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

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TABLE OF CONTENTS

INTRODUCTION 3
SPECIES SYNOPSES 4
Sea lamprey (*Petromyzon marinus*, Petromyzontidae) 4
American and European eel (*Anguilla rostrata, A. anguilla*, Anguillidae) 5
Bay anchovy (*Anchoa mitchilli*, Engraulidae) 6
European anchovy (*Engraulis encrasicolus*, Engraulidae) 6
Japanese anchovy (*Engraulis japonicus*, Engraulidae) 7
Northern anchovy (*Engraulis mordax*, Engraulidae) 8
Atlantic and Pacific herring (*Clupea harengus*, *C. pallasii*, Clupeidae) 9
European sardine (*Sardina pilchardus*, Clupeidae) 10
European sprat (*Sprattus sprattus*, Clupeidae) 11
Roach (*Rutilus rutilus*, Cyprinidae) 11
Zebrafish (*Danio rerio*, Cyprinidae) 12
Arctic charr (*Salvelinus alpinus*, Salmonidae) 13
Atlantic salmon (*Salmo salar*, Salmonidae) 14
Brown trout (*Salmo trutta*, Salmonidae) 15
Atlantic cod (*Gadus morhua*, Gadidae) 16
Haddock (*Melanogrammus aeglefinus*, Gadidae) 17
Pouting (*Trisopterus luscus*, Gadidae) 18
Inland silverside (*Menidia beryllina*, Atherinopsidae) 18
Medaka (*Oryzias latipes*, Adrianichthyidae) 19
Mummichog (*Fundulus heteroclitus*, Fundulidae) 20
Threespine stickleback (*Gasterosteus aculeatus*, Gasterosteidae) 21
European seabass (*Dicentrarchus labrax*, Moronidae) 21
Largemouth bass (*Micropterus salmoides*, Centrarchidae) 22
Pumpkinseed (*Lepomis gibbosus*, Centrarchidae) 24
White crappie (*Pomoxis annularis*, Centrarchidae) 25
Eurasian and yellow perch (*Perca fluviatilis*, *P. flavescens*, Percidae) 26
Walleye and pikeperch (*Sander vitreus*, *S. lucioperca*, Percidae) 27
Pebbled butterflyfish (*Chaetodon multicinctus*, Chaetodontidae) 27
Spiny chromis (*Acanthochromis polyacanthus*, Pomacentridae) 28
Lesser sandeel (*Ammodytes marinus*, Ammodytidae) 29
Longjaw mudsucker (*Gillichthys mirabilis*, Gobiidae) 29

Turbot (*Scophthalmus maximus*, Scophthalmidae) 30
Plaice (*Pleuronectes platessa*, Pleuronectidae) 30
Winter flounder (*Pseudopleuronectes americanus*, Pleuronectidae) 31
Sole (*Solea solea*, Soleidae) 31
REFERENCES 32

INTRODUCTION

The document contains supporting information about the effect of energy acquisition and allocation on egg production in relation to reproductive strategies of 39 fish species. We developed these synopses based on our own reviews of the literature and our participation with the Northwest Atlantic Fisheries Organization's (http://www.nafo.int/) Working Group on Reproductive Potential. Other experts were consulted during the review process as well (see "Species selection" and "Acknowledgements" in the main article). The final list is also presented in Table 1 of the main article.

A specific goal was to include a broad phylogenetic diversity, and the 39 species reviewed here are from 21 families and 12 orders. A few species represent each biogeographic zone (boreal, temperate, subtropical, tropical) and aquatic biome (marine, estuarine, freshwater) including diadromous fishes (i.e., sea lamprey, American and European eel, salmonids). Other selected species have been introduced or invaded habitat outside their native range, such as sea lamprey and the centrachids. Many species are important fishery species, such as Atlantic cod or largemouth bass. Others are important as experimental models in the laboratory, such as zebrafish, inland silverside, medaka, mummichog, threespine stickleback, and longjaw mudsucker. Many have specific spawning migrations, such as populations of sea lamprey, American and European eel, Atlantic and Pacific herring, roach, Atlantic salmon, brown trout, Arctic charr, Atlantic cod, walleye and pikeperch, Eurasian and yellow perch, plaice, and winter flounder. Fish names follow Nelson *et al.* (2004) for North American fishes and Wheeler (1992) for European fishes; any exceptions were checked against Eschmeyer and Fong (2008) and fishbase (www.fishbase.org).

Viviparous species were not tabulated (Table 1 of main article) or summarised here because of potential complications regarding non-lecithotrophic sources of nutrition (matrotrophy, oophagy, adelphophagy; Trexler 1997). There are several well-studied viviparous teleosts mentioned in the main article, except that we could not find sufficient information on any species of Chondrichthyes.

The format for each synopsis is standardised, usually in a two paragraph format. Each synopsis begins with a general description of the geographic range and habitat occupied by the species. Next, the reproductive strategy is outlined with respect to the following: 1) breeding opportunity (semelparous or iteroparous); 2) synchrony of oocyte development with respect to vitellogenesis (synchronous, group synchronous, or asynchronous) and oocyte maturation or ovulation (total or batch spawning); and 3) methods used to describe and calculate fecundity (determinate or indeterminate). Terminology regarding reproductive strategies is similar to that used by Murua *et al*. (2003) and Kjesbu (2009).

These aspects of reproductive strategies are followed by a statement whether we consider the species as: 1) extreme capital breeders if females did not feed immediately prior to or during spawning, 2) mixed capital-income breeders if females mostly rely on capital for breeding, 3) mixed income-capital breeders if females mostly rely on income, and 4) 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 also include specific evidence regarding the ways in which energy (e.g., food amount or type) affects the numbers or size of eggs produced per year, and whether this is based on observation, field or laboratory experimentation, or modeling of individual fish or at a population level (see also Table 1 of main article). A statement about any noteworthy context, particularly as it may relate to future research directions, concludes each synopsis.

SPECIES SYNOPSES

Sea lamprey (*Petromyzon marinus*, Petromyzontidae)

An anadromous species distributed in the North Atlantic Ocean, sea lamprey has also invaded the North American Great Lakes (Hubbs and Pope 1937; Beamish 1980). It is a semelparous breeder: females enter rivers and streams in spring, at 5-7 years old, spawn in summer, and die within a few days of spawning (Applegate 1950; Wigley 1959; Hardisty 1965). Oocytes develop synchronously from primary growth to secondary growth to mature stages throughout the life of the lamprey (Fig. 3a-f of main article; Applegate 1950; Lewis and McMillan 1965). The absolute fecundity is established in the first year (ammocoete) and remains high in individuals from anadromous populations. In contrast, half or more of the oocytes in landlocked females do not undergo vitellogenesis or ovulate, but because these landlocked females are smaller, their relative fecundity is higher than anadromous populations (Appelgate 1950; Hardisty 1963, 1964). In both forms, lifetime fecundity can be estimated prior to spawning using the determinate fecundity method, and ranges from 20,000 to 100,000 in landlocked populations and from 124,000 to 260,000 in anadromous populations (Applegate 1950; Vladykov 1951; Wigley 1959; Hardisty 1963). Females can be best characterised as total ovulators that behaviourally spawn in batches; they ovulate their eggs in a single wave, from the posterior to the anterior of the ovary. Fully ripe eggs are shed into the coelom, and 20-40 eggs are released at a time into a nest, at intervals several minutes apart, lasting from 16 hours to 3.5 days (Appelgate 1950).

Sea lamprey is an extreme capital breeder. Sea lamprey cannot feed during the spawning run because their digestive tract degrades (Applegate 1950). Instead, they derive their spawning energy requirements from the catabolism of energy stored during the pre-maturation feeding phase (Beamish 1979; Beamish *et al*. 1979). Hardisty (1963; p. 17) notes that “the wide range of variability in oocyte numbers [is the result] of variations in nutritional and other environmental factors.” Individuals of both anadromous and landlocked populations initially produce a similar number of oocytes but in landlocked lampreys there is a dramatic downregulation of oocyte numbers later in life; this suggests that in landlocked conditions, food is either limiting, the smaller body size achieved limits the advancement of all potential oocytes, or both (Hardisty 1963; Applegate 1950). Sea lamprey size, which is related to fecundity, is positively related to their prey abundance (Heinrich *et al*. 1980) or even related to prey type (*Salvelinus namaycush* vs. *Coregonus clupeaformis*; Kitchell and Breck 1980). Smith and Marsden (2007) report a positive correlation between prey (lake trout) abundance and sea lamprey fecundity in the Great Lakes. The introduction of sea lamprey into landlocked ecosystems, while generally a nuisance to existing fisheries, represents a potential evolutionary model to explore, via the comparative method, the nutritional mechanisms that affect egg production.

American and European eel (*Anguilla rostrata, A. anguilla*, Anguillidae)

These catadromous species are widely distributed in the North Atlantic Ocean, living most of their lives in freshwater systems of North America or Europe, respectively (Tesch 1977; van Ginneken and Maes 2005). They are semelparous breeders, spawning in the Sargasso Sea at 10 or even 20 years old (Vøllestad 1992; Oliveira and McCleave 2000). Oocytes develop synchronously from primary growth to secondary growth to mature stages (Palstra *et al*. 2005). The spawning cue is not well known but maturation is stimulated by sustained swimming activity (Palstra and van den Thillart 2010). The gonadosomatic index is low for females as they leave coastal habitat (1-2% of their body weight is gonad), but increases dramatically to 40-60% in spawning females (van Ginneken *et al*. 2005). Lifetime fecundity ranges from 1 to 4 million (*A. anguilla*; Boëtius and Boëtius 1980; van Ginneken *et al*. 2005) and 2 million to 20 million eggs (*A. rostrata*; Barbin and McCleave 1997). Spawning has only been observed in tanks where it appears to result in a nearly instantaneous release of all eggs (van Ginneken *et al*. 2005; Oliveira and Hable 2010).

Both species are extreme capital breeders. Pankhurst and Sorensen (1984) observed the degradation of the stomach during experimentally-induced maturation, and several modeling studies show that females can mature a clutch of eggs entirely from catabolism of their energy stores (e.g., Boëtius and Boëtius 1985; Amin 1991; van Ginneken and van den Thillart 2000). There are many hypotheses about what triggers the spawning migration of "silver" eels, but among the biotic-oriented mechanisms, Vøllestad (1992) dismisses age or size because they are too variable among this life phase. Larsson *et al*. (1990) note that fat stores in silver eels are higher than pre-migratory phase yellow eels, so they propose that energy content triggers migration and maturation; although intuitive, this hypothesis remains largely untested. Van Ginneken and van den Thillart (2000) create an energy budget indicating that migrating females use about 40% of their stored energy for swimming, leaving 60% for egg production. Although they successfully argue that mature females have sufficient energy reserves to make it to the Sargasso Sea, Kettle *et al*. (2011) note that this may not be true for all adult source areas, and further research is needed to explain the 20-fold variation in fecundity estimates for these species. Tagging methods that would allow direct examination of naturally maturing females in the ocean are promising (Methling *et al*. 2011) but have yet to reveal insights into the likely relationship between available energy and egg production in *Anguilla*. Stock assessment working groups are beginning to evaluate condition indices of escaping silver eels for their potential to forecast reproductive potential of adults leaving freshwater systems (WGEEL, 2012).

Bay anchovy (*Anchoa mitchilli*, Engraulidae)

A marine-estuarine species of the western North Atlantic Ocean, bay anchovy lives for a maximum of 3-4 years and is an iteroparous breeder: females start spawning in estuaries at 3-10 months old (Luo and Musick 1991; Zastrow *et al*. 1991). The reproductive season is usually from spring to autumn, shorter at northern latitudes but may extend throughout the year at southern latitudes within its range (Houde and Lovdal 1984; Vouglitois *et al*. 1987; Luo and Musick 1991; Zastrow *et al*. 1991; Lapolla 2001; Bassista and Hartman 2005). Annual fecundity is indeterminate. Oocytes develop from primary growth to secondary growth stage asynchronously and mature in batches (Luo and Musick 1991). Batch fecundity varies seasonally and geographically and ranges from 429 to 1186 eggs g^{-1} ovary-free weight (Luo and Musick 1991; Zastrow *et al*. 1991; Bassista and Hartman 2005). Spawning fraction is typically high (> 0.5) with nearly all females spawning daily during the peak of the spawning season (Luo and Musick 1991; Zastrow *et al*. 1991, Bassista and Hartman 2005).

