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The implications of pelvic reduction in threespine stickleback for long-term persistence of populations

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ABSTRACT

Questions: Do threespine stickleback populations that exhibit pelvic reduction exist at lower densities than populations expressing the full pelvic girdle? Does population size fluctuate more in pelvic-reduced populations? Does trout stocking contribute to fluctuations, if they are present?

Organisms: Twenty-three populations of lake-dwelling freshwater threespine stickleback (*Gasterosteus aculeatus*). Populations are of three types: 12 full-pelvic populations, all but two with predatory rainbow trout; five pelvic-reduced populations lacking trout; and six pelvic-reduced populations originally lacking trout, but into which trout are now stocked.

Time and place: Annual field collections within the Cook Inlet region of Alaska, 1993–2010.

Analytical methods: Nested ANOVAs (lake nested within population type) of logCPUE (catch-per-unit-effort), pooling all samples from each lake category in each year. ANOVA on coefficient of variation (CV) across populations and types. ANOVAs followed by planned comparisons.

Results: Pelvic-reduced populations of both types exist at about one-third the density of full-pelvic populations. However, the coefficient of variations did not differ significantly. No effect of trout stocking was evident.

Conclusions: Although catch-per-unit-effort values are only relative rather than absolute population size estimates, if our values of CPUE are comparable across populations, then populations that have evolved pelvic reduction have lower population densities than do full-pelvic populations. The small size of lakes supporting these unique populations and their lower fish density suggest that this rare type of stickleback population may be at elevated risk of extinction.

Keywords: adaptive radiation, conservation, extinction, population fluctuation, stickleback.

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INTRODUCTION

Small population sizes are of concern to conservation biologists (Spielman *et al.*, 2004). Small populations may be more susceptible to inbreeding and genetic drift (Daniels *et al.*, 2000; Griffen and Drake, 2008a; Palstra and Ruzzante, 2008), and they may be at increased risk of extinction simply due to environmental stochasticity (Shaffer, 1981; Lynch *et al.*, 1995; Inchausti and Halley, 2003; Legendre *et al.*, 2008). Although small population size is the principal problem, an additional important determinant of long-term population persistence may be fluctuation in population abundance (Primack, 1998; Legendre *et al.*, 2008). Loss of genetic diversity during substantial population declines may also impair fitness (Keller *et al.*, 1994; Vrijenhoek, 1994; Newman and Pilson, 1997; Nieminen *et al.*, 2001), making small populations that are subject to altered selection (e.g. predator introduction) even more vulnerable to extinction (Ohta, 1972; Saccheri *et al.*, 1998; Shirley and Sibly, 2001; Keller and Waller, 2002).

The concept of an ‘endangered’ species was developed to protect organisms that were deemed to be in danger of extinction. The term can denote a true taxonomic species, and when it does so it typically refers to one with a very limited geographic range, for example the snail darter (Plater, 2004). However, it may also refer to a subspecies, or in vertebrates to a ‘distinct population segment’ (USFWS-NMFS policy 61 FR 4722: 7 February 1996). For instance, sockeye salmon comprise a diverse assemblage including sea/river, lake, and landlocked kokanee forms, with the latter two types having repeatedly evolved from the ancestral sea/river form [the recurrent evolution hypothesis (Wood *et al.*, 2008)]. In Chinook salmon, repeated, parallel evolution of different run-time variants in separate geographical regions has occurred (Waples *et al.*, 2008). In Pacific salmon, individual populations may be considered ‘evolutionarily significant units’ (ESUs) worthy of protection in the same manner as distinct species (Waples, 1995), even though the biological species as a whole is not in imminent danger of extinction. Evolutionarily significant units may be defined by geographic separation, genetic differentiation, or by local adaptation driven by natural selection, and thus they comprise populations or population segments that are largely reproductively isolated from other populations of the same species. In addition, an ESU must represent *an important component of the evolutionary diversity* of the species to which it belongs (Waples, 1991). The implication of this last requirement is that, for some biological species, the conservation value derives from the entire *evolutionary system* encompassed by the species.

The situation with the biological species threespine stickleback (*Gasterosteus aculeatus*) parallels that of the salmon. This fish is extremely abundant in coastal areas throughout the northern hemisphere (Wootton, 1976; Bell and Foster, 1994), with perhaps hundreds of thousands of extant populations. The species consists of an extant ancestral lineage that has existed phenotypically unchanged in northern hemisphere oceans for more than 10 million years (Bell, 1994), and a complex of variably differentiated freshwater populations derived from this common oceanic ancestor. The most recent widespread colonization event occurred following the last glacial period, which ended in areas such as the Cook Inlet Basin only about 10,000 years ago. The newly founded freshwater populations have diverged adaptively in a variety of traits from the ancestral oceanic stickleback (Bell and Foster, 1994), and the radiation has been an exemplary system for studying a wide variety of evolutionary processes. These include numerous aspects of behaviour (Huntingford *et al.*, 1994; Foster *et al.*, 1996; Messler *et al.*, 2007), rapid evolution (Bell *et al.*, 2004; Baker *et al.*, 2011; Aguirre and Bell, 2012; Bell and Aguirre, 2013; Hendry *et al.*, 2013), ecological diversification within allopatric (Baumgartner, 1995; Walker, 1997; Baker *et al.*, 1998, 2008; Aguirre, 2009; Ravinet *et al.*, 2013b; Reimchen *et al.*, 2013), parapatric (Hendry *et al.*, 2002; Kaeuffer *et al.*, 2012; Ravinet *et al.*, 2013a), and sympatric (McPhail, 1994; Baker *et al.*, 2005; Karve *et al.*, 2013) scenarios, plasticity (Wund *et al.*, 2008, 2012), and host–parasite dynamics (Heins and Baker, 2008; Konijnendijk *et al.*, 2013), to name just some.

