ARTICLE

Divergent reproductive life histories in Haida Gwaii stickleback (*Gasterosteus* spp.)

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Abstract: To assess intraspecific variability in fecundity of threespine stickleback (*Gasterosteus aculeatus* L., 1758) as a test of life-history trade-offs, we quantified egg traits, morphological characters, and habitat variables in 43 allopatric and morphologically diverse populations from Haida Gwaii off the west coast of Canada. Mean mature egg size and total egg count (12 eggs per female and 8 gravid females per locality) were both positively and significantly correlated with standard length (SL) of the fish ($r = 0.58$ and 0.84, respectively). Egg size was ~10% larger in freshwater localities than in similar-sized stickleback in adjacent marine localities ($P < 0.02$). Multiple regression and Akaike's information criterion (AIC) analyses of residual egg size against morphological and lake habitat variables yields a negative correlation with lake pH (partial $r = -0.34$, $P < 0.05$) and no association with lake size, aquatic spectra, gill raker number, defense armor, or predation regime. Relative to stickleback from continental regions, Haida Gwaii stickleback life histories appear to be *K*-shifted (large but few eggs) possibly because of cool temperatures, low aquatic productivity, low community diversity, predation regime, and occasional iteroparity.

Key words: archipelago, body size, egg number, egg size, fecundity, Queen Charlotte Islands, threespine stickleback.

Résumé : Afin d'évaluer la variabilité intraspécifique de la fécondité des épinoches à trois épines (*Gasterosteus aculeatus* L., 1758) en tant que test des compromis associés au cycle de vie, nous avons quantifié des caractères des œufs, des caractères morphologiques et des variables de l'habitat dans 43 populations allopatriques et morphologiquement variées de l'archipel Haida Gwaii de la côte ouest du Canada. La taille moyenne des œufs matures et le nombre total d'œufs (12 œufs par femelles et 8 femelles gravides par emplacement) présentaient des corrélations positives et significatives avec la longueur standard (SL) du poisson ($r = 0.58$ et 0.84, respectivement). La taille des œufs était de ~10 % supérieure pour les épinoches en eau douce que pour les épinoches de taille semblable dans des localités marines attenantes ($P < 0.02$). L'analyse par régression multiple et du critère d'information d'Akaike (AIC) de la taille résiduelle des œufs par rapport à des variables morphologiques et de l'habitat lacustre fait ressortir une corrélation négative avec le pH du lac (r partiel $= -0.34$, $P < 0.05$), mais aucune association avec la taille du lac, le spectre aquatique, le nombre de branchictènie, l'armure de défense ou le régime de prédation. Comparativement à ceux d'épinoches de régions continentales, les cycles de vie des épinoches de Haida Gwaii semblent montrer un déplacement de type *K* (des œufs de grande taille, mais en moindre quantité), possiblement en raison de basses températures, de la faible productivité aquatique, de la diversité limitée des communautés, du régime de prédation et d'une itéroparité occasionnelle. [Traduit par la Rédaction]

Mots-clés : archipel, taille du corps, nombre d'œufs, fécondité, îles de la Reine-Charlotte, épinoche à trois épines.

Introduction

Intraspecific variability in fecundity of fishes involves a trade-off between egg size and egg number (Fleming and Gross 1990; Baker 1994). Egg size is particularly important because it is highly correlated with hatchling size (Ponce de León et al. 2011), which in turn characterizes gape and dietary opportunities (Wootton 1984), interactions with predators (Reznick and Endler 1982; Cowan et al. 1996), and the extent of parental care (Sargent et al. 1987). Small eggs and high fecundity are a response to increased food availability, high growth rates of small fry, and possibly higher predation intensity on early age classes (Reznick and Endler 1982; Elgar 1990; Teletchea and Fontaine 2010, 2011; Walsh and Reznick 2010; Ponce de León et al. 2011), and as well can be influenced by a complex of life history, demographic, niche, and habitat attributes (Winemiller and Rose 1992). Genetic variability underlies many of these adaptations, but phenotypic plasticity in response to cues such as temperature and chemical cues from predators can also be important (Baker and Foster 2002; Baker et al. 2005; Laptikhovski 2006).

