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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; Vrtilek 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 THREESPINE 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 (Bertechy 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,

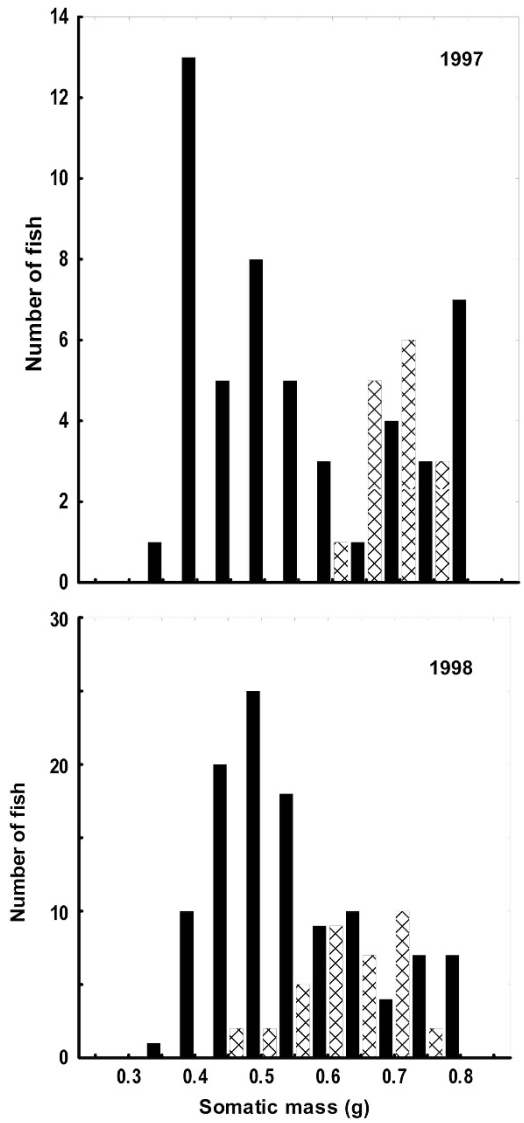

Figure 1 Size frequency of age-1 female threespine stickleback in Cornelius Lake, Alaska. Solid bars indicate nonbreeding females, confirmed by dissection; hatched bars indicate females that were in the clutch-production cycle (Baker *et al.*, 1998). Breeders are clearly primarily the larger fish, although 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 (Metcalfe 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.