Bay anchovy is an extreme income breeder. Luo and Musick (1991) present calculations showing that the overall egg production for the 1988 spawning season in lower Chesapeake Bay was 45110 eggs per female (55-mm fork length) which is equivalent to 346% of a female's body energy. During peak spawning, daily spawning output was 6.3% of body energy. The authors conclude that most spawning energy was derived from daily feeding, not fat reserves. Wang and Houde (1994) showed that somatic growth increases significantly in bay anchovy during the spawning season (32-33% increase in gutted weight and 26% in total weight), so feeding not only meet energy requirements for daily spawning but also provides surplus energy for growth. Finally, bay anchovy egg abundance in the field is correlated with the abundance of calanoid copepods, the principal prey item for adults (Peebles *et al*. 1996; Peebles 2002). The correlation between instantaneous prey availability and egg production is expected to be higher in income breeders, i.e. when spawning energy derives primarily from recent feeding.

European anchovy (*Engraulis encrasicolus*, Engraulidae)

A marine species of the eastern Atlantic Ocean, the Mediterranean Sea, the Black Sea and the Azov Sea, European anchovy lives for a maximum of 4-5 years and is an iteroparous breeder: at about 1 year old females start to spawn. They spawn usually from spring to autumn, but spawning duration ranges from 2.5 months to year-round depending on stock and temperature cycles (Palomera and Rubies 1996, Somarakis *et al*. 2004). In the Black Sea, some young-of-the-year (65-95 mm) may spawn towards the end of the spawning season when they are 2-3 months old (Lisovenko and Andrianov 1996). Annual fecundity is indeterminate and oocytes develop from primary growth to secondary growth stage in an asynchronous manner (Motos 1996; Schismenou *et al*. 2012). Batch fecundity and spawning frequency varies widely between seasons, years and stock areas especially in the Mediterranean Sea (Motos 1996; Somarakis *et al*. 2004; 2012). For example, estimates of spawning fraction range from 0.06 to 0.40 (Somarakis *et* *al*. 2004; 2007; 2012) but values up to 1.00 have been reported in the Black Sea during the peak of the spawning period (Lisovenko and Andrianov 1996). In the Bay of Biscay, spawning fraction is consistently ~0.4 at peak spawning (Uriarte *et al*. 2012).

There is substantial field evidence and some comparative studies suggesting that European anchovy are largely income breeders. However, energy gained and stored before the spawning period might also affect its annual reproductive output. Lisovenko & Andrianov (1996) report an increase of up to 49% for mean female gutted weight from the beginning to the end of the spawning period in the Black Sea whereas, in the Aegean Sea, anchovy exhibits its highest somatic and liver condition during the reproductive period (May-June, Somarakis unpublished data). These observations suggest that food intake during the reproductive period might be sufficient to support both somatic growth and egg production. The high variability of spawning fraction and batch fecundity estimates for European anchovy in the Mediterranean Sea has been attributed to the respective high spatial and temporal variability in plankton production characteristic of this basin (Somarakis *et al*. 2004; 2007). In the North Aegean Sea, anchovy exhibited better somatic condition and produced more eggs (higher batch fecundity) and at higher rates (higher spawning fraction) during June 1993 when zooplankton concentration (adult prey) was significantly higher compared to June 1995 (Somarakis 2005). Recently, a strong linear relationship has been demonstrated between daily specific fecundity (eggs g^{-1} of the population) and the ratio of zooplankton biomass and anchovy biomass (index of per capita food availability) indicating that egg production is controlled by a density-dependent mechanism (Somarakis *et al*. 2012). Finally, in the Strait of Sicily, chlorophyll concentration before the onset of the reproduction period was correlated with fish condition and reproductive intensity (i.e., mean gonadosomatic index during the spawning season) which implies that the level of primary production during the winter-early spring bloom might affect reproductive output in the subsequent spawning period in summer through the increased condition of adult fish (Basilone *et al*. 2006). Also in the Strait of Sicily, interannual fluctuations in egg abundance are positively related to primary productivity (Basilone *et al*., in press).

Japanese anchovy (*Engraulis japonicus*, Engraulidae)

A marine species of the western North Pacific Ocean, Japanese anchovy lives for a maximum of 4 years and is an iteroparous breeder: at about 1 year old females start to spawn, and they typically spawn from early spring to late autumn (Tsuruta and Hirose 1989; Kawaguchi *et al*. 1990; Funamoto and Aoki 2002; Funamoto *et al*. 2004). Annual fecundity is indeterminate and oocytes develop from primary growth to secondary growth stage in an asynchronous manner (Imai and Tanaka 1994). There is strong experimental and field evidence that batch fecundity increases and egg size decreases with increasing temperature (Tsuruta and Hirose 1989, Kawaguchi *et al*. 1990; Imai and Tanaka 1997; Imai and Kajitori 2000; Funamoto *et al*. 2004; Takasuka *et al*. 2005). Spawning fraction varies from 0.71 to 0.23, within a year, among years, and among stocks (Tsuruta and Hirose 1989; Funamoto and Aoki 2002; Takasuka *et al*. 2005). A positive relationship has been recently demonstrated between spawning fraction and sea surface temperature (Takasuka *et al*. 2005).

Japanese anchovy are largely income breeders as evidenced by laboratory experiments (Tsuruta and Hirose 1989; Kawaguchi *et al*. 1990) demonstrating that food availability affects imminent reproductive potential. In a starvation experiment (Kawaguchi *et al*. 1990), fish continued to spawn for 22 days at 19°C after the onset of starvation but with decreasing rate. Egg volume decreased as well. In another study, Tsuruta and Hirose (1989) investigated the effect of the amount of food and fish density on egg production. Lower levels of food increased the inter-spawning interval and decreased batch fecundity and egg size. The condition of fish declined during the experiments which indicated that allocation of energy to reproduction was prioritised. Food intake affected egg production with a two-week lag. At constant food supply, egg production decreased in tanks with high density of fish. However, somatic growth was better in the high density tank. This implied that a density dependent mechanism (amount of food per individual fish) controlled the allocation of energy to growth or reproduction. At high fish density, growth was prioritised. When sea water from the high density tank was transferred into the low density tank, egg production decreased in the low density tank.

Northern anchovy (*Engraulis mordax*, Engraulidae)

A marine species of the eastern North Pacific Ocean, northern anchovy is an iteroparous breeder: at about 1-year (central subpopulation) or 2-years (northern subpopulation) old, females start to spawn (Hunter and Macewicz 1980; Laroche and Richardson 1980; Blaxter and Hunter 1982). Some spawning occurs throughout the year, but the central subpopulation (35°N) spawns primarily in winter (February-March) (Hunter and Macewicz 1980; Blaxter and Hunter 1982), whereas the northern subpopulation (45°N) has a more precise and much shorter spawning season that peaks in July (Laroche and Richardson 1980; Blaxter and Hunter 1982). Annual fecundity is indeterminate. Oocytes develop from primary growth to secondary growth stage in an asynchronous manner. Hydration begins in early morning and the eggs are completely hydrated by sunset (Hunter and Macewicz 1980; Hunter and Leong 1981; Hunter and Macewitz 1985a). Batch fecundity estimates for the central subpopulation from Daily Egg Production Method applications (peak spawning) range from 445 to 622 eggs g^{-1} whole body weight and spawning fraction from 0.09 to 0.16 (Hunter and Macewitz 1985a; Hunter *et al*. 1985; Somarakis *et al*. 2004). Parrish *et al*. (1986) demonstrated that the fraction of females with hydrated eggs or with day-1 postovulatory follicles increased with female size, and despite a number of simplifications and assumptions in their approach, determined annual fecundity to be age-dependent. An average 4+ yr-old female produces 10 times as many eggs as a 1-yr old female. The difference was mainly due to the increase in the spawning period with increasing age.

Northern anchovy are largely capital breeders. Fat accumulates in the body during summer (April and July), associated with the annual spring bloom of zooplankton. It usually remains high through the end of autumn (December) and then declines to a minimum during the winter spawning period (Hunter and Leong 1981). Thus, fat stored from the previous spring and summer may be used the following year to support reproduction (Hunter and Leong 1981). According to calculations by these authors, about 2/3 of the annual cost of egg production can be accounted for by the annual decline in fat stores. There is evidence that feeding conditions may not affect greatly the batch fecundity (Hunter and Leong 1981): Females matured in the laboratory were fed a high ration and grew about four times faster than those in the sea, yet the batch fecundity was about the same as field-caught specimens, which consume a lower ration. At least over the first few months of spawning, batch fecundity does not change significantly, implying that it is more stable than other reproductive traits. In laboratory experiments (Hunter and Macewicz 1985b), female northern anchovies reacted very quickly to adverse feeding conditions by resorbing oocytes and they recovered rapidly when sufficient food was available. Females with low levels of alpha atresia (< 50% yolked oocytes affected) spawned about half as frequently as did those with no alpha stage atresia. Finally, during 'El Niño' years, small pelagic fish populations in the California and Humboldt Current systems may exhibit markedly lower egg production (Blaxter and Hunter 1982; Alheit 1989).

Atlantic and Pacific herring (*Clupea harengus, C. pallasii*, Clupeidae)

These marine species are widely distributed in the North Atlantic Ocean (*Clupea harengus*), including the Baltic Sea, and in the North Pacific (*Clupea pallasii*). They are iteroparous breeders with group-synchronous oocyte development with respect to vitellogenesis (Hickling and Rutenberg 1936; Kurita, *et al*. 2003). Herring have a very distinct mode of advanced yolked oocytes from which to measure potential annual fecundity (Hickling 1940), but it has been demonstrated that smaller vitellogenic oocytes of this mode are downregulated by atresia prior to spawning (Kurita *et al*. 2003). The fecundity of 34 cm fish, from the spring-spawning herring population decreased significantly, over 50%, from 113,000 in July to 49,200 in February/March (Kurita *et al*. 2003). Herring is a total spawner that ovulates all mature oocytes in a single batch (Geffen 2009). Once mature, females normally deposit their eggs on gravel or rocks in coastal and offshore bank habitats. Skip spawning by herring was reported to be very high as inferred indirectly from fish scales (Engelhard and Heino 2005), but more recent, direct examinations of herring gonads during different migratory phases indicated much more modest skip spawning rates (Kennedy *et al*. 2010).

The herring is an extreme capital breeder (Kennedy *et al*. 2010). During the spawning migration, body reserves accumulated during summer feeding are the only source of energy for reproduction, migration, and routine metabolism (Slotte 1999). Potential fecundity is a function of the whole body weight for Icelandic summer-spawning herring (Óskarsson and Taggart 2006). Wood (1958) and references therein have shown conclusively that the fat content of the herring is related to both feeding and time of spawning. Further it was observed that low fat content in females, caused by a scarcity of food, can reduce the number of eggs produced (Hempel 1971). During summer feeding, when the amount of materials to be invested in reproduction has not yet been decided, fish produce high numbers of small vitellogenic oocytes independently of condition. In autumn, when the possible amount of investment is determined, and more material is needed for oocyte growth, the number and quality of oocytes is downregulated depending on nutritional condition (Brooks *et al*. 1997; Kurita *et al*. 2003). Fecundity of both Atlantic herring (Ma *et al*. 1998) and Pacific herring (Hay and Brett 1988) is known to vary due to nutritional condition of the spawning fish, and its annual variation is related to differences in food intake (Hempel 1971; Bowers and Holliday 1961). Differentiating between recruit and repeat spawners is potentially important because the timing of oocyte growth, and seasonal change in intensity of atresia can be different between the two (Slotte and Fiksen 2000; Óskarsson *et al*. 2002). Food availability also affects the onset of maturity by 1 year in Atlantic herring (Cushing and Burd

1956). Skip spawning is related to condition and may follow climate signals (Engelhard and Heino 2006). Kennedy *et al*. (2010) showed how individuals that did not reach a Fulton's condition factor above 0.70 during the feeding season are less likely to begin ovary maturation. Below this threshold, the ovary developed later, had a higher intensity of atresia, or were likely to skip spawn in the coming spawning season. For both herring species there is extensive information about the reproductive biology and the connection between feeding and reproductive potential. This is an excellent example of a capital breeder, but herring typically over commit to yolked eggs and adjust realised fecundity via atresia.