As pointed out by Bell and Ortí (1994), Foster *et al.* (2003), and von Hippel (2008), the conservation danger resides in the threat to a relatively small number of unique elements – populations and metapopulations – in the biological radiation of this species. Examples of these unique elements include the British Columbia sympatric species pairs (McKinnon and Rundle, 2002; see also Cresko and Baker, 1996), parapatric stream–lake stickleback (Bolnick *et al.*, 2009; Hendry *et al.*, 2013), anadromous–lake resident pairs (Karve *et al.*, 2013), black–red pairs (McPhail, 1969), and the unique white stickleback in Nova Scotia (Blouw and Hagen, 1990).

The conservation value of species such as the stickleback cannot be measured using the same metrics important for more restricted species (e.g. number of viable populations remaining, population size, geographic range). Rather, the primary value of the threespine stickleback is as an *evolutionary system* – and one whose most unique elements may be at the greatest risk (Bell and Ortí, 1994; Foster *et al.,* 2003). One of these unique elements comprises a very small set of populations that have evolved a condition known as pelvic reduction. A fully formed pelvic girdle is a bilateral structure comprised of a pelvic spine, anterior and posterior processes, and an ascending process on each side of the ventral midline (Bell *et al.*, 1993; Bell and Ortí, 1994) for a total of eight components. The ancestral state is a robust, fully formed girdle. The pelvic girdle is presumed to function to protect the stickleback from gape-limited predators such as trout (Reimchen, 1994; Reimchen *et al.*, 2013). Pelvic reduction is widespread geographically, but unevenly distributed, being reported from Alaska, Scotland, southern British Columbia, the Haida Gwaii Archipelago, Quebec, southern California, and Norway (Klepaker *et al.*, 2013). In most of these regions, the number of populations exhibiting pelvic reduction is small; for example, only four populations with pelvic reduction out of more than 200 Norwegian populations surveyed (Klepaker *et al.*, 2012). However, within the Cook Inlet region of Alaska, samples collected since the mid-1980s demonstrate that pelvic reduction is relatively common, with 47.5% of 204 populations studied by Bell and Ortí (1994) having at least a few individuals exhibiting the phenotype. Nonetheless, even in Alaska fish with reduced pelvic structures predominate in relatively few populations. This is because in Alaska selection appears to strongly favour the reduced phenotype only under certain conditions, notably a lack of predatory fish and low calcium concentrations (Bell *et al.*, 1993; Bell and Ortí, 1994).

Lakes in Alaska that support stickleback populations with substantial pelvic reduction are invariably small. Of 215 lakes surveyed in the Cook Inlet region of Alaska in 1990 by M.A. Bell, the mean surface area of 30 lakes with at least some degree of pelvic reduction was 19.9 ha, and in 185 lakes without pelvic reduction the mean size was 37.9 ha. These lakes are also located within nutrient-poor watersheds, and lack permanent inlet streams that could bring nutrients to the lakes. In addition, the major predatory fish (rainbow trout, *Oncorhynchus mykiss*) in Cook Inlet lakes requires either an inlet or outlet stream to reproduce, and thus is absent naturally from many of our small, isolated study lakes. In our south-central Alaska study area, pelvic reduction seems to be associated with low calcium concentrations, and low calcium is also associated with low primary productivity [$r = 0.28$, $n = 80$ Alaskan lakes, $P < 0.008$ (J.A. Baker, unpublished data)]. In particular, lakes in which pelvic-reduced fish predominate show a low yield of chlorophyll per unit of phosphorus (Jones *et al.*, 2003) and thus in their original (unaltered by human influence) state they should support relatively small populations of stickleback per unit size (Griffen and Drake, 2008b).

In this study, we take advantage of our long-term collecting programme in the Cook Inlet Region of Alaska to investigate whether lakes in which pelvic reduction has evolved support smaller densities of stickleback than do lakes in which pelvic reduction has not evolved. If they do, and if our estimated densities proportionally reflect actual population size, then these unique populations may be at an increased risk of loss. M.A. Bell initiated the collections during the 1980s, with the first broad-scale collections made by him in 1990. Collections have continued annually by J.A. Baker and D.C. Heins and their students from 1992 to the present. M.A. Bell and students have also continued to collect from selected populations during this period. The combined collections are estimated by J.A. Baker to include more than 400,000 preserved stickleback from more than 250 populations. The collections were made for a variety of purposes, and as is often the case with such general collections, they are not always ideal for addressing detailed conservation questions (Reznick *et al.*, 1994). Nevertheless, we believe that they are sufficient for our needs. We do not perform a formal population viability analysis, and we follow the advice of Fieberg and Ellner (2000) in not attempting to estimate the probability of extinction for our populations, but rather focus on how ecological factors may drive population dynamics.

