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Resources are more important than predation in driving the size at maturation of freshwater threespine stickleback (*Gasterosteus aculeatus*)

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ABSTRACT

Background: Resource availability and predation are thought to be the most important ecological factors shaping age at maturation. They are expected to have a similar effect in causing populations to mature earlier, but a contrasting effect on size at maturation. Greater resource supplies have a positive effect on size at maturation by increasing growth rate, whereas heavier predation has a negative effect since it induces populations to mature earlier (and thus at smaller size).

Question: Is resource availability or predation pressure more important in shaping the size at maturation when resources and predation covary in the environment?

Organism: Freshwater threespine stickleback (*Gasterosteus aculeatus*).

Field site: Natural lochs on the Scottish island of North Uist.

Methods: We estimated size at maturation using two different approaches: probabilistic maturation reaction norm (PMRN) and Stearns' size at maturation.

Results: Size at maturation was strongly influenced by resource supply but not by predation. We obtained this result with both approaches: PMRN and Stearns' size at maturation. Populations in higher resource environments, even with higher predation, tend to mature as larger and older individuals. The large increase in fecundity achieved by delaying maturation could provide an explanation for this. Populations living in resource-rich environments also clearly have a faster growth rate, as indicated by a larger average size of individuals at age one year. On the other hand, populations with higher predation have a significantly lower life span, as indicated by a lower proportion of fish older than one year.

Keywords: maturation event, PMRN, predation, resources, threespine stickleback.

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INTRODUCTION

Time of maturation is a crucial event in the life history of an organism, since it will affect other life-history traits such as future growth, fecundity, adult survival rate, and the survival rate of the next cohort. The most important thing to consider in optimizing the time of maturation, in terms of age and size at maturation, is fitness: the balance of costs and benefits of maturing earlier or later (Stearns, 1992). Maturing earlier reduces generation time and the probability of death before maturation (Stearns, 1992). However, delaying maturation, if growth is still possible, has a direct positive consequence for fecundity because larger body size results in a greater number and/or larger size of propagules (Stearns and Koella, 1986; Roff, 1992). As larger propagules tend to increase fitness in the next generation, delaying maturation is likely to have an indirect positive effect on the survival rate of the next cohort. Delaying maturation can also extend growth and increase adult survival if there is a trade-off between growth and reproduction (Reznick, 1983), or a negative relationship between adult survival and age at maturation (Stearns, 1992).

From a life-history perspective, time of maturation is strongly influenced by growth rate, and juvenile and adult mortality rate. Most authors agree that individuals or populations with a faster growth rate are expected to mature earlier and at a bigger size (Stearns and Koella, 1986; Reznick *et al.*, 1990; Roff, 1992; Heino *et al.*, 2002). However, if the faster growth leads to increased adult or adult and juvenile mortality, this general pattern can reverse to produce later maturation at a bigger size (paraboloid and keel-shaped reaction norms) (Stearns and Koella, 1986). In populations with higher juvenile mortality, selection should favour later maturation, since this will result in increased reproductive investment and correspondingly more and/or larger offspring, increasing the probability of producing surviving offspring. In contrast, higher adult mortality should favour earlier maturation to reduce the risk of being killed before maturation (Roff, 2001).

Resource availability and predation are thought to be the most important ecological factors shaping the evolution of age and size at maturation of organisms (Abrams, 2011). This is because resource availability is the most important factor in shaping growth, while predation strongly affects the survival rate of organisms. Better resources will lead to faster growth rates, while higher predation will increase the probability of dying before reproduction. For these reasons, resources and predation have a similar impact in causing populations to mature earlier, but have a contrasting effect on size at maturation. Higher resources have a positive effect on size at maturation by increasing growth rate, while heavier predation has a negative effect since it induces populations to mature earlier (and thus at smaller size).

