

REVIEW

Life-history plasticity in female threespine stickleback

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The postglacial adaptive radiation of the threespine stickleback fish (*Gasterosteus aculeatus*) has been widely used to investigate the roles of both adaptive evolution and plasticity in behavioral and morphological divergence from the ancestral condition represented by present-day oceanic stickleback. These phenotypes tend to exhibit high levels of ecotypic differentiation. Population divergence in life history has also been well studied, but in contrast to behavior and morphology, the extent and importance of plasticity has been much less well studied. In this review, we summarize what is known about life-history plasticity in female threespine stickleback, considering four traits intimately associated with reproductive output: age/size at maturation, level of reproductive effort, egg size and clutch size. We envision life-history plasticity in an iterative, ontogenetic framework, in which females may express plasticity repeatedly across each of several time frames. We contrast the results of laboratory and field studies because, for most traits, these approaches give somewhat different answers. We provide ideas on what the cues might be for observed plasticity in each trait and, when possible, we inquire about the relative costs and benefits to expressed plasticity. We end with an example of how we think plasticity may play out in stickleback life history given what we know of plasticity in the ancestor.

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INTRODUCTION

Life-history traits are those features of organisms that are directly and intimately connected to reproductive output. Although life-history traits may have low average heritability, they typically possess sufficient additive genetic variation to respond rapidly to selection (Mousseau and Roff, 1987). In addition, life-history traits commonly exhibit substantial plasticity (Mousseau and Fox, 1998; Nylin and Gotthard, 1998). This ability to respond to environmental challenges via rapid evolution, plasticity or both may be a hallmark of life-history traits. Individual life-history traits are integrated within a complex network of positive and negative (tradeoff) relationships not just among themselves (Stearns, 1989; Roff, 1992), but also with many other aspects of the phenotype (Forsman, 2014). This complexity places limits on the extent to which individual traits can shift plastically and still cumulatively produce the maximum reproductive fitness (Brown and Shine, 2007; Hamel *et al.*, 2014). This complexity is particularly important for female animals because of the large per-offspring investment that females make.

Core reproductive life-history traits in female animals commonly include the age (or size) at maturation, the level of reproductive effort, egg or offspring size, clutch size (eggs or offspring produced during one relatively short period of reproduction) and reproductive frequency (Reznick *et al.*, 2000). Growth rate is sometimes considered to be a life-history trait (see, for example, Arendt, 1997). However, in this review we differentiate it from those traits listed above because although growth rate contributes to reproductive potential (for example, by potentially increasing size at each reproductive event), it is involved as an outside influence on the set of traits we consider (see 'Initiation of Maturation' section below). In iteroparous animals, these

female traits may be considered to be developmentally inducible, although not in the usual ontogenetic sense. Rather, they represent iteratively inducible traits that are expressed repeatedly throughout the life of the organism (Foster *et al.*, 2015). Even the most rapid plastic responses in female life-history traits cannot be considered activational (*sensu* Snell-Rood, 2013), a common characteristic of behavioral traits. Nevertheless, life-history plasticity may be expressed at several very different timescales—from clutch-to-clutch adjustments (Kolm, 2001; Vrtilik and Reichard, 2014), to a gradual adjustment in reproductive traits as the breeding season approaches (Kennedy *et al.*, 2008), to year-to-year shifts (Lee *et al.*, 2012) and across generations via maternal effects (Bashey, 2006; Galloway and Etterson, 2009).

Most trait expression probably comprises a mixture of constitutive and plastic components (Grimaldi *et al.*, 2005; Bourdeau, 2012). With respect to life history, all normal females express a set of traits associated with reproduction—a nonzero level of reproductive effort, egg or offspring size, clutch or brood size; and frequency of reproduction. In this respect, these are constitutive traits, and each female presumably has some genetically determined level of expression based on allelic variation associated with the individual traits. In many species, life-history traits also show considerable inducible plasticity—adjustments to the constitutive expression made in response to an environmental cue. Trait expression, achieved by whatever mechanism, is presumably optimized as part of the overall phenotype (Lancaster *et al.*, 2010).

In this paper, we review data for the threespine stickleback (*Gasterosteus aculeatus*), and our use of the word 'stickleback' for brevity refers to that species only. However, much of what we conclude may apply to other stickleback species, and even many

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other teleosts. As we demonstrate, life-history traits of female stickleback show varying degrees of apparent plasticity. The likelihood that plasticity will evolve in a particular trait depends on several factors, one of which is the response time between exposure to a cue and the expression of an appropriate response (Moran, 1992; Padilla and Adolph, 1996). Thus, female stickleback life-history traits may require different cues with different lag times before expression of the phenotype (DeWitt *et al.*, 1998). The reliability of the cue is also important (DeWitt and Scheiner, 2004). The relative costs and benefits of plasticity in individual traits may differ, and this may also contribute to differences in levels of plasticity (Relyea, 2002; Koivula *et al.*, 2003). Finally, traits are linked both genetically and functionally, and thus expressed plasticity in one trait would seem to require simultaneous plastic expression in at least one other trait, and perhaps more. In such cases, we may discover a hierarchy of trait plasticity that reflects the relative importance of each trait in determining fitness.

The threespine stickleback adaptive radiation has proven a model for understanding evolutionary processes in general (Bell and Foster, 1994), and for investigating behavioral (Foster and Wund, 2011; Foster *et al.*, 2015) and morphological (Wund *et al.*, 2008, 2012) plasticity specifically. In contrast, there has been much less discussion of life-history plasticity in this model species. In this paper we seek to summarize what we do know, and hopefully prompt researchers to take fuller advantage of this easily studied species. For each core reproductive trait noted earlier we provide a brief general overview of plasticity in the trait, highlighting studies of fish where possible. This is not a comprehensive review of plasticity *per se*, and hence the studies we highlight are illustrative only; we minimize the number of references for brevity. We indicate what we understand about plasticity of each trait in stickleback, and the evidence that supports our inference. We attempt to identify the cue that females use to adaptively adjust trait expression, the reliability of the cue and the likely time lag in response. In the last section we speculate on how plasticity may operate within the overall life history of threespine stickleback, discussing possible constraints, and costs and benefits where possible.

THE THREESPIKE STICKLEBACK ADAPTIVE RADIATION

G. aculeatus comprises a very large complex of differentiated populations including a number of clear, but unnamed biological species (Bell and Foster, 1994; McKinnon and Rundle, 2002). The complex is broadly distributed in marine, brackish and coastal fresh waters in boreal and temperate regions of the northern hemisphere, encompassing fully marine, estuarine, anadromous and freshwater lifestyles. Freshwater populations in northern regions covered by ice during the last glacial maximum must have been colonized in the past 12 000 years (Reger and Pinney, 1996), whereas populations in unglaciated regions can be much older (Oravec and Reimchen, 2013). Freshwater populations in postglacial regions have generally been shown to display pronounced parallelism in the divergence of behavior and morphology among populations in response to foraging opportunities ('benthic-limnetic continuum': Foster *et al.*, 1998; Rundle *et al.*, 2000), and to differences in predation levels (Messler *et al.*, 2007) that can offer significant insights into the adaptive value of particular phenotypes (Schluter, 2000). The impressive levels of parallelism in morphology and behavior appear not to be mirrored in the patterns of differentiation of female life-history attributes (Baker *et al.*, 1998, 2005, 2008).

A second attribute of the threespine stickleback adaptive radiation that is unusual, and of value with respect to understanding evolutionary pattern, is the continued existence of oceanic stickleback, considered to be reasonable surrogates for the ancestors that gave rise

to the postglacial freshwater radiation within regions (see, for example, Hohenloe *et al.*, 2012; Foster, 2013). This attribute of the radiation permits inference of the direction of evolutionary transitions, and allows us to ask questions about the patterns of evolutionary change in population contrasts.

INITIATION OF MATURATION

The size or age at which an organism begins to divert resources to reproduction is a critical life-history trait (Henderson and Morgan, 2002; Barot *et al.*, 2004). This may be especially important when breeding opportunities are limited, as in semelparous fish (Crespi and Teo, 2002), in monocarpic plants (Burd *et al.*, 2006) and in short-lived organisms such as threespine stickleback (Baker *et al.*, 2008) and guppies (Reznick *et al.*, 1990). Plasticity for size/age at reproduction has been extensively modeled (Berrigan and Koella, 1994; Marty *et al.*, 2011), comprehensively reviewed recently in insects (Teder *et al.*, 2014) and has been demonstrated in a wide array of fish species (Morita and Fukuwaka, 2006; Hutchings and Jones, 2008). Early-life reproduction is likely to be particularly important in short-lived species living in strongly seasonal environments that constrain breeding to a short period of the year (Adolph and Porter, 1996; Merila *et al.*, 2000). Except for obligate annual species, the age at which an organism matures is almost always plastic (Day and Rowe, 2002). In long-lived iteroparous organisms, this maturation plasticity may permit the organism to skip reproductive events entirely (Rideout *et al.*, 2005; Skjæraasen *et al.*, 2012). Some of the established determinants of the expression of plasticity for maturity in fishes include early-life growth rate (Bertecky and Fox, 1999; Copp and Fox, 2007), size (Teder *et al.*, 2014) and energetic status (for example, lipid content; Thorpe, 2007).

Females in most threespine stickleback populations can expect to breed in only 1–2 seasons (Baker *et al.*, 2008; but see Oravec and Reimchen, 2013), even though in many populations older females are often present. Seasonal constraints on the timing of the reproductive period in most populations mean that if a female does not breed at age 1, she must wait an entire year. Early reproduction, on average, produces a higher intrinsic rate of increase because of reproductive 'compounding' (Roff, 2000; Anguilletta *et al.*, 2004), and thus selection should favor plasticity because of the high value of reproducing at an early age when it is profitable. Age and/or size at first breeding has been shown to have a heritable basis in stickleback (McPhail, 1977; Snyder and Dingle, 1989; Snyder, 1991), but several lines of evidence strongly suggest that it is plastic as well. We have studied more than 130 freshwater populations over the past 20 years in Alaska and southern British Columbia. In virtually all of these populations, a (variable) proportion of first-year females is included in the breeding pool in the wild (Figure 1). Although this could result from populations consisting of a mixture of females that are genetically determined to breed at either age 1 or age 2, and then die, the most likely explanation is that females exhibit plasticity for initial age of breeding. Such plasticity was nicely documented by Saito and Nakano (1999) who demonstrated that females in one population bred either at age 2 or age 3, depending upon the size they reached in the previous year. We have raised more than 30 populations in the laboratory, and have found that most females can become reproductive (given appropriate light cues) at age 1, even in populations where age-1 breeders are uncommon in nature (for example, Walby Lake; Heins *et al.*, 2010). Furthermore, in the laboratory, the fish that fail to breed at age 1 are nearly always unusually small individuals. These results must be viewed with some caution, as our laboratory-reared fish typically receive maximum rations throughout their first year of life,

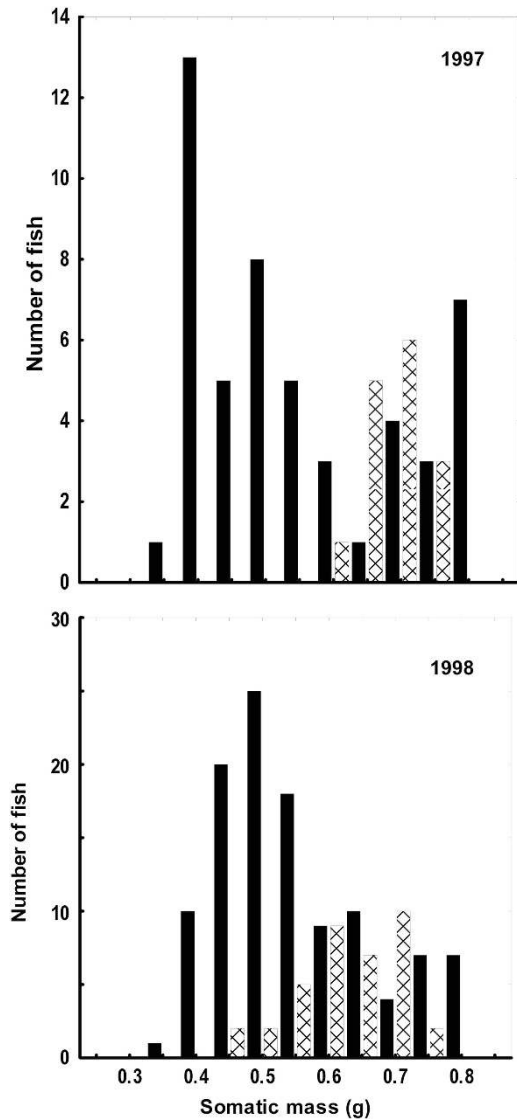


Figure 1 Size frequency of age-1 female threespine stickleback in Cornelius Lake, Alaska. Solid bars indicate nonbreeding females, confirmed by dissection; hatched bars indicate females that were in the clutch-production cycle (Baker *et al.*, 1998). Breeders are clearly primarily the larger fish, although size is not a perfect predictor, as some larger fish are not breeders. The main group of breeding females in this population are age-2 individuals.

and this may not be typical. Finally, Snyder (1991) showed that stickleback could become reproductive as early as 195–220 days of age, given sufficient growth and appropriate environmental cues.