Threespine stickleback (*Gasterosteus aculeatus* L.,1758) are found in a wide diversity of marine and freshwater habitats of the northern hemisphere and vary in reproductive life histories (Wootton 1976; Bell and Foster 1994; Baker et al. 2005). Freshwater populations are more variable in egg characteristics than adjacent marine populations (Baker 1994; Baker et al. 2008). Low-calcium lakes in Alaska lacking predatory fish have stickleback with larger mean egg sizes than those in adjacent high-calcium habitats (Baker et al. 1998) while in a sympatric benthic–limnetic species pair, benthic ecotypes produce fewer and larger eggs than sympatric limnetic forms (Baker et al. 2005).

Stickleback from the Haida Gwaii archipelago, 100 km off the coast of British Columbia, are exceptionally diverse in adult body size and defense morphology (Moodie and Reimchen 1976; Reimchen 1994). Life-history traits among these endemic populations have received limited attention. Extended longevity and yearly iteroparity in one lake (Reimchen 1992; Gambling and Reimchen 2012) predict fewer and larger eggs (Poizat et al. 1999). In the current article, we quantify egg size and egg number among 43 populations that

Fig. 1. Distribution of major localities used for direct measures of egg size and number of threespine stickleback (*Gasterosteus aculeatus*) from Haida Gwaii and adjacent mid-coast of British Columbia. Selected lake photographs and Google Earth images available at http://web.uvic.ca/~reimlab/haidagwaiilakes.

encompass the full range of aquatic habitat diversity in the archipelago and assess whether population variability is present, and if so, to identify the extent to which morphology and habitat predicts the variability. Habitats include estuaries, oligotrophic lakes with high water clarity, and dystrophic lakes and ponds that are deeply stained, as well as those differing in predation regimes, with 12 localities that lacked predatory fish. Populations differed in adult body size (range 30–90 mm standard length), in lateral plates morph frequencies (complete morph through to naked phenotypes), and in trophic ecotypes (limnetic through to benthic) (Reimchen 1994). To provide a broader geographical context to the Haida Gwaii data, we also quantified egg traits in four lake populations close to the British Columbia mainland (Reimchen and Nosil 2006) and extracted published data on egg traits from stickleback in continental North America, Europe, and Asia.

We predict a trend towards increased egg sizes in freshwater relative to estuarine habitats (Teletchea and Fontaine 2011); a trend towards larger eggs in cooler rather than warmer waters (Laptikhovski 2006); and an inverse relationship between egg size and egg number among populations (Stearns 1977).

Materials and methods

We used stickleback collected during surveys by T.E.R. from 1975 to 2000 (mainly May and June). Among over 100 stickleback populations identified from throughout the archipelago (Reimchen 1994; Spoljaric and Reimchen 2007), we were able to obtain gravid females in 43 populations from 39 lakes and 4 estuaries (Fig. 1). All

of these sites except one were ecologically intact with minimal historical alteration. The exception was the previously barren eutrophic Mayer Pond that had recently (1993) been stocked with giant stickleback from the large dystrophic Mayer Lake as a field experiment to evaluate morphological and genetic changes of colonists to an ecologically divergent habitat (Leaver and Reimchen 2012). All collections were preserved in 10% formalin for at least several years and then transferred to 95% ethanol. We found no significant differences in egg size among individuals stored for 20 years in formalin compared with those stored for several years. We examined all adult females in the samples and were able to obtain data from 2 to 12 individuals (mean 8) per population and on each of these recorded total number of mature eggs in the body cavity and maximum diameter of 12 randomly selected mature eggs. We restricted our analyses to females that were exclusively category RE (ripe stage), containing eggs which were fully matured and ready to be spawned (Baker et al. 1998). These individuals were easily identifiable due to ovarian and egg morphology; matured eggs were located postero-ventrally within the ovary, while oocytes were restricted to antero-dorsal regions (as opposed to MA-mature stage, and MR-ripening stage females, in which maturing eggs and undifferentiated oocytes were mixed within the ovaries), and the chorion of RE eggs was clearly separated from the spherical yolk. Chorion diameter was directly comparable between RE individuals within and among populations due to similar preservation procedures; although MA and MR females are both useful for determining number of eggs within a clutch,

