

# Parasitism, water temperature and life history characteristics of the freshwater fish *Gobiomorphus breviceps* Stokell (Eleotridae)

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**Abstract** – Life history traits can vary among populations of the same fish species in response to selective pressures exerted by the local environment. Here we used inter-population comparisons to investigate the effects of parasitism and variability in water temperature on life history traits in a New Zealand freshwater fish, the upland bully. Although age and size at maturity varied among populations, they were not significantly related to either temperature regime or average parasite load. Trade-offs between egg size and clutch size were only apparent in one of the seven populations when populations were analyzed separately but became clear when all data were pooled. However, neither average population clutch size or egg size was related to the population's mean parasite load or the local temperature regime. Although the latter two parameters may influence other life history variables, such as the number of clutches produced per season and the partitioning of eggs among clutches, there was no evidence that they influenced life history strategies of the upland bully populations investigated here.

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**Key words:** age at maturity; clutch size; egg size; inter-population comparison; trade-offs; trematodes

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**Un resumen en español se incluye detrás del texto principal de este artículo.**

Variation in life history characteristics among populations of the same species has been attributed to factors ranging from latitudinal clines (Fleming & Gross 1990; Vøllestad & Abée-Lund 1990) to differences in predation regime (Crowl & Covich 1990; Reznick et al. 1990; Fraser & Gilliam 1992; Belk 1998). Effects of parasitism on life history traits have mostly been ignored. Theoretical models predict that a host that matures earlier or at a smaller size in response to parasitism could reduce the impact of parasites on its reproductive success (Hochberg et al. 1992). Such a change in life history strategy could give the host a selective advantage over conspecifics that mature later or at a larger size. For instance, in a comparison among populations, Lafferty (1993) found that snails matured at a smaller size in populations where the prevalence of larval trematode parasites was high.

In fish, parasites are known to lower physical condition or to reduce growth and reproductive output (e.g., Pennycuik 1971; McPhail & Peacock 1983; Lemly & Esch 1984; Poulin 1993). These proximate effects can influence fish fitness, and if levels of parasitism are relatively constant over time in given populations, parasites can play selective roles in fish evolution. Therefore, we might expect fish in heavily parasitized populations to evolve different life history strategies, to compensate for the effects of parasitism, than fish in other populations.

The optimal age at maturity is a trade-off between present reproduction and the probability of future reproduction (Stearns 1989, 1992). Because fecundity usually increases with fish size (Wootton 1991), individuals allocating energy to growth can expect an increased future reproductive success. In

populations where parasites that lower host survival are abundant, however, the probability of future reproduction is reduced. We might thus expect individuals from heavily parasitized populations, where future reproduction is compromised, to mature earlier and/or at a smaller size than individuals from populations experiencing weaker selective pressures from parasitism. Phenotypic plasticity could, to some extent, obscure evolutionary divergence between populations, but it is unlikely to mask it completely. Also, when fish populations are compared to evaluate the effect of a variable such as parasitism, it is difficult to exclude the potential influence of other factors that also vary among populations. At the very least, one should attempt to control for variables for which data is readily obtained. Among abiotic factors, for instance, water temperature is easily quantified and it is known to have important effects on fish growth rates, age and size at maturity, and other life history traits (Wootton 1991). In particular, fish egg sizes vary across populations with respect to water temperature, either on a latitudinal scale (Fleming & Gross 1990) or on a seasonal basis (Mills & Eloranta 1985), and temperature can therefore influence the trade-off between egg size and egg numbers. It is thus important to assess the role of this variable along that of parasitism.

Here, we used inter-population comparisons to investigate how age and size at maturity, clutch size and egg size in upland bullies (*Gobiomorphus breviceps* Stokell) vary in response to variation in parasitism and water temperature. Upland bullies are one of the most common fish species in streams of New Zealand's South Island (McDowall 1990). All the bully populations we studied are parasitized by larvae of the digenean trematode parasite *Telogaster opisthorchis* (MacFarlane 1945). The larvae encyst in the visceral organs, muscles and body cavity of bullies, reducing the fish's physical condition and affecting its responses to predators and its parental care behavior (Poulin 1993; Stott & Poulin 1996). The abundance of this parasite varies greatly among fish populations (Hamilton et al. 1997). Furthermore, its abundance has remained stable in the only one of our study streams for which we have long-term data: in the Linnburn stream, prevalence of *T. opisthorchis* has remained 100% and the mean number of cysts per fish has not varied significantly between 1992 and 1997 (Poulin 1993; Hamilton et al. 1997). Variation among fish populations and stability over time make this parasite a potential agent of selection. For instance, it appears to have caused differences in the evolution of secondary sexual traits among bully populations (Hamilton & Poulin 1999). It is therefore also likely to be a key determinant of

variation in life history traits among bully populations.

