development. In such fish, where there is a point at which the standing crop of secondary oocytes will equal the number of eggs produced per annum, it is said that they have 'determinate' fecundity. Counting oocytes at this point, where the annual clutch size has been determined and is readily identifiable, can even be automated with digital image processing (Thorsen and Kjesbu 2001; Witthames *et al.* 2009). In contrast, measuring the fecundity of fishes with asynchronous oocyte development is confounded by the production of multiple, overlapping clutches of secondary oocytes within a spawning season (*de novo* vitellogenesis; Rideout *et al.* 1999; Murua *et al.* 2003). In such cases, fecundity is said to be 'indeterminate', because there is no single point in time to measure the standing crop of secondary oocyte as a predictor of annual fecundity (Hunter and Goldberg 1980; Abaunza *et al.* 2003; Korta *et al.* 2010; Schismenou *et al.* 2012). Moreover, in many of these same species, a remaining portion of vitellogenic oocytes is resorbed at the end of the spawning season (Kjesbu and Witthames 2007). Consequently, measuring indeterminate fecundity is more challenging, costly and prone to error.

Hunter and Macewicz (2003), who had first proposed the terms determinate and indeterminate, later criticized these terms, because all fish show indeterminacy at some point in the reproductive cycle. Still, these terms describe well the dynamics of oocyte recruitment in relation to energy allocation, although reference to determinate fecundity does not automatically imply that the standing stock of secondary, vitellogenic oocytes equals annual realized fecundity. Unless fecundity is estimated close to the spawning season, downregulation of secondary oocytes by atresia may reduce the final number of eggs ovulated (Murua *et al.* 2003; Kjesbu 2009; McElroy *et al.* 2013; Witthames *et al.* 2013). This is particularly true for capital breeders, who set the cohort of secondary oocytes well in advance of spawning, typically at much higher numbers than will be realized. In such cases, downregulation by atresia is the only mechanism available to match the full development of these eggs with the surplus energy that accumulates over a several month process (see 'Capital breeding' and Supporting Information).

Additionally, one might assume that determinate fecundity would be strongly associated with capital breeding, and indeterminate fecundity would be a prerequisite for income breeding; however, these categories do not correspond in all fishes. Some fishes with polymodal and overlapping sizes of primary and secondary oocytes (i.e. with asynchronous development) may stop *de novo* vitellogenesis prior to spawning so that they exhibit determinate fecundity (Alonso-Fernández *et al.* 2008; Grau *et al.* 2009; Muñoz *et al.* 2010). Alternatively, some fishes with a clear size hiatus between primary and secondary oocytes (i.e. group synchrony) may produce more than one clutch of secondary oocytes per year; if so, they do not have determinate annual fecundity (e.g. spiny chromis, *Acanthochromis polyacanthus*, Pomacentridae; Nakazono 1993). Wuenschel *et al.* (2013) examined black sea bass (*Centropristis striata*, Serranidae) reproduction using fish collected at extremes of its considerable latitudinal range (25°N–45°N) and speculated that the northern stock was more determinate, whereas the southern stock was more indeterminate. Exceptions such as these are either rare or poorly understood, but they deserve more attention because they suggest that our awareness of these processes may be incomplete (Ganias 2013).

Further complicating the estimation of fecundity is that it can vary with fish age. Young, mature females may abort their first clutch of eggs (Ramsay and Witthames 1996), they may not produce the same number of eggs per unit of maternal biomass (i.e. relative fecundity; Green 2008; Sogard *et al.* 2008), or they may not produce eggs of the same quality as older females (Ross 1984; Murawski *et al.* 2001; Pankhurst *et al.* 2008). These age-specific variations arise as a consequence of younger fish having lower condition, occupying poorer habitat or demonstrating cognitive inexperience. Exertion of high reproductive effort may increase fecundity in the short term, but it will likely threaten survival (Fig. 4; Gunderson and Dygert 1988; Lambert and Dutil 2000; Nielsen *et al.* 2012). Consequently, short-term gains in fecundity will reduce future egg production (i.e. reproductive value) if surplus energy allocated to reproduction is unavailable for metabolic maintenance, feeding or predator avoidance. A shortfall in energy can increase the risk of starvation, predation or disease concurrent with or shortly after spawning (Stearns 1989; Thompson *et al.* 1991). Energy allocated to current reproduction is not available for growth, which lowers reproductive value because fecundity, particularly in determinate spawners, is a function of female body size (Rideout and Morgan 2010).

Many species do not spawn annually (Rideout *et al.* 2005; Secor 2008; Rideout and Tomkiewicz 2011). For some, this may simply be a physiological constraint, such that it takes more than one year to develop a clutch of eggs (Roussow 1957; Carrier *et al.* 2004; Kennedy *et al.* 2011; Scarnecchia *et al.* 2011). For others, skip spawning is an environmentally driven conditional reproductive strategy. Skip spawning in white sucker (*Catostomus commersonii*, Catostomidae) is positively correlated with hypoxia and negatively correlated with forage abundance (Trippel and Harvey 1989). The cui-ui (*Chasmistes cujus*, Catostomidae) does not make a spawning migration in drought years (Scoppettone *et al.* 2000). Nutritional cues will typically inhibit an annual clutch of vitellogenic oocytes from forming (Fig. 2c), which immediately reduces reproductive costs and effort while increasing the likelihood of surviving and spawning in the future (Fig. 4; Burton 1991; Rideout and Tomkiewicz 2011; Skjæraasen *et al.* 2012). At much older ages, an individual's reproductive value is reduced if survival declines or reproductive senescence occurs (Rideout and Burton 2000; Reznick *et al.* 2004; Scarnecchia *et al.* 2011).

Egg quality may also confound the interpretation of the egg quantity, because there are specific nutritional controls on egg quality as well as egg numbers (Brooks *et al.* 1997; Chambers 1997; Kamler 2005); however, environmental rather than genetic effects appear to dominate effects on egg size (Chambers and Leggett 1996). As such, egg size is not necessarily a selected trait of a reproductive strategy, but its association with egg number cannot be ignored. Although many fishes can grow to a length in excess of 1 m, approximately 70% of marine and freshwater fishes produce eggs from 0.5 to 1.5 mm diameter (Kamler 2005). Egg volume can vary several folds within a subfamily (Thresher 1982; Beacham and Murray 1993), suggesting little genetic effect by historic, phylogenetic constraints. At an intraspecific level, Kinnison *et al.* (2001) document a trade-off between upstream migration energetics and the resulting egg size (and egg numbers) between populations of Chinook salmon (*Oncorhynchus tshawytscha*; Salmonidae). Egg size variation is also constrained by a number of processes, such as osmotic regulation (Finn *et al.* 2000), fertilization rates (Levitan 1998), period of development (van Damme *et al.* 2009) and the egg's own energetics (Finn *et al.* 1995a,b; Kamler 2005; Régnier *et al.* 2013). Small fish, in particular, with relatively smaller body cavities, may not produce proportionally smaller eggs, but they can produce more eggs by spawning multiple batches.