European sardine (*Sardina pilchardus*, Clupeidae)

A marine species of the eastern North Atlantic Ocean, the Mediterranean Sea and the Black Sea, European sardine is an iteroparous breeder: depending on stock or year, females start to spawn at 1-4 years old (Somarakis *et al*. 2006a; Silva *et al*. 2006; 2008), usually from autumn to spring (Somarakis *et al*. 2006a; Ganias *et al*. 2007; Stratoudakis *et al*. 2007). The duration of the spawning period is variable and depends on temperature (preference for spawning at 14-15^{o}C and avoidance at < 12^{o}C and > 16 ^{o}C; Stratoudakis *et al*. 2007). Annual fecundity is indeterminate. Oocytes develop from primary growth to secondary growth stage in an asynchronous manner (Ganias *et al*. 2004), however, a clear hiatus is established in the oocyte size frequency distributions at the late stages of vitellogenesis (tertiary yolk globule stage) (Ganias *et al*. 2004). Mean batch fecundity at peak spawning shows low variation between years and stocks and is highly and closely related to average female weight (Ganias *et al*. 2004; Somarakis *et al*. 2006b). Spawning fraction estimates range from 0.03 to 0.24 (Ganias *et al*. 2003; Somarakis *et al*. 2006b).

Sardine is primarily a capital breeder. There is a strong inverse relationship between ovarian condition and somatic condition in the eastern Mediterranean (Ganias *et al*. 2007) implying that egg production relies on energy reserves accumulated during the summer growing season. Recently, Mustać and Sinovčić (2009) have described a similar inverse relationship between fat content and the sexual cycle of sardine in the Adriatic Sea. Off the Iberian Peninsula, Zwolinski *et al*. (2001) report a 25% decrease in mean gutted weight of sardine from the beginning (October) to the end (March) of the spawning season. Furthermore, Silva *et al*. (2008) have demonstrated that the Iberian stock grows and improves condition outside the main spawning season (when temperature and food availability are higher). Nonetheless, there is field evidence (Ganias 2009) that, besides capitalised energy, current income may fine-tune its reproductive effort. In the eastern Mediterranean, Ganias (2009) reports that reproductive activity, incidence of recent spawning, and relative batch fecundity were higher in areas with increased Chl *a* concentration. Relative fecundity was significantly higher at sites with increased zooplankton. The author therefore concluded that, besides stored energy, sardine also uses current income to support egg production.

European sprat (*Sprattus sprattus*, Clupeidae)

A marine-estuarine species distributed in the eastern North Atlantic Ocean, European sprat is also distributed in the North, Baltic, Mediterranean, and Black Seas (Bailey 1980). It is an iteroparous breeder: adults mature at age 1 or 2 (yr) (Bailey 1980; Polivaiko 1980). Oocytes develop from primary growth to secondary growth stages asynchronously (Haslob *et al*. 2012). Sprat ovulates eggs in batches (Petrova 1960; Polivaiko 1980; George 1987; Alheit 1988). No skip spawning or atretic down regulation of vitellogenic oocytes has been reported. All parameters required to estimate fecundity via an indeterminate method vary both spatially and temporally. The size at maturity is larger in the Baltic Sea (10-11 cm, Kraus and Köster 2004) than in the Black Sea (5.2-11.5 cm; Giragosov 2002). The generally protracted spawning season (5-6 months) is longer in warmer waters, and peak spawning varies with latitude: April-August in northern vs. November-April in southern European waters (Petrova 1960; Grauman 1969; Dulĉić 1998; Giragosov 2002). Individual sprat spawn from 2 to 4.5 months (Alekseev and Alekseeva 2005; Giragosov 2002). Number of batches per year ranges from 4 (Shkitsky 1967) to 13-17 (Alekseev and Alekseeva 2005) in the Baltic sprat and is 34.5 on average in the Black Sea sprat (Giragosov 2002). A spawning interval during the main spawning time was estimated of approximately 4 days for Baltic sprat (Kraus and Köster 2004; Haslob *et al*. 2012), and of 2 days for Black Sea sprat (Giragosov 2002). Batch fecundity varies in relation to fish size and sampling month, region, and year (Polivaiko 1980; Haslob *et al*. 2005; Alekseev and Alekseeva 2005; Haslob *et al*. 2011, 2013). For example, batch fecundity of Baltic sprat ranges from 206 to 4,244 eggs per female. Absolute individual fecundity of Black Sea sprat has been estimated to average 28,193 oocytes (Giragosov 2002).

European sprat is a mixed income-capital breeder. Feeding by Black Sea sprat declines but continues during the spawning period, which provides energy for sprat reproduction. Daily rations of fish at age 1+ and 2+ during the spawning period were 2.6 - 2.5% of body weight; outside the spawning period maximum daily rations were 8.8-7.7%. After spawning, the gonad rest and energy reserves accumulate. During the spawning period, lipid amount in muscles and viscera decreased to 3-5 %, whereas in the non-spawning period lipid values rise to 12-15 % (Shulman *et al*. 1985). Feeding effects on sprat reproduction are inferred from a negative correlation between batch fecundity and stock size (Haslob *et al*. 2005, 2011); however, individual fish condition is not correlated with batch fecundity (Haslob *et al*. 2011) and abiotic factors may have confounding effects (Haslob *et al*. 2005, 2011). Sprat in the Baltic lives at the northern boundary of the geographical distribution of this species (Muus and Nielsen 1999) and years with a higher temperature may result in better growth, earlier maturation and enhanced gonad development leading to a higher egg production. Low water temperatures reduce and delay the onset of the spring zooplankton production in the Baltic (MacKenzie *et al*. 1996) especially availability of warm-adapted prey species (Grauman and Yula 1989; Möllmann *et al*. 2000), which in turn may negatively affect individual fecundity (Haslob *et al*. 2005).

Roach (*Rutilus rutilus*, Cyprinidae)

A freshwater species, the roach has a native distribution throughout Europe and Asia and is introduced widely (Vila-Gispert and Moreno-Amich 2000). It is an iteroparous breeder: at about 3 years old females spawn in spring (Mann 1973; Bastl 1995; Nõges and Järvet 2005). Oocytes develop from primary growth to secondary growth stages in a group-synchronous manner (Rinchard and Kestemont 1996). Oocytes develop from secondary growth to mature stages a synchronous manner (Rinchard and Kestemont 1996). We are not aware of reports regarding skip spawning or atretic down regulation of this advancing clutch of vitellogenic oocytes by this species. Potential annual fecundity varies by age from about 1 to 50 thousand eggs per female (MacKay and Mann 1969; Mann 1973; Townsend *et al*. 1990; Bastl 1995). Females are best characterised as total ovulators that behaviourally spawn in batches; they ripen their eggs in a single wave and fully ripe eggs are released in several dozen spawning events over several days (Rinchard and Kestemont 1996; Wedekind 1996).

Roach is an extreme capital breeder. It spawns in spring, and after a brief period when the gonad rests, growth of secondary oocytes resume in late summer concurrent with a drawdown of visceral fat reserves (Lyagina 1972; Rinchard and Kestemont 1996). MacKay and Mann (1969) document low potential fecundity in roach that fed primarily on detritus; they also cite earlier studies that indicate that both food type (i.e., animal versus plant) and amount could affect roach fecundity. Several studies of roach populations – in reservoirs or rivers – show that roach fecundity varies widely from year to year, and the authors qualitatively attribute this to positive associations with feeding conditions (Lyagina 1972, 1975; Kuznetsov and Khalitov 1978; Vøllestad and L'Abée-Lund 1990; Bastl 1995). Some of these studies specifically note that when potential fecundity was lower, the egg size is larger, suggesting some compensatory effect that improves individual offspring fitness. Cryer *et al*. (1986) demonstrate that large year classes of age-0 roach in Alderfen Broad could overgraze their prey, which reduces absolute fecundity of conspecific adults (see also Perrow *et al*. 1990). Wyatt (1988) examined roach in Slapton Ley, without such a food limitation, and reported growth rates so fast that maturation occurred a year earlier than normally reported. In both systems, population size cycled in a similarly stable manner. Townsend *et al*. (1990) modeled roach dynamics in Alderfen Broad and Slapton Ley to demonstrate how two different reproductive responses to food could create stable 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, which explains why population cycles are not commonly observed for this relatively long-lived fish that typically switches prey types at older ages.

Zebrafish (*Danio rerio*, Cyprinidae)

A freshwater species native to Asia, zebrafish is a common biological model used in laboratory experiments (Ulloa *et al*. 2011). It is a semelparous breeder: females spawn spring-autumn, offspring mature as early as 10-11 weeks, and females do not live more than one year in nature (Eaton and Farley 1974a,b; Spence *et al*. 2007). Primary growth oocytes develop asynchronously into secondary growth oocytes so that annual fecundity is indeterminate (Selman *et al*. 1993; Forbes *et al*. 2010). In the presence of a male, females spawn daily batches of 2-5 dozen eggs; spawning frequency decreases when separated from a male or over long periods of spawning (Eaton and Farley 1974a).

Zebrafish are income breeders. 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), increased numbers of oocytes, but lower egg size and reduced hatching rates (Forbes *et al.* 2010).

Arctic charr (*Salvelinus alpinus*, Salmonidae)

Widely distributed among streams, oligotrophic lakes, and the marine environment, Arctic charr are found throughout the arctic, subarctic, boreal and temperate climate regions of the Holarctic ecozone. It is often the only fish species in alpine lakes, spawning in the summer and autumn (Sandlund *et al.* 1992; Klemetsen *et al.* 2003). Reproduction is iteroparous: age at first maturity ranges from 2 to 6 years in small resident populations, from 4 to 8 years in anadromous populations (Nordeng 1983). More than one year is required for post-spawners to restore their energy reserves to the same level as mature, non-reproductive charr (Dutil 1986), and the time needed increases as fish length increases. Bimodal populations (both large [normal] and small [dwarf] morphs occurring within a cohort) increase in frequency with latitude and are characteristic of large, deep lakes with few fish species (Griffiths 1994). Griffiths (1994) suggests that much of the variation in charr size structure is a consequence of increased seasonality in food supply in more northerly environments, coupled with feeding size thresholds. The latter result in larger members of a cohort being able to maintain growth rates on seasonally abundant prey while smaller individuals, which cannot catch these items, form a second mode of more slowly growing fish. Oocytes develop from primary growth to secondary growth stages in a group-synchronous manner and from secondary growth to mature stages a synchronous manner (Frantzen *et al*. 1997). Fecundity is determinate, and annual fecundity ranges from between 13 and 9200, increasing with body size (Sandlund *et al*. 1992; Dempson & Green 1985). Ovulation occurs in a single wave (Frantzen *et al*. 1997), and female lays the eggs in a nest (Sandlund *et al.* 1992; Seppä *et al*. 2001).