## Methods

Upland bullies were collected from 7 distinct stream populations in the Otago province of the South Island, New Zealand, during three breeding seasons (austral spring and summer, 1994–1995 to 1996–1997). All streams were similar with respect to width (2–4 m) and depth (<50 cm), and all had the same predator species (brown trout *Salmo trutta* and eels, *Anguilla* spp.) and similar faunas of invertebrate prey. Water temperature ranges were collected monthly in all streams, using maximum-minimum thermometer. Severe flooding events prevented complete annual thermal records. Fish were segregated by population and sex and kept in large tanks for 1–2 days before being killed by an overdose of anesthetic (2-phenoxy ethanol). Fish were wet weighed and measured to the nearest mm before dissection. The number of cysts of *T. opisthorchis* found in each fish was recorded, as was the number of eggs in each female. Using only females from which eggs could be expelled by a gentle pressure on the body sides prior to dissection, we also took measurements of egg sizes. A random sample of 15 well-developed eggs from each of these clutches was measured using a binocular microscope to obtain an average egg size per clutch. Since bully eggs are slightly ovoid in shape, egg size was taken as the maximum egg length.

Scales and otoliths were removed from each fish for age analyses. Age was determined using annulus formation in both scales and otoliths. Upland bullies display scale annuli formed when growth slows down during winter (Staples 1975). When circuli followed an annulus, fish were classified into a “+” age class. Analysis of bully otoliths was used as a confirmation of ages determined using scales. Otoliths were ground by sanding until the annuli could be discerned under a light microscope. When possible (some otoliths disintegrated during grinding), both otoliths were used for age determination. There was no significant difference, in any of the populations, between ages calculated with either left or right otoliths (paired *t*-tests, all  $P > 0.50$ ). There were also no significant differences between ages obtained from scales or otoliths from the same fish, in any of the populations (paired *t*-tests, all  $P > 0.20$ ). Still, the average of scale and otolith age was used to categorize fish into various age classes (0+, 1, 1+, etc.). Age and size at maturity, for each population, were taken as the age and length of the youngest/smallest fish in which mature gonads were present.

We used parametric statistics after  $\log_{10}$  transformation of the data that needed normalization (parasite load, total fish length, fish weight, clutch size). Using total length (gravid female fish only) and egg size as independent variables, we performed multiple regressions with clutch size as the dependent variable. This was done separately for each population as well as on pooled data. This procedure allowed us to test for a trade-off between egg size and egg numbers while controlling for female body size, both within particular streams and among all fish independently of stream of origin.

Then, pooling data from all populations, we regressed clutch size on total length and used the residuals as measures of clutch size standardized for body size. These residuals were then averaged in each of the seven populations, to give mean population values independent of the population's body sizes. Similarly, measures of parasite load corrected for body size were obtained, separately for male and female fish, from regressions against total length across pooled data, with the residuals then averaged for each population. The monthly water temperature ranges obtained in each stream were also averaged to give mean population values. Average mid-range temperatures were similar for all streams, therefore the effect of temperature variability (measured as the average of monthly temperature ranges) seemed more likely to provide informative results than the median temperature. Multiple regression analyses were used to assess the relationships, among mean population values, between parasite load and the range in water temperature (independent variables) on the one hand, and female clutch size, egg size, and male and female age/size at maturity (dependent variables) on the other hand.

## Results

Clutch size and egg size varied among female bullies, both within and across populations (Fig. 1). When populations were treated separately, clutch size was usually positively related to total fish length rather than negatively related to egg size (Table 1). Only in the Garden Bush High stream was there a significant negative relationship between egg size and clutch size after correcting for fish size, thus suggesting a trade-off. Fish in the Shag Trib bully population showed no relationship between clutch size and either egg size or female size. When data for all seven populations are pooled, a strong positive relationship between clutch size and female size emerges, as well as a strong negative relationship (a trade-off) between egg size and clutch size (Table 1).