There are many observations that eggs size varies inversely with egg number, but it is not always clear whether egg stage or the effects of nutrition or downregulation are controlled for in such field studies. Experiments to clarify these issues can also be difficult to control because egg size may vary with female size (Bagenal 1969; Jonsson and Jonsson 1997; Witthames *et al.* 2013) or over successive batches (McEvoy and McEvoy 1991, 1992; Chambers and Waiwood 1996; Trippel 1998). In one example, egg size and quality were conserved in threespine stickleback (*Gasterosteus aculeatus*, Gasterosteidae), while spawning rate and batch fecundity declined in response to reduced rations (Fletcher and Wootton 1995; Wootton and Fletcher 2009). In contrast, reduced rations fed to zebrafish actually increased the numbers of oocytes although egg size and hatching success declined (Forbes *et al.* 2010). In a common garden experiment, female Atlantic silversides (*Menidia menidia*, Atherinopsidae) collected from northern populations produced larger eggs, spawned more frequently and spawned with higher efficiency than those collected from southern populations (Klahre 1998). Experiments by Einum and Fleming (2000) examining the effect of Atlantic salmon (*Salmo salar*, Salmonidae) egg number and offspring survival demonstrated stabilizing phenotypic selection, where optimal egg size was close to the average size observed in the population. They concluded that at least for iteroparous fishes, adult females appear to prioritize their own maternal fitness rather than immediate offspring survival. The high mortality of early life stages is likely to limit the benefit from increases in investments per egg, and Charnov *et al.* (2013) concluded that drivers affecting egg size are uncoupled from drivers that affect selection of age at maturity, adult mortality and reproductive effort. As will be shown in our review, egg size did not respond predictably to energy acquisition or allocation, perhaps because it is so flexible and decoupled from these other traits.

Fecundity and energetics

Available data that connect fecundity to food availability are typically reported for economically important fishes or small fishes used as experimental models. Despite such a bias, this section provides an historical review of observational, experimental and modelling studies that document the progression from discovery, to verification, to a mechanistic understanding of fecundity dynamics as related to acquisition of energy for diverse taxa from a range of aquatic habitats.

Earlier descriptive studies (prior to 1980) associated improved feeding conditions with early maturity. Examples include char (*Salvelinus alpinus*, Salmonidae; Runnström 1951), herring (*Clupea harengus*, Clupeidae; Cushing and Burd 1956) and flounders (Pleuronectiformes; Kändler 1932; Gross 1949; Bagenal 1966), whereas poor-feeding conditions delayed maturity or lowered fecundity in brown trout (*Salmo trutta*, Salmonidae; McFadden *et al.* 1965), roach (*Rutilus rutilus*, Cyprinidae; MacKay and Mann 1969; Lyagina 1975; Kuznetsov and Khalitov 1978), goldfish (*Carassius auratus*, Cyprinidae; Bekker 1958), yellow bass (*Morone mississippiensis*, Moronidae; Bulkley 1970), white crappie (*Pomoxis annularis*, Centrarchidae; Mathur *et al.* 1979) and Eurasian perch (*Perca fluviatilis*, Percidae; Alm 1953). Such studies focused on species with determinate fecundity, presumably because fecundity is easier to measure for such fish, but also because of the large, organized fisheries and corresponding research at higher latitudes, where species with determinate fecundity are more common.

More recently, growing time series continue to document correlations between indices of available food or fish condition and reproductive potential (e.g. Marshall *et al.* 1999, 2003; Marshall 2009). Specific indices of secondary production are positively correlated with annual reproductive potential of Gadiformes in open marine systems (Kjesbu *et al.* 1998; Ajiad *et al.* 1999; Kraus *et al.* 2002; Rideout and Morgan 2010; Fig. 5). Similar patterns are evident for Clupeiformes (Peebles 2002; Somarakis *et al.* 2012; Fig. 5). In another study on haddock (*Melanogrammus aeglefinus*, Gadidae), Friedland *et al.* (2009) reported a strong correlation between autumn primary productivity and the year class strength from spawning the following spring on Georges Bank (Fig. 5); they concluded it was due to parental condition. A similar association was noted between food availability for or amount of surplus energy by adult walleye (*Sander vitreus*, Percidae) and subsequent year-class strength (Henderson and Nepszy 1994; Madenjian *et al.* 1996).