Arctic charr are extreme capital breeders (Nordeng 1983). They display considerable phenotypic plasticity and variability in life-history traits, including in responses to food availability. In females but not in males, the gonadosomatic index was predicted by growth rates in the months leading up to maturation, and among the females that matured, faster growing fish produced more eggs (Adams and Huntingford 1997). Within a single cohort of Arctic charr, fish that grow faster and ultimately become larger during the year prior to maturation were more likely to mature than those that grow less well (Woodhead 1960; Adams and Huntingford 1997). To the contrary, Sandlund *et al*. (1992) suggest that early encounters with sticklebacks in juvenile stage can induce a shift to predation on stickleback in the largest juveniles of planktivorous/ piscivorous morphs, resulting in increased growth rate and delayed maturation, e.g. diet shift from invertebrates to piscivory as juveniles results increased growth rate and delayed maturation in resident lake charr. The latter is in accordance with study by Rikardsen and Elliott (2000), who conclude that under unfavourable feeding and competition conditions the charr grow slower and mature earlier. They therefore have a disadvantage when migrating to the sea because of their small size, and therefore the proportion of resident individuals is higher (Rikardsen and Elliott 2000). But according to Nordeng (1983), an increase in amount of food accelerates the development in the offspring and increases the proportion of resident individuals, which shows that the pattern of segregation to morphs depends upon genetic constitution and access to food (Nordeng 1983). In conclusion, food quantity has a positive effect on gonadosomatic index and fecundity, but there is no clear pattern whether the food amount and type affects the onset of maturation and the proportion of resident individuals in case of Arctic charr.

Atlantic salmon (*Salmo salar*, Salmonidae)

An anadromous species inhabiting temperate and arctic zones of the North Atlantic Ocean, there are also landlocked stocks of Atlantic salmon in large deep lakes (Klemetsen *et al.* 2003) and a non-migratory male type. Atlantic salmon is an iteroparous breeder: most will mature after 1-3 winters at sea, but there is considerable variation in age at maturity within and between populations (Jonsson *et al*. 1991a; Klemetsen *et al.* 2003). Younger fish tend to spawn more often but expend less energy per spawning event than older females (Jonsson *et al*. 1991b; Klemetsen *et al.* 2003). Oocytes develop from primary growth to secondary growth stages in a group-synchronous manner and from secondary growth to mature stages a synchronous manner (Taranger *et al*. 2010). Fecundity estimation is determinate. Potential annual fecundity varies by body size from about 33 eggs to 18 thousand eggs per female (Gibson *et al*. 1996, Randall 1989, Klemetsen *et al.* 2003) and egg numbers are typically correlated with egg size (Klemetsen *et al.* 2003). The eggs are ovulated in a single batch, and can remain in the body cavity for around one week prior to egg deposition (spawning) and fertilisation (Taranger *et al*. 2010). Eggs are laid in a number of separate nests with the average of 24 h between successive spawning events (Fleming 1996).

Atlantic salmon is an extreme capital breeder. Maturing sea-run salmon feed heavily and store body reserves in the spring prior to spawning, which means that cues associated with the accumulation of surplus energy are decoupled from cues associated with spawning (Rowe and Thorpe 1990; Kadri *et al.* 1996; Simpson *et al.* 1996). Also, in laboratory or in caged conditions, individual life-history decisions to smolt or mature is made in the previous year, and is influenced by growth rate, metabolic rate, lipid stores and social status of the fish (Kadri *et al.* 1996; Simpson *et al.* 1996). Kadri *et al.* (1996) additionally demonstrated that differences in feeding motivation lead to differences in growth, lipid deposition and body condition between immature and maturing adult Atlantic salmon. This is regarded as an example of an endogenous modulation of appetite which ensures that fish will only reproduce if they are in adequate condition (Kadri *et al.* 1996). Maturing females are already larger and have higher fat contents than non-maturing fish after the grilse stage (first sea winter) (Schaffer and Elson 1975). It is concluded that fish that have been growing well are more likely to subsequently adopt the development pathway of early maturation (Simpson *et al.* 1996) and if spring growth is inadequate, maturation is switched off physiologically (Rowe and Thorpe 1990). Another aspect found is that the faster the parr grow in fresh water before smolting, the smaller their relative egg size becomes when they attain maturity. This phenotypic response has been explained as an adaptation to the potential growth opportunities in their nursery river. This assumes that feeding opportunities the parents experienced as juveniles in rivers is a good predictor of what their offspring experience (Jonsson *et al.* 1996; Klemetsen *et al.* 2003).

Brown trout (*Salmo trutta*, Salmonidae)

Inhabiting both fresh and salt waters, brown trout spawns in small streams as well as large rivers from the Atlas Mountains in North Africa to the Barents Sea, and from the western limits of the European coastline to the Ural Mountains and Caspian Sea. It has also been introduced widely outside Europe, spawning in autumn at northern latitudes and in winter further south (Klemetsen *et al.* 2003; Jonsson and Jonsson 2006). Brown trout are iteroparous: mean age at maturity ranges from 1 to 5 years in resident populations and from 2 to 8 years in anadromous populations (Jonsson and Jonsson 2006). Younger females spawn every year, older females spawn every other year (Jonsson *et al.* 1991c). Vitellogenic eggs develop group synchronously and mature eggs ovulate in a single wave (Billard 1987). Females spawn only a portion of eggs at the time, in nests, and may be reproductively active over a few days (Klemetsen *et al.* 2003). Fecundity estimation is determinate, and potential annual fecundity ranges from about 300 eggs to 1500 eggs per female, increasing with body size (Klemetsen *et al.* 2003)

Anadromous brown trout (sea trout) exhibit an alternative life-history strategy compared to resident trout, where the juveniles migrate to the estuary or coastal areas for feeding and return to freshwater for spawning or wintering. The profit of migration is increased food consumption with higher growth rate, energy density and reproductive potential than those of resident fish. Increased reproductive potential results from larger body size, higher gamete production and improved competitive ability during spawning. The cost to migration includes high mortality at sea and the energy need to move between the spawning and nursery grounds in fresh water and the sea (Jonsson and Jonsson 1993; Jonsson and Jonsson 2006). Jonsson and Jonsson (1993) therefore suggest that anadromous individuals adopt migration as a consequence of energetic limitation in fresh water (Jonsson and Jonsson 1993). In experiments, Wysujack *et al*. (2009) reported that low food availability increased the numbers of migratory fish.

Anadromous forms are extreme capital breeders (Ruzzante *et al*. 2004). Bagenal (1969) concluded from the tank experiments with brown trout that more of the better fed fish were mature, they grew faster and they contained significantly more and smaller (by dry weight) eggs, even after adjusting for fish size. Also there were indications of earlier spawning time (Bagenal 1969). However, Jonsson and Jonsson (1997) found that heavy feeding as sub-adults gave large eggs even in small females, evening out the variation due to fish size (Jonsson and Jonsson 1997). According to stomach content study by Jonsson *et al*. (1999), the age and size at which brown trout became piscivorous decreased with increasing individual growth rate of the fish. Age at sexual maturity increased with the age at which the fish became piscivorous. The growth rate for a trout feeding on invertebrates was slower than that of a fish-feeder. It is assumed that fish may have increased their net reproductive rate by postponing maturity after switching to fish-feeding (Jonsson *et al.* 1999). Comparison of trout from infertile and fertile streams indicated that fish originating from infertile streams were older at first sexual maturity and produced fewer eggs because of smaller average size than trout from fertile streams (McFadden *et al.* 1965). Fish of the same size produced a smaller total weight of eggs in infertile waters than in fertile waters. In low productivity systems, few eggs are produced per adult but such low reproductive rates keep these brown trout populations in equilibrium with the low basic productivity of the environment (McFadden *et al.* 1965).

Atlantic cod (*Gadus morhua,* Gadidae)

A marine boreal species widely distributed in the eastern and western parts of North Atlantic as well as around Greenland, Iceland, and Faroe Islands, Atlantic cod is an iteroparous breeder. In general, cod spawn in coastal areas as well as inlets and fjords in spring (ICES 1990, 1991). Considerable variation in age and size at maturity has been observed among stocks inhabiting different geographical areas (Lambert *et al*. 2003 and references therein). Mean age and size at 50% maturity for cod have been observed to vary among stocks by as much as 1.5 to 9.5 years of age and 27 to 72 cm in length. Baltic cod demonstrates a more prolonged period of spawning (March-October) possibly connected with match or mismatch of environmental conditions in the spatially-limited spawning grounds of the Baltic Sea, where there are strong variations in salinity and oxygen concentrations that frequently reach the species' tolerance limits. Fall spawning is also known in populations along western parts of North Atlantic (Chambers and Waiwood 1996).

Oocytes develop from primary growth to secondary growth stages as well as from secondary growth to mature oocytes in a group-synchronous manner (Shirokova 1977; Burton 1998; Kjesbu *et al.* 1998). Atretic down regulation appears to play an important role in final annual fecundity generation (Skjaeraasen *et al.* 2006; Thorsen *et al.* 2006). Therefore a determinant fecundity method to estimate potential annual fecundity is more accurate shortly prior to spawning, when difference between potential and realised fecundity is minimal. Annual potential fecundity, which ranges from 0.1 to 19 million ova per female (Serebryakov *et al*. 1984; Kjesbu 1988), is dependent on fish size, age, condition, feeding regime (or a ration in pre-spawning year) and prey availability (Kraus *et al.* 1997, 2000; Lambert and Dutil 2000; Marshall *et al*. 2003). In the field, Atlantic cod spawn 3-8 batches (Sorokin 1957), and as many as 19-20 batches in laboratory conditions (Kjesbu 1989). In lab, batch fecundity changes with a dome-shape pattern: rises from the start of spawning (60-70 thousand eggs) to the maximum (300-310 thousand eggs) in the 10-13th batch and then decreases again; total number of batches and inter-batch intervals are associated with the sizes and levels of female condition (Kjesbu 1989).

Atlantic cod is a capital breeder. After spawning in spring, there is a period of the gonads resting. New portions (clutches) of vitellogenic oocytes for the following year begin to develop in fall. Some mature fish in low condition might skip spawning. Experimental work on captive fish has demonstrated that skipped spawning is highly influenced by individual energy reserves (Skjæraasen *et al*. 2009, 2012). In the field, skip spawning appears to range from almost zero noted in Baltic cod (Kraus *et al*. 2002) to 30-40 % reported for various cod populations (Walsh *et al*. 1986; Burton *et al*. 1997; Rideout *et al*. 2000; Skjæraasen *et al*. 2012). Onset of maturation in a population varies also by years and appears to be affected by the feeding conditions experienced by fish in the pre-spawning season (Ajiad *et al.* 1999; Yaragina *et al.* 2003); portions of mature fish demonstrate a density dependent effect (Cardinale and Modin 1999; O'Brien 1999). Sherwood *et al*. (2007) note from field studies that a food type can affect reproductive potential; they report that a more pelagic diet (particularly capelin rather than shrimp) produced higher somatic condition, higher liver index (lipid stores) and greater spawning potential (decreased incidence of atresia). Quality of eggs larvae can depend on fish attributes like size, condition and age of females (Marteinsdottir and Steinarsson 1998).

Haddock (*Melanogrammus aeglefinus*, Gadidae)

Haddock is a marine demersal fish of the eastern and western North Atlantic Ocean. Reproduction is iteroparous, in the winter-spring, with females maturing at 2-3 years of age (Clark 1959; Wigley 1999). Oocyte development is group synchronous, and there is a well defined gap in size between previtellogenic and vitellogenic oocytes (Hickling and Rutenberg 1936; Robb 1982; Clay 1989). Ovulation and spawning of pelagic eggs occurs in multiple batches (Hislop *et al*. 1978; Trippel and Neil 2004), however additional recruitment of vitellogenic oocytes during the spawning season does not occur, permitting annual fecundity estimation via determinate methods (Alonso-Fernandez *et al*. 2009). Fecundity estimates increase with size and age, and across different haddock stocks range from < 100K to > 1500K (summarised in Blanchard *et al*. 2003; Skjæraasen *et al*. 2013).