Prevalence of *T. opisthorchis* infection was 100%

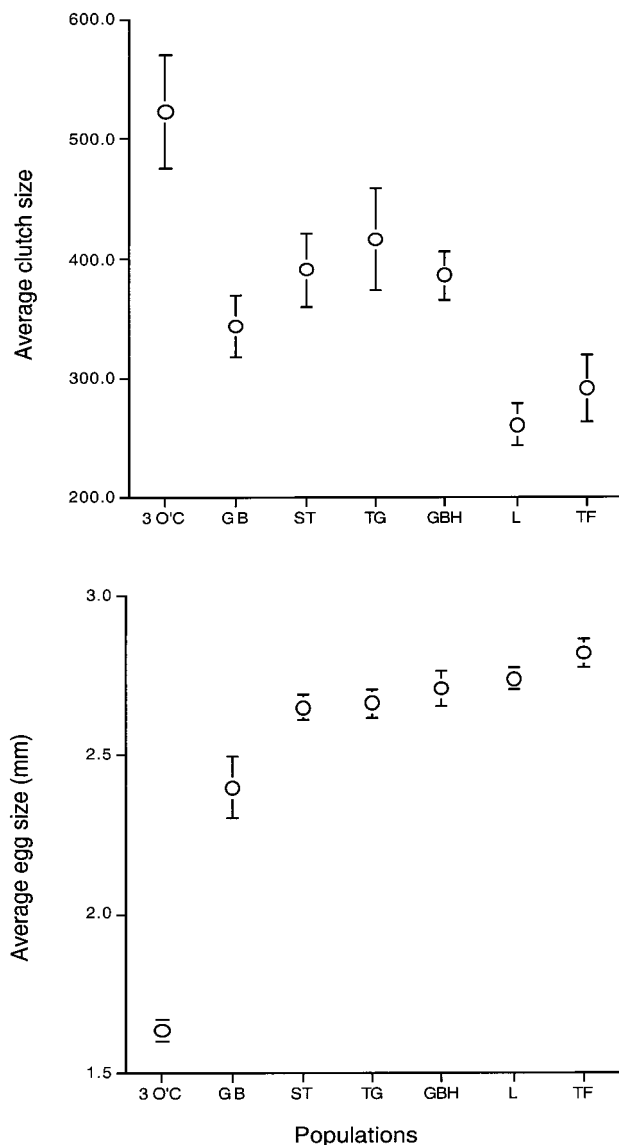


Fig. 1. Average clutch size and average egg size for each of the seven upland bully populations. Bars indicate standard error. Populations are ranked in increasing order of egg size. Key to stream of origin: 3 O'C=3 O'Clock stream; GB=Garden Bush stream; ST=Shag Trib stream; TG=Trotters Gorge stream; GBH=Garden Bush High stream; L=Linnburn stream; TF=Tommy Flat stream

in all streams except the Shag Trib stream (93%). The variance-to-mean ratio in numbers of parasites per fish was clearly greater than one in all streams, indicating that the parasites were not randomly distributed among fish. However, it only ranged between 32 and 74 among the streams, showing that the parasites were not highly aggregated among fish hosts. The high prevalence and modest aggregation of the parasites suggest that most fish in a population were subjected to their selective pressure.

Average age and size at maturity of both male

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Table 1. Relationships between clutch size and both total female length and egg size, in each of seven upland bully populations and across pooled data. Results are standardized coefficients from multiple regression analyses.

Stream of origin	<i>n</i>	Coefficient	<i>P</i>
3 O'Clock			
Total length	25	0.717	0.0001
Egg size		-0.044	0.7724
Garden Bush			
Total length	29	0.678	0.0008
Egg size		-0.113	0.5314
Garden Bush High			
Total length	68	0.487	0.0001
Egg size		-0.307	0.0045
Linnburn			
Total length	61	0.281	0.0290
Egg size		-0.220	0.0852
Shag Trib			
Total length	39	0.315	0.0734
Egg size		0.089	0.6055
Tommy Flat			
Total length	42	0.659	0.0001
Egg size		-0.129	0.3881
Trotters Gorge			
Total length	32	0.887	0.0001
Egg size		-0.113	0.3516
Pooled data			
Total length	296	0.575	0.0001
Egg size		-0.334	0.0001

and female bullies varied slightly across the seven populations (Fig. 2). The independent variables, mean parasite load and mean temperature range, also varied across populations (Fig. 3). However, neither mean parasite load nor temperature range correlated significantly with mean population clutch size, egg size, or male and female age and size at maturity (multiple regressions, all  $P > 0.54$ ).