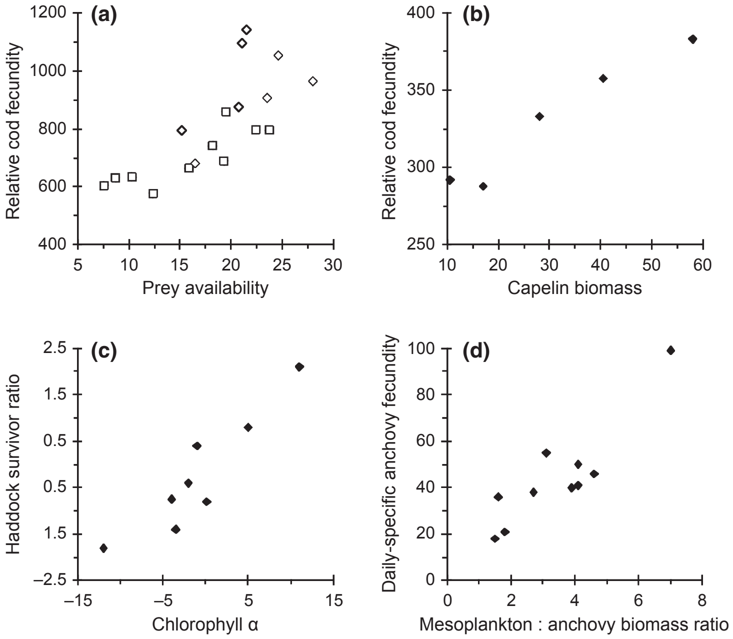

Figure 5 Correlated fluctuations between environmental productivity and reproductive potential or year-class strength. (a) Relative fecundity (eggs g^{-1}) of Baltic cod, *Gadus morhua callarias*, and prey availability (total biomass of sprat and herring age 0–2 divided by adult cod biomass). Data are annual estimates from 1987 to 2004 ($R = 0.75$; $N = 18$; P approximately 0.01). Squares are from Kraus *et al.* (2002). Diamonds are updated values using prey index from multispecies virtual population analysis (Teschner *et al.* 2010) and fecundity estimates from Martina Bleil (Institute for Baltic Sea Fisheries, unpublished data). (b) The relationship between Atlantic cod, *Gadus morhua morhua*, mean relative fecundity (eggs g^{-1}) in year t and biomass of their common prey, capelin in the previous year ($\times 10^3$ t) offshore of Newfoundland ($N = 5$; correlation not reported; data redrawn from Rideout and Morgan 2010); (c) the relationship between survivor ratio of haddock recruits per spawning stock biomass and chlorophyll α from the autumn bloom [mg m^{-3} × (8 days)$^{-1}$] as measured for Georges Bank; data are differenced to remove potential autocorrelation ($R = 0.88$; $N = 9$; $P < 0.01$; redrawn from Friedland *et al.* 2009); (d) the relationship between European anchovy daily specific fecundity (eggs g^{-1}) and mesozooplankton biomass [dry weight ($\times$ 10^{-4}), standardized to acoustic estimates of anchovy biomass] in the Aegean Sea ($R = 0.91$; $N = 10$; $P < 0.01$; redrawn from Somarakis *et al.* 2012).

Early experiments offer compelling evidence regarding the effect of nutrition on spawning periodicity and maturation. In general, decreased food availability caused gonad regression, and increased food availability caused earlier maturation and higher fecundity in species as disparate as brown trout (McCay *et al.* 1930; Scott 1962; Bagenal 1969), haddock (Hislop *et al.* 1978), medaka (Hirshfield 1980), threespine stickleback (Wootton 1973, 1977, 1979) and longjaw mudsucker (*Gillichthys mirabilis*, Gobiidae; de Vlaming 1971). Experimentally starved Atlantic herring can survive for months if sufficient fat reserves exist (Wilkins 1967), but low food availability reduces the number of eggs produced (Hempel 1971; Hay and Brett 1988; Ma *et al.* 1998). Experimental work on captive Atlantic cod and winter flounder (*Pseudopleuronectes americanus*, Pleuronectidae) demonstrates that skipped spawning is influenced by individual energy reserves available at the initiation of a new cohort of secondary oocytes (Tyler and Dunn 1976; Burton and Idler 1987; Kjesbu *et al.* 1998; Skjæraasen *et al.* 2009, 2012). Some experiments have shown that a decrease in food ration stimulates reproduction, such as for Mozambique tilapia (*Oreochromis mossambicus*, Cichlidae), but this paradox occurs because somatic growth stops, so that energy allocation leading to higher fecundity is a result of stunting (Mironova 1977). Other experiments that specifically controlled for fish size have demonstrated positive effects of food on reproductive potential, such as zebrafish (*Danio rerio*, Cyprinidae; Forbes *et al.* 2010) and turbot (*Scophthalmus maximus*, Scophthalmidae; Bromley *et al.* 2000).

Some of the earliest and most comprehensive experimental work on this topic has been with viviparous fish, particularly lecithotrophic species. Hester (1964) demonstrated across three parturition periods that guppies (*Poecilia reticulata*, Poeciliidae) on the lowest rations had less than half the number of oocytes for future reproduction than those on the full ration. Several other experiments demonstrate that high food availability to guppies is associated with increased body size, litter size and reproductive allotment (Reznick 1983, 1990; Reznick *et al.* 1992, 1996; Reznick and Yang 1993). Some of these relationships were quite complex. For example, females could respond to low food amounts by producing heavier offspring using their own fat reserves (Reznick and Yang 1993) or by producing fewer offspring with more fat reserves at birth (Reznick *et al.* 1996, 2001).

Bioenergetic models that simulate energy allocation to reproduction in yellow perch (*Perca flavescens*, Percidae) provide evidence that high fecundity in spring – and strong recruitment to follow – is related to the condition of females in the preceding autumn (Henderson *et al.* 2000). A state-dependent model designed to track lifelong energy allocation in Atlantic cod successfully predicted indeterminate somatic growth and skipped spawning, and that an energetically costly spawning migration enhanced growth and survival of propagules (Jørgensen and Fiksen 2006; Jørgensen *et al.* 2006, 2008). A model designed to predict the reproductive bioenergetics of the inland silverside (*Menidia beryllina*, Atherinopsidae), a short-lived fish with a brief, intense spawning period (Chizinski *et al.* 2008), was unsuccessful. Still, in other examples of dynamic energy budget models, the reproductive dynamics of small, short-lived fishes have been successfully modelled. One model predicted variability in spawning season of the European anchovy (*Engraulis encrasicolus*, Engraulidae; Pecquerie *et al.* 2009), and another described variability in body size, fat storage and gonad size of capelin (*Mallotus villosus*, Osmeridae; Einarsson *et al.* 2011).

In the case of roach, the integration of observational, experimental and modelling approaches provides evidence that intraspecific competition for food can affect reproductive potential. Observational studies coupled with enclosure experiments showed that large year classes of age 0 roach in a shallow lake could overgraze the prey base and thereby reduce fecundity of adults (Cryer *et al.* 1986; Perrow *et al.* 1990). In contrast, Wyatt (1988) examined roach in another shallow lake without such a food limitation, where juvenile growth rates were sufficient to support maturation a year earlier than normally reported, which increased total egg production. Nonetheless, population abundance was cyclical in both systems. Townsend *et al.* (1990) modelled roach dynamics in both systems to demonstrate how two different reproductive responses to food could create population cycles for relatively long periods. They also demonstrated that such cycles were a special condition of very high mortality rates and an overlapping forage base between juveniles and adults found in certain lakes, but otherwise such cycles are uncommon for this long-lived fish when its diet changes with age.

Capital–income strategies

Species selection

Notwithstanding the biases towards larger species of economic importance and the smaller species used as experimental models, we believe that sufficient materials exist to synthesize the effects of food acquisition and allocation on egg production in relation to female fish reproductive strategies. No simple keyword search could extract the relevant literature on this multifaceted topic. Instead, as an expert panel having worked on fish reproduction from boreal to tropical habitats, we identified a long list of candidate species, and we received feedback on and added to this list based on presentations to the larger Northwest Atlantic Fisheries Organization's Working Group on Reproductive Potential and at related scientific conferences. Using an iterative approach to search using Boolean logic (Eells *et al.* 2012), we scanned the published literature, pursued related articles identified by search engines and assembled publication lists for each species. Species synopses were developed by all co-authors for fishes that appeared promising, and these synopses were shared among co-authors for further review and feedback. Approximately twice as many species were investigated as made the final list. The 39 species that did make the final selection (Table 1; see also species synopses in Supporting Information) all had complete information on:

1. The reproductive strategy, specifically: semelparity or iteroparity, synchrony of oocyte development with respect to secondary (vitellogenic) oocytes, indeterminate or determinate annual fecundity, and batch or total spawning. Few articles consistently address all of these reproductive traits (but see Murua and Saborido-Rey 2003). We reviewed the original articles and have summarized the details for further interpretation by others (see Supporting Information).
2. The ways in which energy (e.g. food amount or type) affects these reproductive traits. In a few cases, we include proxies for direct food consumption, such as a fish condition index, if these species were not addressed in an earlier review about proxies for food consumption (Lambert *et al.* 2003).