Fig. 2. Relationship between population mean egg diameter and standard length in gravid threespine stickleback (*Gasterosteus aculeatus*) from Haida Gwaii, western Canada. Habitat symbols show lake size (small lakes: <900 m³; large lakes: ≥900 m³), as well as presence or absence of predatory fish and of estuarine or freshwater lakes.

they do not provide reliable estimates of final egg diameter and so were not included in the analysis (Heins et al. 1992).

Egg traits were analyzed for potential associations with morphology of stickleback and biophysical variables of the habitat. In addition to standard body length (SL) and body depth for each individual, we also used previously determined population means for number of gill rakers, number of bony lateral plates (Reimchen 1989; Reimchen et al. 1985), and general habitat data (estuary vs. freshwater habitats, lake area, volume, pH, and aquatic spectra measured as percent transmission at 400 nm). To control for the positive relationship between body size and fecundity, both egg size and egg number ($\log_{10}$-transformed) were regressed against fish SL within each population, and the mean population residuals were used in subsequent analyses. Multiple stepwise linear regressions were performed on mean age size and number and morphological characteristics to assess which variables best predicted life-history characteristics across populations; all reported variables represent population mean values unless otherwise indicated. The use of Akaike's information criterion (AIC) was also employed to examine the best models.

For geographically large-scale comparisons, we obtained egg size and egg number from published data (Wallace and Selman 1979; Mori 1987; Baker 1994; Ali and Wootton 1999; Kume 2011)

and measured egg traits on lake populations previously investigated from Dewdney and Barnard islands near the adjacent British Columbia mainland (Reimchen and Nosil 2006). Among these 40 allopatric populations, we were able to obtain fully mature females from four populations and used the same protocol as characterized above. We extracted residuals of egg size and egg number ($\log_{10}$-transformed) against SL for the entire data set (Haida Gwaii, North America, Europe, Asia). All analyses were performed using SPSS version 17.0 or SPSS version 19 (IBM Corporation 2008, 2010).

Results

Mean population morphological and habitat characteristics are summarized in supplementary Table S1[1]. Among the 43 populations examined from Haida Gwaii, substantial variation in egg size occurred and the extent of this variation differed with respect to stickleback morphology and habitat. Egg diameter among populations ranged from 1.73 to 2.27 mm (1.98 ± 0.11 mm, mean ± SE), comprising a 30% difference in diameter and a 126% difference in volume. Egg diameter was most strongly associated with SL (Fig. 2) ($r = 0.58$, $N = 43$, $P < 0.001$), negatively associated with number of lateral plates ($r = -0.33$, $N = 43$, $P < 0.04$), and weakly associated with

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[1]Supplementary Table S1 is available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/dx.doi.org/10.1139/cjz-2012-0175.

Table 1. Comparison of models describing residual egg size variation in Haida Gwaii threespine sticklebacks (*Gasterosteus aculeatus*) evaluated using Akaike's information criterion (AIC), with lake volume, pH, and water spectra as predicting variables.