We test three specific predictions for our study system. The first is that catch-per-unit-effort (CPUE) of stickleback will be lower in populations expressing pelvic reduction than in populations that retain the full pelvic girdle, correcting for lake size if necessary. Second, we predict that pelvic-reduced populations that have been stocked with rainbow trout will have a lower CPUE than those that are not stocked. Finally, we predict that populations that have evolved pelvic reduction will show greater annual variation in CPUE. We assume that CPUE reflects density in at least a rank-order manner, and thus variations in CPUE reflect variations in population size.

METHODS

Our study populations are a subset of those in a previous, more general study (Baker *et al.*, 2010). In that study involving a larger set of populations ($N = 77$) from the same study area, we showed that pelvic-reduced populations subjected to trout stocking had a significantly greater probability of dropping to an ‘unusually low population size’ during our 1990 to 2010 collection period. In that paper, ‘abundance’ was scored as a two-state variable, ‘within the typical range’ or ‘unusually low’, and we analysed the relative proportions of ‘unusually low’ abundance estimates. For the present study, we focused on a subset of the original populations for which quantitative data were available. Twenty-three populations with a relatively consistent sampling record between 1993 and 2010 were chosen for inclusion in the present study (Table 1). Criteria for inclusion were that a quantitative set of collections had been made in at least 9 of the 18 years spanned by our study, and that the samples had been collected using a standardized protocol. Some of the populations with pelvic reduction had been stocked with rainbow trout by the Alaska Department of Fish and Game. Our final data set included: 12 full-pelvic populations (FP), 10 of which exist with native rainbow trout (trout are also stocked annually in most of these lakes); five pelvic-reduced populations that lack trout (PR-NS: trout not native, none stocked); and six pelvic-reduced populations that had been stocked with rainbow trout (PR-ST). Hereafter, we refer to these as population types, using the acronyms for brevity. The pelvic-reduced populations used in this study represent the only ones available within our study area for which we have sufficient numerical trap-catch data. The 12 FP populations were randomly

Table 1. Study lakes

Lake	Predatory fish	Depth (m)	Elevation (m)	SA (ha)	RLA index	Pelvic phenotype	Annual samples
Beverly	NT	2.9/6.1	113	17	80	FP	11
Big Beaver	NT	3.0/5.5	64	61	42	FP	16
Cornelius	NT	7.0/16.5	122	18	34	FP	15
Falk	None	3.5/4.0	30	6	40	FP	12
Kashwitna	NT	1.9/4.0	57	64	100	FP	14
Lazy	NT	2.9/5.5	52	10	65	FP	16
Lynda	NT	3.5/6.0	52	7	50	FP	12
Pup	None	2.5/4.0	134	5	100	FP	15
South Rolly	NT	8.2/19.2	58	44	22	FP	12
Stepan	NT	2.5/4.3	73	23	34	FP	17
Tern	NT	2.0/3.5	205	55	90	FP	17
Willow	NT	1.7/3.0	91	58	100	FP	18
Bear Paw	ST	3.0/5.8	88	17	100	PR	18
Boot	ST	2.3/2.7	113	11	100	PR	17
Bruce	ST	2.9/5.0	51	10	60	PR	17
Dawn	ST	2.5/5.2	84	5	52	PR	11
Kalmbach	ST	4.0/7.3	44	54	48	PR	17
Vera	None	3.4/6.7	61	45	47	PR	14
Solid Rock	None	2.0/3.5	66	12	100	PR	16
Echo	None	2.5/4.5	61	15	41	PR	11
Jean	None	6.0/8.0	162	17	45	PR	15
Trouble	None	2.0/3.0	119	2	100	PR	9
Whale	None	3.5/6.5	67	5	60	PR	16

Note: Predatory fish: NT = native rainbow trout; ST = stocked trout. Depth is mean/max. Elevation = metres above mean sea level. SA = surface area. RLA = proportion of littoral vs. limnetic habitat (e.g. 100 indicates a shallow lake with only littoral habitat). Latitude and longitude for each lake are available in Baker *et al.* (2010). FP = full pelvis; PR = reduced pelvis.

selected from a slightly larger pool of such populations such that they represented approximately the same range of lake sizes. Because the sampling was performed as permitted by time and resources during the execution of other studies, not all lakes were sampled each year.

The standardized protocol specified collection of threespine stickleback from the breeding grounds in each lake using un-baited ¼-inch mesh (97.5% of all traps) or ⅛-inch mesh (2.5% of traps) metal minnow traps. All collections were made during the height of the breeding season. Typically, 10 traps were set per sampling effort, spaced at irregular intervals along the shoreline, usually within 5 m of the bank in depths typically less than 1–2 m. Traps were allowed to soak for 20–24 h (mean = 20 h; median = 21 h). All stickleback captured were counted. If two sampling efforts were made in any individual population in a single year, the data were pooled. Throughout the study, seining and visual surveys via snorkelling were used as time permitted to corroborate the trap-derived abundances. Final disposition of captured specimens varied by year and population. On average, in lakes where capture rates were high, ~80% of captured fish were immediately released after trap counts were made in the field. Collections were being made for other studies, however, and so in most lakes gravid females and a random selection of adult males and subadult fish were retained. Fish retained were euthanized with an overdose of MS-222 and preserved in 10% formalin, isopropyl alcohol, or 100% ethanol depending upon our needs. In lakes where capture rates were extremely low, all fish captured were counted and released.