Viviparous species were not included in our review (Table 1) because of complications regarding non-lecithotrophic sources of nutrition (matrotrophy, oophagy, adelphophagy; Trexler 1997). Later, viviparity is discussed, although we could not find sufficient information on any species of Chondrichthyes, which is a conspicuous gap in our coverage.

Based on this information, we categorized reproductive strategies along a capital–income continuum, assigning each species into four categories: (i) extreme capital breeders if females did not feed immediately prior to or during spawning; (ii) mixed capital–income breeders if females mostly rely on capital for breeding; (iii) mixed income–capital breeders if females mostly rely on income; and (iv) extreme income breeders if females feed during the spawning period and show no evidence of storing energy for growth of gonads or accessory breeding activities.

We limited our treatment to females mainly to manage the scope of this review. It is accepted that the female reproductive strategy typically exerts the greatest influence over the dynamics of the population, as producing eggs is more costly than producing sperm, or at the very least, sexual selection can involve different measures of fitness by males (Bateman 1948; Williams 1966; Coleman and Jones 2011). We are well aware that research demonstrates the relevance of male strategies to influence effective fecundity and recruitment dynamics (Simpson *et al.* 1996; Levitan 1998; Trippel 2003), but for the reasons stated above and because of the expansive scope of the topic already, we do not include male reproductive strategies in this review.

Capital breeding

Capital breeding 'describes the situation in which reproduction is financed using stored capital' (Stephens *et al.* 2009). In semelparous, total spawners, such as the sea lamprey (*Petromyzon marinus*, Petromyzontidae) and the European eel (*Anguilla anguilla*, Anguillidae), feeding ceases prior to spawning, accompanied by atrophy of the gastrointestinal organs (Applegate 1950; Pankhurst and Sorensen 1984), leaving little doubt that such species are extreme capital breeders. Sea lampreys derive their spawning energy requirements from the catabolism of energy stored during the pre-maturation feeding phase (Beamish 1979; Beamish *et al.* 1979). European eels store fats throughout a pre-migratory 'yellow' phase, and Larsson *et al.* (1990) propose that a threshold of energy content is needed to trigger transformation to the mature and migratory 'silver' phase.

Iteroparous, total spawners are also capital breeders. In these fishes, reproductive potential – the rate of oocyte development, the number of eggs produced or even whether or not spawning will occur – is affected by the amount of energy acquired many months earlier. As an example, maturing sea-run Atlantic salmon feed heavily and store body reserves in the spring prior to spawning (Rowe and Thorpe 1990; Kadri *et al.* 1996; Simpson *et al.* 1996). In laboratory or in caged conditions, individual life-history decisions to smolt or mature are made in the previous year and are influenced by hatch date, growth rate, metabolic rate, lipid stores and social status (Metcalfe and Thorpe 1992; Kadri *et al.* 1996; Simpson *et al.* 1996). The decision to skip spawning is related to the energetic condition many months prior to the spawning season in both yellow perch and the related Eurasian perch (Henderson *et al.* 2000; Holmgren 2003), as well as the unrelated Atlantic herring (van Damme *et al.* 2009) and winter flounder (Burton and Idler 1984, 1987; Burton 1991, 1994).

Batch spawners with group-synchronous oocyte development may also be capital breeders. European plaice (*Pleuronectes platessa*, Pleuronectidae) stop feeding prior to spawning, without regard to the availability of food (Rijnsdorp 1989), and approximately half of their gonad growth is subsidised from body reserves stored during the growing season (Rijnsdorp 1990). Reduced rations fed to turbot 4 months prior to spawning, when secondary oocytes were present, prevented oocyte maturation in significant numbers of females (Bromley *et al.* 2000). If reduced rations were scheduled earlier, by another 4 months, which preceded development of secondary oocytes, followed by full rations during secondary oocyte development, this had less of an effect but still produced smaller gonads and lower fecundity (Bromley *et al.* 2000).

Capital-breeding fishes, regardless of total or batch spawning, demonstrate a critical period of nutritional control for oogenesis at some point between initial energy acquisition and eventual energy allocation for reproduction (Boulcott and Wright 2008).

Because stored energy requires maintenance itself, capital breeders are not maximizing conversion efficiency (Jönsson 1997), but '[by] storing resources, an adult could then shift them to a time when it is advantageous for the young to be born' (Reznick and Braun 1987). Environmental cues that capital breeders use to initially determine fecundity are disassociated from cues regarding environmental conditions that affect egg or larval survival, but final adjustment to realized fecundity can still be tuned to the environment of the adults in the period leading up to spawning. Capital breeders do this by setting the maximum (potential) number of vitellogenic oocytes well ahead of the spawning season and adjusting this number downward closer to the spawning season (Kjesbu and Witthames 2007; Witthames *et al.* 2013). For example, during the spawning migration of Atlantic herring, a total spawner, body reserves accumulated during summer feeding are the only source of energy for reproduction, migration and routine metabolism (Milroy 1908; Slotte 1999). Initially, a female herring produces high numbers of small secondary oocytes independently of condition, whereas closer to the spawning season, when the available energy is apparent, the number and quality of oocytes are downregulated by atresia to optimize the reproductive investment (Brooks *et al.* 1997; Kurita *et al.* 2003; van Damme *et al.* 2009). The transfer of energy from somatic tissue to gonad tissue has also been noted in haddock, a batch spawner (Russell 1914). Months prior to spawning, the potential annual fecundity of haddock is set in relation to stored energy (Marshall and Frank 1999; Blanchard *et al.* 2003; Alonso-Fernández *et al.* 2009), but low rations closer to the spawning season can cause oocytes to downregulate (Hislop *et al.* 1978). A decline in egg size for individual females as spawning progresses is another mechanism for capital-breeding batch spawners to adjust for depleted energy by the end of the spawning season (McEvoy and McEvoy 1991, 1992; Trippel and Neil 2004).