In the wild, female oceanic stickleback in Alaska breed primarily at age 2 (Baker *et al.*, 1998, 2008; Karve *et al.*, 2013; RW King, unpublished data). Narver (1969) suggested that the ‘estuarine’ population in Chignik Lagoon, Alaska, bred at age 1; however, the sizes of fish reported in that study (65–90 mm) are clearly age 2 based on our extensive spatial and temporal sampling of ancestral populations in Alaska. Presumably, age-1 fish were not present on the breeding grounds where Narver (1969) collected. Despite generally breeding at age 2, a small and annually variable proportion of age-1 Alaska fish do breed (Figure 2). In British Columbia (JA Baker, unpublished data) and the St Lawrence River estuary (Picard *et al.*, 1990), breeders are also a variable mix of age-1 and age-2 fish. As with

freshwater stickleback, oceanic stickleback reared in the laboratory (six populations from Alaska and three from British Columbia) all show a very high probability of reproducing at age 1. These multiple lines of evidence suggest that plasticity is the ancestral condition. In most freshwater populations we observe at least two age classes of breeding females, suggesting that many females can reproduce in multiple years, as they do in the laboratory. Females from both ancestral and freshwater populations that reproduce in the laboratory at age 1 show a high probability of surviving to age 2 and breeding the following year.

The cue initiating maturation is probably an aspect of the maternal phenotype itself (Metcalf and Monaghan, 2003), such as body size (Weeks and Quattro, 1991; Saito and Nakano, 1999) or energy state (Morgan, 2004; Vitousek *et al.*, 2010). Our current work (ML Reyes and JA Baker, unpublished data) suggests that size may be the most important variable cueing reproduction at age 1 in stickleback, as fish encountering a period of low rations late in their first growing season recover size instead of lipid stores if ration is increased (Figure 3). This also corresponds with the observation that size is the best predictor of female reproductive output per clutch (Wootton, 1973a; Wootton, 1977; Ali and Wootton, 1999a; Baker *et al.*, 2008), with energy state or current ration level having smaller effects (Ali and Wootton, 1999a) or no detectable effect at all.

Experiments (Wootton, 1973b; Inness and Metcalfe, 2008) show that high rations increased the proportion of female stickleback that matured at age 1, and that size is probably the best indicator of the probability of maturing. Subsequently, Ali and Wootton (1999b) found that breeding and nonbreeding first-year females did not differ in average size, but they collected their fish from the wild in ‘mid-winter’, when females may have already made a decision to mature or not. Females begin mobilizing energy into ovarian and support tissue in winter (Wootton *et al.*, 1978, 1980; Wootton, 1994; Sokolowska and Kulczykowska, 2006), indicating that a response (mature, or not) may be determined several months before the reproductive season begins. This suggests that the cue is likely to be highly reliable, because reproducing when size or energy is insufficient likely leads to low survival to age 2 (see, for example, Vitousek *et al.*, 2010), and failing to breed when size or energy is sufficient surrenders the compounding advantage of early reproduction.

Reproduction at age 1 would be favored if it resulted in a lifetime reproductive output exceeding that of females that delayed breeding to age 2 (Roff, 2002). Because female size has the greatest influence on clutch size, reproduction at age 1 should be favored only when it does not substantially diminish survival to, or size at, age 2 (Hutchings, 1999). The enormous reproductive effort made by female stickleback prevents most individuals from growing substantially during the reproductive season (Wootton *et al.*, 1978). However, in Alaska, breeding ends by mid-July in most populations (Heins *et al.*, 1999), providing females up to 3 months of growth before the next winter. This suggests that females of sufficient size and energy state that breed at age 1 will be able to offset some of the growth cost of reproduction, and will attain the highest lifetime output of potential offspring, whereas smaller and/or less energetic females may do better by waiting until age 2, favoring plasticity for this trait. This is the explanation for the alternating reproductive age pattern observed by Saito and Nakano (1999), in which seasonally late-hatched fish did not achieve the minimum reproductive size until age 3, whereas early hatched fish grew large enough to reproduce at age 2.

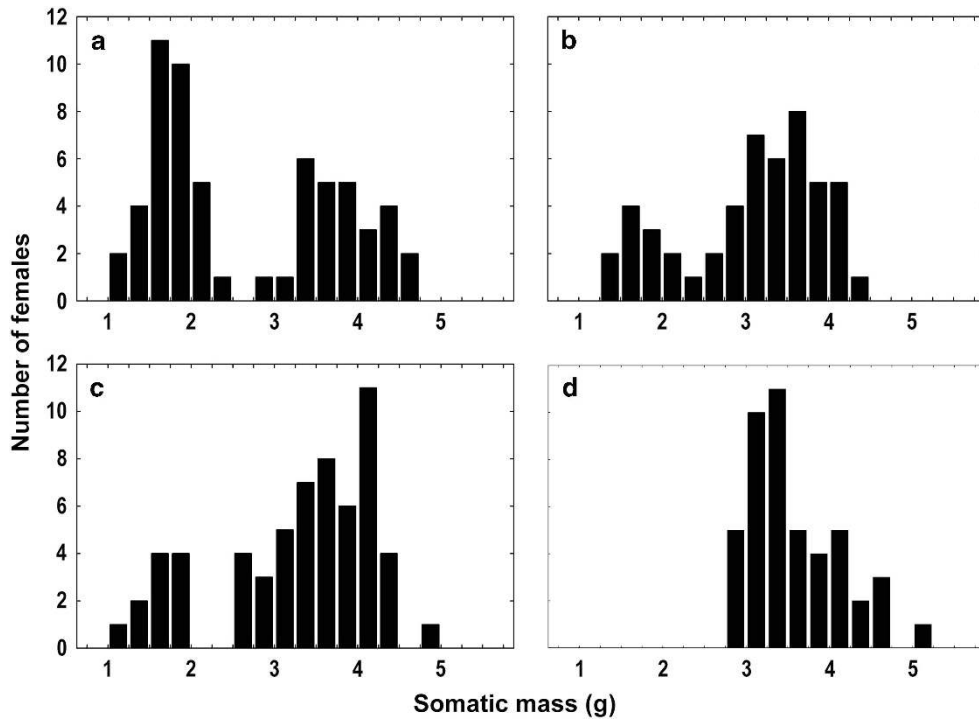


Figure 2 Size frequency of anadromous threespine stickleback on the breeding ground in two Alaskan populations. (a–c) Anchor River population 1995–1997. (d) Mud Lake population (Karve *et al.*, 2013). All fish are reproductive females captured on the breeding grounds. The clear size modes in Anchor River represent age-1 and age-2 breeders; only age-2 breeders make the extended migration up the Knik River system and tributaries to spawn in Mud Lake.

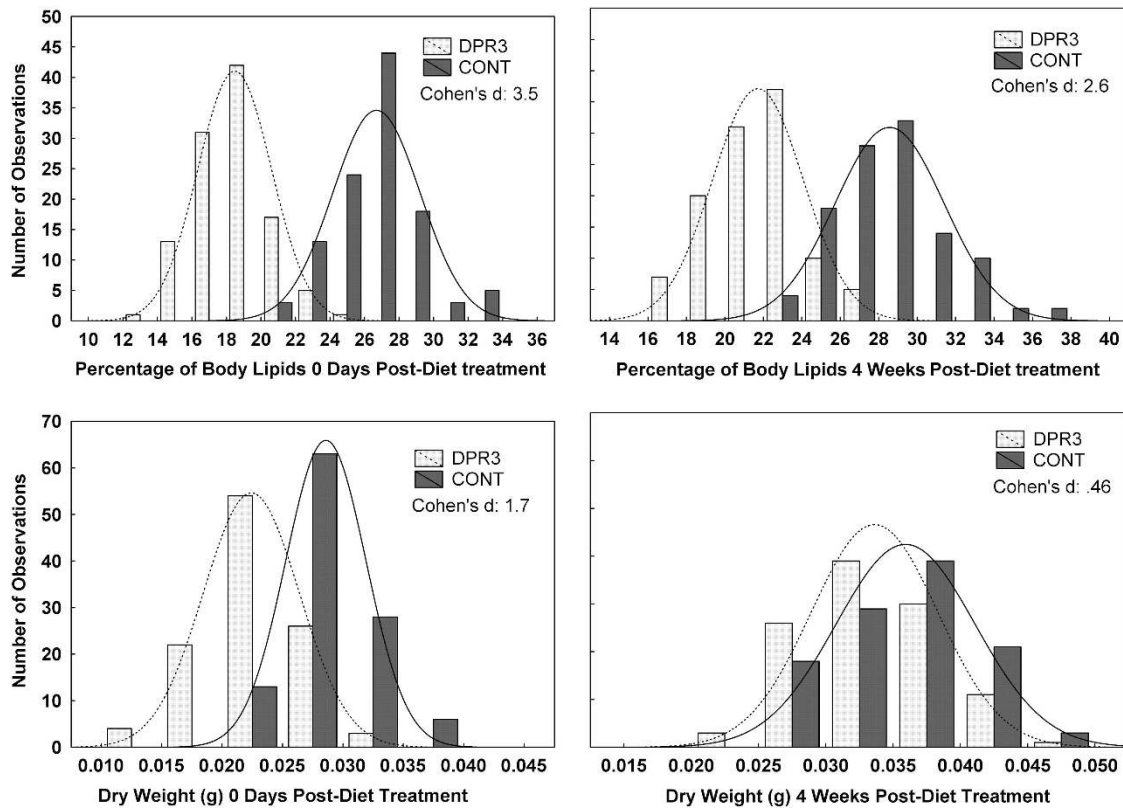


Figure 3 Comparison of compensatory responses in somatic mass and lipid content of threespine stickleback in experimental (DPR3) and control (CONT) fish that experienced a 50% reduction in ration in their fourth month of life (~2 months before over-wintering). The left panels show values at the end of 1 month of reduced ration; the right panels show values after a return to full ration for 1 month. The magnitude of the differences between control and experimental fish for each panel is indicated by an effect size metric (Cohen's *d*).