In theoretical studies of life-history evolution, agents of selection, such as resource availability and predation, are generally assumed to be independent of one another, but this may not always be true. There are good reasons to believe that resources and predation may covary in natural environments (MacColl, 2011; MacColl *et al.*, 2013), since naturally richer environments may support more complex food webs (and hence more predators) (Grenouillet *et al.*, 2002), or because predation reduces prey population size (Abrams and Rowe, 1996; Reznick *et al.*, 2001; Abrams, 2011). A study by Martin *et al.* (2011) on broods of passerine birds found that high predation risk can force individuals to grow faster even when they have fewer resources. On the other hand, a study by Arendt and Reznick (2005) on Trinidadian guppies (*Poecilia reticulata*) found that higher resources decreased the negative effect of predation on growth rate. Starting from these unpredicted results, we address the question of which one is more important in shaping the size at maturation if resources and predation covary.

Maturation has traditionally been quantified as a deterministic reaction norm linking age and size for individuals or populations (Stearns and Koella, 1986; Stearns, 1992). Individuals are assumed to mature as they pass a critical point along the maturation curve at a fixed age and size. More recently, it has been suggested that it is more accurate to view maturation as a probabilistic phenomenon, in which the likelihood of maturing is a function of size and age called the probabilistic maturation reaction norm (PMRN) (Heino *et al.*, 2002; Dieckmann and Heino, 2007). Heino and co-workers argue that not all individuals will mature at the same age or size because they have different growth curves. Quantifying maturation as PMRNs reduces the effect of variation in growth among populations on the maturation function, reducing the effects of phenotypic plasticity. For this reason, PMRNs are used widely to analyse selection, especially in harvested populations (e.g. Law, 2000; Conover and Munch, 2002; Ernande *et al.*, 2004). Even though PMRNs cannot be ascribed purely to genetic variation (Kraak, 2007), we can assume they are mostly shaped by the selection they have experienced.

To date, the use of PMRNs has been mostly applied to marine populations and in particular the impacts of commercial fishing (Pérez-Rodríguez *et al.*, 2013; Marty *et al.*, 2014; Hunter *et al.*, 2015). It is well established that intensive fishing will decrease the age and size at maturation (Heino and Godo, 2002; Jørgensen *et al.*, 2007; Kokkonen *et al.*, 2015). However, the PMRN approach has seldom been applied to the study of life-history responses to ecological circumstances in freshwater fish species (e.g. Kokkonen *et al.*, 2015). Here, we investigate the role of natural variability (i.e. resources and predation) on inter-population variation in the PMRNs of freshwater threespine stickleback (*Gasterosteus aculeatus*; hereafter stickleback) from the Scottish island of North Uist.

The stickleback has become a model fish in evolutionary ecology due to its rapid adaptive radiation and its scientific tractability. Stickleback can spawn multiple times within years, and are therefore iteroparous (Baker *et al.*, 2015), but most stickleback populations on North Uist are short-lived (annual) populations with less than 15% reaching their second winter (Rahman, 2017). There is a strong covariance between resource availability and density of predators in these populations (MacColl *et al.*, 2013; MacColl and Aucott, 2014). As a result, there is also a contrast in stickleback adult size, size at maturation, and number and size of offspring between alkaline, meso- to naturally euthrophic lochs (lakes) on the west side of the island and acidic, oligotrophic lochs in the east (MacColl *et al.*, 2013; Rahman, 2017). The main question for this study was which factor is more important in shaping size at maturation: resources or predation?

METHODS

Study area and populations

North Uist (57°36′N, 7°20′W) is a small island of only 303 km^2 in the Western Isles of Scotland. There are more than 180 lochs (lakes) – and many smaller lochans (ponds) – on the island, ranging from alkaline in the west to acidic in the central and eastern parts of the island (Giles, 1981). These lochs vary greatly in size but are generally shallow (MacColl *et al.*, 2013). Many of them are completely isolated from the marine environment, while others are tidal or have streams running to the sea. Populations of stickleback in North Uist are free from fishing activities, and lochs on the island contrast strongly in water chemistry, such as calcium availability (Giles, 1981) and pH, which correlate with resource availability (Waterston *et al.*, 1979) and stickleback body size (MacColl *et al.*, 2013). The lochs also vary in the size and density of their main predator, the brown trout (*Salmo trutta*) (MacColl and Aucott, 2014). The brown trout is the dominant predator of stickleback on North Uist, although other predators such as birds, eel, salmonids, and Arctic charr also occur in some lochs (MacColl *et al.*, 2013). Avian predators include divers (*Gavia* spp.), terns (*Sterna* spp.), and herons (*Ardea cinerea*), but none are common in freshwater lochs. Stickleback are found in most water bodies across North Uist and vary greatly in body size (MacColl *et al.*, 2013), but have not previously been the subject of studies of life-history variation.