Due to the nature of our sampling we do not have direct population size estimates. Instead, we used our trap catches to calculate catch-per-unit-effort (CPUE), calculated as the total catch of stickleback per trap-hour. The CPUE is widely used in fishery research as an index of abundance (Harley *et al.*, 2001), and has been employed in studies similar to ours (e.g. Townsend *et al.*, 1990; Wootton, 2008; Mickle *et al.*, 2010). Because we have only CPUE data available, we do not know the form of the relationship of CPUE to population size (Harley *et al.*, 2001), a point to which we return in the Discussion.

We used a nested analysis of variance (ANOVA), with population nested within type and individual samples as the base-level data to determine whether CPUE differed across the three types of stickleback populations. Type was considered a fixed effect and population and year were random effects in this analysis. Because not every population could be adequately sampled in each year, year could not be used as a fixed effect (e.g. a blocking factor). The test for the main effect of type used Satterthwaite's denominator synthesis method to construct the *F*-ratio. Following ANOVA, we computed two specific contrasts to test whether: (a) FP populations had greater CPUE than pooled PR populations; and (b) the two types of PR populations differed. Catch rates were $\log_{10}$-transformed prior to analysis. Variance equality and normality were evaluated using Levene's test and the Shapiro-Wilks test, respectively. The approximate relative contribution of population type and individual population to CPUE variation was determined using a variance components analysis in which type was considered random.

We assume that our CPUE estimates will be proportional to population size. However, trap catches may be affected by at least two other physical features of our lakes – the size of the lake, and the relative amount of littoral versus limnetic habitat. In larger lakes there is a greater chance that catches at our specific sampling site(s) may not be representative in every year, particularly if multiple spawning sites are used and their use varies across years. For the second factor, in a lake with a large limnetic volume some juvenile and adult (age 1 and older) fish may forage sufficiently far offshore that they are less vulnerable to our traps. For most of our study lakes, we performed snorkelling surveys in random years concurrent with trapping to ensure that both juvenile and adult stickleback were indeed using primarily the shallow littoral areas. In many of our study lakes we also studied male reproductive behaviour, and general observations made in these studies were also used to qualitatively assess the general validity of our trap catches. In all our study lakes except one (South Rolly Lake), surveys showed that nearly all juvenile and adult stickleback foraged in the littoral habitat during the breeding season. Lake surface area was determined from Alaska Department of Fish and Game lake records, or estimated by us from Google Earth imagery. Relative littoral area (RLA) values were provided by J.A. Walker of the University of Southern Maine at Portland (personal communication; Walker, 1997), or estimated using a similar methodology. RLA attempts to estimate the proportion of the lake habitat that would be benthic as opposed to limnetic habitat. For each of these factors we calculated the correlation coefficient with CPUE, using data for FP and PR populations separately. Both parametric and non-parametric correlations were computed. If a significant relationship was detected, we re-ran our ANOVA of CPUE taking the trend into account.

Additional variance in our CPUE estimates could arise if the population sizes were changing systematically through time. This consideration is quite plausible, given that we have documented more than two-fold productivity increases in a set of 30 south-central Alaskan lakes between 1990 and 2008 (J. Loux-Turner, unpublished data). To evaluate this possibility, we calculated the correlation between log CPUE and sampling year for each population. We did not compute significance levels for the individual correlations, but rather tested whether their distribution was centred on zero and was normally distributed. If abundance changes across time were due simply to random fluctuations, we would expect them to have a mean of zero and to be normally distributed. A general increase in CPUE through time would be indicated by a mean correlation that exceeded zero.

We evaluated whether the three population types showed different levels of variability in CPUE across years by calculating the coefficient of variation [CV; adjusted for small sample sizes as suggested by Sokal and Rohlf (2012)] for each population across all available annual samples, and then performing a one-way ANOVA. In this analysis, each population contributed a single measure of CV for its type, and thus sample sizes are quite low. Because we had an *a priori* expectation that FP > PR-NS > PR-ST, we incorporated this ordering by adjusting the P-value as suggested by Rice and Gaines (1994). We also compared the ratio of maximum to minimum CPUE across years for each population, as this measure of abundance fluctuation may also be of value (see Baker *et al.*, 2010).

RESULTS

CPUE was not correlated with the proportion of benthic habitat for either FP ($r = 0.06$, $n = 12$, $P = 0.90$) or PR ($r = 0.03$, $n = 11$, $P = 0.95$) populations. CPUE was correlated with lake surface area (Fig. 1), but only for FP populations ($r = 0.63$, $n = 12$, $P = 0.03$), not PR populations ($r = 0.17$, $n = 11$, $P = 0.74$). There was an overall trend for log CPUE to increase throughout the 18-year study period. A total of 19 of the 23 population correlations were positive, and only four negative (Fig. 2), a significant deviation from the null expectation of equal frequencies of positive and negative values ($\chi^2 = 9.78$, d.f. = 1, $P = 0.0018$). The correlations were approximately normally distributed, with a mean of 0.24 (95% confidence limits 0.12 to 0.36).