REPRODUCTIVE EFFORT

The relationship between current and future performance is manifested in one of the principal tradeoffs shaping life-history evolution—the ‘cost of reproduction’ (Reznick *et al.*, 2000; Kuparinen *et al.*, 2011). The level of effort put toward reproduction can affect the probability of survival (Gunderson, 1997; Moore and Attisano, 2011), future reproduction via reduced growth (Roff, 2000; Tsiklris *et al.*, 2007) or both (Koivula *et al.*, 2003), depending upon environmental conditions (Shine, 1980; Hamel *et al.*, 2014). Plasticity in level of reproductive effort has been documented in a variety of ectotherms, including insects (review in Nylin and Gotthard, 1998), fish (Pampoulie *et al.*, 2000; Kolm, 2001), snakes (Brown and Shine, 2007) and marine iguanas (Vitousek *et al.*, 2010). In animals, plastic expression can range from clutch-to-clutch adjustments (Wisenden, 1993) to the sudden abandonment of reproduction and resorption of eggs (Vitousek *et al.*, 2010; Moore and Attisano, 2011). In some fish, annual opportunities for spawning may be skipped (Trippel and Harvey, 1989; Skjæraasen *et al.*, 2012). In iteroparous organisms like the threespine stickleback, which are capable of producing multiple clutches in multiple years, plasticity of reproductive effort may exist at three levels: (1) within years across sequential clutches, (2) within years for the number of clutches and (3) across years. These could represent different plastic response mechanisms or different manifestations of a single plastic mechanism.

The mass of the eggs spawned in a single clutch is a common proxy for the relative amount of energy devoted to reproduction by a female during the time interval required to produce the clutch (Roff, 2002). Scaled to female body mass, this metric constitutes one of the most widely used indices of reproductive effort (gonadosomatic index: Gunderson and Dygert, 1988; relative clutch mass; Heins and Baker, 1993). On this basis, threespine stickleback make a relatively large effort per clutch. Averaged over 83 populations, Alaskan stickleback produce clutches that weigh more than one-fourth the somatic weight of the female (mean = 26.6%, Figure 1 in Baker *et al.*, 2008), and oceanic females produce clutches that weigh >36% their body weight (Baker *et al.*, 1998). Similar values were observed for stickleback from British Columbia (Baker *et al.*, 2013; JA Baker, unpublished data). Wootton and Fletcher (2009) reported values of ~16% for their highest ration; however, they used a different measure of female mass in their calculations. An approximate adjustment indicates that their values are similar, or only slightly lower, than ours.

Reproductive effort can also be evaluated over an entire season by incorporating the frequency of clutch production. Our data for multiple laboratory-reared populations, and that of Wootton for Welsh populations (Wootton, 1973b; Wootton and Fletcher, 2009) show that healthy, well-fed females can produce 8–9 clutches, and occasionally more, at intervals of 3–9 days within a season, producing up to 1000 eggs before ceasing reproduction (see also Brown-Peterson and Heins, 2009). Thus, a female stickleback may produce eggs that represent 1.4 times (Wootton and Fletcher, 2009) to 2.25 times (JA Baker, personal observation) and to possibly 3–4 times her somatic mass in one season (Wootton, 1973b). The careful experiments of Wootton, 1973b indicated that larger and better fed females produced more clutches, but not larger relative clutch masses (scaled for body size). This effect has been reported in other species (Donelson *et al.*, 2008; Hamel *et al.*, 2009). Similarly, Hooker (1988) reported in an experimental study of two stream stickleback populations from extreme southwestern British Columbia that females could produce up to 9 clutches per season, and a maximum total of about 850 eggs. However, interclutch intervals ranged more widely (10–30 days), and Hooker (1988) found that smaller females actually produced more

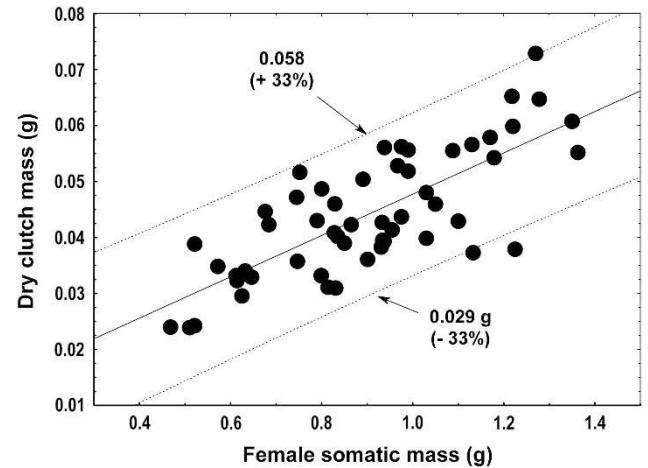


Figure 4 The relationship between dry clutch mass (an indicator of reproductive effort) and female somatic mass in Big Beaver Lake, Alaska, 1997. Each symbol indicates an individual female. At the mean somatic mass of 0.90 g, female clutch mass can vary higher or lower by as much as one-third from the expected value along the regression line.

clutches, so that seasonal fecundity was almost independent of female size.

The balance of experimental evidence thus suggests that clutch-to-clutch plasticity in reproductive effort in threespine stickleback is limited, and that females may generally reproduce near the maximum level for their body size and energy state. These conclusions are also consistent with the finding that the average level of reproductive effort per clutch across stickleback populations closely tracks average body size (Baker *et al.*, 2008). Nevertheless, there is often substantial individual variation in the clutch mass to body mass ratio among wild-caught females (Figure 4) that is difficult to reconcile with the experimental studies of Wootton, 1973b). Field data suggest that, as the breeding season nears, individual females integrate cues from their current state (body size, lipid stores, liver glycogen level) and ration level to set the level of per-clutch reproductive effort for that season (Vitousek *et al.*, 2010) that, under certain circumstances, may result in considerable individual variation about the population effort-size trajectory. At present, we do not know how much of this variation is due to constitutive (allelic variation) or plastic effects.

Reproductive effort in fish tends to remain fairly consistent throughout a reproductive season (examples in Vrtilik and Reichard, 2014), and therefore within-season plasticity of reproductive effort may be mediated primarily via the number of clutches in many cases. Studies by Ali and Wootton (1999a) and Wootton and Fletcher (2009) show that once stickleback females begin reproducing, they maintain their initial strategy of making a size-appropriate clutch mass regardless of subsequent changes in ration levels. In contrast, inter-clutch interval is sensitive to ration, lengthening under low rations. This plasticity for interclutch interval may simply be a nonadaptive response to resource reduction. However, it may also indicate adaptive plasticity if the resources required to maintain the original interclutch interval would result in a somatic cost (for example, poorer condition or immune system function), leading to a lower survival probability.

Our evidence for substantial plasticity for reproductive effort also includes comparisons of many populations assayed in the wild and raised in a common laboratory environment. In the presumably benign laboratory environment, effort is typically lower per clutch for

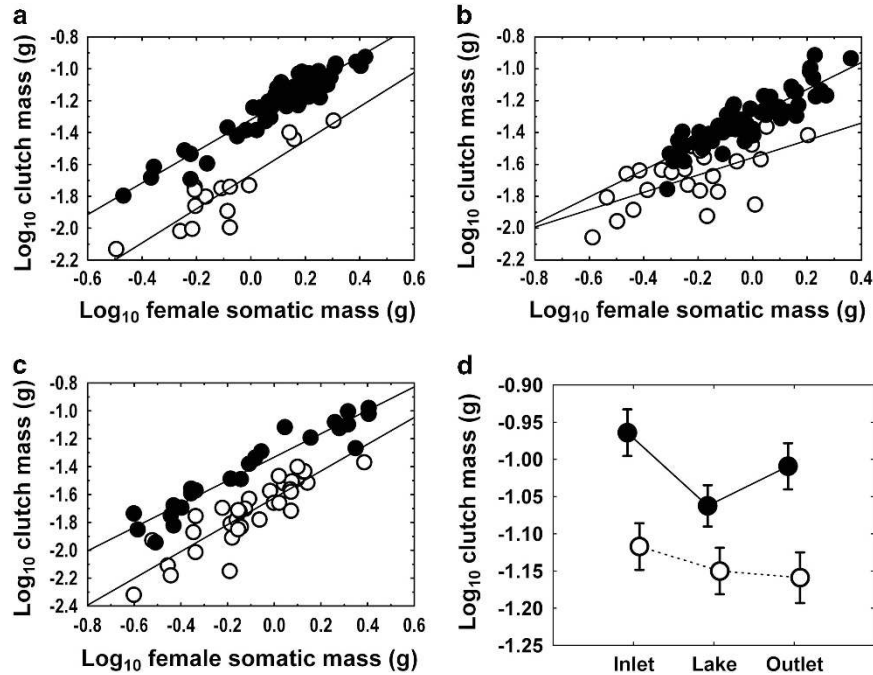


Figure 5 Relationships between clutch mass and body mass in female threespine stickleback from four populations studied in the wild (solid circles) and in the lab (open circles). (a) Lynne Lake, Alaska—limnetic body shape. (b) Cornelius Lake, Alaska—intermediate body shape. (c) Willow Lake, Alaska—benthic body shape. (d) Shown are clutch masses for stickleback from three distinct habitats within the Misty Lake ecosystem, British Columbia, adjusted to a common female mass of 2.45 g. In panels a–c, fish less than ~1 g are age 1 individuals.

first-year females than in the field (Figure 5; Baker *et al.*, 2013). Oceanic and estuarine populations, in which the majority of females appear to breed in just 1 year, with few lifetime clutches (Narver, 1969; Crivelli and Britton, 1987; Boulé and FitzGerald, 1989), show a relatively small change compared with freshwater populations. Freshwater populations can produce many clutches in a single breeding season (Wootton, 1973b; Wootton and Evans, 1976; Copp *et al.*, 2002; Wootton and Fletcher, 2009), and probably in more than a single year in many populations (Baker *et al.*, 2008; Lee *et al.*, 2012). The smaller reduction by ancestral stickleback in the laboratory suggests that more limited plasticity of reproductive effort is the ancestral condition. Reproductive effort also appears to be reduced with length of migration in anadromous stickleback in Alaska (Karve *et al.*, 2013; JA Baker, personal observation), but at present we do not know whether this represents plasticity or population-specific adaptive variation.

The energetic needs of reproduction may be met in two ways—stored energy or energy consumed as reproduction proceeds, corresponding to the ends of a continuum from capital to income breeding (Houston *et al.*, 2007; Stephens *et al.*, 2009). It is likely that stickleback fall somewhere between these extremes because even fed maximum rations (16% body weight per day; Wootton and Fletcher, 2009), stickleback reproductive effort declines over a spawning season. Stickleback might express adaptive plasticity for this trait as well (as do aspik vipers; Lourdais *et al.*, 2002). Stickleback emerge from a 5–6-month winter in early May in Alaska, and have 0.5–1.0 months to regenerate lipid stores and liver glycogen for reproduction. Thus, depending on their energy state emerging from the winter, and early-season food quantity, females may enter the reproductive period with varying levels of reproductive capital that then may cue plastic adjustments in traits that depend critically on energy flow for reproduction (Madsen and Shine, 1999; Casas *et al.*, 2005).

A plausible explanation for the difference between data derived from experimental versus wild-caught populations is that Wootton worked with largely annual populations (for example, Wootton and Fletcher, 2009), whereas our data come mostly from populations in which females may reproduce over 2–3 years. Annual versus longer-lived populations might be anticipated to evolve differently with regard to the expression of plasticity in reproductive effort, and indeed probably in most traits. Thus, our data suggest that stickleback may exhibit more substantive plasticity, by setting an appropriate level of reproductive effort before the breeding season—even though they do not change that effort throughout a season.