Ecological and stickleback sampling

In 2013, data on the following water chemistry variables were collected as proxies for resource availability: pH, conductivity, the concentrations of calcium (Ca^{2+}) and sodium (Na^{+}) ions, and dissolved organic carbon (DOC). These variables were chosen because they are commonly used measures of environmental variation in aquatic systems, and have previously been found to covary with resource availability in Uist lochs (Waterston *et al.*, 1979; MacColl *et al.*, 2013). To estimate trout density, we used data collected by the local North Uist Angling Club (MacColl and Aucott, 2014). Between 1956 and 2006, they recorded the number of trout caught during fishing competitions on many different lochs. For these competitions they also recorded the amount of time spent fishing and the number of anglers. This made it possible to calculate the average number of trout caught per person per hour for many lochs (catch per unit effort, CPUE). The size of trout landed during these competitions was also recorded, allowing estimates to be made of the average size and catch rate of trout in different lochs (MacColl and Aucott, 2014). The absence of trout from some lochs was confirmed by gill-netting in 2013.

Females from six different populations of North Uist stickleback were sampled in 2014–2015 (Table 1), with the aim of obtaining at least 50 immature and 50 mature females from each population. Most samples (more than 93%) were collected from the lochs in 2014, with the remaining sampled in 2015. These six populations were chosen because of their apparent diversity in yearling (1+) size (MacColl *et al.*, 2013), resource availability, and predation intensity (Table 1). We chose three pairs of populations across the resource gradient. In each pair of populations, trout were present in one and absent from the other, to ensure the greatest contrast in predation potential. Based on genome-wide data (~9000 SNPs) from RADseq, each of the six populations analysed here forms its own clearly distinct genetic unit (Magalhaes *et al.*, 2016).

Fish sampling was carried out using unbaited minnow traps that were set overnight from the shore in water 0.3–3.0 m deep. The trapped stickleback were emptied into buckets and were sorted on the loch shore to exclude males as far as possible, since the PMRN analysis was restricted to females. The remaining samples were selected haphazardly and brought to a field laboratory for dissection and measurement. Remaining male fish were excluded from data collection once their sex had been established by visual inspection of dissected gonads.

For each individual stickleback, we recorded standard length in millimetres, weight in grams, reproductive status (maturing/mature or immature), and weight of gonads. Reproductive status was checked by dissection of the body cavity and observation of the ovaries under a binocular microscope (~16–40×). If the ovules were all small and the same size, then fish were recorded as immature. If any of the ovules were of larger size such that there was conspicuous variation in size between ovules, then the fish was recorded as maturing/mature. Fish were preserved in ethanol for later determination of age by otolith analysis (Singkam and MacColl, 2018). Using the otolith data, we estimated average size (length) at one and two years old, and the proportion of fish older than one year (most stickleback in these populations mature at about one year of age). One-year-old fish were defined as those that had one clear winter/transparent ring (hatched in the previous breeding season to that of sampling, and approximately 10–13 months old) (Singkam and MacColl, 2018). We used the average size in each year class as an estimate of the growth rate in each population, while the proportion of older fish was used as an estimate of life expectancy.

Data analysis

Principal components analysis was performed to summarize the resource variables (concentration of calcium and sodium ions, pH, conductivity, and dissolved organic carbon), and the first principal component (PC1) used as an overall summary of 'resource availability'. A generalized linear model (GLM) with normal errors and identity link function was used to test for differences in size at one year of age. In comparisons of age distributions between lochs, fish were coded as one year of age or older, and the data were analysed by GLM with a binomial error distribution and a logit link function. Regression analysis was then used to examine the relationships of mean size at one year and the 'proportion of older' fish in each population with measures of resource availability and predation (brown trout CPUE).