Income breeding

Income breeding 'refers to the use of concurrent intake to pay for a reproductive attempt' (Stephens *et al.* 2009). In many small, batch-spawning fishes with asynchronous oocyte development, spawning can be frequent and prolonged – even daily, lasting for months – leaving little doubt that such species are extreme income breeders. In the bay anchovy (*Anchoa mitchilli*, Engraulidae), daily spawning output was 6.3% of body energy. Over the spawning season, bay anchovy egg production was equivalent to 346% of a female's body energy, which requires that spawning energy is derived from direct feeding (Luo and Musick 1991). For this species, egg abundance is positively correlated with the abundance of calanoid copepods, the principal prey item for adults (Peebles *et al.* 1996; Peebles 2002).

Income breeders can show a rapid response relative to nutritional control of oogenesis. Experimentally starved mummichog (*Fundulus heteroclitus*, Fundulidae) stopped producing mature oocytes within 3 days, but oocyte maturation could be restored within three additional days following resumption of feeding (Wallace and Selman 1978, 1980). Experiments with threespine stickleback suggest that spawning rate was more sensitive than batch fecundity to reduced rations – although both reproductive parameters declined – a result that argues for further work to determine whether there is a hierarchical response of reproductive effort to food restrictions in income breeders (Fletcher and Wootton 1995; Ali and Wootton 1999; Wootton and Fletcher 2009).

Income breeding is metabolically efficient and has the advantage of fine-tuning reproductive output relative to the current environment pertaining to both maternal condition and potential survival of the offspring. Peebles (2002) reported a 1-day lag – therefore no capital storage – between available food and daily spawning rates by bay anchovy. Furthermore, because larval anchovies ate a younger stage of the same prey consumed by adult anchovies, Peebles proposed that this plasticity in spawning rates reduces starvation risks of their young offspring. Females of the annual species, inland silverside, achieve only about 27% of their total growth by winter (Huber and Bengtson 1999b). By spring, female silversides are emaciated – indicating no remaining energy stores – but rapid growth of soma, liver and gonad resumes simultaneously in the field, a phenomenon that can be replicated in the laboratory (Huber 1995; Huber and Bengtson 1999a,b). In the field, females produce 200–2000 eggs per batch on a lunar cycle for several months (Hubbs 1982; Middaugh and Hemmer 1992; Sherrill and Middaugh 1993).

Although batch spawning can reduce the energy required per spawning bout relative to total spawning and income breeding can provide a measured level of energy for each batch, the cumulative energy expended across a spawning season can still be substantial. Huber and Bengtson (1999b) concluded that metabolic burnout of spawning inland silversides cumulated in a disappearance of mature fish by the end of their second summer (see also Chizinski *et al.* 2007). In this context, we have categorized inland silversides, and a few other batch-spawning species (Table 1), as semelparous. Although semelparity has been applied to species that 'reproduce only once in a lifetime' (Cole 1954), even semelparous, total spawners typically spawn in multiple and discrete bouts despite the fact that they ovulate their eggs in a single, uninterrupted manner (see Supporting Information). Therefore, our definition of semelparity is focused on the inability for a fish to recover from their first spawning period, whether brief or prolonged. The risk of metabolic exhaustion may explain why food is not the only cue for spawning among many income breeders. For example, mature females of the short-lived iteroparous mummichog stopped spawning after several months in the laboratory in spite of continued feeding (Taylor 1986; Hsiao *et al.* 1994).

Continued experiments and more rigorous analyses of income breeding fishes are likely to reveal broad effects of food on different aspects of their reproductive potential. In the case of zebrafish, experiments demonstrate that food amount interacts with nearly the entire suite of reproductive traits. Higher food amounts cause female-biased sex ratios (Lawrence *et al.* 2008), earlier maturation (Uusi-Heikkilä *et al.* 2011) and increased numbers of oocytes, but smaller egg size and reduced hatching rates (Forbes *et al.* 2010).

Mixed-breeding strategies

Although fishes with asynchronous oocyte development appear predisposed to income breeding, these multiple-spawning fishes often demonstrate evidence of at least supplementing their egg production with stored energy. Well-fed Japanese anchovy (*Engraulis japonicus*, Engraulidae) continue to spawn for a few weeks if starved – demonstrating some availability of capital stores – but spawning frequency, batch fecundity and egg size declined (Kawaguchi *et al.* 1990). Females of the annual species, medaka, that ate more food during the spawning period produced more eggs, but females with the most fat stores lay more eggs early in the spawning period and especially at high temperatures (Hirshfield 1980). At some point, however, more food no longer increased reproductive effort and was even associated with higher mortality (Hirshfield 1980). In the longjaw mudsucker, ovaries regressed when food was withheld completely prior to spawning, suggesting income breeding. But ovaries also recrudesced when food was withheld from post-spawning, regressed females, although at great cost to stored energy (de Vlaming 1971). Female pebbled butterflyfish (*Chaetodon multicinctus*, Chaetodontidae) spawn continuously for months, but Tricas (1986) noted that both sexes deposit large visceral fat stores prior to the reproductive season. Summer is their primary feeding season, which coincides with maximal growth of corals. Corals with the highest energy content and lowest handling costs are preferred prey for pebbled butterflyfish. Nonetheless, corals are inherently low in energy so these fish spend more than 90% of their time budget feeding on scleractinian coral polyps (Tricas 1989a,b; Aeby 2002). Thus, regardless of the energy gained by feeding during a protracted spawning period (e.g. income breeding), Tricas (1986) concluded that the length of the spawning period itself was limited by the amount of energy stored as fat during the preceding summer.

The Clupeiformes exhibit a wide diversity of reproductive strategies, from extreme capital (Atlantic herring) to extreme income (bay anchovy), and a variety of mixed-breeding strategies. In northern anchovy (*Engraulis mordax*, Engraulidae), fat accumulates in spring–summer associated with the annual spring bloom of zooplankton, remains high through autumn and then declines to a minimum during the winter spawning period (Hunter and Leong 1981). According to Hunter and Leong (1981), about two-third of the annual cost of egg production can be accounted for by the annual decline in fat stores. In European anchovy, chlorophyll concentration before the onset of the reproduction period is correlated with fish condition and energy allocated to reproduction, suggesting a capital-breeding pattern (Basilone *et al.* 2006); however, during the spawning season, interannual fluctuations in European anchovy egg abundance are also positively related to synoptic measures of primary productivity, suggesting an income-breeding pattern (Basilone *et al.* 2013). In European sardine (*Sardina pilchardus*, Clupeidae), energy stores rise rapidly in spring/summer and are used later for reproduction in autumn/winter (Ganias *et al.* 2007). Nonetheless, Ganias (2009) found a correlation between European sardine spawning rate and Chl *a* concentration on the spawning grounds indicating that direct allocation of energy to the gonad was also occurring during the spawning season.