Haddock is a capital breeder. Variability in fecundity for different stocks and years has been related to various measures of condition including relative condition, Fulton’s condition factor, and hepatosomatic index (Blanchard *et al*. 2003; Alonso-Fernandez *et al*. 2009). Laboratory studies have demonstrated increased fecundity and dry weight of eggs with increased ration (Hislop *et al*. 1978), but the fecundity of high ration haddock was not much higher than wild fish of the same weight. They concluded, therefore, that the upper limit of fecundity had been set prior to ration manipulations (which began in November), indicative of a capital spawning pattern. Although maximum fecundities may be established during early oocyte development, it appears that haddock are able to ‘tune’ (downregulate) fecundity in response to food quantity during the months leading up to spawning (evidenced by the ration effect they observed). The recruitment of haddock on the Scotian Shelf was found to be positively related to growth (length at age-4) and condition (weight at 50 cm), and they concluded true reproductive potential of the stock was poorly described by spawner biomass (Marshall and Frank 1999). More recently, Friedland *et al*. (2008, 2009) demonstrated strong correlations between recruitment of Georges Bank haddock and magnitude of the fall phytoplankton bloom the prior year, which they suggested enhanced the quantity of reproductive output. Thus, haddock appear able to exploit pulses of environmental productivity (more or better quality food) to increase their reproductive output. Condition can, however, have a variable effect on fecundity across years (Blanchard *et al*. 2003), possibly due to the timing of energy inputs available to produce eggs in relation to oocyte development/ovarian organization. This timing can be segregated into two major periods: 1) initially, fairly soon in the post-spawning period, the maximum number of eggs is set when the vitellogenic cohort is determined by group synchronous development; 2) later, closer to but still prior to spawning, downregulation may occur to right-size the egg numbers relative to the cumulative energy actually acquired and needed for oocyte maturation and ovulation. The relative importance of these two modes of fecundity regulation likely depends on properties of both the ecosystem (timing and type of energy pulses) and stock (biomass or condition).

Pouting (*Trisopterus luscus*, Gadidae)

A marine species found in the eastern North Atlantic Ocean, pouting is distributed from the Skagerrak and the British Isles to southern Morocco and into the western Mediterranean (Wheeler 1978; Whitehead *et al*. 1986). Pouting is an iteroparous breeder: females mature as age 1-2 for this short-lived species (5-9 yr) (Labarta *et al*. 1982; Puente 1988; Merayo 1996). Primary growth oocytes develop into secondary growth oocytes asynchronously, and mature oocytes develop group-synchronously, for an average of 20 batches during the spawning season (Alonso-Fernández *et al*. 2008). Despite the lack of a hiatus between primary and secondary oocytes, indicating asynchronous vitellogenesis, there appears to be no *de novo* vitellogenesis once a female becomes ripe, so determinate methods have been used to estimate potential annual fecundity for this species (Alonso-Fernández *et al*. 2008). Batch fecundity ranges from 1,900 to 80,000 eggs and potential annual fecundity ranges from 0.025 to 1.6 million follicles (Alonso-Fernández 2011). Potential annual fecundity, batch fecundity, spawning period length, and also egg size increase with fish size (Merayo 1996; Alonso-Fernández *et al*. 2008; Alonso-Fernández *et al*. 2011; Alonso-Fernández 2011; Alonso-Fernández and Saborido Rey 2011).

Pouting are mixed capital-income breeders (Alonso-Fernández and Saborido Rey, 2012). They accumulate energy reserves as lipids stored in the liver and use this for oocyte recruitment; however, energetic provision through concurrent feeding during a protracted (4–5 months) spawning season may also contribute to egg production. Spawning rates in the field and laboratory vary 3-4 fold (every 2-7 days), so it is possible that income breeding processes could affect batch sizes and spawning frequencies (Alonso-Fernández *et al*. 2011). No direct information regarding food effect is available for pouting; however, significant effects of energy reserves on reproductive potential have been detected. Potential annual fecundity and egg dry mass are positively related to fish size and energy reserves (Alonso-Fernández 2011). Also timing of gonad development seems to be affected by level of energy reserves, i.e., gonad development starts earlier in those females that acquire adequate levels of stored energy sooner than those that do not achieve such reserves (Alonso-Fernández and Saborido Rey 2011).

Inland silverside (*Menidia beryllina*, Atherinopsidae)

An estuarine and freshwater species of eastern North America, inland silverside has been introduced throughout the continent (Hubbs 1982, Coorey *et al*. 1985, Stoeckel and Heidinger 1988) and is used widely in laboratory experiments (Hemmer *et al*. 1992). Inland silverside is a short-lived (2 years), semelparous breeder. It typically matures in its second season, spawning during a short summer season in the north or a longer (spring-summer) season in the south (Middaugh and Hemmer 1992). In the south, temperatures may become too hot by late summer for continued spawning (Hubbs 1982), but when growth conditions are favorable, larger young-of-year females mature in their first year, which produces a minor, autumn-spawning pulse (Hubbs 1982; Middaugh and Hemmer 1992). Primary growth oocytes develop asynchronously into secondary growth oocytes so that annual fecundity is indeterminate (Coorey *et al*. 1985). Females produce batches of 200-2000 eggs; size-specific fecundity is much higher in freshwater lakes than estuaries (Hubbs 1982, Middaugh and Hemmer 1992). Inland silversides spawn cyclically, on or near the full and new moons (Hubbs 1982, Sherrill and Middaugh 1993).

Inland silversides are income breeders. Growth occurs principally in two discrete stanzas. First, rapid somatic growth occurs primarily in the first year, when approximately 27% of its total growth is completed prior to the onset of winter (Huber and Bengtson 1999b). In laboratory experiments, increasing temperatures without increasing photoperiod increase liver and visceral fat weight, which appears to be a pre-overwintering response rather than storage of surplus energy for reproduction (Huber and Bengtson 1999a). Silversides emerge emaciated from the winter and once temperatures and photoperiod increase sufficiently (~May) rapid growth of soma, liver, and gonad occurs simultaneously (Huber and Bengtson 1999a, b). In a short (< 2 month) laboratory experiment, more food provided to overwintered females induces larger fish with relatively larger gonads (Huber 1995). Hubbs (1982) remarked that ~14% daily ration produced ~7% egg production, and Huber and Bengtson (1999b) concluded that metabolic burnout of spawning adults cumulated in a disappearance of mature fish by the end of the second year. In some systems, where inland silversides are the dominant planktivore, this may be an important mechanism to reduce intraspecific competition (Chizinski *et al*. 2007). Efforts to extend these observations and experiments by use of bioenergetic models failed to predict growth of actively spawning adults, leading Chizinski *et al*. (2008) to conclude that such models require further development for short-lived species that experience such a brief, intense spawning period.

Medaka (*Oryzias latipes*, Adrianichthyidae)

A freshwater species of the western Pacific rim, medaka is a semelparous breeder: females spawn spring-autumn, offspring mature as early as 10-12 weeks, and females do not live more than one year in nature (Yamamoto and Yoshioka 1964; Howard *et al*. 1998; Dhillon and Fox 2004). Primary growth oocytes develop asynchronously into secondary growth oocytes so that annual fecundity is indeterminate (Wallace and Selman 1981a). Females can spawn daily batches of eggs over several months to typically produce 1000-2000 eggs in a lifetime (Yamamoto and Yoshioka 1964; Howard *et al*. 1998). Medaka is a small, short-lived, eurythermal fish, widely used in laboratory studies (Shima and Mitani 2004).

Medaka are primarily income breeders. In laboratory experiments, fish fed more food during the spawning period produced more eggs in general (Hirshfield 1980), but Hirshfield (1980) also showed that fatter fish laid more eggs early in the spawning period, especially at high temperatures that are associated with above average batch size. There was a cost to high reproductive effort, since the proportion of a female's energy budget allocated to reproduction was greater at higher temperature, and at some point more food no longer increased reproductive effort and was even associated with higher mortality. Dhillon and Fox (2004) showed that higher food consumption prior to maturation caused medaka to grow faster and mature earlier, at least up to the highest thermal limit (~33^{o}C); however, at this upper thermal limit length and age at maturity increased, thereby demonstrating the independent effect of temperature at this extreme limit of bioenergetics.

Mummichog (*Fundulus heteroclitus*, Fundulidae)

An estuarine species of the east coast of North America, from the Gulf of Maine to Florida, mummichog has subpopulations north and south of New York and New Jersey (Able and Felley 1986). It is an iteroparous breeder: maturation occurs in the first or second year for this short-lived (4 years) fish (Fritz and Garside 1975; Able 1990). Females spawn from spring to autumn (Wallace and Selman 1981b; Able 1990) and fecundity estimation is indeterminate. Primary growth oocytes develop asynchronously into secondary growth oocytes (Hsiao *et al*. 1994), and females ovulate batches either continuously in the north or with lunar periodicity in the south (Fig. 3m-r of main article; Taylor *et al*. 1979; Wallace and Selman 1981b; Hsiao *et al*. 1996). Egg size varies for a variety of reasons: it increases with female size; it is both larger and more variable in the southern population; it decreases as the season progresses (Marteinsdottir and Able 1988; Hsiao *et al*. 1994).

Mummichog is an income breeder, as evident from laboratory experiments. Fish starved for as few as three days stop maturing new oocytes, but renewed feeding for three days restores oocyte maturation (Wallace and Selman 1978). In a related experiment, oocyte maturation resumes in starved fish by injecting them with human chorionic gonadotropin, leading Wallace and Selman (1980, p. 352) to conclude: “Available food supply thus may be the ultimate control for egg production in the [northern] population”. In the south, where mummichog has a more protracted spawning season, mature females kept and fed in the laboratory still stopped spawning after 5-8 cycles, demonstrating that other factors – particularly photoperiod influence on gonadotropin regulation – control length of the spawning season (Taylor 1986; Hsiao *et al.* 1994). Conover (1990) and Schultz *et al*. (1996) used a counter-gradient hypothesis to explain that northern fish spawn early and frequently compared to southern fish because the growing season is shorter in the north and size-selective predation is a selective mechanism during the overwintering period. Taylor (1986) experimentally increased feeding in spawning females, reporting that somatic growth increased but egg number did not, suggesting at an upper limit of batch size exists after which energy is diverted to maternal soma. Field work relating food amount to fecundity was pioneering but equivocal. In an early comparative study, Fritz and Garside (1975) compared fecundity between two lakes to suggest that higher fecundity was found in the lake that appeared to have lower productivity; however, this study inappropriately used a determinate fecundity method to measure annual fecundity. In addition, they did not provide direct estimates of productivity at the appropriate trophic level for mature mummichog. In a review of field data, Wallace and Selman (1981b) asked if latitudinal differences in spawning frequency were related to food, but they concluded that this approach was confounded by the subpopulation structure across latitudes. Although egg size variations are well documented within and among mummichog populations, and larger eggs are associated with higher egg and larval survival (Marteinsdottir and Able 1992), we are not aware of any work investigating food effects on mummichog egg size or other proxies for egg quality. Dramatic variations in mummichog spawning ecology occurs over very small spatial and temporal scales (meters, days; Able and Hagan 2003; Hunter *et al*. 2009), and common garden experiments are possible, so continued work with this species as an experimental model is warranted.

Threespine stickleback (*Gasterosteus aculeatus,* Gasterosteidae)

Residing in both freshwater and coastal systems of the northern hemisphere, the threespine stickleback is an iteroparous breeder: Females start to spawn at 2-3 years old and most (but not all) fish die after their first breeding season (Reimchen 1992). Several clutches of eggs are produced over a breeding season that lasts from spring to early summer (Wootton 1973; Wallace and Selman 1979; Ali and Wootton 1999a). Annual fecundity is indeterminate. Oocytes develop from primary growth to secondary growth stage in an asynchronous manner (Wallace and Selman 1979). The minimum observed inter-spawning interval is 3 days (Fletcher and Wootton 1995).