Stickleback that can breed in more than a single season also often display season-to-season plasticity in level of effort, expressed ontogenetically as an increasing commitment to reproduction as they age. That is, allometric slopes (model II, reflecting error in both x and y variables) relating clutch mass to body mass are >1 in many populations we have studied (Figure 6). Such an increase is expected under lifetime allocation models of reproductive effort (Roff, 2002), and thus represents adaptive plasticity. All of our data bearing on this phenomenon are from cross-sectional studies of females of multiple ages collected at one time, and we know of only one study (Lee *et al.*, 2012) that has tracked individual stickleback across multiple years. However, numerous experiments by Wootton cited above suggest that the population-level trends relating reproductive effort to body size/age may mirror those of the individual females themselves. This form of plasticity should be expressed even within a breeding season in annual populations, and indeed this was observed by Poizat *et al.* (1999) in the Camargue estuary, southern France. These data suggest that plastic adjustments to reproductive effort between years is adaptive, most likely because lower than maximum levels of reproduction at young ages can enhance survival to one or more subsequent breeding years (minimize survival cost; Bertschy and Fox, 1999) in most freshwater populations. The energy state of the female, perhaps

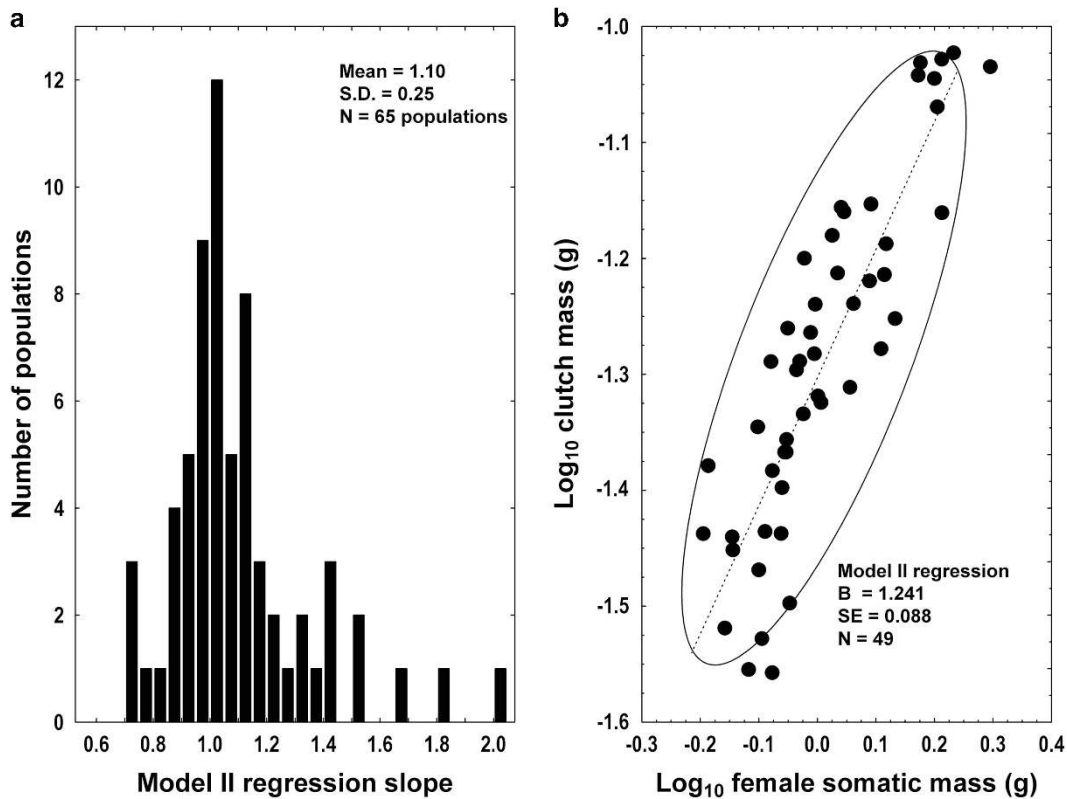


Figure 6 (a) The distribution of population-level regression slopes (model II) for 65 Alaskan populations of threespine stickleback. A slope of >1 indicates that relative reproductive effort increases with size/age. (b) An example of a one population's relationship; each filled circle represents an individual female. A 99% bivariate probability ellipse is fitted to the data, with the model II regression trend indicated by a dashed line.

in combination with current income, may be a cue to adjust the overall level of reproductive effort to maximize survival to older ages, at least in populations where older females commonly breed. In contrast, older females may commit greater resources to reproduction as they have reduced probability of breeding in future years.

Body size is the best predictor of clutch size in stickleback (Fletcher and Wootton, 1995; JA Baker, personal observation), and a population's clutch mass to body mass regression trend may approximate the constitutive expression of reproductive effort across the lifetime (the trajectory). Individual females may have constitutively lower or higher efforts at each size, but may generally follow the population trajectory. However, females could adaptively modify this expression by either increasing or decreasing reproductive effort to maximize their expected lifetime output of offspring. The cue is likely to be female energy state, and current feeding conditions, and must act in just a few weeks before first breeding of each season, and thus the lag time between cue and response is relatively short. This is a clear case of iterative developmental plasticity in which females are able to adjust reproductive effort in relation to perceived food availability, individual condition and expectation of future reproductive opportunities.

EGG SIZE

Offspring size is a critical life-history trait (Bernardo, 1996), and selection on offspring size is often strong. It may be particularly pronounced in fish (Kingsolver *et al.*, 2001), and in which it commonly favors larger size in the youngest fish (Duarte and Alcaraz, 1989; Perez and Munch, 2010). In egg-laying species, an additional complicating feature is that the females produce eggs, and thus the egg-to-offspring mapping must also be taken into account.

Although egg size itself may be under direct selection (Einum and Fleming, 2000b; Simons, 2008), the primary target of selection in most cases appears to be the size and performance of the fry. Thus, there is often found to be a positive correlation between egg size and fry size or capability (Einum and Fleming, 2000a; Segers and Taborsky, 2011). Because even small differences early in life can lead to large variations in fry fitness (Anderson, 1988; Perez and Munch, 2010; JA Baker, unpublished data) plasticity should be a considerable advantage to females. Egg-size plasticity has been well studied, and it is widespread in both egg-laying (Kolm, 2001; Gagliano and McCormick, 2007) and live-bearing (Rodd *et al.*, 1997; Auer, 2010) fish. Complicating the issue is the fact that egg size is a property of both the female and offspring phenotype (Bernardo, 1996), and therefore the best egg size for fry may not be the optimal egg size for females (Einum and Fleming, 2000b). Females may express egg-size plasticity in at least four ways (Marshall and Uller, 2007), three adaptive for themselves and/or the fry (anticipatory, selfish and bet-hedging), and one nonadaptive (transmissive).

Baker and Foster (2002) notwithstanding, egg size appears to show no appreciable short-term adaptive plasticity in stickleback based on experimental manipulation of female diet or condition (Fletcher and Wootton, 1995; Ali and Wootton, 1999b; Inness and Metcalfe, 2008), on comparisons across sequential field collections throughout a breeding season (JA Baker, personal observation) or on sequential clutches when reared in the laboratory (JA Baker, unpublished data). In one population in Wales studied experimentally by Fletcher and Wootton (1995), a significant, positive correlation was observed between egg size and ration size as ration increased from 2 to 16% body weight per day, suggesting adaptive plasticity with energy income

as the cue. However, this pattern was entirely generated by a reduced egg size at only the lowest ration, suggesting nonadaptive plasticity instead. Even under such widely varying rations, the lipid–protein ratio of eggs remained unchanged (confirmed by Wootton and Fletcher, 2009), a finding similar to that in Atlantic salmon (Berg *et al.*, 2001), although different from live-bearing guppies (Reznick and Yang, 1993). In addition, unlike reproductive effort, we observed no consistent difference in egg size between lab-raised and wild-caught fish in most populations. Studies show that the cestode parasite *Schistocephalus solidus* almost always reduces stickleback egg size (Heins and Baker, 2003), and in most populations egg size is inversely related to severity of parasitism, strongly implicating nonadaptive nutrient theft (Heins and Baker, 2008; Heins *et al.*, 2014). However, a recent study found potential adaptive plasticity for egg size in two populations (Heins and Baker, 2014), but in these cases the females have a reliable cue—the parasite within them.

The most plausible explanation for the lack of clutch-to-clutch egg-size plasticity is that females have no reliable cue to guide an appropriate response. The highest mortality rate in most fish populations occurs at the youngest ages (Houde, 1987; Perez and Munch, 2010), and is often attributed to starvation. If so, the cue for provisioning eggs should accurately predict fry feeding environment if the plasticity is to be adaptive. The duration from onset of vitellogenesis to exogenously feeding stickleback fry is at least 14 days at mid-summer Alaska water temperatures (5–6 days to produce a clutch, 6–7 days to hatch and 2–3 days to complete development and begin exogenous feeding), and it is even longer at the cool temperatures experienced early in the breeding season (JA Baker, unpublished data). If female stickleback plastically established a target egg size at the onset of vitellogenesis based on current information on the food availability for fry, this cue would need accurately to predict conditions 2–3 weeks later. Unpredictable variability in weather, competing fry

density and temperature make it unlikely that such a cue could be sufficiently accurate.

Despite the apparent lack of short-term plasticity in egg size, approximately half of all freshwater, and all oceanic, populations we have studied exhibit egg-size plasticity between reproductive seasons (iterative ontogenetic plasticity). This is expressed as a positive relationship between egg size and female size or age (Figure 7; Fletcher and Wootton, 1995; Baker *et al.*, 1998, 2008, 2013). This pattern implies that the ‘decision’ to produce eggs of a particular size might be reset annually, cued by the size, age or energy state of the female when she begins breeding in a particular year, a possibility supported by modeling studies such as those by Kindsvater and Otto (2014). However, this relationship is not displayed in all freshwater populations in Alaska. Because the ancestor displays the relationship, this indicates that some Alaskan populations may no longer express this plasticity. If the cue is indeed internal to the female herself, this could indicate that they have actually lost the ancestral ability to plastically respond. Further evidence of age-related plasticity in egg size is evident from plots comparing clutch size and egg size with female size in one of our long-term study populations (Figure 8). In this population in 1990–1993, females produced body size-appropriate clutches throughout life, but the oldest females appeared to maintain their fecundity by decreasing egg size. It is important to note that this inferred plasticity is based only on cross-sectional studies thus far (females of different sizes and ages within a collection).

CLUTCH SIZE

Clutch size may be the most fundamental life-history trait, as it represents the maximum number of offspring that can result from a single reproductive event. As a result, the diversity and evolution of clutch sizes have been subjects of intense interest (Godfray *et al.*, 1991). As opposed to reproductive effort, clutch size is relatively easily defined, and relatively easily quantified if done so just before

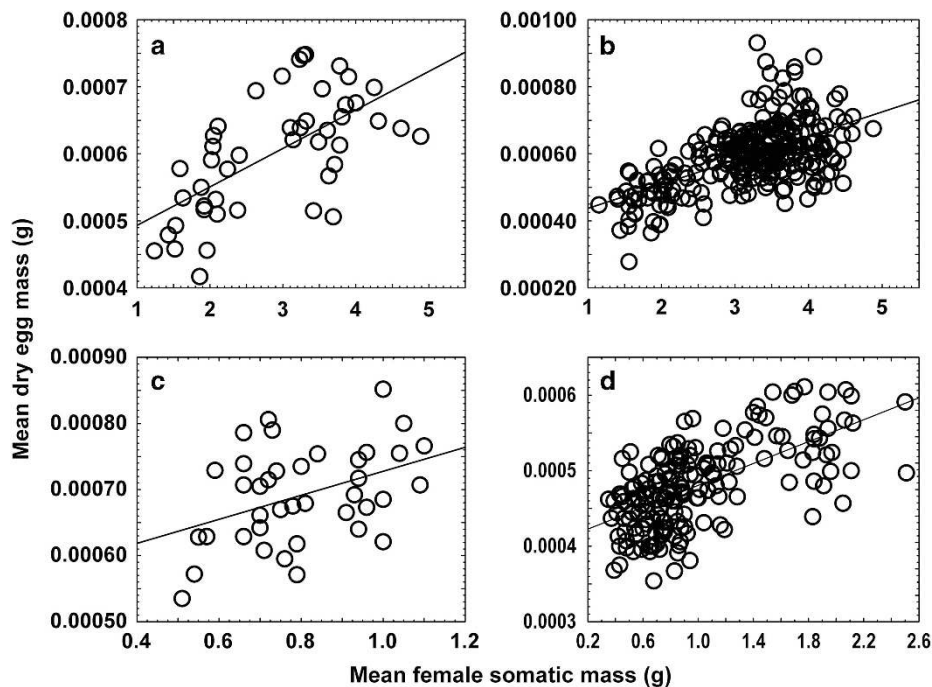


Figure 7 The relationship between egg size (mean dry mass) and female somatic mass (blotted, eviscerated) in four populations of Alaskan threespine stickleback. (a) Resurrection Bay marine; (b) Anchor River anadromous; (c) Daniels Lake fresh water; (d) Bear Paw Lake fresh water.