Species with wide latitudinal ranges may exhibit intraspecific variation in capital–income breeding strategies (Schultz and Conover 1997; Ganias 2013; Wuenschel *et al.* 2013). Temperature is an obvious scalar that can affect energetics. Among eight populations of sole (*Solea solea*; Soleidae), populations from colder environments had higher rates of energy acquisition and reproductive investment, matured earlier and grew to a smaller size than populations from warmer environments (Mollet *et al.* in press); perhaps the ambiguity of whether sole is primarily a capital or income breeder (see Supporting Information) is because of this species' flexibility along the capital–income continuum. One mixed-strategy breeder, the longjaw mudsucker, is not only distributed across a wide latitudinal range but also eurythermal and euryhaline. It frequently inhabits marginal environments that demand high maintenance costs, which may select for a mixed-breeder strategy. Species that have been widely distributed by human activities, such as the largemouth bass (*Micropterus salmoides*, Centrarchidae), appear to express a mixed-breeding strategy that may facilitate its success as an introduced species. Other species, such as the capital-breeding brown trout or the income-breeding inland silverside, have also been widely introduced outside their native range. Comparative research of reproductive energetics is a powerful approach to understanding life-history trade-offs (Glebe and Leggett 1981; Jørgensen *et al.* 2008; Scarnecchia *et al.* 2011). These taxa may serve as excellent models for studies of plasticity and adaptation of breeding strategies to new environmental conditions.

Viviparous species

Krumholz (1948), observing introduced populations of the western mosquitofish (*Gambusia affinis*, Poeciliidae), reported that the spawning frequency was related to pond productivity; however, the number of broods produced by an individual also depended on the age at which maturity was reached. Overwintering females are virgins, reach maturity at approximately 9 months and spawn three to four broods over a 10- to 15-week period.

Offspring from the first few batches of the season become mature at approximately 5 weeks old and spawn only one to two broods over 4–10 weeks. This is an early example of spawning seasonality as a conditional strategy, where birth order can alternative between generations. Schultz *et al.* (1991), investigating the dwarf perch, also observed that birth order affected timing of spawning and that delays in first spawning proportionally benefited smaller over larger females. In such cases, females with large reserves are the capital breeders, while conspecifics with smaller reserves adopt an income breeding strategy. Experimental demonstrations of the effects of food on the reproductive potential of the guppy were reviewed earlier, and similar effects are also evident in research on the congener, swamp guppy (*Poecilia picta*, Poeciliidae; Reznick *et al.* 1992).

Accessory reproductive activities

Accessory reproductive activities such as migrations, territorial defence and parental care may compete with the allocation of surplus energy to gonad development (Jager *et al.* 2008). For example, van Ginneken and van den Thillart (2000) estimate that migrating silver eels use about 40% of their stored energy for swimming, leaving 60% for egg production. Longer or otherwise more costly migrations of Chinook salmon reduce gonad size and egg size (Kinnison *et al.* 2001). In studies that we reviewed, migration was common and consistently associated with total or group synchrony at vitellogenesis and capital energy allocation (Supporting Information). The cost of anadromous migrations includes mortality at sea and the risks of acquiring the energy needed to move between the spawning and nursery grounds between fresh water and the sea (Jonsson and Jonsson 1993, 2006). Jonsson and Jonsson (1993) suggest that anadromous individuals have adopted migration as a consequence of energetic limitation in fresh water. In experiments, Wysujack *et al.* (2009) reported that low food availability increased the numbers of migratory fish. Castro-Santos and Letcher (2010) considered the practical energetic costs of decisions made on the spawning grounds by iteroparous populations of the anadromous American shad (*Alosa sapidissima*, Clupeidae), noting that building more upstream passage at dams may increase immediate spawning success but at the expense of reduced iteroparity if downstream passage is not facilitated as well.

There are also examples of accessory activity in the form of territorial defence and maternal care. In the pebbled butterflyfish, monogamous pairing occurs wherein the female shares territorial defence with the male. As indicated earlier, the duration of the spawning period can depend upon fat stores gained from eating coral polyps during the period of peak coral growth. Territorial defence is hypothesized to maintain adequate feeding areas because coral is a relatively low-energy food source (Tricas 1989a,b; Aeby 2002). In another case, spiny chromis, females participate in biparental care of eggs and fry (Robertson 1973; Donelson *et al.* 2008). Spiny chromis is primarily a capital breeder with the potential to produce multiple clutches depending on stored energy reserves. Typically, only one or two clutches are produced, and if successful, energy is diverted to parental care rather than further egg production. Species in which the females are the sole provider of care and those that exhibit biparental care are associated with reduced opportunities for females to feed and produce multiple clutches (Blumer 1979; Smith and Wootton 1995; Tacon *et al.* 1996), and thus, capital allocation patterns may be typical in those situations.

Among fishes that exhibit parental care, most often males are solely involved (Blumer 1979; Smith and Wootton 1995). In these cases, accessory activities by females may be minimal in terms of demands on surplus energy. Examples include pipefishes (Syngnathidae), for whom maintaining a brood is costly to males (Lyons and Dunne 2003), and the centrarchids, which all exhibit male care in nest building, territorial defence and brood protection (Blumer 1979; Cooke *et al.* 2006). In our review, pumpkinseed sunfish (*Lepomis gibbosus*, Centrarchidae) spawn during summer and show attributes of income breeding, whereas white crappie spawn in early spring, before the seasonal pulse of productivity, and they show attributes of capital breeding (see Supporting Information).

Summary and implications

The capital–income continuum

An early postulation that ectotherms are capital breeders (e.g. Bonnet *et al.* 1998) is not true for fishes. The synchrony and rate of oogenesis, together with flexible modes of energy allocation and the range of accessory activities, produce a broad scope of conditional breeding strategies in fishes. This extends from unambiguous capital breeders to unambiguous income breeders and includes a variety of mixed-breeding strategies. Synchronous secondary oocyte development was associated with extreme capital breeders. Group-synchronous secondary oocyte development was associated with fishes that use capital sources for breeding. Asynchronous secondary oocyte development was common to fishes that use income sources of energy for breeding, but many of these fishes augment egg production with a capital mode of energy storage. All total spawners were capital breeders. Batch spawners did not exist among extreme capital breeders, but otherwise, they were interspersed along the capital–income continuum.