Threespine stickleback is largely an income breeder. There is strong experimental evidence of the effect of food amount on egg production (Wootton 1973; 1977; Ali and Wootton 1999a, b; Fletcher and Wootton 1995; Wootton and Fletcher 2009). Specifically, low food intake during the breeding season increases the inter-spawning interval, which reduces annual fecundity. Spawning frequency is very sensitive to food intake but batch fecundity is less so (although it is significantly lower at low rations) and egg characteristics (size, quality) are relatively conservative. Mean reproductive investment per inter-spawning interval is higher at the highest rations but it declines over successive spawnings irrespectively of ration. The study of Wooton and Fletcher (2009) is one of the most comprehensive studies of the effect of food amount on reproductive parameters of a batch spawner along the course of the breeding season.

European seabass (*Dicentrarchus labrax*, Moronidae)

A marine species of the eastern North Atlantic Ocean, European seabass ranges from the British Isles to North Africa (Vinagre *et al*. 2009). It is an iteroparous breeder: at about three years old females start spawning offshore during winter-spring (Felip *et al*. 2001; Pawson *et al*. 2007; Vinagre *et al*. 2009). Oocytes appear to develop from primary growth to secondary growth stage and from secondary growth to mature oocytes in a group-synchronous manner, but the size hiatus that characterises group-synchrony is not unambiguous (Mayer *et al*. 1990). Annual potential fecundity, measured with a determinate method, is dependent on fish size, and ranges from 0.5 to 2.0 million (Wassef and Emary 1989; Mayer *et al*. 1990). European seabass spawn 3-4 batches during the spawning season; batch fecundity declines rapidly with each successive batch (Mylonas *et al*. 2003).

European seabass appear to be a mixed capital-income spawner, although experimental studies, together with the ambiguity of oocyte synchrony, make this conclusion preliminary. In the lab, reduced food provided to females spawning for their second time produced no obvious effects on immediate reproductive potential (Cerdá *et al.* 1994a). Compared to females fed full rations, females fed half rations spawned about the same number of eggs, and although these eggs were smaller, the egg quality was about the same (i.e., as measured by percent buoyant and larval survival to day 40). Nonetheless, females fed half rations grew less, in both length and weight, and had significantly lower condition than females fed full rations so that reproduction is prioritised over somatic growth. Therefore, a reduced food amount does not immediately reduce reproductive potential but presumably lowers future reproductive potential (see above, size effect on fecundity). European seabass is cultured for food, particularly around the Mediterranean Sea, so the lack of knowledge of the effect of food quality on reproductive potential is a bottleneck for hatchery production (Carrillo *et al*. 1995; Bell *et al*. 1997; Bruce *et al*. 1999). Artificial diets have produced poor egg quality, in terms of buoyancy and hatch rates, compared to natural diets (Navas *et al*. 2001). Fish fed artificial diets with about 32-33% protein and carbohydrate showed several adverse effects compared to fish fed diets with higher protein and lower carbohydrate compositions (Cerdá *et al.* 1994b). The former group produced fewer eggs, these eggs were less buoyant, fewer hatched, and there were more deformities among those eggs that did hatch. A better understanding of how diet composition affects reproductive potential relative to the reproductive strategy of European seabass has immediate practical importance.

Largemouth bass (*Micropterus salmoides*, Centrarchidae)

A freshwater species native to North America, largemouth bass originate in the St. Lawrence (Great Lakes), Mississippi River basin and Atlantic drainages. This popular sport fish has been widely introduced elsewhere including the tropics and high elevation lakes (Dadzie and Aloo 1990; Martin *et al*. 1999; Lorenzoni *et al*. 2002; Curtis and Wehrly 2006; Neal and Noble 2006). Within the native range, northern largemouth bass (*M. salmoides salmoides)* is considered genetically distinct from Florida largemouth bass (*Micropterus salmoides floridanus)*, naturally occurring in south Florida, but these types interbreed to yield an intergrade subspecies (Isely *et al.* 1987; Kassler *et al*. 2002; Rogers *et al*. 2006). Males exhibit parental care by building and defending nests, and post-spawning brood care can last up to a month. Largemouth bass are iteroparous breeders: maturity occurs by age 3-5 years and longevity is 24 years in the northern extent of the range (Beitinger and Fitzpatrick 1979; Curtis and Wehrly 2006). However, introduced populations in the tropics show very different traits, where maturity occurs as early as four months and longevity decreases to as few as three years (Beitinger and Fitzpatrick 1979; Neal and Noble 2006). Similarly, spawning duration shows a clear latitudinal gradient: less than a month in Canada, about two months in northern temperate areas of the U.S., 3-4 months in southern temperate areas, more than four months in S. Florida and S. Texas, six months in Puerto Rico and eight months in Equatorial Kenya (Lamkin 1900; Stranahan 1908; Clugston 1966; Jackson 1979; Maraldo and MacCrimmon 1981; Isely *et al*. 1987; Dadzie and Aloo 1990; Gran 1995; Gross *et al*. 2002; Rogers *et al*. 2006; Waters and Noble 2004; Curtis and Wehrly 2006). Rogers *et al*. (2006) demonstrated both a temperature and genetic influence on spawning periodicity of largemouth bass for Florida and intergrade subspecies just within the latitudinal range of Florida (31–25^{o}N). Growth rates increase from the northern range to the subtropics, but at more tropical locations it appears that excess allocation to reproduction results in a trade-off with annual growth (Neal and Noble 2006).

Based upon field and controlled rearing studies, individual female largemouth bass have been noted to ovulate multiple batches (Lamkin 1900; Stranahan 1908; Kelley 1962; Jackson 1979; Gran 1995). Their oocytes appear to develop asynchronously from the primary to the secondary growth phase and group synchronously through maturation (comparing figures of oocyte size progression in Kelley 1962; Timmons *et al*. 1980; and Gran 1995). While investigators recognise the potential for extended seasonality and multiple spawning in Florida and intergrade largemouth bass (Rogers 2006; Neal and Noble 2006) there may be some uncertainty over the seasonality and consequent reproductive potential of northern largemouth bass. Recent interpretations of the reproductive timing describe northern largemouth bass having evolved fairly brief spawning periods so that offspring match the seasonal peak in prey availability (DeVries *et al*. 2009). These interpretations may in part be based upon earlier investigations of reproductive histology that suggest northern largemouth bass have only one spawning episode (James 1946; Goubier *et al*. 1997). Jackson (1979), noted contrary results to James (1946) and the latitudinal trend (above) certainly suggests that extended seasonality and multiple spawnings occur throughout much of the natural and introduced range. Further, Carlson (1973) and Jackson (1979) have induced protracted spawning in northern largemouth bass by manipulating photoperiod and temperature which suggests a good deal of plasticity may exist. Adult *Micropterus spp*. (largemouth and smallmouth bass) have been noted to be inhibited from spawning (skipped spawning) due to several factors including temperature, photoperiod, eutrophication, dietary steroids, crowding and sensitivity to rearing conditions (Osburn 1923; Chew 1972, 1974; Smith 1976; Jackson 1979; Cantin 1987; Raffetto *et al*. 1990; Rosenblum *et al*. 1995; Martin *et al*. 1998, 1999). The descriptions of inhibited spawning appears similar in that secondary oocytes begin maturation but become arrested, followed by prolonged resorption of degenerating follicles. Workers often referred to this condition as “over-ripened” however in a review of omitted annual reproduction, Rideout *et al*. (2005) referred to this as the “reabsorbing” type of omission.

All fecundity references to date applied a determinate methodology (Kelley 1962; Timmons *et al*. 1980; Dadzie and Aloo 1990; Brown and Maceina 2002; Lorenzoni *et al*. 2002; Rodriguez-Sanchez *et al*. 2009). However, there is strong evidence that largemouth bass exhibits an indeterminate fecundity type: 1) There is no hiatus between primary and secondary growth oocytes suggesting asynchronous development 2) they are a batch spawner with extended (two to several months) spawning season that increases from temperate to tropical reaches of their range, and 3) they exhibit a tropical growth pattern that can be energetically accounted for in females by substantial energy allocation to reproduction in the form of an indeterminate multiple spawning strategy (Neal and Noble 2006).

Largemouth bass show a high degree of capital energy allocation based upon studies conducted in temperate areas. Condition indices reflect annual feeding and energy allocation patterns (Heidinger and Crawford 1977; Adams *et al*. 1982; Brown and Murphy 2004). Somatic growth is maximised and females build gonads and store visceral fat in the fall. This coincides with a piscivore foraging advantage in this season (Adams *et al*. 1982; Brown and Murphy 2004). There is evidence for winter to early spring translocation of more energy from muscle, mesenteric and visceral stores, and liver to complete gonad development by early spring; the liver appears not to be the long-term storage organ seen in other fish families (Adams *et al*. 1982; Brown and Murphy 2004). Consumption (by females) increases in spring and remains high during spawning and post-spawning periods. So some degree of income allocation to spring reproduction may occur in temperate areas (Adams *et al*. 1982). An inference from Neal and Noble (2006) is that there is much higher energy allocation to reproduction in the tropics, where there is less seasonal pattern to consumption: thus energy allocation should follow an increased income pathway. The latitudinal shift from capital to income allocation was independently predicted using a dynamic state model incorporating largemouth bass bioenergetic functions (Garvey and Marschall 2003). But the model limited reproductive allocation to no more than 10% of wet mass (deterministic assumption) and the prediction of income investment at lower latitudes was only distinguishable when high rations were provided. The few investigations of food and reproduction have been directed at broodstock management. Pelleted diets with increased lipid, protein and balanced archidonic acid content resulted in increased growth, mesenteric fat and fecundity in comparison to either pellets or forage fish with lesser amounts of these ingredients (Snow 1970; Rosenblum *et al*. 1994; and Rosenblum *et al*. 1995). There is some evidence that energetic allocations are likely a function of size or age. Goodgame and Miranda (1993) cite an M.S. thesis (Reagan 1969) that made proximate analysis measures and documents that fat percentage increases exponentially with length. Goodgame and Miranda (1993) suggest that length-related differences in energy reserves may allow larger largemouth bass to spawn earlier, which they documented, but gave no inference about the potential to spawn more times over a longer duration. Largemouth bass is probably one of the best known species regarding energetics of growth, feeding and metabolism but surprisingly little is known regarding the effects of food on female reproductive allocation. A clear gradient of life history response to latitude is evident with potentially much higher reproductive allocation moving towards the tropics. Renewed investigation of the reproductive biology would likely improve our understanding of largemouth bass life history tradeoffs and recruitment.

Pumpkinseed (*Lepomis gibbosus*, Centrarchidae)

A freshwater species native to eastern temperate habitats of North America, New Brunswick to South Carolina, pumpkinseed has been broadly introduced throughout North America, South America and Europe and is considered invasive in some areas (Copp *et al*. 2004). It is an iteroparous breeder, wherein males build nests and exhibit parental care. Pumpkinseed live to about 8 years in the wild and mature between ages 2 to 5, but these traits vary across the range and in introduced populations (Deacon and Keast 1987). There is a spring-summer spawning season in temperate areas but spawning occurs year-round in the tropics (Magalhães and Ratton 2005). Females are best characterised as multiple ovulators, spawning in batches (Fox and Crivelli 2001; Zieba *et al*. 2010). While pumpkinseed fecundity has most often been estimated using determinate methodology (Deacon and Keast 1987; Crivelli and Mestre 1988; Fox and Keast 1991; Gutiérrez-Estrada *et al*. 2000; Vila-Gispert and Moreno-Amich 2000) there is strong evidence that the fecundity type is indeterminate due to batch spawning, extended spawning seasons across a latitudinal gradient and lack of size hiatus between primary and secondary growth oocytes supporting *de novo* vitellogenesis. An indeterminate approach was undertaken by Fox and Crivelli (1998) who showed that populations in Canada and France allocated between 11.5 and 27% of prespawning biomass to reproduction. Fox and Crivelli (1998) considered these levels of allocation to be relatively low compared to other multiple spawning species.