## Discussion

While there was variability in life history characteristics both within and among upland bully populations, there were no consistent trends to suggest constraints or selective pressures imposed by parasites or temperature regimes. There were no relationships between the latter two variables and either clutch size, egg size, or age and size at maturity. It may be that seven populations is not a number large enough to permit weak relationships to be detected statistically. It is also possible that an effect of parasitism is masked by other environmental variables not examined in this study. Still, based on the present results, neither parasitism nor temperature variability appear linked with inter-population variations in bully life history strategies.

As in other studies on fish, clutch size was re-

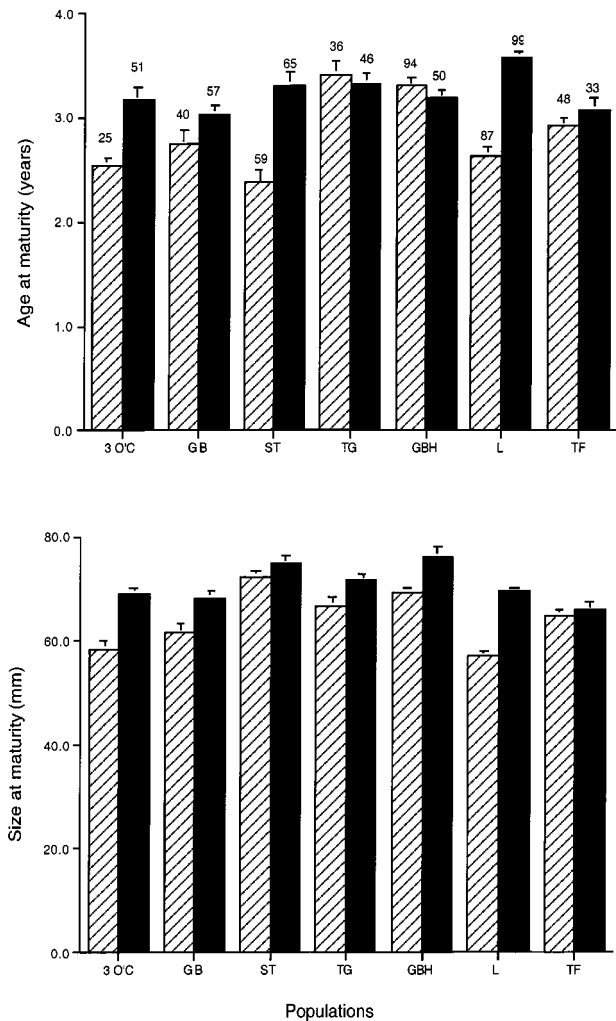


Fig. 2. Average age and size at maturity for each of the seven upland bully populations. Bars indicate standard error. Data for females are indicated by hatched bars, data for males by shaded bars. Numbers above bars are sample sizes. Key to populations as in Fig. 1

lated to female size. There has been a suggestion that, in the upland bully, egg size should be influenced by fecundity (McDowall & Eldon 1997). When our seven populations were analyzed separately, however, the trade-off between egg size and clutch size was only statistically apparent in one population. This suggests that the trade-off is not very pronounced, since the numbers of mature females examined (see Table 1) are large enough for moderate correlations to be detectable. When data on all populations are pooled, the trade-off becomes clear (Table 1), as it does when one looks at trends in mean population values (Fig. 1). Both theory (Stearns 1992) and empirical results (e.g. Fleming & Gross 1990) show that energy must be partitioned between egg size and egg numbers, such that a trade-off must exist. It is possible that