Large, longer-lived fishes appear more likely to use capital sources, and small, short-lived fishes are more likely to use income sources for breeding. Under conditions where higher annual fecundity confers higher fitness, asynchronous oocyte development, batch spawning and income breeding will be selected for in smaller fishes whenever the optimal fecundity threshold is greater than the limits of their body cavity. In addition, a metabolic allometry arises as smaller fish must use proportionally more of their fat stores when food is limiting (Shuter and Post 1990; Schultz *et al.* 1998; Adams 1999). The sizes or ages associated with capital–income breeders are not well defined in our review, and closer scrutiny is warranted.

Spawning frequency is a conditional strategy for both capital and income breeders. Skip spawning is a term typically associated with capital breeders with group-synchronous oocyte development, as they are omitting a spawning opportunity for an entire year. Income breeders with asynchronous oocyte development presumably do not skip spawning opportunities for an entire spawning season, but they may reduce the number of batches produced in response to poor-feeding conditions. The temporal scales may be different for each breeder type, but the underlying processes are the same in both cases: advancing a clutch of oocytes to maturation is inhibited, typically due to nutritional deficiencies (Rideout and Tomkiewicz 2011).

Strong, seasonal fluctuations in food availability at high latitudes promote capital responses to energy acquisition, whereas more moderate or prolonged seasonal cycles at low latitudes promote income responses (Schultz and Conover 1997). However, not all environmental contrasts are latitudinal, as in the Mediterranean Sea, where small, zooplanktivorous pelagic fish species that reproduce concurrent with the annual peak in zooplankton production (e.g. European anchovy) are primarily income breeders, whereas species that spawn in periods of low production (e.g. European sardine) are primarily capital breeders (Somarakis *et al.* 2004; Ganias *et al.* 2007).

Generalized vs. specialized foraging modes may also explain a species' place on the capital–income continuum. For example, the pumpkinseed, an income breeder known for plasticity of life-history traits and opportunistic foraging, feeds predominately on mollusks and zooplankton (Justus and Fox 1994; de Magalhães and Ratton 2005). By comparison, the confamilial largemouth bass and white crappie are larger-bodied piscivores that take advantage of abundant fish prey in the summer and (particularly) autumn in temperate areas. As a result, they both show distinct seasonal condition cycles (Bunnell and Marschall 2003; Brown and Murphy 2004; Bunnell *et al.* 2007) and allocate energy as capital breeders.

There is likely an inherited component of capital–income breeding, but it is also evident that energy allocation for breeding has a non-genetic component, so overlaid on heritable reproductive strategies is tactical flexibility that enables fishes to maximize lifetime fecundity in response to variations in ecosystem productivity. We postulate that female fish breeding is largely a conditional strategy, whereby an individual's genotype is capable of expressing itself along this capital–income continuum in response to both its physiological condition and its phenotypic status relative to other conspecifics and the characteristics of the environment. Individuals or species switching between extreme capital and income breeding is not suggested nor likely, but our conclusions should lead researchers to investigate the flexibility of conditional breeding strategies.

Continued investigations of fish reproductive strategies will benefit by applying the most appropriate method – at the most appropriate spatial and temporal scale for the target species – for measuring the dynamics of fecundity and relating this to the dynamics of the specific ecosystem (Koops *et al.* 2004; Morrongiello *et al.* 2012). In terms of comparative research, investigating a few species in great detail could tease apart the heritable and ecophysiological components of these reproductive strategies (Schoener 2011). Alternatively, the relationship between simple yet broadly applicable metrics of energy density and reproductive condition could be applied to a larger number of species (Nunes *et al.* 2011; Wuenschel *et al.* 2013).

It may be, however, that the capital–income typology is simply too restrictive, such that this information should be integrated into a larger body of knowledge about allometric relationships, accessory activities and demographic models, or to consider more than two strategic end points (e.g. McCann and Shuter 1997; Reznick *et al.* 2002; Jager *et al.* 2008; Shoval *et al.* 2012; Charnov *et al.* 2013) similar to what happened to r/K selection theory (Roff 2002). We are particularly interested in the potential for such studies in explaining recruitment dynamics, so we complete this essay with further thoughts on this topic.

Reproductive potential and success

Egg production is critical to sustainable fisheries, but in evolutionary terms, it is not a complete measure of fitness. The number of secondary oocytes produced is referred to here as a measure of potential fecundity or reproductive potential. Nonetheless, a full measure of reproductive success requires tracking these propagules to measure whether they survive and reproduce themselves (Stearns 1992; Roff 2002). This is difficult if not impossible to do for most fishes (Schultz 1993; Vincent and Giles 2003; Clutton-Brock and Sheldon 2010).

Extremely high mortality of the egg and larval stages is evident in many fish species, which led Russell (1932) to state: ‘there is no necessary connection between the number of eggs produced in a particular spawning season and the amount of fry which survives… The fate of the year class is probably settled at a somewhat later stage, possibly in the larval or post-larval stage’. Russell’s sentiments have been restated by many, including Paulik (1973), an advocate for multi-life-stage recruitment processes. We are aware that mortality among early life stages of oviparous fish can be high, difficult to measure or predict and arise from complex abiotic and biotic sources (Houde 2008; Fassler *et al.* 2011). Nonetheless, we agree with others who do not regard production vs. mortality hypotheses as mutually exclusive. As examples, Peebles (2002), when referring to an income breeder, proposed that spawning modulation in response to food would prevent catastrophic mismatches between bay anchovy larvae and their food. Presumably, income breeders can recover and spawn earlier than a capital breeder when good-feeding conditions are re-established. Such an adult-centric hypothesis regarding the benefits of bet-hedging spawning strategies is an alternative to those hypotheses that focus on the benefits to larval survival. Friedland *et al.* (2009), when referring to a capital breeder, test for relationships in the early life history to support match–mismatch at first feeding but instead find more support for ‘parental condition’ affecting subsequent recruitment in haddock.

If adults in better condition, or in years with higher productivity, have higher relative fecundity, why has this been so hard to see in terms of recruitment or reproductive success? As pointed out earlier, measuring fecundity is very difficult for some species; fecundity is rarely measured routinely, even in species for which it is relatively easy to measure; and the number of eggs may be correlated with egg size, which itself is quite plastic. In addition, measurements of fish condition or environmental productivity need to be matched appropriately – spatially and temporally – with measures of reproductive investment, especially relative to the potential lag between energy acquisition and allocation (Koops *et al.* 2004).

Also affecting interpretation of results is that some responses are dramatic, such as skipped spawning in fishes with determinate fecundity, but more nuanced responses, such as slight variations in spawning frequency or batch fecundity in fishes with indeterminate fecundity, can still have an significant but difficult-to-measure impact over the course of a protracted spawning season (Peebles 2002; Fitzhugh *et al.* 2012). Even among capital breeders, some of these patterns can be complex, such as when younger Atlantic salmon tend to spawn more often but expend less energy per spawning event than older females (Klemetsen *et al.* 2003). Our knowledge of the range of these effects could be biased towards those species that are easiest to measure or that exhibit only simple responses.