Pumpkinseed females exhibit an income pattern of energy allocation to reproduction with evidence that energy for oocyte maturation is gained just prior to or during the reproductive period (Justus and Fox 1994). Overall body condition shows little seasonal fluctuation, however, the liver and gonad both increase in mass coincident with the onset of spawning (Crivelli and Mestre 1988). Field studies support the linkage between food and reproduction with observations of stunted growth, poor condition, reduced fecundity, and reduced egg size attributed to intra-specific competition and low food availability (Deacon and Keast 1987; Danylchuk and Fox

1994; Copp *et al*. 2004). A high proportion of small mature females may not reproduce, or may delay reproduction in a given season if food resources are inadequate (Danylchuk and Fox 1994). In general, a high degree of plasticity of growth, maturity and fecundity is noted although effects are not isolated in field studies. This plasticity together with increased reproductive allocation moving towards the tropics and high r-selected life history endpoints may explain success in introductions and invasions.

White crappie (*Pomoxis annularis*, Centrarchidae)

A freshwater species native to temperate areas of eastern North America (Canada to the northern coast of the Gulf of Mexico) and introduced to western North America, white crappie is an iteroparous breeder: it matures from age-1 to age-3 and lives about 10 years (Hansen 1951; Carlander 1977; Bunnell 2002). Similar to other centrarchids, males build and defend nests. There is a latitudinal gradient in spawning duration; about 1 month in the northern range and 2-3 months in Florida (Pine and Allen 2001). Spawning also begins about a month earlier in the southern range (late March-May in Texas) compared to the northern range (May-June in Ontario) (Schloemer 1947; Thomas and Kilambi 1981). Previous studies assume a determinate fecundity type (Mathur *et al*. 1979; Thomas and Kilambi 1981; Baker and Heidinger 1994; Dubuc and DeVries 2002) and one to a few ovulations per mature individual per season have been noted (Siefert 1968; Thomas and Kilambi 1981) which supports this assumption. Vitellogenesis appears to be group synchronous but no clear size hiatus is evident between primary and secondary growth oocytes (Thomas and Kilambi 1981; Pope *et al*. 1996) indicating some uncertainty.

White crappie gain and store energy for reproduction months before the spawning period consistent with being a capital breeder. Following the summer growth period, condition increases and gonads develop in the fall well ahead of spring spawning (Neumann and Murphy 1992; Gabelhouse 1991; Bunnell and Marshall 2003). Field studies, rearing experiments and model observations link the effect of food on reproductive output. Based upon field studies accounting for lake productivity, high food availability is associated with high fall condition (total lipids, relative weight, and liver weight), which in turn is correlated with ovarian development in the pre-spawning period (Neumanm and Murphy 1992). Further, condition level and ovarian energy density is a function of size or age (Neumann and Murphy 1992; Gablehouse 1991; Dubuc and DeVries 2002; Bunnell *et al*. 2005). Based on an outdoor pool experiment established four months prior to spawning, Bunnell *et al*. (2007) found that high-fed females increased egg size and built both liver mass and gonads directly. In contrast, intermediate- and low-fed females sacrificed liver stores to develop gonads. They also found that 8% of low- and intermediate-fed females did not develop gonads which is similar to the average reported (9%) from 7 reservoirs. As a criterion to match gonad investment patterns observed in field studies, an individual-based model predicted that fall allocation to ovaries occurred in response to the risk of poor spring feeding conditions rather than recent summer feeding success (Bunnell *et al*. 2003). While field studies reveal that productivity of closed freshwater systems affects adult condition and reproductive development, the results are equivocal regarding reproduction and recruitment success. Spawning stock biomass is a significant predictor of recruitment in one study (Bunnell *et al*. 2006) but not in others (Maceina 2003). Crappies are notorious for variable recruitment in lakes and reservoirs—presumably reflecting differing productivity levels and hydrodynamic conditions acting on both adult and larval stages. As a consequence, explanatory mechanisms are often based upon inference due to uncontrolled effects (Maceina 2003; Bunnell *et al*. 2006).White crappie appear to be rather fixed in their reproductive timing and capital allocation pattern over a broad latitudinal gradient in contrast to other centrarchids.

Eurasian and yellow perch (*Perca fluviatilis*, *P. flavescens*, Percidae)

Two freshwater species of temperate and subarctic regions of Eurasia and North America, the Eurasian and yellow perch became separated about 8 million years ago (Craig 2000); they are so similar in morphology, physiology, behavior and ecology that they can be considered biologically equivalent (Thorpe 1977). Both species are iteroparous and spawn once a year in spring (Thorpe 1977; Treasurer 1981; Craig 2000; Heibo *et al*. 2005). There is considerable variation in the rates of growth, maturation, and fecundity of perch populations, which demonstrates lower reproductive investment at higher latitudes (Heibo *et al*. 2005) and life history tradeoffs resulting in stunting (Jansen 1996). Several aspects of perch reproduction are worth mentioning: two primordial ovaries are fused into a single organ, and all eggs are shed at once in a single gelatinous ribbon (Treasurer and Holliday 1981). In addition to total spawning at the individual level, spawning is highly synchronised at the population level often concentrated to a few days (Tsai and Gibson 1971). Perch have group-synchronous oocyte development, with a distinct cohort of advancing oocytes suitable for determinate fecundity estimation (Treasurer and Holliday 1981; Sulistyo *et al*. 1998). Fecundity increases with perch size and age, and varies widely both annually and across populations (Tsai and Gibson 1971; Sztramko and Teleki 1977; Thorpe 1977; Treasurer 1981; Jansen 1996; Lauer *et al*. 2005).

Perch are extreme capital breeders. Perch feed opportunistically on insects, crustaceans, crayfish and fish (Craig 1980; Thorpe 1977) which can influence age at first reproduction (Hayes and Taylor 1990). If suitable fish prey are present, perch become piscivorous and attain greater growth rates and sizes but delay maturation (Heibo *et al*. 2005). After spawning, they recover rapidly, as a new batch of oocytes may begin vitellogenesis as soon as one month after spawning (Treasurer and Holliday 1981). The bulk of energy investment into the gonad occurs during autumn but continues through the winter as perch feed even under the ice. Several studies have suggested some of the annual variation in fecundity of perch is related to food supply (Petrovski 1960; Tsai and Gibson 1971; Thorpe 1977; Craig 1980). The inclusion of energy allocated to reproduction in yellow perch bioenergetic models also provides 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). It is also apparent that not all mature perch females spawn annually (i.e. skip spawning), and this skipped spawning is related to the energetic condition in the preceding year (Henderson *et al*. 2000; Holmgren 2003). There is no evidence of downregulation of fecundity through atresia in perch, but occasionally spawning may be disrupted (due to environmental or behavioral factors), as evident by observations of egg-bound females and massive postovulatory degeneration (Treasurer and Holiday 1981).

Walleye and pikeperch (*Sander vitreus*, *S. lucioperca*, Percidae)

Two freshwater species of temperate and subarctic regions of North America and Eurasia, walleye and pikeperch are closely related (Sloss *et al*. 2004). Both species are iteroparous and spawn once a year in spring (Hokanson 1977; Lappalainen *et al*. 2003; Rennie *et al*. 2008). There is wide variation in the rates of growth, maturation and fecundity of *Sander* populations across latitude (Lappalainen *et al*. 2003; Rennie *et al*. 2008). They are total ovulators and lay their eggs in a benthic nest (Hokanson 1977; Lappalainen *et al*. 2003). They have group-synchronous oocyte development (Malison *et al*. 1994; Malison and Held 1996), suitable for determinate fecundity estimation (Carlander 1945; Wolfert 1969). Fecundity increases with size and age (Lappalainen *et al*. 2003). Slower growing populations live longer so they have an equivalent lifetime egg production compared to faster growing populations (Craig *et al*. 1995).

Sander are extreme capital breeders. After spawning, they begin to store energy and develop a new batch of vitellogenic oocytes (Golovanenko *et al*. 1970). Ovarian lipids are derived from visceral fat deposits, and gonadal development will stop if there is insufficient surplus energy through the winter (Henderson *et al*. 1996). Relative fecundity was positively correlated with higher ovarian lipids, but whole-body lipid concentrations was negatively correlated with smaller egg size, suggesting a compensatory mechanism that could limit reproductive potential (Moles *et al*. 2008). Annual variation in fecundity has been related to fish age, habitat quality (i.e., dissolved oxygen), and food supply (Lappalainen *et al*. 2003). Increased population density is associated with delayed maturity (Schueller *et al*. 2005), decreased population density was associated with higher fecundity (Baccante and Reid 1988), and a newly transplanted population of walleye had extraordinarily high fecundity (Maule and Horton 1985). Year class strength has been positively correlated with the amount of surplus energy available to spawners (Henderson and Nepszy 1994). Madenjian *et al*. (1996) reported a correlation between shad abundance and subsequent walleye recruitment.

Pebbled butterflyfish (*Chaetodon multicinctus*, Chaetodontidae)

A tropical, marine species, pebbled butterflyfish is endemic to the Hawaiian Islands (Craig *et al*. 2010). It is a semelparous breeder: maturation occurs at about 13 months and a series of multiple spawning bouts, primarily in winter-spring, last as long as one year (Tricas 1986; Tricas and Hiramoto 1989). Fecundity estimation is indeterminate. Primary oocytes develop asynchronously to the secondary growth stage, and secondary growth oocytes develop group-synchronously to the mature stage (Tricas 1986; Tricas and Hiramoto 1989). Batch fecundity, which range from 1,000 to 20,000 eggs, increases with fish size, but other factors such as season or lunar cycle confound the fecundity-size relationship (Tricas 1986).

Pebbled butterflyfish are mixed capital-income breeders. Females spawn continuously for months, but Tricas (1986) noted that both sexes deposit large visceral fat stores during summer, prior to the reproductive season. Summer coincides with maximal growth of corals, their primary prey. Living in pairs, large males defend the largest territories and mate with the largest females (Tricas 1986; Driscoll and Driscoll 1988). Corals with the highest energy content and lowest handling costs are preferred prey, and territory size is a function of food abundance and competitor density; however, corals are inherently low in energy so pebbled butterflyfish spend over 90% of their time budget feeding on scleractinian coral polyps (Tricas 1986; 1989a; 1989b; 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 appeared to be limited by the amount of energy stored as fat during the summer preceding this period.

Spiny chromis (*Acanthochromis polyacanthus*, Pomacentridae)

A reef-associated marine species of the Indo-West Pacific (Allen 1991, Planes *et al*. 2001), spiny chromis is an iteroparous breeder: breeding generally begins in 3-year old fish (Thresher 1985) but may occur among 2-year olds on outer-shelf reefs (Kingsford and Hughes 2005), and as early as nine months among juveniles hatched and reared in captivity (Kavanagh 2000). Spawning occurs between monogamous pairs, mostly during austral spring and early summer (October-January) (Thresher 1985; Hilder and Pankhurst 2003). Primary growth oocytes develop group synchronously into secondary growth oocytes, but they can do so multiple times within a year, so that annual fecundity is indeterminate (Nakazono 1993; Pankhurst *et al*. 1999). Several hundred eggs are produced per ovulated batch (Donelson *et al*. 2008). Typically only one or two batches of mature eggs are produced each season (Thresher 1985), but up to five batches were produced in laboratory conditions with high ration (Donelson *et al*. 2008). Although they have the capacity to spawn more than one batch in a season, in nature, multiple broods are a response to loss of a mate or egg predation. Another special reproductive feature of this species is that parental care occurs for both eggs and fry (there is no independent planktonic larval stage), which makes this species a reliable experimental model in the laboratory (Robertson 1973; Donelson *et al*. 2008).