CPUE varied significantly across the three population types (nested ANOVA: $F_{2,20.4} = 17.39$, $P < 0.001$; note the fractional denominator degrees of freedom estimated by the analysis). All ANOVA assumptions were satisfied for this analysis. Linear contrasts showed that FP populations had significantly higher CPUE than the pooled PR populations ($P < 0.001$), but there was no difference between the two types of PR populations ($P > 0.33$). Log CPUE for FP populations averaged 0.2896 (1.95 fish per trap-hour), while the CPUE for PR-NS and PR-ST catches averaged only −0.1675 and −0.2147 (0.68 and 0.61 fish per trap-hour, respectively) – a 2.87-fold to 3.19-fold difference between FP and PR populations. Adjusting FP populations to the average lake surface area for all lakes with FP populations reduced slightly the magnitude of the difference between FP and PR populations, but the overall pattern remained robust and significant. Population type accounted for 37.0% of the overall variance in CPUE, and population-within-type accounted for 12.6%.

Populations of all three types varied considerably across the sampling period (Figs. 3 and 4). Following P-value adjustment, the ANOVA of population-level CVs indicated no significant differences across the three population types ($P = 0.15$). The ranking of populations was: FP (mean CV = 0.798), PR-NS (mean CV = 0.851), PR-ST (mean

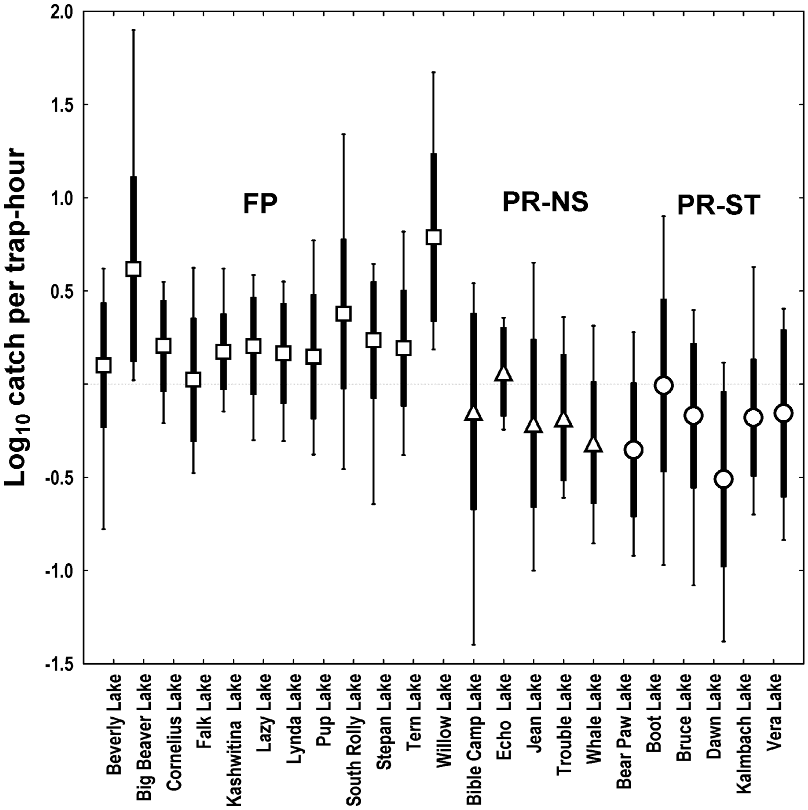

Fig. 1. CPUE ($\log_{10}$ fish per trap-hour) for 23 populations of threespine stickleback from the Cook Inlet region of Alaska. Symbols indicate means, boxes indicate standard errors, and whiskers indicate minimum and maximum observed values. The dashed line at log0 (one fish per trap-hour) is included to help when comparing population types: squares (full-pelvic populations); triangles (pelvic-reduced populations lacking predatory trout); circles (pelvic-reduced populations that have been stocked with predatory trout).

CV = 0.934). Ratios of maximum to minimum population CPUEs were not significantly different between FP and PR populations ($t_{21} = 0.92$, $P = 0.37$; mean ratio = 23.5 for FP populations and 31.8 for PR populations).

DISCUSSION

Both average population size and variation in population size are important in determining population persistence. Although we did not measure population size directly, our data do permit us to infer differences in at least rank-order population size across our populations, and to couple this with estimates of annual variation. Very few reports of threespine stickleback abundance have been published (Wootton and Smith, 2001), and four of these were performed either in very large lakes (Krokhin, 1970; Eggers *et al.*, 1978; Adams and Maitland, 1998) or in open river systems (Power *et al.*, 2000) that are likely quite different from our small lakes. Gíslason *et al.* (1998) estimated abundance in a moderate-size lake in Iceland, but the only

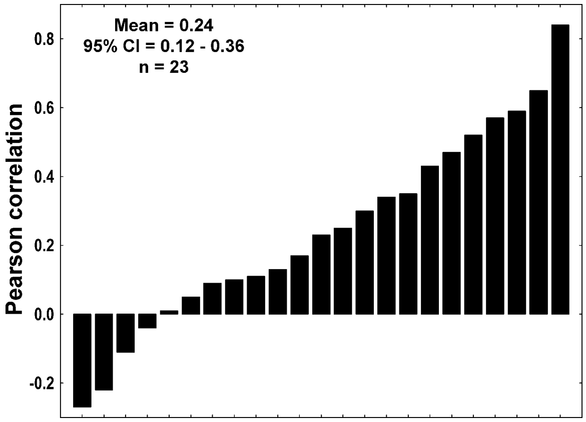

Fig. 2. The distribution of correlations between log CPUE and year for 23 populations of threespine stickleback from the Cook Inlet region of Alaska.

estimates for relatively small lakes are for a pond in Wales (Wootton and Smith, 2001; Wootton *et al.*, 2005; Wootton, 2007, 2010), Drizzle Lake in the Haida Gwaii Archipelago (Reimchen, 1990), and Misty Lake on Vancouver Island (Hendry *et al.*, 2002). These studies suggest a tremendous density range across populations, from hundreds to hundreds of thousands of stickleback per hectare.