PMRN analysis was conducted using a GLM with binomial errors and a logit function, following Heino *et al.* (2002). Maturation of each fish (0 or 1) was used as the response variable. Size, age (in years from otoliths), and loch of origin were included in the fixed model. Size at 50 per cent probability of maturation (Lp50) was calculated for each loch following Heino *et al.* (2002). Lp50 was then regressed on environmental (resource and predation) variables.

A GLM with normal errors and identity link function was used to test for differences in the size and age (square root transformed) of the mature fish. The average length and age of these mature fish in each population were then used to estimate traditional maturation reaction norms (Stearns and Koella, 1986). Estimated means were regressed on resource availability and brown trout CPUE. We also estimated the difference – or 'bias' (Heino *et al.*, 2002) – between mean size at maturation and the Lp50, and examined how this was related to mean body size in each population using simple regression analysis. All statistical analyses were conducted in Genstat (VSN International, 2011).

RESULTS

Principal components analysis of resource factors summarized 73% of variation in PC1 and 20% of that in PC2. Principal components scores for each loch are shown in Table 1. All of the resources factors, except DOC, tended to have similar weightings on PC1, while PC2 was associated with variation in DOC. Details of trout CPUE, trout size, and number of mature and immature samples from each population are summarized in Table 1.

There were significant differences in size at one year old (Wald $F_{5,540} = 68.71$, $P < 0.001$) and age distributions (Wald $F_{5,667} = 10.56$, $P < 0.001$; analyses based on individual fish) between populations (Table 2). Larger size at one year of age was clearly associated with measures of resource availability (Wald $F_{1,4} = 37.08$, $P = 0.004$; analyses based on lochs), but

Table 1. Sample sizes, size of yearling threespine stickleback, and indices of resources and predation for six North Uist lochs in the present study

Loch:	a'Bharpa (Bhar)	Ialaidh (Iala)	Chadha Ruaidh (Chru)	nan Struban (Stru)	Hosta (Host)	na Reival (Reiv)
Coordinates	57°34′N, 7°17′W	57°37′N, 7°12′W	57°36′N, 7°12′W	57°34′N, 7°21′W	57°37′N, 7°29′W	57°37′N, 7°31′W
pH	6.03	6.36	6.57	7.05	8.33	8.95
Conductivity (μS/cm)	140.20	185.00	149.00	164.50	339.50	433.25
Ca^{2+} (mg/L)	3.4×10^{-5}	6.0×10^{-5}	5.0×10^{-5}	8.5×10^{-5}	72.0×10^{-5}	45.0×10^{-5}
Na^{+} (mg/L)	8.0×10^{-4}	9.2×10^{-4}	8.1×10^{-4}	10.8×10^{-4}	11.9×10^{-4}	17.5×10^{-4}
DOC (μmol/L)	7.07	15.90	9.37	10.83	7.43	9.82
PC1 resource score	−1.48	−1.40	−1.29	−0.66	2.00	2.84
PC2 resource score	−1.14	1.57	−0.43	0.22	−0.83	0.61
Yearling size (mm)*	30.8	30.1	29.5	30.4	40.6	38.1
Trout catch rate[#]	0.26	0.0	0.0	0.51	0.16	0.0
Mean trout size (mm)	303.7	n/a	n/a	264.2	449.3	n/a
No. of stickleback:						
Immature	50	24	44	50	51	51
Maturing/mature	71	81	58	69	54	60
Total	121	105	102	119	105	121

* Data from MacColl *et al.* (2013), DOC = dissolved organic carbon, [#] trout per person per hour.

Table 2. Population mean (± S.E.) values of size and age at maturation of three-spined stickleback in six North Uist lochs. See text for details