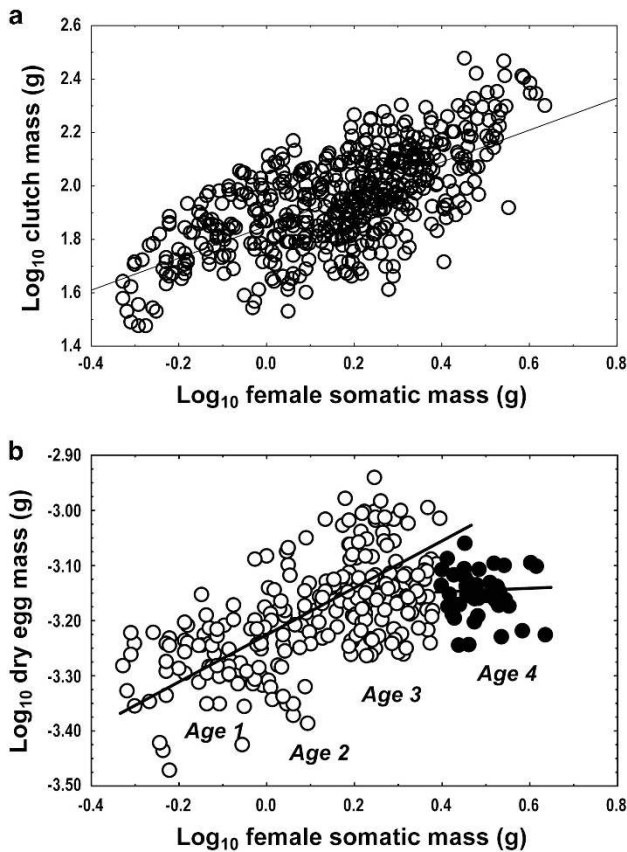


Figure 8 (a) The relationship between clutch size and female body size (3 years pooled) in the Solid Rock, Alaska, population. (b) The relationship between egg size and female body size in the same population for the same samples. Note that the oldest females (estimated to be age 4) produce appropriate clutches for their body size, but produce smaller eggs than expected.

reproduction. Plasticity for clutch size has been documented in a wide array of poikilotherms (Roff *et al.*, 1999; Klemetsen *et al.*, 2003), including numerous fish (Kennedy *et al.*, 2008; Evans *et al.*, 2010). Little clutch-to-clutch size fluctuation is reported in ectotherms, but there is evidence for long-term plasticity cued by energy acquisition during the prespawning period when the gonads are developing. In many exploited marine species, for example, downregulation of fecundity is common as the spawning season approaches (Kennedy *et al.*, 2007, 2008, 2009), and is likely an adaptive adjustment of spawning season fecundity to match nutrient levels.

Female stickleback are group-synchronous spawners (Wallace and Selman, 1979), rapidly and synchronously enlarging a clutch of eggs via vitellogenesis and then spawning all quickly in the nest of a single male. This process may be repeated as many as 9 times in a single season in freshwater populations (Wootton and Fletcher, 2009; JA Baker, personal observation), although oceanic populations appear to produce many fewer, though larger, clutches (Boule and FitzGerald, 1989; Dufresne *et al.*, 1990; RW King, personal observation). Clutch size mirrors reproductive effort in threespine stickleback (Baker *et al.*, 1998, 2008; Wootton and Fletcher, 2009), with population-level correlations between these traits ranging from 0.79 to 0.90 ($N=83$ populations; JA Baker, unpublished data). High correlations between these traits are typical of other species as well (Su *et al.*, 1997; Kinnison *et al.*, 2001). As with reproductive effort, clutch size is primarily a

function of female size, and under a normal ration does not change appreciably across spawnings (Wootton and Fletcher, 2009; JA Baker, personal observation). Clutch size does show a tradeoff with egg size, once female size effects have been removed (Baker *et al.*, 1998, 2005; Oravec and Reimchen, 2013). Stickleback may not be capable of downregulating clutch size to the extent observed in many marine species, but at present the potential for this to occur is unexplored.

It may be difficult to disentangle the effect of plasticity in reproductive effort from that in clutch size or seasonal fecundity in species like stickleback. Reproductive effort for a female of some specified size can be approximated as clutch size \times egg size. Plastic reductions in reproductive effort would likely be achieved via reductions in the number of follicles recruited into vitellogenesis (assuming no change in egg size) and, as a result, clutch size will decline proportionally to reproductive effort. The data cited earlier for downregulation of fecundity in many marine fishes could thus represent plasticity for level of reproductive effort instead. The distinction is important because traditional life-history theory distinguishes reproductive effort, clutch size and egg size as linked traits, but individually free to respond to natural selection (Jorgensen *et al.*, 2011; but see Winkler and Wallin, 1987).

PLASTICITY WITHIN AN OVERALL LIFE HISTORY

In this last section, we try to provide an illustration of how multivariate plasticity might play out within the life history of a fish like the threespine stickleback. For brevity and simplicity, we confine ourselves to events that might occur during the reproductive portion of the lifespan, although it is clear that events earlier in life may change how the reproductive portion of the life history plays out (Lee *et al.*, 2012). Plasticity for egg or offspring size is one of the most widely reported aspects of fish life histories, and here we use it as a central trait to explore how multivariate life histories may evolve. We first examine the effect of egg-size plasticity in a hypothetical species that possesses this ability. We then ask how stickleback might differ, given their apparent lack of short-term egg-size plasticity. We also explore the direction of evolution in fresh water given the known ancestral condition.

Contemporary phenotypic evolutionary ecology emphasizes the importance of the integration of multiple traits (Pigliucci, 2003; Reynolds, 2009; Robinson and Beckerman, 2013). DeWitt and Langerhans (2004) expand on this idea by differentiating between constitutive and plastic aspects of integrated phenotypes. The effect of plasticity, and the degree to which plasticity in one trait may be linked to plasticity in other traits, depends upon the limits of plasticity in each trait (Polačik *et al.*, 2014), and the forms of the functions relating specific trait values to fitness, modified by the effects of body size, somatic condition (Reznick and Ghalambor, 2001; Ghalambor *et al.*, 2007), density (Leips *et al.*, 2009) and perhaps growth rate. The increase in maternal fitness derived from a plastic response (for example, increased offspring survival or growth) should equal or exceed the expected loss because of negatively correlated traits (for example, the egg-size vs clutch-size tradeoff). This linkage has implications for the evolutionary trajectory of life-history traits, and for the evolution of plasticity in them.

If a plastic increase in egg size is cued by the environment (presumably to maintain fry fitness), then to preserve the original, presumably optimal, multivariate female life history, there must be a plastic decrease in reproductive effort (\sim fecundity) to balance the increased cost of reproduction. This is a logical adaptive tradeoff, as a plastic increase in offspring size would likely only occur when conditions (for example, food abundance) worsen. Without reducing

reproductive effort, future survival or reproduction would be compromised, lowering lifetime fitness. In fish that produce several clutches per season, the lowered reproductive effort could be accomplished via a reduction in the number of eggs produced per clutch, to reduce per-clutch cost (an immediate tradeoff), or a reduced number of clutches to reduce 'cumulative' seasonal reproductive cost (a 'delayed' tradeoff). Which of these tactics confers greater fitness depends upon their relative costs and benefits. Increased per-clutch effort seems most likely to exact relatively immediate survival costs (Siegel *et al.*, 1987; Rodewald and Foster, 1998; Sinervo, 1999), whereas longer-term costs may involve survival probability between reproductive season, or future reproduction costs mediated by lower growth or reduced condition (examples above) or physiological stress (Edward and Chapman, 2011; Schwartz and Bronikowski, 2011). The gain from a specified amount of expressed egg/offspring size plasticity will be determined only partly by the shape of the offspring size-fitness function (likely to be sigmoidal; Smith and Fretwell, 1974; Jorgenson *et al.*, 2011). In this example the amount of expressible plasticity in egg size will also be constrained by the shape of the function relating the level of reproductive effort to its cost. The shape of this cost function is less clear. In addition, the total fitness gain in the above example will depend upon female size, as in organisms like stickleback both

fecundity (always) and egg size (often) are positive functions of female size.

Female stickleback show a complex pattern of plasticity across the traits we examined, and as indeterminate growers the life-history traits are also strongly affected by body size (Wootton 1973a; Baker *et al.*, 1998, 2008). A typical set of correlations among life-history traits, female size and somatic condition are shown in Figure 9. Female threespine stickleback show no clutch-to-clutch plasticity in egg size and, therefore, if ration level for females is reduced for a length of time sufficient to deplete energy capital, stickleback are unable to increase egg size to buffer potential environmental effects on their offspring. Adaptive plasticity may be expressible only by reduction in reproductive effort that, as indicated above, is probably mediated in one of (or a combination of) the three ways: (1) via a reduction in the number of follicles recruited into vitellogenesis (that is, reduced clutch size) as body size/energy content declines, (2) via a longer interclutch interval or (3) by earlier cessation of reproduction (produce fewer seasonal clutches). If fluctuations in adult ration are mirrored by reductions in fry ration (via density effects, for example; Allen *et al.*, 2008), this means that fry fitness would also be reduced as the environment now requires a larger fry while, in addition, clutch size is also reduced—a double hit to within-season fitness. Thus, the principal fitness benefit of life-history plasticity must be survival to reproduce in a subsequent