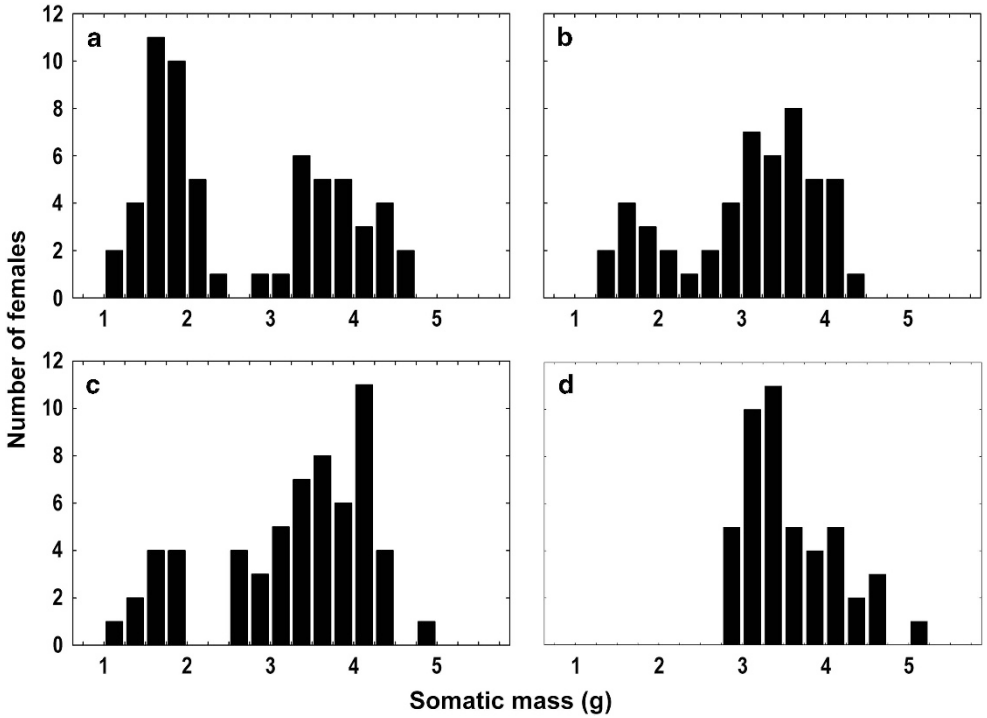

Figure 2 Size frequency of anadromous threespine stickleback on the breeding ground in two Alaskan populations. (**a–c**) Anchor River population 1995–1997. (**d**) Mud Lake population (Karve *et al.*, 2013). All fish are reproductive females captured on the breeding grounds. The clear size modes in 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.

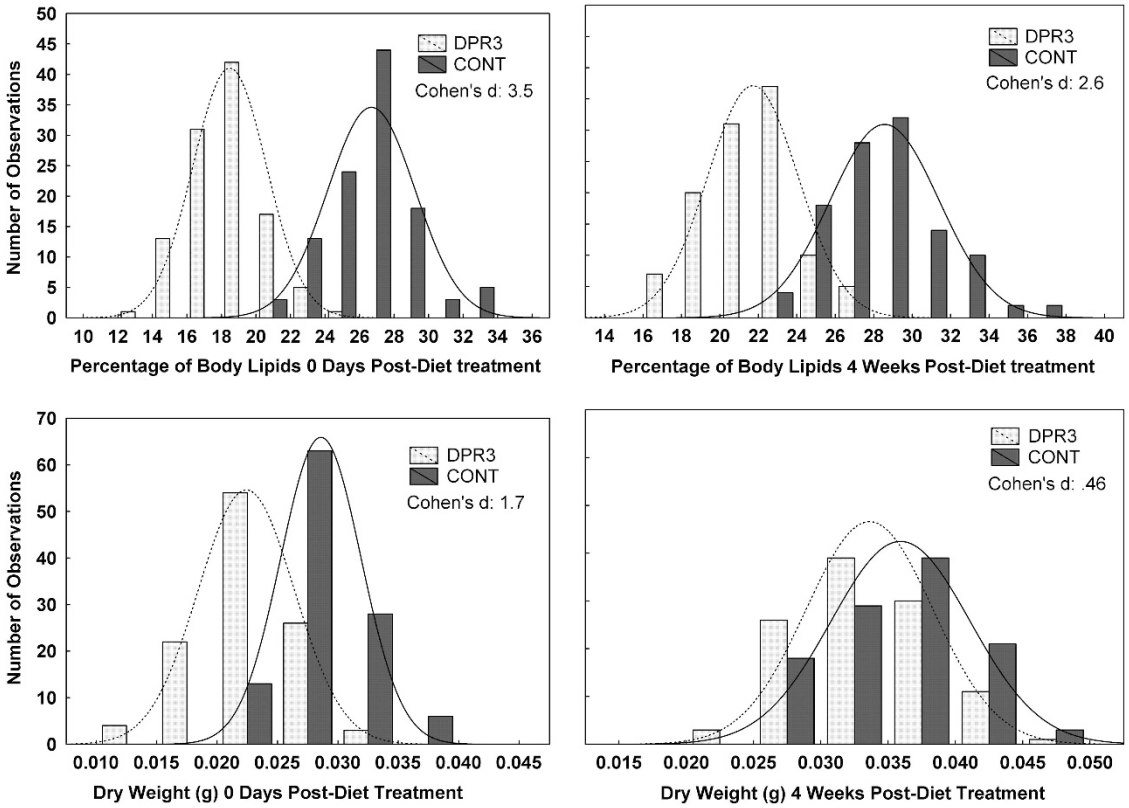

Figure 3 Comparison of compensatory responses in somatic mass and lipid content of threespine stickleback in experimental (DPR3) and control (CONT) fish that experienced a 50% reduction in ration in their fourth month of life (~2 months before over-wintering). The left panels show values at the end of 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; Skjæeraasen *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 clutches, so that seasonal fecundity was almost independent of female size.