Model	r^2 adjusted	AIC_c	ΔAIC_c
pH	0.23***	−11.34	0.00
Spectra	0.07*	−9.01	2.32
pH × spectra	0.23**	−7.28	4.06
Log_{10}volume	0.05	−5.63	5.70
pH × log_{10}volume	0.24**	−4.87	6.47
Spectra × log_{10}volume	0.12	−2.51	8.83
pH × spectra × log_{10}volume	0.25*	5.49	16.82

Note: Models are listed in ascending order of AIC scores. Residuals are extracted from regression of egg size against standard length (SL). *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

with number of gill rakers ($r = -0.25$, $N = 39$, $P = 0.13$). With SL as the covariate, adjusted egg size differed significantly among populations ($F_{[1,40]} = 102.5$, $P < 0.001$). Estuarine populations had eggs about 10% smaller than those in freshwater populations after adjustment for body size effects (ANOVA, $F_{[3,38]} = 6.8$, $P < 0.02$). Among freshwater populations, there was also considerable variability in egg sizes corrected for body size. For example, Mayer Lake, which has giant adult stickleback, had unusually small eggs yet Drizzle Lake, also with giant stickleback, had some of the largest egg size. We also examined residual egg size in relation to lake pH, lake volume (log_{10}-transformed), aquatic spectra, and presence or absence of predatory fish. Saturated model was not significant ($F_{[1,38]} = 2.2$, $P = 0.09$, adjusted $r^2 = 0.11$), although pH contributed significantly to the model (pH: partial $r = -0.34$, $P < 0.05$) with negligible effects for the remaining variables (lake volume: partial $r = 0.11$, $P = 0.53$; spectra: partial $r = 0.17$, $P = 0.32$; predatory fish: partial $r = -0.05$, $P = 0.8$). We computed multiple ANOVA with residual egg size as a dependent and habitat variables as covariates including all single, two-way, and three-way interactions. Although each of the variables and interactions accounted for some of the residual egg size, the best AIC model included only pH, consistent with multiple linear regression analyses (Table 1).

Number (log_{10}-transformed) of eggs per female varied widely among individuals and among populations. Overall, this ranged from 16 to 415 (mean = 105.3) with population means being strongly correlated with SL ($r^2 = 0.71$, $P < 0.001$). The four estuarine populations had similar egg number relative to those in freshwater populations ($F_{[1,42]} = 0.54$, $P = 0.5$) but were significantly higher after adjustment for body size ($F_{[1,42]} = 12.8$, $P < 0.001$) (Fig. 3). Among all freshwater populations, a saturated multiple regression model of residual egg number with pH, spectra, lake volume, and presence or absence of predatory fish was significant ($F_{[1,38]} = 3.5$, $P < 0.02$, adjusted $r^2 = 0.21$) with the largest effect of spectra (partial $r = 0.4$, $P < 0.02$) and pH (partial $r = -0.36$, $P < 0.04$) and minor effects of lake volume (partial $r = 0.19$, $P = 0.28$) and predation regime (partial $r = -0.27$, $P = 0.12$). Further analyses of the residuals were performed using ANOVA with single, two-way, and three-way interactions of the habitat variables. The best AIC model, which accounted for only 11% of the variance, included only lake volume (Table 2).

Egg size and number of the giant Mayer Lake stickleback were evaluated three generations (6 years) after their transplant into a small eutrophic pond (Mayer Pond) that was an ecological contrast of the source population. Gravid females exhibited a 30% reduction in body size (87 vs. 65 mm: $t_{[18]} = 5.8$, $P < 0.001$), a concordant and predicted decrease in egg number (172 vs. 74: $t_{[18]} = 4.4$, $P < 0.001$) but no change in mean egg size (2.01 vs. 2.00 mm: $t_{[18]} = 0.26$, $P = 0.8$) (Figs. 2, 3).

We compared our data on egg size and egg number with that from stickleback populations in southern British Columbia, Cali-