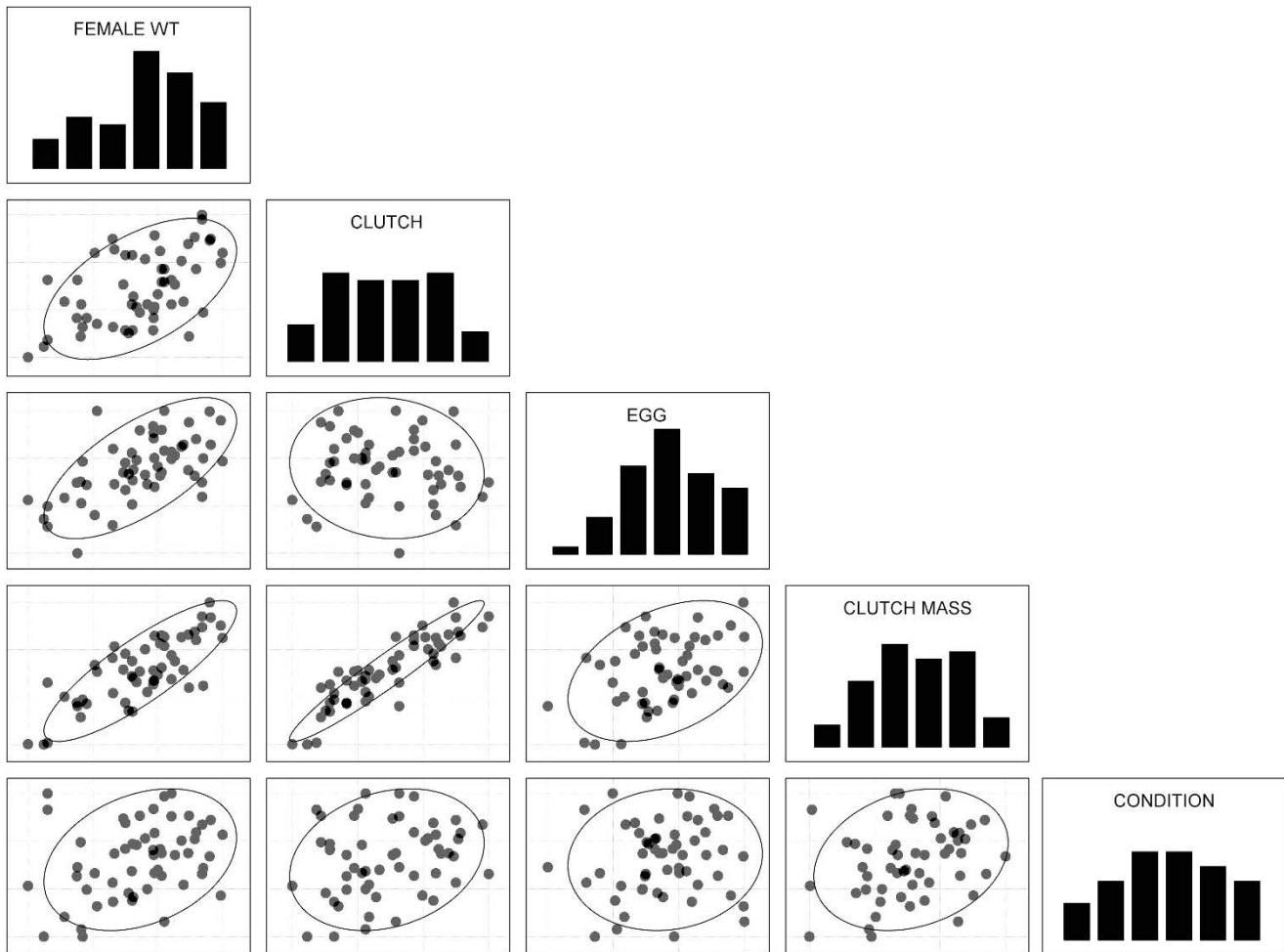


Figure 9 Matrix plot showing the relationships between female life-history traits, body mass and somatic condition in Big Beaver Lake, Alaska. The 99% probability ellipses are plotted for each pairwise combination of traits. Correlations were based on log values for female somatic mass, clutch size, egg size and clutch mass. Condition was the residual from a regression of log somatic mass on log SL.

year. This option is available only to populations that can spawn in multiple years, and as a result annual and longer-lived stickleback populations could evolve differently with respect to their expressible life-history plasticity.

The apparently limited within-season reproductive plasticity suggests that much of the annual variation seen in stickleback populations (Baker *et al.*, 2008) might derive from variation in the relative abundance of different genetically based phenotypes in response to fluctuating natural selection. The oceanic stickleback that colonized freshwater habitats following the most recent glaciation, and which gave rise to the present-day adaptive radiation, appears to possess no appreciable clutch-to-clutch plasticity for egg size. As suggested earlier, this is likely because of the lack of an appropriate cue to fry conditions on the spawning grounds. As a result, freshwater populations appear to lack this plastic ability as well, and to date there is no indication that any population has evolved this ability, although admittedly few have been studied in sufficient detail. This situation appears parallel to that shown by brown trout, in that local adaptation to different streams was detected without substantial evolution of plasticity (Rogell *et al.*, 2012).

About half of all stickleback populations we have studied in Alaska and British Columbia possess what we are calling season-to-season plasticity in egg size, expressed as a positive relationship between egg size and female size or age. The phenomenon is widespread (Roff, 1992), but a general explanation for why egg/offspring size should increase with female size/age has not yet been found, although several theoretical models (for example, Parker and Begon; Falster *et al.*, 2008; Kindsvater and Otto, 2014) suggest some possibilities. Unfortunately, we can suggest no explanation for stickleback that fits with any of the possibilities in their models. Despite the lack of an explanation, the interesting fact is that the positive relationship is ancestral, and it appears that perhaps half of all populations no longer express it. This loss of response is almost certainly because of relaxed selection by some unknown factor, and understanding the conditions that differ between these types of populations may help to resolve the general issue, although to date this has not been attempted.

In summary, the threespine stickleback adaptive radiation has been widely used to investigate both adaptive change and phenotypic plasticity in behavioral and morphological traits. Similarly, presumably adaptive variation in life history has been documented for many populations. However, the potential for using this system to understand life-history plasticity, and to contrast it to evolutionary change, has not been widely appreciated. The widespread geographic and habitat distribution (Bell and Foster, 1994), the tremendous variation of all life-history traits (Baker *et al.*, 2008) and the relative ease of studying stickleback in both nature and the laboratory make this species ideal for such investigations.

DATA ARCHIVING

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.c69m7>

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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- Adolph SC, Porter PP (1996). Growth, seasonality, and lizard life histories: age and size at maturity. *Oikos* **77**: 267–278.
- Ali M, Wootton RJ (1999a). Coping with resource variation: effect of constant and variable intervals between feeding on reproductive performance at first spawning of female three-spined sticklebacks. *J Fish Biol* **55**: 211–220.
- Ali M, Wootton RJ (1999b). Effect of variable food levels on reproductive performance of breeding female three-spined sticklebacks. *J Fish Biol* **55**: 1040–1053.
- Allen RM, Buckley YM, Marshall DJ (2008). Offspring size plasticity in response to intraspecific competition: an adaptive maternal effect across life-history stages. *Am Nat* **171**: 225–237.
- Anderson JT (1988). A review of size dependent survival during pre-recruit stages of fish in relation to recruitment. *J Northwest Atl Fish Sci* **8**: 55–66.
- Anguilleta MJ Jr., Steury TD, Sears MW (2004). Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integr Comp Biol* **44**: 498–509.
- Arendt JD (1997). Adaptive intrinsic growth rates: an integration across taxa. *Q Rev Biol* **72**: 149–177.
- Auer SK (2010). Phenotypic plasticity in adult life-history strategies compensates for a poor start in life in Trinidadian guppies (*Poecilia reticulata*). *Am Nat* **176**: 818–829.
- Baker JA, Foster SA, Heins DC, Bell MA, King RW (1998). Variation in female life-history traits among Alaskan populations of the threespine stickleback, *Gasterosteus aculeatus*, L. (Pisces: Gasterosteidae). *Biol J Linn Soc Lond* **63**: 141–159.
- Baker JA, Foster SA (2002). Phenotypic plasticity for life-history traits in a stream population of the threespine stickleback, *Gasterosteus aculeatus* L. *Ecol Freshw Fish* **11**: 20–29.
- Baker JA, Cresko WC, Heins DC, Foster SA (2005). Life-history differentiation of benthic and limnetic ecotypes in a polytypic population of threespine stickleback (*Gasterosteus aculeatus*). *Evol Ecol Res* **7**: 121–131.
- Baker JA, Heins DC, Foster SA, King RW (2008). An overview of life-history variation in female threespine stickleback. *Behaviour* **145**: 579–602.
- Baker JA, Räsänen K, Moore J-S, Hendry AP (2013). Genetic and plastic contributions to trait divergence between parapatric habitats: female life-history traits in threespine stickleback within the Misty Lake System. *Evol Ecol Res* **15**: 473–487.
- Barot S, Heino M, O'Brien L, Dieckmann U (2004). Long-term trend in the maturation reaction norm of two cod stocks. *Ecol Appl* **14**: 1257–1271.
- Bashey F (2006). Cross-generational environmental effects and the evolution of offspring size in the Trinidadian guppy *Poecilia reticulata*. *Evolution* **60**: 348–361.
- Bell MA, Foster SA (1994). Introduction to the evolutionary biology of the threespine stickleback. In: Bell MA, Foster SA (eds) *The Evolutionary Biology of the Threespine Stickleback*. Oxford University Press: Oxford, pp 1–27.
- Berg OK, Hendry AP, Svendsen B, Bech C, Arneklev JV, Lohrmann A (2001). Maternal provisioning of offspring and the use of those resources during ontogeny: variation within and between Atlantic Salmon families. *Funct Ecol* **15**: 13–23.
- Bernardo J (1996). The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. *Am Zool* **36**: 216–236.
- Bertschy KA, Fox MG (1999). The influence of age-specific survivorship on pumpkinseed sunfish life histories. *Ecology* **80**: 2299–2313.
- Berrigan D, Koella JC (1994). The evolution of reaction norms: simple models for age and size at maturity. *J Evol Biol* **7**: 549–566.
- Boule V, FitzGerald GJ (1989). Effects of constant and fluctuating temperatures on egg production in the threespine stickleback (*Gasterosteus aculeatus*). *Can J Zool* **67**: 1599–1602.
- Bourdeau PE (2012). Intraspecific trait cospecialization of constitutive and inducible morphological defences in a marine snail from habitats with different predation risk. *J Anim Ecol* **81**: 849–858.
- Brown-Peterson NJ, Heins DC (2009). Interspawning interval of wild three-spined stickleback *Gasterosteus aculeatus* in Alaska. *J Fish Biol* **74**: 2299–2312.
- Brown GP, Shine R (2007). Repeatability and heritability of reproductive traits in free-ranging snakes. *J Evol Biol* **20**: 588–596.
- Burd M, Read J, Sanson GD, Jaffre T (2006). Age-size plasticity for reproduction in monocarpic plants. *Ecology* **87**: 2755–2764.
- Casas JS, Pincebourde N, Mandon F, Vannier R, Pujol R, Giron D (2005). Lifetime nutrient dynamics reveal simultaneous capital and income breeding in a parasitoid. *Ecology* **86**: 545–554.
- Copp GH, Fox MG (2007). Growth and life history traits of introduced pumpkinseed (*Lepomis gibbosus*) in Europe, and the relevance to its potential invasiveness. In: Gherardi F (ed) *Biological Invaders in Inland Waters: Profiles, Distribution, and Threats* vol. 2, *Invasive Nature—Springer Series in Invasion Ecology*. Springer: Netherlands, pp 289–306.
- Copp GH, Kovac V, Blacker F (2002). Differential reproductive allocation in sympatric stream-dwelling sticklebacks. *Gasterosteus aculeatus* and *Pungitius pungitius* **51**: 337–351.