Single-population or single-year studies will not identify the complexities of these reproductive strategies. For example, in low productivity systems, few eggs are produced by brown trout; in such conditions, low reproductive rates keep these populations in equilibrium. As such, the energy–egg relationship is only evident if highly productive systems are also included in the analysis (McFadden *et al.* 1965). Among years, strong year classes may be infrequent, requiring extensive time series of data, few of which exist. Vert-pre *et al.* (2013) used a meta-analysis to reveal that fluctuations in environmental productivity were the most common mechanism associated with fluctuations in fish surplus abundance. They combine somatic and recruitment sources of biomass, but in the context here, we believe that the processes of capital and income breeding are relevant mechanisms to connect environmental productivity to fishery productivity.

If the expectation is to accurately predict year-class strength, then choosing a life stage later in the life history will provide a better outcome than using an earlier life stage such as eggs. But observing extreme swings in egg production may still be of practical value to fishery managers and industry in terms of forecasting major trends in the population. The focus then should be on the dual criteria of the life stage that is easiest to measure and has the most predictive power (Friedland *et al.* 2009). We do not expect that this will be a simple task: the relationship between energy and egg production could be nonlinear, such that parental effects may be more important when poor environmental conditions exist (Taylor 1986; Peebles *et al.* 1996; Donelson *et al.* 2009); or extremely low densities of spawners in patchy environments may impede reproductive success by Allee effects (Stoner *et al.* 2012) or fail to numerically overwhelm egg and larval predators (Richardson *et al.* 2011). Separating individual-level and possible contingent-level (*sensu* Secor 1999) processes may also be important to understanding how reproductive potential may relate to recruitment. In particular, the fitness of the mean individual may not be representative of the subsequent pool of survivors, given that the numbers of successful spawners in any year are typically much, much smaller than actual population size (Hedgecock and Pudovkin 2011). Approaches that account for individual, year-class-specific, age-based or contingent levels of variation are likely to be informative in relating environmental effects on egg production and recruitment (Chambers 1993; Wright and Trippel 2009; Moyes *et al.* 2011).

Conclusions

To our knowledge, this review provides the broadest taxonomic coverage of the patterns and processes of energy acquisition and allocation to fish egg production. The focus is on oogenesis, as a universal but flexible process that underlies many reproductive traits. A wealth of data, based on a broad scope of research approaches, unequivocally connects feeding conditions to reproductive potential. Potentially maladaptive responses such as delays in maturity, skipped spawning and lower than average annual fecundity can often be explained in the context of conditional reproductive strategies that attempt to maximize adult fitness in response to fluctuating environmental conditions. More often, reproductive potential is poorly measured, and time series of data are not available to test the outcomes of environmental variation on egg production. We find that although there are several unambiguous examples of capital and income breeders, selection has not been disruptive. There are many mixed breeder types across a diverse set of taxa, which has not been well recognized in the literature. Capital and income breeding processes have far reaching effects on reproductive traits and possibly on other aspects of population dynamics. This review summarizes recent advances and examples of how to measure reproductive potential to encourage investigation of the evolutionary, ecological and fisheries-related consequences of these breeding strategies.

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Glossary Terms commonly used in the text, tabulated and defined here for quick access. See also Murua and Saborido-Rey (2003), Kjesbu (2009), Tomkins and Hazel (2007) and Charnov *et al.* (2013) for further details and related terminology.

Asynchronous oocyte development	Secondary oocytes arise throughout the spawning season (*de novo* vitellogenesis), resulting in overlapping size cohorts of primary and secondary oocytes during at least the early part of the spawning season
Atresia	Resorption of the follicle, particularly referring to atretic secondary oocytes which reduces annual realized fecundity (see downregulation)
Batch spawner	Ovulation occurs in more than one discrete event within the spawning season
Capital breeders	Individuals who use energy stored prior to the spawning season to produce eggs later
Conditional strategy	A decision rule governed by a conditional (rather than a genetic) clause (e.g. mature if larger than other fish). See reproductive tactic
Determinate fecundity	Annual (iteroparous species) or total (semelparous species) potential fecundity becomes set prior to the spawning season so it can be measured at a single point in time
Downregulation	The process of atresia that reduces the number of viable oocytes. Typically referring to atresia of secondary (vitellogenic stage) oocytes, to account for a difference between potential and realized fecundity
Group-synchronous oocyte development	A discrete cohort of secondary oocytes advances from a reservoir of primary oocytes, resulting in a size hiatus between the two classes of oocytes
Income breeders	Individuals who use energy available during the spawning season to produce eggs in that season
Indeterminate fecundity	Annual potential fecundity is not set prior to the spawning season because primary oocytes continue to develop into secondary oocytes after spawning commences, and these have the potential to be spawned in the current season
Iteroparous	Individuals that have the capacity to reproduce in more than one spawning period
Potential fecundity	The number of secondary oocytes produced prior to (determinate method) or during (indeterminate method) the spawning season
Realized fecundity	The final number of eggs spawned
Relative fecundity	The number of secondary oocytes divided by body weight to standardize for differences in fish size
Reproductive effort	Reproductive investment and any accessory reproductive costs
Reproductive investment	The amount of mass or energy used to produce eggs
Reproductive potential	A measure of population productivity. Commonly described in fishery models as biomass of the mature population. Specific reference here is to the number of eggs produced by an individual or population. There may be other indices of reproductive potential (e.g. number of repeat spawners, spawner age diversity, etc.)
Reproductive strategy	A genetically based decision rule regarding a reproductive trait (or combination of traits)
Reproductive success	Relative to a spawning individual, the number of its propagules that live to reproduce themselves
Reproductive tactic	The phenotype generated by a decision rule (see reproductive strategy)
Reproductive traits	Specific reproductive characters such as age at maturity, spawning frequency, batch fecundity, etc. These may be under genetic and environmental control
Semelparous	An individual that reproduces entirely within one spawning period and then dies during the post-spawning interval
Skipped spawners	Individuals that have matured and spawned in the past that do not spawn in a given year
Surplus energy	Energy available to the individual above that needed for routine metabolism
Synchronous oocyte development	Only a single cohort of oocytes progresses from primary to secondary status and ovulates during the fish's life
Total spawner	Ovulation occurs in a single, uninterrupted wave within the spawning season

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Supporting information about the effect of energy acquisition and allocation on egg production in relation to reproductive strategies of 39 fishes (species synopses).

Table S1. A list of species mentioned in the text.