fornia, western Europe, and Japan. Across this distribution, there was an 86% and 546% increase in egg diameter and egg volume, respectively, between the populations with the smallest and the largest eggs and a 21-fold increase (23 vs. 506 eggs) between the lowest and the highest mean population fecundity per female. For both estuarine and freshwater populations and across a wide range of body sizes, Haida Gwaii stickleback have larger eggs than those in other geographical areas (estuarine: 1.82 vs. 1.49 mm, respectively, $F_{[1,15]} = 15.0$, $P < 0.001$; freshwater: 2.00 vs 1.62 mm, respectively, $F_{[1,48]} = 92.0$, $P < 0.001$). Covariance adjustment for differences in adult body size does not remove this effect (estuarine: $F_{residual} = 16.3$, $P < 0.001$; freshwater: $F_{residual} = 103.7$, $P < 0.001$). Total egg number also differs but to a lesser extent between these major geographical areas with Haida Gwaii stickleback having fewer eggs than those in other geographical areas across multiple body sizes (estuarine: 107 vs. 239, respectively, $F_{[4,16]} = 6.1$, $P < 0.02$; freshwater: 89 vs. 128, respectively, $F_{[39,11]} = 5.2$, $P < 0.03$). Adjustment for differences in adult body size eliminates this effect in estuarine habitats ($F_{residual} = 2.1$, $P = 0.17$) but differences in freshwater habitats persist ($F_{residual} = 37.7$, $P < 0.001$).

We examined the body-size-corrected residuals of egg size against egg number for all populations as a general proxy of *r*–*K* reproductive strategies. A significant negative relationship occurs between these traits ($r = -0.71$, $P < 0.001$) that is combined with a strong trend for Haida Gwaii populations to be *K*-shifted relative to other geographical areas, the effect being most accentuated in freshwater populations (Fig. 4). To test whether this trend was associated with the geographical insularity of the archipelago, we also examined egg size and egg number from four allopatric lake populations on the Dewdney and Barnard islands at the same latitude as Haida Gwaii but immediately adjacent to the mainland (Fig. 1). These populations did not differ from those on Haida Gwaii either for egg size ($F_{[1,42]} = 0.06$, $P = 0.81$) or for egg number ($F_{[1,42]} = 0.03$, $P = 0.87$).

Discussion

Egg size in fishes has been quantified in a large assemblage of marine and freshwater fishes with the smallest and largest mature eggs within a species differing by up to 560% (mean 100%) by volume (Bagenal 1971). Our data from Haida Gwaii showed a maximum difference of 126% among populations and was therefore representative of intraspecific variability among other taxa. Inclusion of additional egg-size data from throughout the circumboreal distribution of *Gasterosteus* (reviewed in Baker 1994) increases the overall range in volumes to 550%, representing one of the most variable for any fish species. Different preservation protocols, which can influence the quantification of egg size (Heins and Baker 1988), might contribute to this large range but if the data are reliable, the results further reflect the remarkable diversity exhibited by this taxon (Wootton 1984; Bell and Foster 1994).

Closely related fishes found in both marine and freshwater habitats differ in mean mature egg sizes with larger eggs occurring in freshwater habitats (Bagenal 1971; Teletchea and Fontaine 2011). Although we found that egg size in freshwater populations can be both smaller and larger than nearby marine populations (see also Baker et al. 2008), our data are consistent with the broader taxonomic trend and indicate a 10% mean increase in egg diameter comparable with that reported for stickleback in other geographical regions including Alaska and Japan (Baker 1994). Freshwater habitats tend to have lower productivity than adjacent marine habitats and the production of larger eggs, which results in larger hatchling size, may increase early survivorship in habitats restricted in both prey diversity and abundance (Bagenal 1971; Johnston and Leggett 2002; Taborsky 2006; Johnston et al. 2007; Walsh and Reznick 2010; Ponce de Leon et al. 2011).

In addition to the differences between marine and freshwater habitats, we observed substantial variation in egg size among

Fig. 3. Relationship between population mean egg number and standard length in gravid threespine stickleback (*Gasterosteus aculeatus*) from Haida Gwaii. Habitat symbols show lake size (<900 m³, ≥900 m³), as well as presence or absence of predatory fish and of estuarine or freshwater lakes. *Y* axis shows $\log_{10}$-transformed and untransformed scales.

Table 2. Comparison of models describing residual egg number variation in Haida Gwaii threespine sticklebacks (*Gasterosteus aculeatus*) evaluated using Akaike's information criterion (AIC), with lake volume, pH, and water spectra as predicting variables.