Even fewer reports of density fluctuations in threespine stickleback appear to have been published, and they indicate substantial year-to-year variation in population sizes. Wootton and Smith (2001) reported on mark–recapture estimates across a 26-year period in a pond along the River Rheidol in mid-Wales, during which density fluctuated more than eight-fold. In the smaller north basin of Lake Myvatn (Gíslason *et al.*, 1998), population sizes showed a 42-fold variation over a 7-year period. Power *et al.* (2000) reported 15-fold fluctuations across 18 years in the abundance of stickleback captured over a 3-month period each fall on intake screens of a power station in the Thames River estuary. Adams and Maitland (1998) reported a more than 50-fold variation in catches on intake screens in Loch Lomond, Scotland. Our ratios of maximum-to-minimum CPUE were much higher than those of Wootton, and more similar to those of the other three studies.

Many of our PR lakes are moderately dystrophic (Jones *et al.*, 2003). If we assume that the density of breeding adults in our PR populations is similar to that in other dystrophic Canadian lakes (about 635 adults per ha), we can explore plausible adult population size, and fluctuations in size, using our CPUE data. Bear Paw Lake is an exemplar of our PR populations, and is one that we sampled in each of our 18 years, across which its mean CPUE of 0.60 was nearly identical to the average for its class (PR-ST populations). The average population size in Bear Paw Lake over our study period would be about 10,800 adults, and would have fluctuated between 2150 and 34,200 adults. Trouble Lake, our smallest at just 3 ha, even though it had an average CPUE nearly 50% higher than that of Bear Paw Lake, would have supported only about 2850 adult stickleback on average, and population size would have fluctuated from 810 to 7400 fish in total.

In drawing our conclusions we have made numerous assumptions. Two of the more important were that our traps sampled stickleback equally well in all 23 study lakes, and that our sampling sites and times within each lake were representative of the lakes in

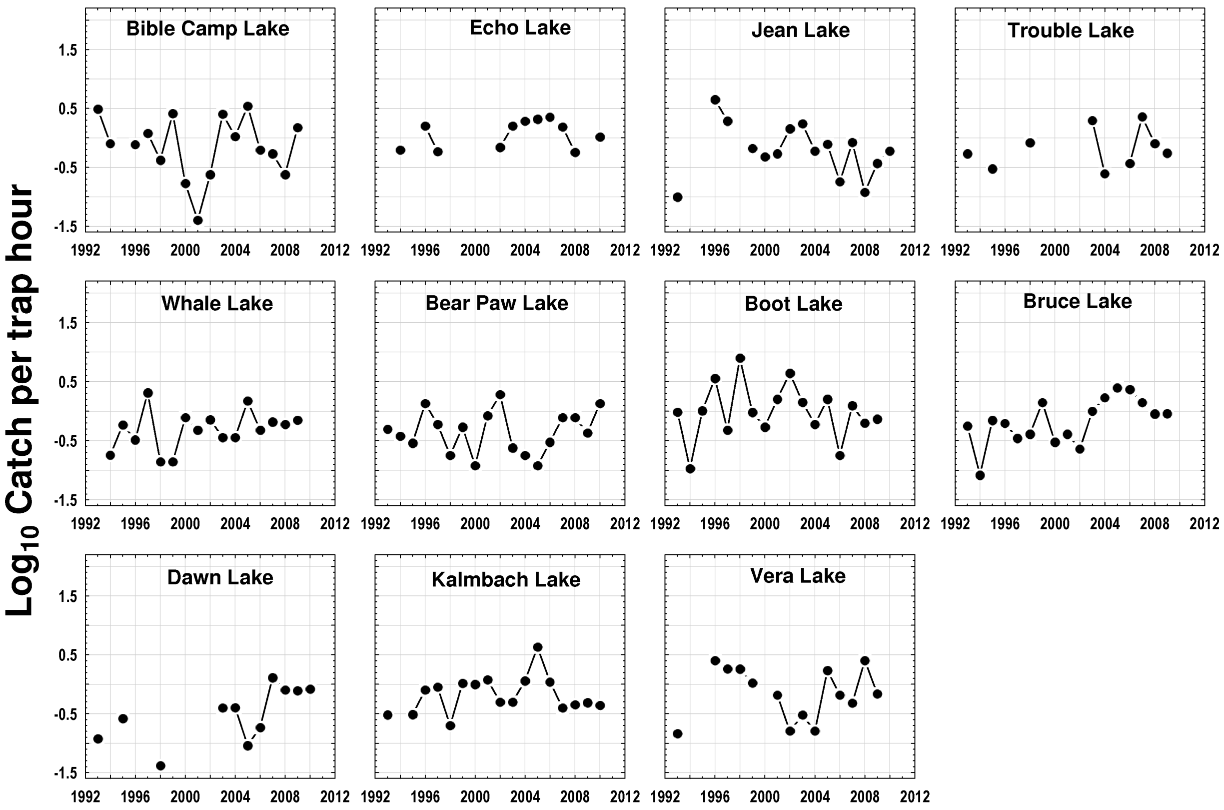

Fig. 3. CPUE values for 11 PR populations of threespine stickleback across an 18-year period. From upper-left to lower-right, the first five panels are PR-NS populations, while the last six panels are PR-ST populations.