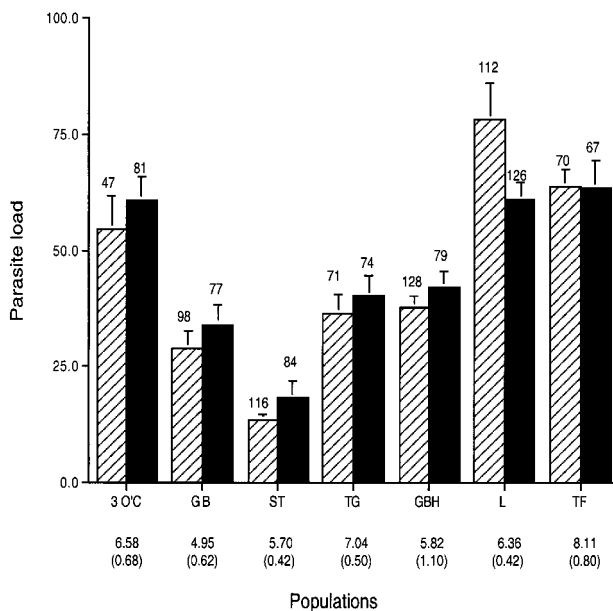


Fig. 3. Average parasite load for each of the seven upland bully populations. Bars indicate standard error. Data for females are indicated by hatched bars, data for males by shaded bars. Numbers above bars are sample sizes. Numbers below bars indicate average monthly temperature range (with standard error in parentheses). Key to populations as in Fig. 1

the reproductive strategy of upland bullies weakens the relationship between egg size and clutch size. Upland bullies can spawn several times per breeding season (Hamilton, unpublished data). These spawning events occur over well-spaced intervals such that the entire season's egg mass is not present in the ovaries at any one time. These multiple spawning events may enable the fish to adjust its reproductive investment in response to its current condition, or the current availability of food or other resources. It also means that the trade-off between egg size and egg numbers may only appear strong when the entire season's egg mass is considered.

Unlike previous laboratory studies of upland bullies (McDowall & Eldon 1997), we found few females with secondary oocytes in their ovaries. The lack of immature oocytes may be an indication that, in wild populations, most females do not produce a new clutch until they have completely deposited their mature eggs. In this species, egg sizes have been found to decrease in clutches produced late in the season (McDowall & Eldon 1997). Therefore, another factor contributing to the fact that we did not observe strong trade-offs in most populations may have been our snap-shot measurement of female fecundity.

Some earlier studies have shown that variation in life history traits among populations often correlates with biotic or abiotic environmental vari-

ables (e.g. Fleming & Gross 1990; Vøllestad & Abée-Lund 1990; Belk 1998). Here we found no evidence that differences in parasitism or temperature regime among upland bully populations had an effect on their life history traits. Adjustments in life history strategies are predicted to be efficient responses against debilitating parasites that reduce the chances of future reproduction (Hochberg et al. 1992; Lafferty 1993). The parasite we studied is the only metazoan parasite of upland bullies in our study populations; it has been shown to reduce expected lifespan by lowering body condition and interfering with normal anti-predator defences in bullies (see Poulin 1993). The reproductive strategy of the upland bully may provide an explanation for the lack of apparent effect in this study. Since bullies spawn several times in a season but only live through one or two breeding seasons once they are mature, perhaps selective pressures from parasites would favour large investments in reproduction early in a breeding season, rather than earlier age at maturity. This would also serve as bet-hedging against a lower probability of breeding in the future and will require further field research.

## Resumen

1. Las características biológicas pueden variar entre poblaciones de la misma especie como respuesta a presiones selectivas ejercidas por ambientes locales. En este trabajo utilizamos comparaciones entre poblaciones para investigar los efectos del parasitismo y de la variabilidad en la temperatura del agua sobre las características biológicas de *Gobiomorphus breviceps*, una especie de Nueva Zelanda.

2. Aunque la edad y el tamaño en la primera madurez varió entre las poblaciones estudiadas, las diferencias no estuvieron relacionadas ni con el régimen de temperaturas ni con la carga media de parásitos. Al analizar las poblaciones por separado, "trade-offs" entre el tamaño del huevo y el tamaño de la puesta aparecieron solamente en una población pero fueron evidentes al combinar todos los datos. Sin embargo, ni el tamaño medio de la puesta o de los huevos por población estuvieron relacionados con la carga media de parásitos ni con el régimen local de temperaturas. Aunque los dos últimos parámetros pueden influir otras variables biológicas tales como el número de puestas producidas por estación del año o la partición de huevos entre puestas, no encontramos evidencia de que influyeran sobre las estrategias biológicas de las poblaciones de *G. breviceps* estudiadas.

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