Model	r^2 adjusted	AIC_c	ΔAIC_c
$\log_{10}$volume	0.13*	−5.63	0.00
Spectra	0.01	−4.47	1.17
pH	−0.02	−4.20	1.43
Spectra × lgvol	0.16*	−1.99	3.64
pH × $\log_{10}$volume	0.08	−0.50	5.14
pH × spectra	−0.03	0.08	5.71
pH × spectra × $\log_{10}$volume	0.31**	5.64	11.28

Note: Models are listed in ascending order of AIC scores. Residuals are extracted from $\log_{10}$ (egg number) against standard length (SL). *, $P < 0.05$; **, $P < 0.01$.

freshwater populations. The principle correlate of this was adult body size, with larger eggs occurring among larger adults. This association has been previously described in European stickleback (Fletcher and Wootton 1995; however, see Baker 1994) and among other teleosts and may reflect in part improved physiological opportunities of large adults to provision resources towards larger eggs (Williams 1967; L'Abee-Lund and Hindar 1990; DeMartini 1991; Hendry and Day 2003; Braga Goncalves et al. 2011; Patimar and Farzi 2011). However, in our data, increased egg size is not a simple isometric or allometric correlate to body size. For example, some

of the smallest- and largest-bodied populations (<50 vs. 90 mm SL) that differ by 800% in mass (Reimchen 1990) had the same mean egg size. Among populations with the same mean adult body size, there were large differences in egg size. Lake primary productivity is not obviously important in egg-size differences among the Haida Gwaii localities, as the majority of lakes are oligotrophic or dystrophic. Some of the variability could be related to predation regime, as this is known to influence early survival of fry (Reznick and Endler 1982). We compared populations with and without predatory fish but found no clear association with egg size and also examined the relationship between number of defensive bony lateral plates, a general proxy for exposure to predatory fish (Hagen and Gilbertson 1972; Moodie and Reimchen 1976; Gross 1977) and egg size, and found no effects. Among seven large lakes, all with abundant predatory fish and all with stickleback as the major prey (Reimchen 1994), three populations had relatively large eggs and four had small eggs. It is possible that the failure to identify support for an effect of predation has been confounded by differences in age-structured predation. In Trinidadian *Rivulus* Poey, 1860, larger eggs are found with a shift towards increased predation on juveniles (Walsh and Reznick 2010). In stickleback, there is evidence for significant conspecific predation on fry (Foster et al. 1988; Reimchen 1994) but only limited data in the Haida Gwaii populations to assess population differences age-structured predation (Reimchen 1990). Large eggs and subsequent large hatchling size may be particularly valuable in these situations,