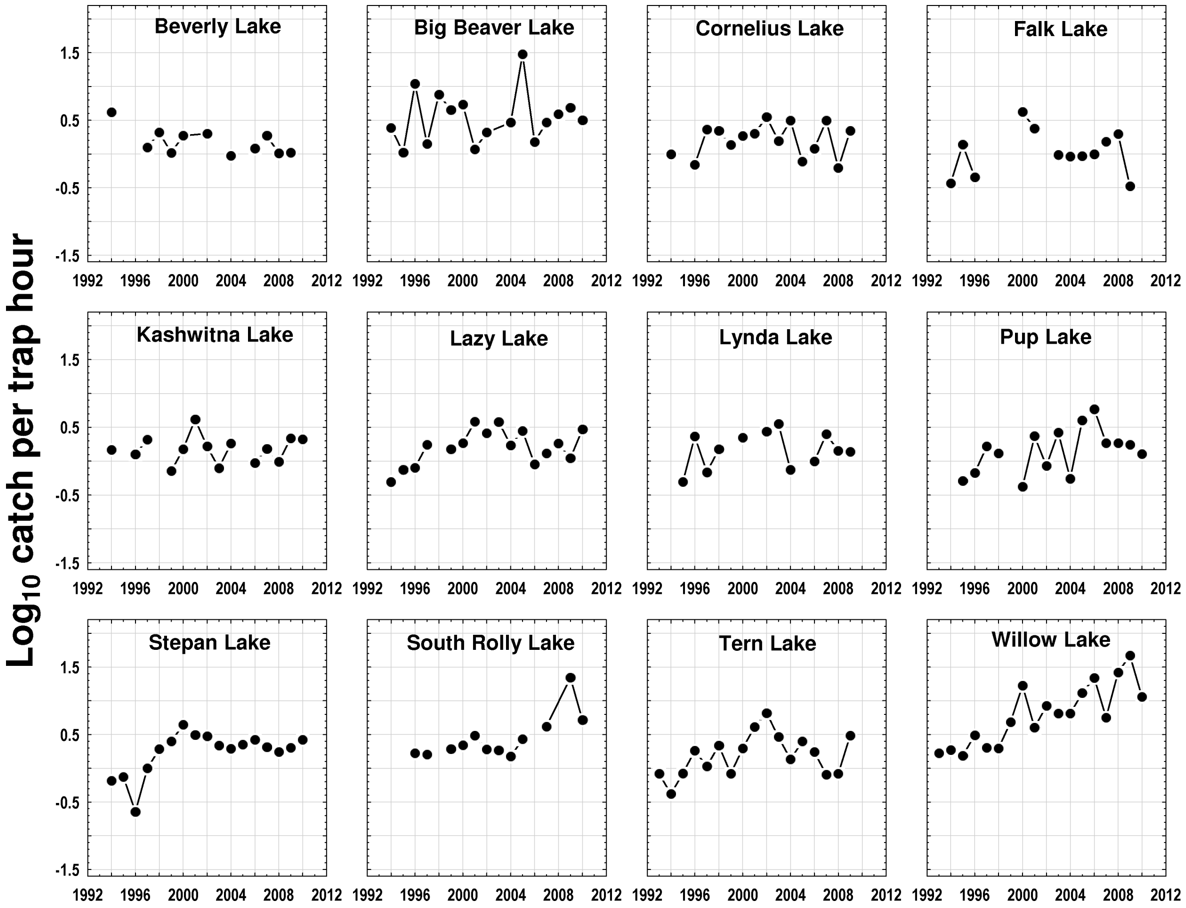

Fig. 4. CPUE values for 12 FP populations of threespine stickleback across an 18-year period.

general. We are confident that the first assumption is valid. All of our lakes are small, and we sample known breeding grounds in each of them. During the breeding season, both our trap catches and snorkelling surveys indicate that all fish age 1 and older, whether they are subadults or breeders, spend the summer months in the shallow, shoreline areas we trap. All populations feed largely on benthos at this time, with the exception of South Rolly Lake fish, which feed on both benthos and plankton (J.A. Baker, personal observation). The second assumption is likely to hold as well. Whenever we have trapped multiple areas of a lake we have obtained similar CPUEs; and on three occasions we have made multiple samples spaced at 2-week intervals in a small set of lakes, again obtaining similar CPUEs. One other point suggests that the differences we observed between FP and PR populations may be conservative. In years in which densities are clearly high, traps appear to fill quickly, and they may saturate in less than our typical 24-h set duration. If so, then CPUE would be underestimated in these situations, which occur far more frequently in FP populations.

Stickleback in some of our PR lakes display a range of pelvic phenotypes, and we have assumed that the different phenotypes are not differentially captured, either via differential avoidance of traps, or because fish with different pelvic phenotypes use different habitats. Reimchen and Nosil (2001) found that stickleback in Boulton Lake, British Columbia did show some habitat assortment by pelvic phenotype, with more asymmetrical phenotypes feeding farther offshore. However, Klepaker *et al.* (2012) found no evidence of assortment by habitat. Our lakes in which PR stickleback exist are quite small and shallow, likely limiting the opportunity for substantial sorting of this type, although we cannot discount it.