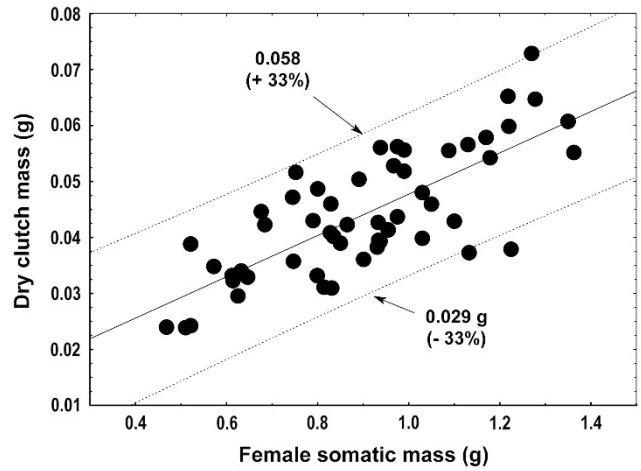

Figure 4 The relationship between dry clutch mass (an indicator of reproductive effort) and female somatic mass in Big Beaver Lake, Alaska, 1997. Each symbol indicates an individual female. At the mean somatic mass of 0.90 g, female clutch mass can vary higher or lower by as much as one-third from the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

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 Vrtilek 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, interclutch 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

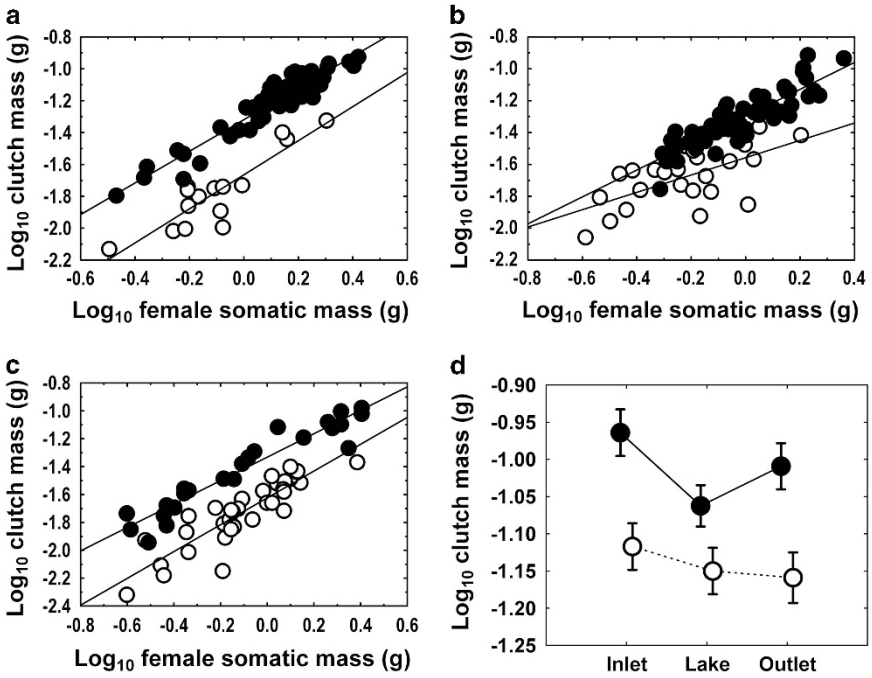

Figure 5 Relationships between clutch mass and body mass in female threespine stickleback from four populations studied in the wild (solid circles) and in the lab (open circles). (**a**) Lynne Lake, Alaska—limnetic body shape. (**b**) Cornelius Lake, Alaska—intermediate body shape. (**c**) Willow Lake, 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 aspic 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