Fig. 4. *K*- vs. *r*-strategies in egg diameter and egg number residuals (body size effects removed) for threespine stickleback (*Gasterosteus aculeatus*) from circumboreal localities. Haida Gwaii localities appear as solid symbols. Four freshwater lakes from Dewdney and Barnard islands on the mid-coast of British Columbia are designated "bcmid". Data on other named localities extracted from the literature (Wallace and Selman 1979; Mori 1987; Baker 1994; Ali and Wootton 1999; Kume 2011).
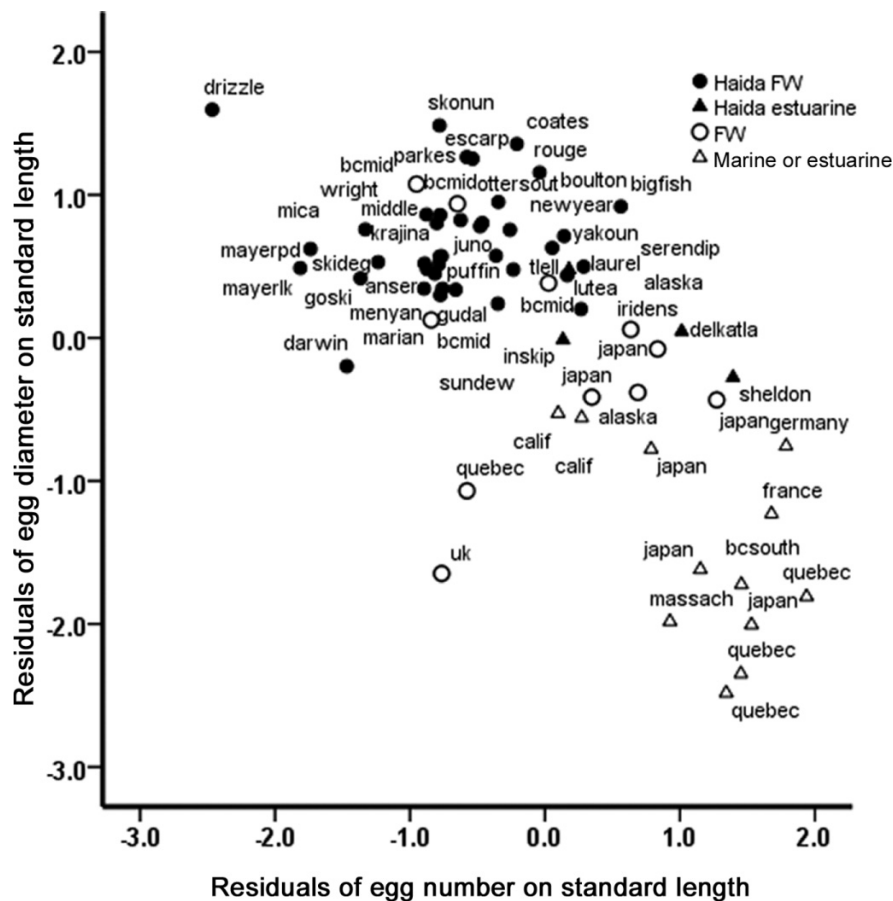
and if true, any population differences in the relative importance of cannibalism by particular age class of these gape-limited conspecifics could facilitate selective differences in egg and hatchling size that are not detectable from general habitat comparisons of predation regime.

In many teleosts, there is an inverse correlation between egg size and water temperature during the spawning period (review in Laptikhovski 2006) and reflects a tendency for increased lipid accumulation in eggs at lower temperatures (Rass 1984, cited in Laptikhovski 2006; Baynes and Howell 1996; Kokita 2003; Bownds et al. 2010). Large deep lakes are colder than shallow pools and as such we predicted larger eggs in larger lakes. Although such a relationship did occur in several cases, among the full data set, lake size was not a significant statistical predictor when the effects of stickleback body size were removed, and as such, temperature does not appear to contribute to the substantial variability in egg size in the archipelago.

Our multiple regression and AIC analyses indicated that SL was the major predictor of egg size, while residuals of egg size against SL were negatively associated with water clarity and with pH. Baker (1994) identified an association between large eggs in stickleback and low calcium levels in several Alaskan lakes, the latter usually associated with lower pH (Cole 1979), which can exert multiple stressors on developing eggs in fishes (Faris and Wootton 1987; Sayer et al. 1993; Finn 2007).

Although we have hitherto assumed that egg-size variability is primarily differentiation of a heritable trait, some of the trends that we observed may reflect phenotypic plasticity. Experimental

life-history studies on cichlid fish that have shown larger eggs occur in direct response to adult detection of predatory chemical cues (Segers and Taborsky 2012) and in response to early food deprivation of the females (Taborsky 2006). In stickleback, seasonal and interannual shifts in egg size within populations have also been described (Poizat et al. 1999, 2002; Baker and Foster 2002; Baker et al. 2005). Extending from a recent transplant experiment of giant limnetic stickleback from a large dystrophic lake with major abundance of predatory salmonids into an adjacent small shallow eutrophic pond lacking all predatory fish (Leaver and Reimchen 2012) resulted in no change in absolute or residual egg size after three generations suggesting a limited role for plasticity in egg size in these physically and biologically divergent habitats.