A study of more than 250 data sets for which both CPUE and abundance were available (Harley *et al.*, 2001) indicated that CPUE and population size are typically not linearly related. Nearly 70% of these authors' data sets showed hyperstability, a situation in which the CPUE overestimates population size as population size declines (indicated by the 'shape' function $\beta < 1$). We have no estimates of β for our populations. However, a study by Gíslason *et al.* (1998) of Lake Myvatn in northern Iceland included both CPUE estimates and population size estimates. In this lake, log CPUE from small traps was linearly proportional to log population density estimates with a slope of close to unity ($\beta = 1.07$). The form of the relationship is critical for drawing correct inferences from CPUE data. For example, if most of our populations show hyperstability (inflated CPUE values at low population sizes), then PR populations may fluctuate to lower sizes than our relative CPUE would suggest. An additional consideration is that Harley *et al.* (2001) used data for exploited marine fish stocks for which all the CPUE estimates were derived from an active gear type (trawls). It is possible that passive gear such as ours may show a different relationship between CPUE and abundance.

Much of the value of the stickleback adaptive radiation is due to the repeated, parallel evolution of specific phenotypes (ecotypes) in multiple geographic regions in response to similar selective pressures (Bell and Foster, 1994). One of the least common of these phenotypes is pelvic reduction. Part of the value of this interesting phenotype stems from its broad geographical distribution (Klepaker *et al.*, 2013), and the fact that its occurrence cannot be explained by factors common to all regions. In Scotland, pelvic reduction is associated with low calcium (Giles, 1983), while in Alaska both low calcium and a lack of piscivorous fish species appear to be important predictors (Bell and Ortí, 1994). Furthermore, selection for reduced armour, particularly spines, may also be favoured if insect predators are abundant, which is more likely when predatory fish are absent, although this link is still considered controversial (Mobley *et al.*, 2013). Nevertheless, low calcium is not associated with pelvic reduction in other areas, and pelvic-reduced stickleback are sometimes sympatric with large predatory fish (Klepaker *et al.*, 2013). Thus, loss of populations in any region diminishes our ability to understand the evolution of this interesting phenotype.

While we did not estimate extinction potential, it is likely that our Alaskan PR populations are in greater danger of extinction than our FP populations, particularly from anthropogenic modification of stickleback habitats (Bell and Ortí, 1994; Foster *et al.*, 2003; von Hippel, 2008; Baker *et al.*, 2010). However, predicting the near- to medium-term fate of these populations is difficult given that each population is subject to its own complex, and likely unique, eco-evolutionary dynamics (Kinnison and Hairston, 2007; Hanski, 2011). These unique eco-evolutionary dynamics are shaped by interactions among numerous factors (Klok and De Roos, 1998; Griffen and Drake, 2008b) such as demographics (including current population size and size variation), variable reductions in genetic diversity due to past selection or bottlenecks, the specifics of the selective landscapes, and changes in selective agents such as the introduction of novel predatory trout and increases in lake productivity. For example, increases in food supply are predicted to decrease extinction risk by increasing carrying capacity (Bayliss and Choquenot, 2003). All of our study lakes are increasing rapidly in productivity, and at least half of our FP populations show evidence of density increases. However, none of the five PR-NS populations have shown any evidence of increased density across our 18-year study period, while two of the PR-ST populations (Bruce and Dawn lakes) have (but without significant change in pelvic phenotype due to trout predation). Finally, at least one lake (Bear Paw Lake) has responded to trout introductions by apparently evolving to use a safer habitat within the lake, instead of re-evolving a complete pelvic girdle.

It is likely that the original evolution of substantial pelvic reduction was an adaptive response to low productivity (associated with low calcium), so that fish allocated scarce minerals such as calcium to reproduction or somatic growth instead of armour (Klepaker *et al.*, 2013). Interestingly, this adaptation may increase extinction probability with respect to recent environmental change [evolutionary suicide (Parvinen, 2005)]. This possibility is obvious in populations in which trout have been stocked but where the stickleback have lost the ability to re-evolve a functional girdle. However, it is possible that such 'suicide' could occur even when the environmental change might be expected to lessen the probability of extinction. For example, we believe that most of the year-to-year fluctuations in our PR populations may stem from density-independent rather than density-dependent mechanisms. We have observed large variations across years in aspects of the regional weather (water temperature; proportion of overcast days that limit primary production) that likely result in dramatic fluctuations in the overall amount of food available for stickleback fry. We expect that our PR stickleback populations will eventually respond to the increasing productivity by increasing their average density. At some point, density-dependent mechanisms may then drive evolutionary change too rapidly, something that we have observed in one of our long-term PR populations (Baker *et al.*, 2011).

Pelvic-reduced populations of threespine stickleback warrant special attention from conservation biologists due to their value in evolutionary, genetic, and ecological research, and the high risk of extinction they experience due to a number of factors. These isolated populations also harbour relatively rare genetic and phenotypic diversity. While external risk factors such as predator introduction have been noted previously, this study presents demographic evidence supporting an additional risk due to smaller than expected population sizes.

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