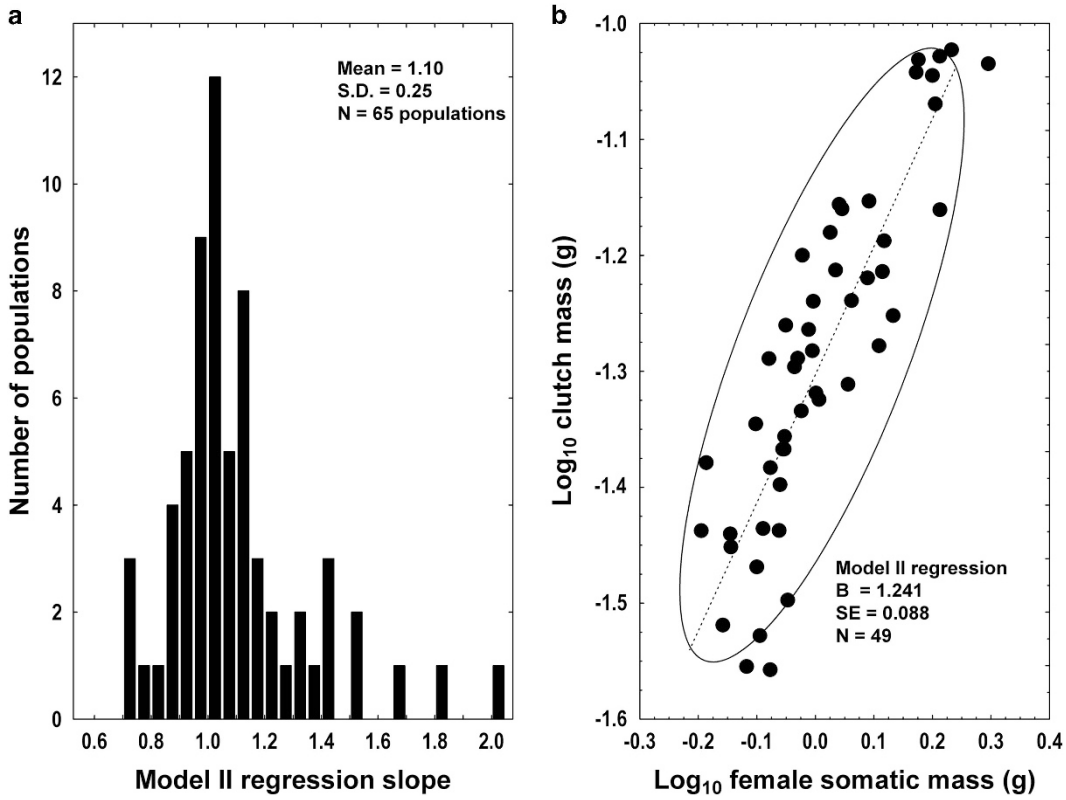

Figure 6 (**a**) The distribution of population-level regression slopes (model II) for 65 Alaskan populations of threespine stickleback. A slope of >1 indicates that relative reproductive effort increases with size/age. (**b**) An example of a one population's relationship; each filled circle represents 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 constituently 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