Loch:	a'Bharpa (Bhar)	Ialaidh (Iala)	Chadha Ruaidh (Chru)	nan Struban (Stru)	Hosta (Host)	na Reival (Reiv)
Mean size (mm) at:						
1 year	30.28 ± 5.57	33.86 ± 4.96	32.44 ± 6.02	31.01 ± 4.31	40.52 ± 8.06	42.34 ± 6.92
2 years	33.80 ± 4.92	37.16 ± 4.23	43.81 ± 5.92	34.13 ± 3.41	51.98 ± 6.95	57.80 ± 7.38
Proportion older fish	15.00 (4.74, 6.23)	35.24 (6.60, 7.13)	17.65 (4.84, 6.01)	2.52 (1.59, 3.65)	17.14 (4.90, 6.10)	27.27 (6.29, 7.30)
Mean size at maturation (mm)	32.82 ± 4.91	37.22 ± 4.23	38.74 ± 5.92	33.78 ± 3.41	48.87 ± 6.95	51.99 ± 7.38
Mean age at maturation (years)	1.21 ± 0.45	1.55 ± 0.76	1.34 ± 0.55	1.03 ± 0.17	1.22 ± 0.42	1.45 ± 0.56
Lp50 of PMRN:						
Size (mm)	28.1 ± 1.96	30.1 ± 2.06	32.1 ± 2.16	29.4 ± 2.03	41.5 ± 2.58	43.6 ± 2.67
Age (years)	0.91 ± 0.68	n/a	0.97 ± 0.77	0.83 ± 0.71	1.11 ± 0.82	1.05 ± 0.78
Deviation (bias):						
Size (mm)	4.72	7.12	4.38	6.64	7.37	8.39
Age (years)	0.30	n/a	0.37	0.20	0.11	0.40

n/a = not available.