- Crespi BJ, Teo R (2002). Comparative phylogenetic analysis of the evolution of semelparity and life history in salmonid fishes. *Evolution* **56**: 1008–1020.
- Crivelli AJ, Britton RH (1987). Life history adaptations of *Gasterosteus aculeatus* in a Mediterranean wetland. *Environ Biol Fish* **18**: 109–125.
- Day T, Rowe L (2002). Developmental thresholds and the evolution of reaction norms for age and size at life-history transitions. *Am Nat* **159**: 338–350.
- DeWitt TJ (1998). Costs and limits of phenotypic plasticity: tests with predator-induced morphology and life history in a freshwater snail. *J Evol Biol* **11**: 465–480.
- DeWitt TJ, Sih A, Wilson DS (1998). Costs and limits of phenotypic plasticity. *Trends Ecol Evol* **13**: 77–81.
- DeWitt TJ, Scheiner S (2004). Phenotypic variation from single genotypes. In: DeWitt TJ, Scheiner SM (eds) *Phenotypic Plasticity: Functional and Conceptual Approaches*. Oxford University Press: New York, pp 1–9.
- DeWitt TJ, Langerhans RB (2004). Integrated solutions to environmental heterogeneity: theory of multimoment reaction norms. In: DeWitt TJ, Scheiner SM (eds). *Phenotypic Plasticity: Functional and Conceptual Approaches*. Oxford University Press: New York, NY, USA, pp 98–111.
- Donelson JM, McCormick MI, Munday PL (2008). Parental condition affects early life-history in a coral reef fish. *J Exp Mar Biol Ecol* **360**: 109–116.
- Duarte CM, Alcaraz M (1989). To produce many small or few large eggs: a size-independent reproductive tactic of fish. *Oecologia* **80**: 401–404.
- Dufresne F, FitzGerald GJ, Lachance S (1990). Age and size-related differences in reproductive success and reproductive costs in threespine sticklebacks (*Gasterosteus aculeatus*). *Behav Ecol* **1**: 140–147.
- Edward DA, Chapman T (2011). Mechanisms underlying reproductive trade-offs: costs of reproduction. In: Flatt T, Heyland A (eds) *Mechanisms of Life History Evolution*. Oxford University Press: Oxford, pp 137–152.
- Einum S, Fleming IA (2000a). Selection against late emergence and small offspring in Atlantic Salmon (*Salmo salar*). *Evolution* **54**: 628–639.
- Einum S, Fleming IA (2000b). Highly fecund mothers sacrifice offspring survival to maximize fitness. *Nature* **405**: 565–567.
- Evans JP, Box TM, Brooshoff P, Tatler JR, Fitzpatrick JL (2010). Females increase egg deposition in favor of large males in the rainbowfish, *Melanotaenia australis*. *Behav Ecol* **21**: 465–469.
- Falster DS, Moles AT, Westoby M (2008). A general model for the scaling of offspring size and adult size. *Am Nat* **172**: 299–317.
- Fletcher DA, Wootton RJ (1995). A hierarchical response to differences in ration size in the reproductive performance of female three-spined sticklebacks. *J Fish Biol* **46**: 657–668.
- Forsman A (2015). Rethinking phenotypic plasticity and its consequences for individuals, populations and species. *Heredity (Edinb)* **115**: 276–284.
- Foster SA (2013). Evolutionary insights from behavioural geography: plasticity, evolution and responses to rapid environmental change. *Evol Ecol Res* **15**: 705–731.
- Foster SA, Wund MA (2011). Ancestral plasticity and adaptive evolution in the threespine stickleback radiation. In: Hallgrímsson B, Hall BK (eds) *Epigenetics: Linking Genotype and Phenotype in Development and Evolution*. University of California Press: Los Angeles, CA, USA, pp 317–336.
- Foster SA, Scott RJ, Cresko WA (1998). Nested biological variation and speciation. *Phil Trans R Soc Lond B* **353**: 207–218.
- Foster SA, Wund MA, Baker JA (2015). Evolutionary influences of plastic behavioral responses to environmental challenges in an adaptive radiation. *Integr Comp Biol*; e-pub ahead of print 10 July 2015.
- Galloway LF, Etterson JR (2009). Plasticity to canopy shade in a monocarpic herb: within- and between-generation effects. *New Phytol* **182**: 103–112.
- Gagliano M, McCormick MI (2007). Maternal condition influences phenotypic selection on offspring. *J Anim Ecol* **76**: 174–182.
- Ghalambor CK, McKay JK, Carroll SP, Reznick DN (2007). Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Funct Ecol* **21**: 394–407.
- Godfray HCJ, Partridge L, Harvey PH (1991). Clutch size. *Annu Rev Ecol Syst* **22**: 409–429.
- Grimaldi AA, Insausti P, Vasellati V, Striker GG (2005). Constitutive and plastic root traits and their role in differential tolerance to soil flooding among coexisting species of a lowland grassland. *Int J Plant Sci* **166**: 805–813.
- Gunderson DR (1997). Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes. *Can J Fish Aquat Sci* **54**: 990–998.
- Gunderson DR, Dygert PH (1988). Reproductive effort as a predictor of natural mortality rate. *J Cons Int Explor Mer* **44**: 200–209.
- Hamel S, Côté SD, Gaillard J-M, Festa-Bianchet M (2009). Individual variation in reproductive costs of reproduction: high-quality females always do better. *J Anim Ecol* **78**: 143–151.
- Hamel S, Yoccoz NG, Gaillard J-M (2014). A standardized approach to estimate life history tradeoffs in evolutionary ecology. *Oikos* **123**: 151–160.
- Heins DC, Baker JA (1993). Reproductive biology of the brighteye darter, *Etheostoma lynceum* (Teleostei: Percidae), from the Homochitto River, Mississippi. *Ichthyol Explor Freshw* **4**: 11–20.
- Heins DC, Baker JA (2003). Reduction in egg size in natural populations of threespine stickleback infected with a cestode macroparasite. *J Parasitol* **89**: 1–6.
- Heins DC, Baker JA (2008). The stickleback-*Schistocephalus* host-parasite system as a model for understanding the effect of a macroparasite on host reproduction. *Behaviour* **145**: 625–645.
- Heins DC, Baker JA (2014). Fecundity compensation and fecundity reduction among populations of the three-spined stickleback infected by *Schistocephalus solidus* in Alaska. *Parasitology* **141**: 1088–1096.
- Heins DC, Singer SS, Baker JA (1999). Virulence of the cestode *Schistocephalus solidus* and reproduction in infected threespine stickleback, *Gasterosteus aculeatus*. *Can J Zool* **77**: 1967–1974.
- Heins DC, Birden EL, Baker JA (2010). Host mortality and variability in epizootics of *Schistocephalus solidus* infecting the threespine stickleback *Gasterosteus aculeatus*. *Parasitology* **137**: 1681–1686.
- Heins DC, Barry KA, Petrauskas LA (2014). Consistency of host responses to parasitic infection in the three-spined stickleback fish infected by the diphyllbothriidean cestode *Schistocephalus solidus*. *Biol J Linn Soc Lond* **113**: 958–968.
- Henderson BA, Morgan GE (2002). Maturation of walleye by age, size and surplus energy. *J Fish Biol* **61**: 999–1011.
- Hohenlohe PA, Bassem S, Currey M, Cresko WA (2012). Extensive linkage disequilibrium and parallel adaptive divergence across threespine stickleback genomes. *Philos Trans R Soc B Biol Sci* **367**: 395–408.
- Hooker LJ (1988). Sexual size dimorphism in two populations of threespine stickleback (*Gasterosteus aculeatus*): female body size and seasonal fecundity in a multiple spawning species. Unpublished M.Sc. Thesis, University of British Columbia, Vancouver, British Columbia, Canada.
- Houde ED (1987). Fish early life dynamics and recruitment variability. *Am Fish Soc Symp Ser* **2**: 17–29.
- Houston AI, Stephens PA, Boyd IL, Harding KC, McNamara JM (2007). Capital or income breeding? A theoretical model of female reproductive strategies. *Behav Ecol* **18**: 241–250.
- Hutchings JA (1999). Influence of growth and survival costs of reproduction on Atlantic cod, *Gadus morhua*, population growth rate. *Can J Fish Aquat Sci* **56**: 1612–1623.
- Hutchings JA, Jones MEB (2008). Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. *Can J Fish Aquat Sci* **55**: 22–47.
- Inness CLW, Metcalfe NB (2008). The impact of dietary restriction, intermittent feeding and compensatory growth on reproductive investment and lifespan in a short-lived fish. *Proc R Soc B* **275**: 1703–1708.
- Jorgensen C, Auer SK, Reznick DN (2011). A model for optimal offspring size in fish, including live-bearing and parental effects. *Am Nat* **117**: E119–E135.
- Karve AD, von Hippel FA, Baker JA (2013). Female life-history traits in a species pair of threespine stickleback in Mud Lake, Alaska. *Evol Ecol Res* **15**: 171–187.
- Kennedy J, Witthames PR, Nash RDM (2007). The concept of fecundity regulation in plaice (*Pleuronectes platessa*) tested on three Irish Sea spawning populations. *Can J Fish Aquat Sci* **64**: 587–601.
- Kennedy J, Witthames PR, Nash RDM, Fox CJ (2008). Is fecundity in plaice (*Pleuronectes platessa* L.) down-regulated in response to reduced food intake during autumn? *J Fish Biol* **72**: 78–92.
- Kennedy J, Gunderson AC, Boje J (2009). When to count your eggs: is fecundity in Greenland halibut (*Reinhardtius hippoglossoides* W.) down-regulated? *Fish Res* **100**: 260–265.
- Kindsvater HK, Otto SP (2014). The evolution of offspring size across life-history Stages. *Am Nat* **184**: 543–555.
- Kingsolver JG, Hoekstra HE, Hoekstra JM, Berrigan D, Vignieri SN, Hill C et al. (2001). The strength of phenotypic selection in natural populations. *Am Nat* **157**: 245–261.
- Kinnison MT, Unwin MJ, Hendry AP, Quinn TP (2001). Migratory costs and the evolution of egg size and number in introduced and indigenous salmon populations. *Evolution* **55**: 1656–1667.
- Klemetsen A, Amundsen PA, Dempson JB, Jonsson B, Jonsson N, O'Connell MF et al. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic char *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecol Freshw Fish* **12**: 1–59.
- Koivula M, Koskela E, Mappes T, Oksanen TA (2003). Cost of reproduction in the wild: manipulation of reproductive effort in the bank vole. *Ecology* **84**: 398–405.
- Kolm N (2001). Females produce larger eggs for large males in a paternal mouthbrooding fish. *Proc R Soc Lond B* **268**: 2229–2234.
- Kuparinen A, Hardie DC, Hutchings JA (2011). Evolutionary and ecological feedbacks of the survival cost of reproduction. *Evol Appl* **5**: 245–255.
- Lancaster LT, McAdam AG, Sinerov B (2010). Maternal adjustment of egg size organizes alternative escape behaviors, promoting adaptive phenotypic integration. *Evolution* **64**: 1607–1621.
- Lee W-S, Monaghan P, Metcalfe NB (2012). The pattern of early growth trajectories affects adult breeding performance. *Ecology* **93**: 902–912.
- Leips J, Richardson JLM, Rodd FH, Travis J (2009). Adaptive maternal adjustments of offspring size in response to conspecific density in two populations of the least killifish, *Heterandria formosa*. *Evolution* **63**: 1341–1347.
- Lourdais O, Bonnet X, Shine R, Denardo D, Naulleau G, Guillon M (2002). Capital-breeding and reproductive effort in a variable environment: a longitudinal study of a viviparous snake. *J Anim Ecol* **71**: 470–479.
- Madsen T, Shine R (1999). The adjustment of reproductive threshold to prey abundance in a capital breeder. *J Anim Ecol* **68**: 571–580.
- Marshall DJ, Uller T (2007). When is a maternal effect adaptive? *Oikos* **116**: 1957–1963.
- Marty L, Dieckmann U, Rochet M-J, Ernande B (2011). Impact of environmental covariation in growth and mortality on evolving maturation reaction norms. *Am Nat* **177**: E98–E118.
- McKinnon JS, Rundle HD (2002). Speciation in nature: the threespine stickleback model systems. *Trends Ecol Evol* **17**: 480–488.
- McPhail J (1977). Inherited interpopulation differences in size at first reproduction in threespine stickleback, *Gasterosteus aculeatus* L. *Heredity* **38**: 53–60.
- Merila J, Laurila A, Laugen AT, Rasanen K, Pakkala M (2000). Plasticity in age and size at metamorphosis in *Rana temporaria* – comparison of high and low latitude populations. *Ecography* **23**: 457–465.
- Messler A, Wund MA, Baker JA, Foster SA (2007). The effects of relaxed and reversed selection by predators on the antipredator behavior of the threespine stickleback, *Gasterosteus aculeatus*. *Ethology* **113**: 953–963.
- Metcalfe NB, Monaghan P (2003). Growth versus lifespan: perspectives from evolutionary ecology. *Exp Gerontol* **38**: 935–940.