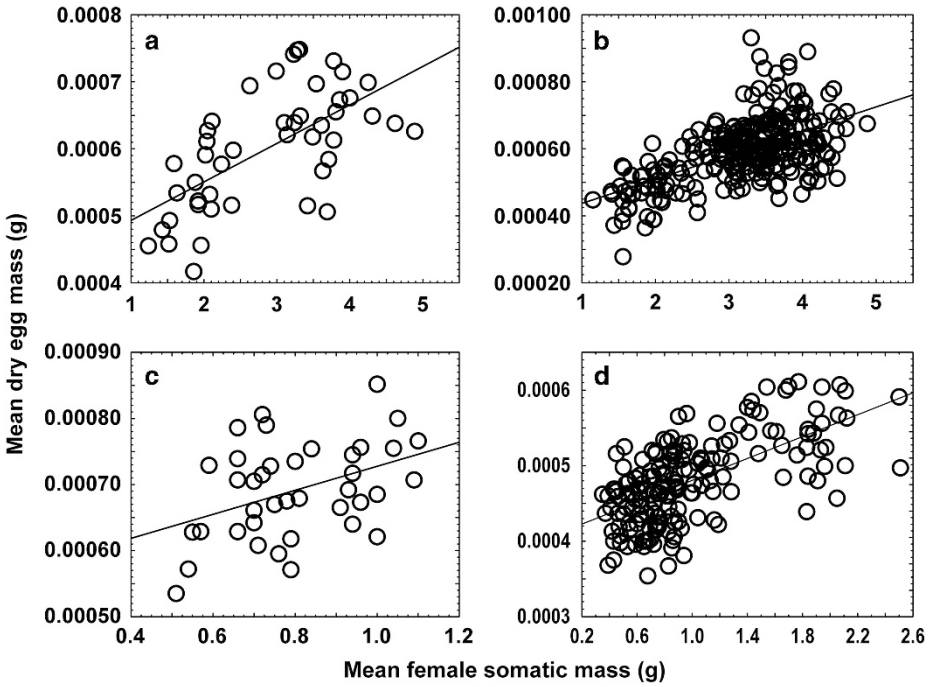

Figure 7 The relationship between egg size (mean dry mass) and female somatic mass (blotted, eviscerated) in four populations of Alaskan threespine stickleback. (**a**) Resurrection Bay marine; (**b**) Anchor River anadromous; (**c**) Daniels Lake fresh water; (**d**) Bear Paw Lake fresh water.

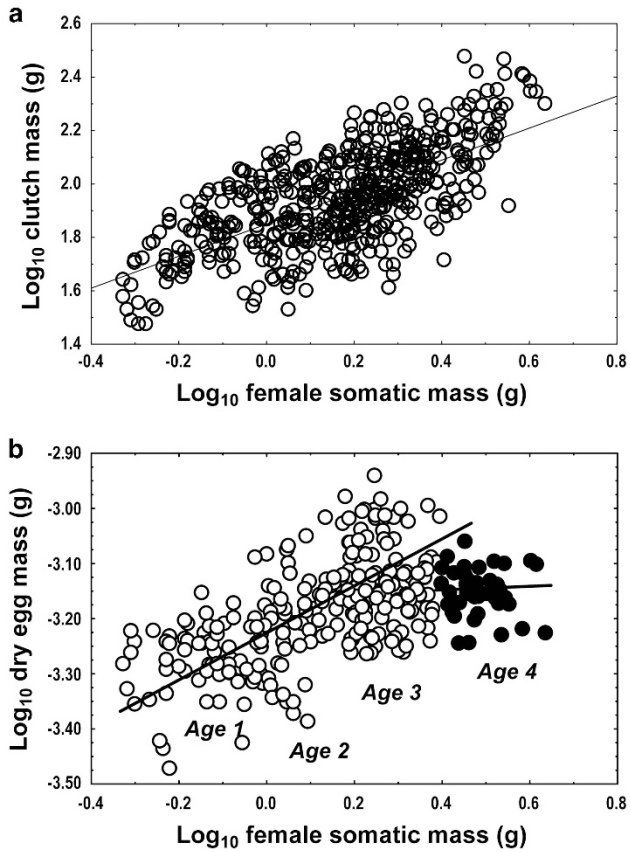

Figure 8 (**a**) The relationship between clutch size and female body size (3 years pooled) in the Solid Rock, Alaska, population. (**b**) The relationship between egg size and female body size in the same population for the same samples. Note that the oldest females (estimated to be age 4) produce appropriate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