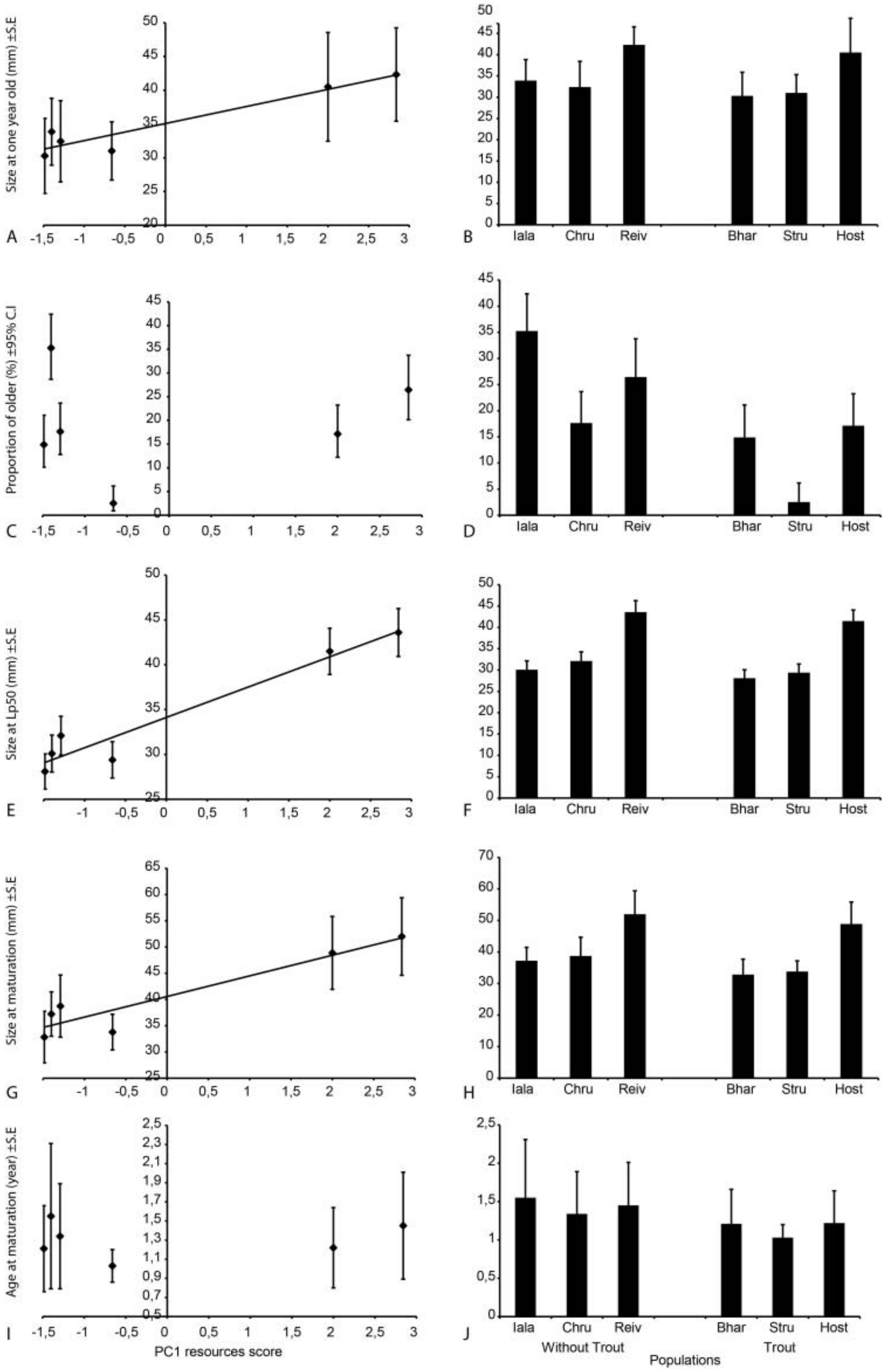

Fig. 1. Relationships between life-history variation (± S.E./CI) and resource availability and predator density among North Uist threespine stickleback. CI = confidence interval.

not with trout catch rate (Wald $F_{1,4} = 1.14$, $P = 0.34$). The proportion of older fish was significantly lower in populations with a higher trout catch rate (Wald $F_{1,4} = 11.42$, $P = 0.028$), but there was no correlation with resources (Wald $F_{1,4} = 0.07$, $P = 0.810$) (see Fig. 1a–d for more detail).

The PMRN analysis showed that there was significant variation in size, but not in age at maturation, among lochs (Tables 2 and 3). The 50% probability of maturing (Lp50) occurred at larger sizes in lochs with richer resources (Wald $F_{1,4} = 62.00$, $P = 0.001$), but differed little regardless of the presence of trout (Wald $F_{1,4} = 0.82$, $P = 0.415$) (Fig. 1e, f).

Mean age and size at maturation (Stearns' approach) differed significantly between populations (Wald $F_{5,396} = 10.62$, $P < 0.001$ for age at maturation; Wald $F_{5,396} = 138.14$, $P < 0.001$ for size at maturation). Again, mean size at maturation was more strongly associated with resource variation (Wald $F_{1,4} = 31.07$, $P = 0.005$), but unrelated to variation in predation (Wald $F_{1,4} = 1.41$, $P = 0.301$) (Fig. 1g, h). Mean age at maturation decreased with increasing trout catch rate (Wald $F_{1,4} = 19.54$, $P = 0.012$), but was unrelated to resources (Wald $F_{1,4} = 0.04$, $P = 0.851$) (Fig. 1i, j).

We also found that populations with higher growth rates, as indicated by a larger mean size at one year of age, matured at a larger size, and this was consistent whether using the PMRN (Wald $F_{1,4} = 102.86$, $P < 0.001$) or mean size at maturation approach (Wald $F_{1,4} = 164.05$, $P < 0.001$). There was some suggestion that populations with a faster growth rate were also more likely to mature at older age (Wald $F_{1,4} = 9.66$, $P = 0.053$ for PMRNs; Wald $F_{1,4} = 0.64$, $P = 0.467$ for Stearns' approach). There was a significant positive correlation between the proportion of older fish in populations and mean age at maturation (Wald $F_{1,4} = 84.14$, $P < 0.001$ for Stearns' approach; Wald $F_{1,4} = 4.52$, $P = 0.123$ for PMRNs), suggesting a negative relationship between earlier maturation and life span.

The bias between size at maturation calculated from the PMRNs and Stearns' mean size at maturation was positively related to body size (size at one year old) (Wald $F_{1,4} = 11.26$, $P = 0.028$). In other words, the expected bias in Stearns' method, compared with the PMRN, is greater in populations with larger body size. The bias on North Uist stickleback ranged from 4.4 mm in the Stru population (average of SL at one year old = 31.0 mm) to 8.4 mm in Reiv (SL = 42.3 mm).