Spiny chromis is primarily a capital breeder. If the first clutch is successful, no further clutches are spawned, and energy and time is diverted to parental care. Field-based studies suggest that food abundance or energy reserves limits spiny damselfish reproductive output. For example, high densities of adults are associated with delayed spawning and reduced initial clutch size (Thresher 1983), as well as reduced steroidogenic capacity and lower fecundity (Pankhurst *et al*. 2008). Also, when multiple clutches are produced within a year, subsequent batches have distinctly reduced reproductive output (Thresher 1985; Pankhurst *et al*. 1999). In laboratory experiments, breeding pairs fed high amounts of food for two months before breeding had better condition, commenced breeding earlier, had higher reproductive output (number of eggs × mean egg volume), and their eggs exhibited increased survival during embryogenesis than breeding pairs fed low rations (Donelson *et al*. 2008). Experimentally manipulated high food rations, resulting in high condition of breeders, also improved larval quality (Donelson *et al*. 2009). Finally, increased temperatures, well above typically encountered now but postulated under certain climate change scenarios, reduce reproductive output of spiny chromis (Donelson *et al*. 2010).

Lesser sandeel (*Ammodytes marinus,* Ammodytidae)

A marine species of the eastern North Atlantic, lesser sandeel inhabitats offshore sandbanks (Mitchell *et al*. 1998). It is an iteroparous breeder: maturation occurs in the first year, and over half the fish are mature in the second year, with a maximum age of three years (Boulcott *et al*. 2007). Females spawn during winter (December-January; Winslade 1974b; Gauld and Hutcheon 1990) and fecundity estimation is determinate (Bergstad *et al*. 2001; Boulcott and Wright 2008). Primary growth oocytes develop group synchronously into secondary growth oocytes during summer (Boulcott and Wright 2008). Specific information on total spawning for lesser sandeel was unavailable, but the congener, *A. personatus*, spawns only one batch per year (Yamada 2009).

Lesser sandeel are extreme capital breeders. They bury in the sediment during most of autumn to spring, such that allocation of energy for reproduction comes from energy stored during the late-spring to summer feeding period (Winslade 1974a; Boulcott and Wright 2008). In a laboratory experiment, the growth of age-1, tagged individuals was followed from early summer (June) to just prior to spawning (November), where Boulcott and Wright (2008) observed a critical period for maturity determination. Fish in better condition during the early summer – but not later – were more likely advance a clutch of secondary oocytes and thereby mature and spawn the following winter.

Longjaw mudsucker (*Gillichthys mirabilis,* Gobiidae)

An estuarine species of the west coast of North America, longjaw mudsucker ranges from central California to Baja California (Barlow 1963). It is an iteroparous breeder: maturation occurs in the first year for this short-lived (4-6 years) fish, and females spawn from spring to autumn (Walker *et al*. 1961; de Vlaming 1972a; McGourty *et al*. 2009). Fecundity estimation is indeterminate. Primary growth oocytes develop asynchronously into secondary growth oocytes (de Vlaming 1972a), and females spawn 2-3 times per spawning season (Walker *et al*. 1961; Barlow and de Vlaming 1972). Barlow (1963) and de Vlaming (1972a) recognised a prolonged spawning season by the population, in association with prolonged seasonal productivity, but the short period of batch spawning by individuals demonstrates that spawning by the population of females was not synchronised.

Longjaw mudsucker are primarily capital breeders. In one experiment, gonads regressed when food was withheld completely from females prior to spawning. In other experiments, gonads recrudesced when food was withheld from post-spawning, regressed females, but at great cost to stored energy (de Vlaming 1971). Under more typical condition, somatic growth is fastest in the hot summer months when gonads are regressed (Walker *et al*. 1961), demonstrating that longjaw mudsuckers typically partition somatic and reproductive growth into separate seasons. This species is tolerant of wide range of environmental conditions (e.g., Gracey *et al*. 2001; Evans and Somero 2008; Logan and Somero 2008), and in addition to food-related effects, the effects of the abiotic and physiological mechanisms on this gobiid’s reproductive biology have been investigated experimentally (de Vlaming 1971; 1972b; 1972c).

Turbot (*Scophthalmus maximus*, Scophthalmidae)

A temperate, marine species of the eastern North Atlantic Ocean, turbot is distributed from Norway to the Iberian peninsula (Millner *et al.* 2005). It is an iteroparous breeder: at 4-5 years old females start spawning during summers (Jones 1974; Roff 1981). Oocytes develop from primary growth to secondary growth stage in a group-synchronous manner, and turbot ovulate in batches (Jones 1974; McEvoy 1984; Bromley *et al*. 2000). Potential annual fecundity, measured with a determinate method, ranges from 1 to 8 million eggs (Jones 1974; Bromley *et al*. 1986). Spawning frequency, batch fecundity, and potential annual fecundity all increase with size and age, but egg diameters decline with each successive, within-year batch (Bromley *et al*. 1986; McEvoy and McEvoy 1991; Mugnier *et al*. 2000).

Turbot are capital breeders, as evident from experimental adjustment to the timing and amount of food with respect to specific stages of vitellogenesis. Reduced rations during vitellogenesis, 4 months prior to spawning, were particularly disruptive by preventing maturation in significant numbers of females (Bromley *et al*. 2000). Reduced rations prior to vitellogenesis, 4-8 months to spawning, followed by full rations during vitellogenesis, had less of an effect, but still produced smaller gonads and lower fecundity (Bromley *et al*. 2000). The experimental design used by Bromley *et al*. (2000) was specifically compelling because all fish started as a similar size, and since they were feed the same amount during the experiment (i.e., the full, half, or reduced rations were staggered), spawning fish were of similar sizes at the end of the experiment. The decline in egg size for individual females as spawning progresses is also evidence of depleted yolk reserves by the end of the spawning season (McEvoy and McEvoy 1991; 1992).

Plaice (*Pleuronectes platessa*, Pleuronectidae)

A temperate, marine species of the eastern North Atlantic Ocean, plaice is distributed from Norway to the Iberian peninsula (Millner *et al*. 2005). It is an iteroparous breeder: nearly all females mature by age 5 in this long-lived fish (Bagenal 1966; Roff 1981; Rijnsdorp *et al*. 1991). Females spawn in spring (Barr 1963) and fecundity estimation is determinate (Horwood 1990; Urban 1991). Primary growth oocytes develop group synchronously into secondary growth oocytes (Horwood 1990). Females spawn in batches, and batch fecundity increases with fish size (Urban 1991).

Plaice are extreme capital breeders. They feed during an extended post-spawning period, when soma growth and total energy increases steadily in summer and autumn (Rijnsdorp 1989; 1990). They fast during winter, prior to spawning, when energy is transferred from the soma to the gonad. They do not feed prior to the spawning season and they draw heavily on protein and lipid reserves for spawning (Dawson and Grimm 1980; Rijnsdorp and Ibelings 1989). Bagenal (1966) and Nash *et al*. (2000) associated high fecundity in stock areas with lower density, inferring better feeding. The decision of how much energy to devote to spawning apparently occurs during the feeding season. In the laboratory, small rations led to skipped spawning, when no vitellogenic clutch developed (Horwood *et al*. 1989; Rijnsdorp 1990; Kennedy *et al*. 2008).

Plaice collected at sea have very low levels of atresia (Armstrong *et al*. 2001), and in the lab, higher levels of atresia induced by small rations is only evident well before spawning (Horwood *et al*. 1989; Kennedy *et al*. 2008). Therefore, plaice set up their annual fecundity irreversibly, well before the spawning season.

Winter flounder (*Pseudopleuronectes americanus*, Pleuronectidae)

A marine-estuarine species of the western North Atlantic Ocean, winter flounder spawn earliest (winter-spring) south of New England and later (spring-summer) in Canada (Pereira *et al*. 1999; Wuenschel *et al*. 2009). It is an iteroparous breeder: females spawn first at about 2-3 years old (Roff 1981; Witherell and Burnett 1993; McBride *et al.* 2013). Oocytes develop from primary growth to secondary growth stages in a group-synchronous manner (Dunn 1970). Oocytes develop from secondary growth to mature stages synchronously (Fig. 3g-l of main article; Topp 1968; Burton 1998; Wuenschel *et al*. 2010; Rowinski *et al*. 2010). Mature females may skip spawning in some years, but if not, one clutch of secondary oocytes develop per year with little evidence of atretic down regulation of this advancing clutch of oocytes (Tyler and Dunn 1976; McElroy *et al*. 2013). Therefore, a determinate fecundity method and estimates of potential annual fecundity should be similar to realised annual fecundity. Potential annual fecundity is typically 100s of thousands of eggs and as high as 1.5 million eggs per female (Smith 1898; McElroy *et al*. 2013). Females can be best characterised as total ovulators that behaviourally spawn in batches; they ripen their eggs in a single wave (Burton 1998). Fully ripe eggs (which are demersal) have been observed to be released in several spawning events over several days (Stoner *et al*. 1999).

Winter flounder are extreme capital breeders. Immediately after spawning, they develop a clutch of vitellogenic oocytes for the following year. However, some mature fish will skip spawn. Whether to skip or spawn depends on nutritional status of the fish early in the feeding season (i.e., summer). As demonstrated experimentally in the laboratory, it is condition not age that determines whether a female will skip; skipping occurs when a vitellogenic clutch of oocytes does not advance in post-spawning females (Tyler and Dunn 1976; Burton and Idler 1984, 1987; Burton 1991, 1994). In the field, skip spawning appears to range from zero on Georges Bank, less than 5% in southern New England, but as high as 10-30% in more northern populations (Burton 1999; Wuenschel *et al*. 2009; McBride *et al*. 2013; McElroy *et al*. 2013). Regulatory options for winter flounder have been considered based on egg-per-recruit models (Boreman *et al*. 1993) but because skip spawning will lower estimates of spawning stock biomass, this needs to be explicitly accounted for (Burton 1999).

Sole (*Solea solea*, Soleidae)

A temperate, marine species of the eastern North Atlantic Ocean, sole is distributed from Norway to the Iberian peninsula (Millner *et al.* 2005). It is an iteroparous breeder: nearly all females are mature by age 4 in this medium-lived (9 years) fish (Roff 1981; Rijnsdorp *et al.* 1991; Teixeira and Cabral 2010). Females spawn in spring, earliest in the south and latest in the north (Koutsikopoulos and Lacroix 1992; Fox *et al*. 2000; Teixeira and Cabral 2010). Various studies have advocated that a determine fecundity method can be used in northern populations (Horwood and Greer Walker 1990; Witthames and Greer Walker 1995; Witthames *et al*. 2009). Nonetheless, primary growth oocytes develop asynchronously into secondary growth oocytes in many if not all populations (Urban 1991; Witthames and Greer Walker 1995; Rijnsdorp and Witthames 2005). Females spawn in batches, and uncharacteristically for a fish, there is no correlation between batch fecundity and fish size (Urban 1991; Witthames and Greer Walker 1995). Potential annual fecundity is related to fish size (Millner *et al*. 1991), but very high levels (~28%) of atretic vitellogenic oocytes have been observed during the spawning season (Witthames and Greer Walker 1995; Armstrong *et al*. 2001).

Sole have been referred to as both capital and income breeders (Witthames *et al*. 1995; Kjesbu and Witthames 2007). A direct connection between feeding and reproductive potential was not established but may be inferred by the relationship that fish with higher condition during the spawning season had higher fecundity (Millner *et al*. 1991). Feeding is reduced during the spawning period but does not stop (Devauchelle *et al*. 1987; Molinero and Flos 1992). The spawning period in the northern part of its range has been estimated at 60 days (Armstrong *et al*. 2001), so it is evident that income contributions can occur during breeding. Laboratory experiments have not, however, focused attention on the link between nutrition or energy and reproductive potential. Nonetheless, Millner *et al*. (1991) report substantial variations in fecundity between stock areas and years, Devauchelle *et al*. (1987) report that fecundity was negatively affected by high temperatures during oogenesis, and Bromley (2003) and Kjesbu and Witthames (2007) report that larger females have higher reproductive potential than smaller females. Since sole appears to straddle the capital-income continuum, demonstrates clinal variation in life history traits along a latitudinal gradient (Türkmen 2003; Mollet *et al*. in press), and is a frequent subject for aquaculture (Imsland *et al*. 2003), this species is well suited for further study.

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