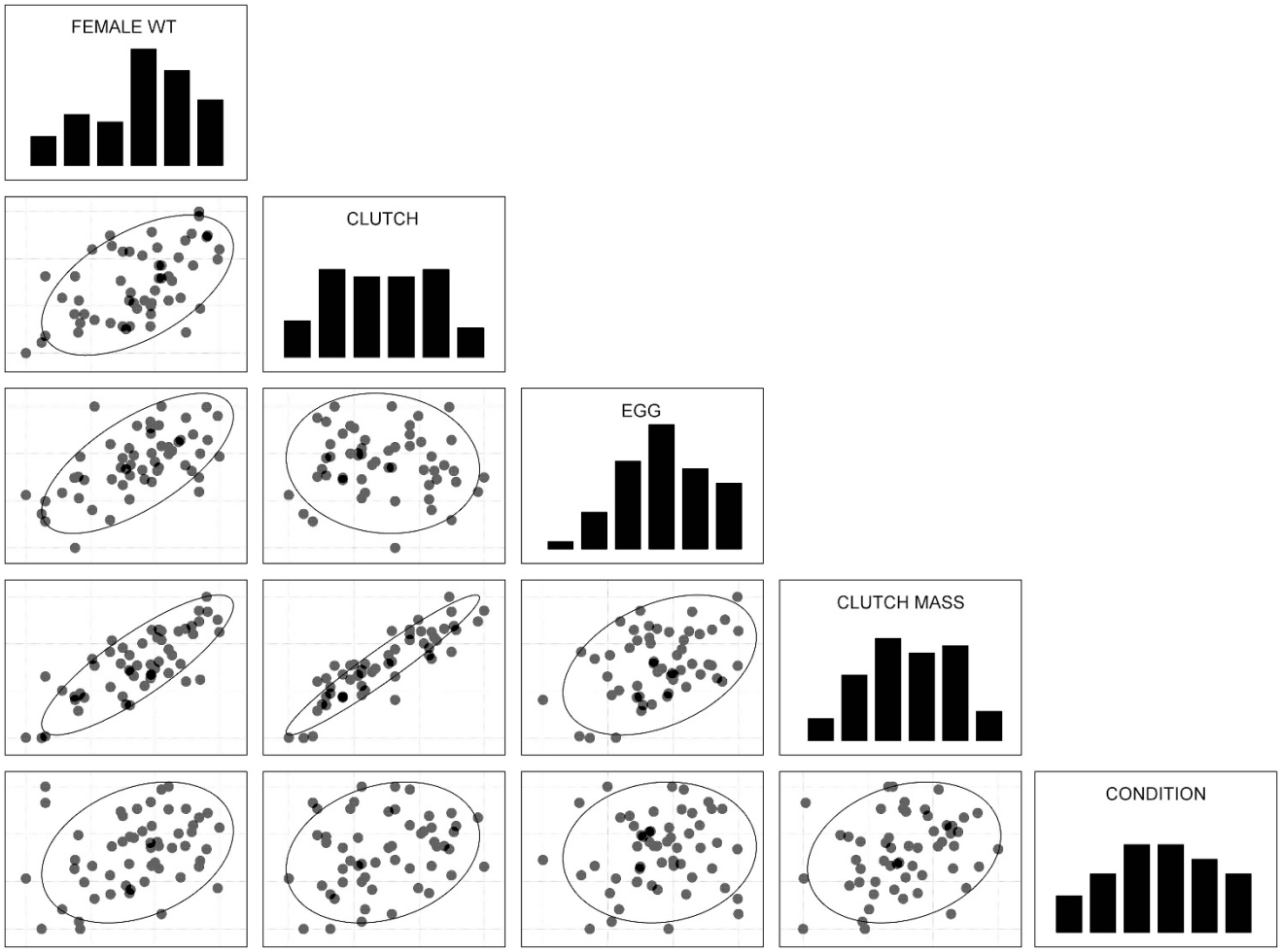

Figure 9 Matrix plot showing the relationships between female life-history traits, body mass and somatic condition in Big Beaver Lake, Alaska. The 99% probability ellipses are plotted for each pairwise combination of traits. Correlations were based on log values for female somatic mass, clutch size,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