Table 3. Results of a GLM to estimate PMRNs in six populations of North Uist threespine stickleback

Explanatory variable	χ^2	*df*	*P*
Loch	42.47	5, 670	<0.001
Length	67.00	1, 666	<0.001
Age	0.07	1, 666	0.798
Loch × Length	39.87	11, 661	<0.001
Loch × Age	8.63	11, 661	<0.001
Length × Age	64.30	3, 669	<0.001

Note: The model fitted 'reproductive status' (0 or 1) as a binary response variable, and used binomial errors and a logit link function.

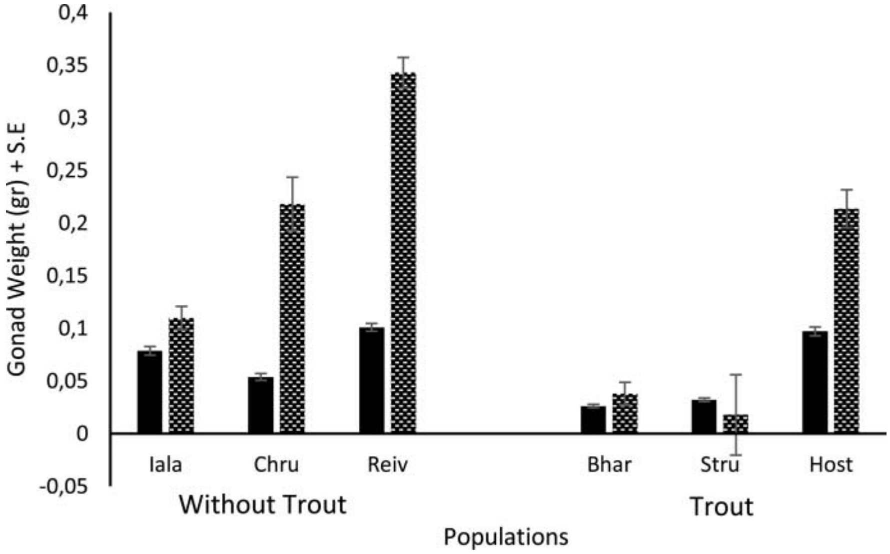

Fig. 2. Changes in mean ovary weights (OW) (± S.E.) between one- and two-year-old mature three-spine stickleback in six populations on North Uist. Solid bars = OW at one year of age, hatched bars = OW at two years of age. Lochs were ordered from the poorest to the richest resources.

Finally, fecundity (measured as gonad weight of mature females) was strongly associated with length (Wald $F_{1,400} = 419.40$, $P < 0.001$) and weight (Wald $F_{1,400} = 723.39$, $P < 0.001$) of the fish. Populations with higher resources experienced a larger increase in investment between their first and second year compared with resource-poor populations (Fig. 2). In Host and Reiv, we observed increases in length of 28.3% and 36.5% respectively between one-year-old and two-year-old fish, while in Bhar and Iala the equivalent increases were only 11.6% and 9.7% respectively. As a result, the fecundity of Host and Reiv increased by 120% and 240% respectively, while the equivalent increases in Bhar and Iala were only 44% and 40% respectively (Fig. 2).

DISCUSSION

The results clearly show that when resources and predation covary, resources are more important in driving evolution of size at maturation in stickleback populations. Our analyses show that the effect of resources overrides the effect of predation on size at maturation. This result is similar to that obtained by Arendt and Reznick (2005) when examining the effect of resources and predation on the growth of Trinidadian guppies. They reported that when resources and predation covary, resources are more important in shaping growth rate. Since optimality of maturation time is highly dependent on costs and benefits (Stearns, 1992), it is interesting to consider how populations overcome the effect of predation.

The most likely way in which the impact of predation can be overcome evolutionarily is that the reproductive advantage of delaying maturation more than offsets the risk of being killed before maturation. The main advantage of delaying maturation is an increase in fecundity, since larger females produce more or bigger offspring (Stearns, 1992; Roff, 2001).

However, if continuing growth is limited due to environmental restrictions (e.g. lack of large prey items for adult stickleback), delaying maturation will become disadvantageous since it will increase the generation time. In our study, we found that the populations which live in higher resource lochs continue growing after they reach one year of age while those from resource-poor populations exhibit little change in size. Delaying maturation in resource-poor populations seems unlikely to outweigh the cost of increasing the generation time.