One of the major sources of variability in reproductive life histories of fishes is fecundity (Helfman et al. 2009). Across a diversity of taxa, total number of eggs per female is largely predicted by adult body size with secondary influences of physiological condition, habitat, and life-history characteristics such as growth rates and size at maturity (Bagenal 1971; Wootton 1976; Winemiller and Rose 1992; Baker 1994; Bone and Moore 2008). In our data, mean egg number ranged over an order of magnitude among populations and body size accounted for 60% of this variability. The highest relative fecundities occurred in estuarine populations (Sheldon, Delkatla) and were about twice as high as any freshwater population of similar body size. This is consistent with previous studies on Alaskan stickleback (Baker et al. 2008) and may result from increased productivity and prey availability for

larval fishes in marine habitats (Teletchea and Fontaine 2011). Among the freshwater habitat variables that we examined, we observed only marginal associations with egg number of which reduced lake volume was the best AIC model contributing to the variance.

Egg size and egg number among multiple taxa are inversely correlated and reflect the widely recognized trade-off between *r* and *K* life histories (Stearns 1977; Law 1979; Baker et al. 1998; Johnston and Leggett 2002; L'Abee-Lund and Hindar 1990; Ponce de León et al. 2011), and are probably structured by a complex of life history, demographic, and habitat features distinctive for each species (Winemiller and Rose 1992). We examined egg traits in threespine stickleback from across their circumboreal distribution and using either raw data or body-size-corrected data, observed an inverse relationship between egg size and egg number, consistent with theoretical predictions. Within this trend, there were habitat associations, as *r*-shifted strategies occurred largely in marine and estuarine populations and *K*-shifted strategies in freshwater populations. This is similar with previous studies on multiple taxa containing both marine and freshwater populations and reflects in part lower productivity in the latter (Teletchea and Fontaine 2011).

Unexpectedly, we found that Haida Gwaii stickleback were substantially shifted towards *K*-strategies in comparison with other geographical areas. Relative egg diameter was approximately 25% higher and relative egg number 50% lower than elsewhere, with differences being accentuated in freshwater habitats. One of the common characteristics of aquatic habitats on Haida Gwaii is that virtually all have low primary productivity and low species diversity (8 vs. 66 species, respectively; Carl et al. 1959; Northcote et al. 1985). In dystrophic lakes, benthic taxa such as dipteran larvae comprise major prey items for stickleback fry (Wootton 1994), which could favour large hatchling size and large gape to access the larger prey. Low productivity and low species diversity increase intraspecific competitive effects and this also favours increased hatchling sizes. An additional factor that may contribute to the *K*-shift in Haida Gwaii sticklebacks is longevity and iteroparity. The most accentuated shift occurred at Drizzle Lake in the *Sphagnum* L. lowlands on northeast corner of Haida Gwaii where residual egg size is approximately twice as large, while size-corrected fecundity was one-half that relative to other geographical areas. There are no single traits that immediately distinguish this lake but potential combinations of factors that could facilitate an additive shift towards a *K*-strategy. Throughout much of their geographical distribution, stickleback have a 1- to 3-year maximum life span (Wootton 1984; Baker 1994) yet stickleback from Drizzle Lake live up to 8 years of age and show evidence for yearly iteroparity (Reimchen 1992; Gambling and Reimchen 2012), which in other taxa is associated with larger and few eggs (Poizat et al. 1999). In addition, Drizzle Lake has low summer temperatures, is deeply stained with low productivity, and stickleback is the dominant fish species in the lake (Reimchen 1990, 1994), all of which are predicted to lead to increased shift towards *K*-strategies (Laptikhovski 2006; Teletchea et al. 2009; Bownds et al. 2010).

If the large variability in egg size and egg number of stickleback within the archipelago and the differentiation from continental regions are confirmed, it further broadens the evidence for the divergent selective and genetic landscapes of the region (summary in Reimchen and Byun 2005). Identifying the actual mechanisms for the variability in reproductive strategies may require the integration of much more additional life-history data such as characterized in the multidimensional life-history models (Winemiller and Rose 1992).

Acknowledgements

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