- Morgan MJ (2004). The relationship between fish condition and the probability of being mature in American plaice (*Hippoglossoides platessoides*). *ICES J Mar Sci* **61**: 64–70.
- Moore PJ, Attisano A (2011). Oosorption in response to poor food: complexity in the trade-off between reproduction and survival. *Ecol Evol* **1**: 37–45.
- Moran NA (1992). The evolutionary maintenance of alternative phenotypes. *Am Nat* **139**: 971–989.
- Morita K, Fukuwaka M (2006). Does size matter most? The effect of growth history on probabilistic reaction norm for salmon maturation. *Evolution* **60**: 1516–1521.
- Mousseau TA, Roff DA (1987). Natural selection and the heritability of fitness components. *Heredity* **59**: 181–197.
- Mousseau TA, Fox CW (1998). The adaptive significance of maternal effects. *Trends Ecol Evol* **13**: 403–407.
- Narver DW (1969). Phenotypic variation in threespine sticklebacks (*Gasterosteus aculeatus*) of the Chignik River System, Alaska. *J Fish Res Board Can* **26**: 405–412.
- Nylin S, Gotthard K (1998). Plasticity in life-history traits. *Annu Rev Entomol* **43**: 63–83.
- Oravec TJ, Reimchen TE (2013). Divergent reproductive life histories in Haida Gwaii stickleback (*Gasterosteus* spp.). *Can J Zool* **91**: 17–24.
- Padilla DK, Adolph SC (1996). Plastic inducible morphologies are not always adaptive: the importance of time delays in a stochastic environment. *Ecol Evol* **10**: 105–117.
- Parker GA, Begon M (1986). Optimal egg size and clutch size: effects of environment and maternal phenotype. *Am Nat* **128**: 573–592.
- Picard P Jr, Dodson JL, FitzGerald GJ (1990). Habitat segregation among the age groups of *Gasterosteus aculeatus* (Pisces: Gasterosteidae) in the middle St. Lawrence estuary, Canada. *Can J Zool* **68**: 1202–1208.
- Pampoulie C, Bouchereau JL, Rosecchi E, Poizat G, Crivelli AJ (2000). Annual variations in the reproductive traits of *Pomatoschistus microps* in a Mediterranean lagoon undergoing environmental changes: evidence of phenotypic plasticity. *J Fish Biol* **57**: 1441–1452.
- Perez KO, Munch SB (2010). Extreme selection on size in the early lives of fish. *Evolution* **64**: 2450–2457.
- Pigliucci M (2003). Phenotypic integration: studying the ecology and evolution of complex phenotypes. *Ecol Lett* **6**: 265–272.
- Poizat G, Rosecchi E, Crivelli AJ (1999). Empirical evidence of a trade-off between reproductive effort and expectation of future reproduction in female three-spined sticklebacks. *Proc R Soc Lond Ser B Biol Sci* **266**: 1543–1548.
- Polačik M, Blažek R, Režucha R, Vrtiliek M, Terzibasí Tozzini E, Reichard M (2014). Alternative intrapopulation life-history strategies and their trade-offs in an African annual fish. *J Evol Biol* **27**: 854–865.
- Reger RD, Pinney DS (1996). Late Wisconsin glaciation of the Cook Inlet Region with emphasis on the Kenai lowland and implications for early peopling. In: David NY, Davids WE (eds) *Adventures Through Time: Readings in the Anthropology of Cook Inlet, Alaska*. Cook Inlet Historical Society: Anchorage, pp 15–35.
- Relyea RA (2002). Costs of phenotypic plasticity. *Am Nat* **159**: 272–282.
- Reznick D, Yang AP (1993). The influence of fluctuating resources on life history: patterns of allocation and plasticity in female guppies. *Ecology* **74**: 2011–2019.
- Reznick DA, Bryga H, Endler JA (1990). Experimentally induced life-history evolution in a natural population. *Nature* **346**: 357–359.
- Reznick D, Nunney L, Tessler A (2000). Big houses, big cars, superfleas and the costs of reproduction. *Trends Ecol Evol* **15**: 421–425.
- Reznick DN, Ghalambor CK (2001). The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica* **112–113**: 183–198.
- Reynolds RJ, Dudash MR, Fenster CB (2009). Multiyear study of multivariate linear and nonlinear phenotypic selection on floral traits of hummingbird-pollinated *Silene virginica*. *Evolution* **64**: 358–369.
- Rideout RM, Rose GA, Burton MPM (2005). Skipped spawning in female iteroparous fishes. *Fish Fish* **6**: 50–72.
- Robinson M, Beckerman AP (2013). Quantifying multivariate plasticity: genetic variation in resource acquisition drives plasticity in resource allocation to components of life history. *Ecol Lett* **16**: 281–290.
- Rodd FH, Reznick DN, Sokolowski MB (1997). Phenotypic plasticity in the life history traits of guppies: responses to social environment. *Ecology* **78**: 419–433.
- Rodewald AD, Foster SA (1998). Effects of gravidity on habitat use and antipredator behavior in three-spined sticklebacks. *J Fish Biol* **52**: 973–984.
- Roff DA (1992). *The Evolution of Life Histories: Theory and Analysis*. Chapman and Hall: New York.
- Roff D (2000). Trade-offs between growth and reproduction: an analysis of the quantitative genetic evidence. *J Evol Biol* **13**: 434–445.
- Roff DA (2002). *Life History Evolution*. Sinauer Associates, Inc.: Sunderland, MA.
- Roff DA, Tucker J, Stirling G, Fairbairn DJ (1999). The evolution of threshold traits: effects of selection on fecundity and correlated response in wing dimorphism in the sand cricket. *J Evol Biol* **12**: 535–546.
- Rogell B, Dannewitz J, Palm S, Petersson E, Dahl J, Prestegard T et al. (2012). Strong divergence in trait means but not in plasticity across hatchery and wild populations of sea-run brown trout *Salmo trutta*. *Molecular Ecology* **21**: 2963–2976.
- Rundle HD, Nagel L, Boughman JW, Schluter D (2000). Natural selection and parallel speciation in sympatric sticklebacks. *Science* **287**: 306–308.
- Saito T, Nakano S (1999). Reproductive-timing-dependent alternation of offspring life histories in female threespine sticklebacks. *Can J Zool* **77**: 1314–1321.
- Schwartz TS, Bronikowski AM (2011). Molecular stress pathways and the evolution of life histories in reptiles. In: Flatt T, Heyland A (eds) *Mechanisms of Life History Evolution*. Oxford University Press: Oxford, pp 193–209.
- Schluter D (2000). *The Ecology of Adaptive Radiation*. Oxford University Press: Oxford.
- Segers FH, Taborsky B (2011). Egg size and food abundance interactively affect juvenile growth and behavior. *Funct Ecol* **25**: 166–176.
- Shine R (1980). “Costs” of reproduction in reptiles. *Oecologia* **46**: 92–100.
- Siegel RA, Huggins MM, Ford NB (1987). Reduction in locomotor ability as a cost of reproduction in snakes. *Oecologia* **73**: 481–485.
- Simons AM (2008). One big, and many small reasons that direct selection on offspring number is still open for discussion. *J Evol Biol* **21**: 642–645.
- Sinervo B (1999). Mechanistic analysis of natural selection and a refinement of Lack’s and Williams’s principles. *Am Nat* **154**: S26–S42.
- Skjærraasen JE, Nash RDM, Korsbrette K, Fonn M, Nilsen T, Kennedy J et al. (2012). Frequent skipped spawning in the world’s largest cod population. *Proc Natl Acad Sci USA* **109**: 8995–8999.
- Smith CC, Fretwell SD (1974). The optimal balance between size and number of offspring. *Am Nat* **108**: 499–506.
- Snell-Rood EC (2013). An overview of the evolutionary causes and consequences of behavioural plasticity. *Anim Behav* **85**: 1004–1011.
- Snyder RJ (1991). Quantitative genetic analysis of life histories in two freshwater populations of threespine stickleback. *Copeia* **1991**: 526–529.
- Snyder RJ, Dingle H (1989). Adaptive, genetically based differences in life history between estuary and freshwater threespine sticklebacks (*Gasterosteus aculeatus* L.). *Can J Zool* **67**: 2448–2454.
- Stearns SC (1989). The evolutionary significance of phenotypic plasticity. *Bioscience* **39**: 436–445.
- Sokolowska E, Kulczykowska E (2006). Annual reproductive cycle in two free living populations of three-spined stickleback (*Gasterosteus aculeatus* L.): patterns of ovarian and testicular development. *Oceanologia* **48**: 103–124.
- Stephens PA, Boyd L, McNamara JM, Houston AI (2009). Capital breeding and income breeding: their meaning, measurement, and worth. *Ecology* **90**: 2057–2067.
- Su G-S, Liljedahl LE, Gall GAE (1997). Effects of inbreeding on growth and reproductive traits in rainbow trout (*Oncorhynchus mykiss*). *Aquaculture* **142**: 139–148.
- Teder T, Vellau H, Tammaru T (2014). Age and size at maturity: a quantitative review of diet-induced reaction norms in insects. *Evolution* **68**: 3217–3228.
- Thorpe JE (2007). Maturation responses of salmonids to changing developmental opportunities. *Mar Ecol Prog Ser* **335**: 285–288.
- Trippel EA, Harvey HH (1989). Missing opportunities to reproduce: an energy dependent or fecundity gaining strategy in white sucker (*Catostomus commersoni*)? *Can J Zool* **67**: 2180–2188.
- Tsikliris AC, Antonopoulou E, Stergiou K (2007). A phenotypic trade-off between previous growth and present fecundity in round sardinella *Sardinella aurita*. *Popul Ecol* **49**: 221–227.
- Vrtiliek M, Reichard M (2014). Highly plastic allocation to growth and reproduction in females of an African annual fish. *Ecol Freshw Fish*; doi:10.1111/eff.12175.
- Vitousek MN, Mitchell MA, Romero LM, Awerman J, Wikelski M (2010). To breed or not to breed: physiological correlates of reproductive status in a facultatively biennial iguanid. *Horm Behav* **57**: 140–146.
- Wallace RA, Selman K (1979). Physiological aspects of oogenesis in two species of sticklebacks, *Gasterosteus aculeatus* L. and *Apeltes quadracus* (Mitchill). *J Fish Biol* **14**: 551–564.
- Weeks SC, Quattro JM (1991). Life-history plasticity under resource stress in a clonal fish (Poeciliidae: *Poeciliopsis*). *J Fish Biol* **39**: 485–494.
- Winkler DW, Wallin K (1987). Offspring size and number: a life history model linking effort per offspring and total effort. *Am Nat* **129**: 708–720.
- Wisenden BD (1993). Female convict cichlids adjust gonadal investment in current reproduction in response to relative risk of brood predation. *Can J Zool* **71**: 251–256.
- Wootton RJ (1973a). Fecundity of the three-spined stickleback, *Gasterosteus aculeatus* (L.). *J Fish Biol* **5**: 683–688.
- Wootton RJ (1973b). The effect of size of food ration on egg production in the female three-spined stickleback, *Gasterosteus aculeatus* L. *J Fish Biol* **5**: 89–96.
- Wootton RJ (1977). Effect of food limitation during the breeding season on the size, body components and egg production of female sticklebacks (*Gasterosteus aculeatus*). *J Anim Ecol* **46**: 823–834.
- Wootton RJ (1994). Energy allocation in the threespine stickleback. In: Bell MA, Foster SA (eds), *The Evolutionary Biology of the Threespine Stickleback*. Oxford University Press: Oxford, pp 114–143.
- Wootton RJ, Allen JRM, Cole SJ (1980). Energetics of the annual reproductive cycle in female sticklebacks, *Gasterosteus aculeatus* L. *J Fish Biol* **17**: 387–394.
- Wootton RJ, Evans GW (1976). Cost of egg production in the three-spined stickleback (*Gasterosteus aculeatus* L.). *J Fish Biol* **8**: 385–395.
- Wootton RJ, Fletcher DA (2009). Effect of spawning number and ration on reproductive performance of the batch-spawning three-spined stickleback *Gasterosteus aculeatus*. *J Fish Biol* **75**: 618–629.
- Wootton RJ, Evans GW, Mills L (1978). Annual cycle in female three-spined sticklebacks (*Gasterosteus aculeatus* L.) from an upland and lowland population. *J Fish Biol* **12**: 331–343.
- Wund MA, Baker JA, Clancy B, Golub J, Foster SA (2008). A test of the ‘flexible stem’ model of evolution: ancestral plasticity, genetic accommodation, and morphological divergence in the threespine stickleback radiation. *Am Nat* **172**: 449–462.
- Wund MA, Valena S, Wood S, Baker JA (2012). Ancestral plasticity and allometry in threespine stickleback fish reveal phenotypes associated with derived, freshwater ecotypes. *Biol J Linn Soc USA* **105**: 573–583.