Another possible explanation for why resource availability is more important than predation in shaping life history in these populations is that larger stickleback may escape the effects of predation because of gape limitation in their predators. However, this seems unlikely in our study system for several reasons. First, the relationship between age at maturation and predation suggests that trout mainly eat adult stickleback, thereby selecting for earlier maturation (Stearns, 1992; Roff, 2001). Second, this is also consistent with the bigger reduction in the proportion of older stickleback in lochs with trout present, and with Scharf and colleagues' (2000) observation that fish predators will take prey up to 20% of their size: even adult stickleback are generally less than 20% of the size of trout. And third, we do find adult stickleback in the stomachs of trout taken by anglers (A.D.C. MacColl, unpublished data). Together, these facts indicate that trout clearly prey upon all sizes of stickleback, although a larger scale analysis by Rahman (2017) suggested that the effects of predation on life history were overridden by the combined effects of competition and resource availability.

Overall, it would appear that maturation occurs earlier with increasing predation (Fig. 1j), and this is consistent with many studies that have examined the effect of commercial fishing (Pérez-Rodríguez *et al.*, 2013; Marty *et al.*, 2014; Hunter *et al.*, 2015; Kokkonen *et al.*, 2015). However, in contrast to those studies, our results showed there was no significant effect of predation on size at maturation. This null effect could be due to a strong positive effect of resources in selecting for larger size at maturation. Since maturing earlier should correlate with smaller size (Stearns, 1992; Heino *et al.*, 2002), our results suggest that if predation is sufficient to drive such changes, they can be offset by increases in resources. This may be relevant to fisheries or wildlife management.

By extension, an unexplained result from this study is that the Reiv population, with high resources, appears to have a lower life span than resource-poor Iala (Fig. 1d). Fish predators are absent from both of these populations, and Reiv has better resources. Since better resources should favour longer life span and there is a trade-off between maturation time and future growth (Reznick, 1983; Stearns, 1992), this result requires an explanation. The most obvious one is that stickleback densities are very high in Reiv, where the competitor species *Pungitius pungitius* is also present (Rahman, 2017).

The Reiv population also has a higher prevalence of most parasites than does Iala (de Roij, 2010), and a higher density of avian predators [terns, *Sterna* spp., although these are still not common (A.D.C. MacColl, personal observations)]. Eighty per cent of Reiv individuals are infected with at least three parasites, of which the most prevalent is *Gyrodactylus arcuatus* (Young and MacColl, 2017). Other parasites than can be found in Reiv are *Schistocephalus solidus*, *Diplostomum gasterostei*, *Proteocephalus filicollis*, and *Dermocystidium* sp. (de Roij, 2010; A.D.C. MacColl, unpublished data). In contrast, only *G. arcuatus* was found in Iala, and with a prevalence of only 18% (A.D.C. MacColl, unpublished data). These facts combined may explain the lower life expectancy in Reiv.

The age structure of stickleback populations on North Uist and in many other locations (dominated by the 0+ age class) suggests that populations are often essentially annual (e.g. Wootton and Smith, 2000), and thus that most fish die after spawning. While there certainly are stickleback populations in which a substantial proportion survive to the age of two or three (MacColl, 2009), it is unclear whether individual females breed in more than one season, rather than waiting to a later age to do so for the first time. Establishing that with certainty would require a large-scale mark-recapture study of individually identifiable fish. However, it is interesting to note that our data are consistent with the possibility that female stickleback breed in multiple years, at least in some populations. In Iala, for example, 76% of females were maturing (leaving only 24% as immature) when we sampled in May, which is relatively early in the breeding season. However, 35% of our sample in this population had survived to two years old. Thus, if this pattern is consistent between years, our data suggest that at least ~10% (35 minus 24%) of females survive until the next spring even after breeding.

Overall, we can conclude that resources are more important than predation in shaping the evolution of size at maturation. On North Uist, the combination of the two factors led to substantial variation in time of maturation. Modelling could be useful to further understand the complex relationship of these two factors to maturation. Lastly, as we expected, the bias between the PMRN Lp50 estimate and mean size at maturation was positively related to body size. This is a useful result, since it is much easier and should be acceptable to estimate the Lp50 from mean size at maturation.

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