



Empirical evidence for competition-driven semelparity in wild medaka

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Recruit-driven generation cycles and the cost of reproduction in wild medaka

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Abstract

35 Metabolic theory predicts that maintenance rate increases faster with animal body size than food intake rate, such that the critical resource density R^* at which ingested energy exactly covers maintenance requirements increases with body size. Small-sized (low R^*) juveniles may thus exclude their larger-sized (high R^*) parents in competition for common resources, resulting in apparent semelparous life histories, and translating at the population level into so-called recruit-driven
40 generation cycles (GC, also known as single-cohort cycles). However, empirical support for such a competition-mediated semelparity and for resultant GC remains scarce. Here, we report a high consistency of cohort dynamics with GC in wild medaka (*Oryzias latipes*). As predicted by the theory, R^* increased with size (as suggested by the allometric increase in stomach fullness). There was also a strong juvenile-adult diet overlap, and all individuals died after reproduction as semelparous age-1+
45 adults, synchronous with dropping abundances of food resources. In addition to the theory, we found evidence for increased reproductive investment under decreasing food levels, translating into increased parasite prevalence (suggesting immune depression), and in a global somatic deterioration. Therefore, semelparity and resultant GC in wild medaka are apparently driven both by intercohort competition for resources and by a parallel energy re-allocation from somatic maintenance to reproduction. The
50 literature data show that the strengths of both intercohort competition and reproductive allocation increase at higher temperatures, pointing to climate warming as a potentially powerful magnifier of GC.

Keywords: Body size; Life-history evolution; Longevity; r and K strategies; Resource competition;
55 Semelparity.

Introduction

The relative size scaling of intake and metabolic rates may be key to determine the size-dependency of dominance in exploitative competition, and its effects on the dynamics of size-structured populations. Often, maintenance requirements increase faster with body size than ingestion capacity, such that the critical resource density R^* (in analogy with Tilman's (1982) theory) at which energy gain from ingestion is exactly balanced by energy loss from maintenance increases with body size (Persson et al 1998; De Roos et al 2003; Persson and De Roos 2006; Kooijman 2010). Consequently, small-sized juveniles may continue growing in size and depleting resources at resource levels at which large adults can not meet their maintenance requirements and starve to death (Persson et al 1998). At the population level, this competitive exclusion of adults by their juveniles is predicted to translate into so-called recruit-driven generation cycles (GC, Persson et al 1998). GC are expected to occur in all organisms in which (i) R^* creases with body size, (ii) resources substantially overlap between juveniles and adults, and (iii) adults can not offset the effects of exploitative competition through interference competition or cannibalism (Claessen et al 2000; Le Boulot et al 2014).

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The theory of GC has been developed from a population dynamics perspective. However, it is also highly relevant to life-history theory and, in particular, to the theory of the cost of reproduction. The cost of reproduction is defined as a trade off between current and future reproduction, such that increased current reproduction incurs costs in terms of reduced future reproduction (Williams 1966). High mortality costs of reproduction due to immune depression (Zuk and Stoehr 2002; Harshman and Zera 2007) or due to increased predation risk (Magnhagen 1991) are expected to favour the evolutionary emergence of semelparity (Charnov and Schaffer 1973), a “suicidal” reproductive strategy in which individuals invest all their energy in their first reproduction at the cost of somatic deterioration

and death. So far, intercohort exploitative competition has not been commonly considered by evolutionists among the mechanisms that make reproduction costly and that may select towards semelparity. Hence, empirical information on GC and the conditions under which they emerge can potentially enrich our understanding of the mechanisms that control population dynamics and mould life-history evolution in wild populations.

Cohort dynamics consistent with GC have been observed in wild populations of roach *Rutilus rutilus* (Cryer et al 1986; Persson et al 1998) and the vendace *Coregonus albula* (Hamrin and Persson 1986; De Roos and Persson 2001). Additionally, growth trajectories consistent with GC have also been reported in the yellow perch *Perca flavescens* (Persson et al 2004). However, despite the large scope for GC in animal populations, empirical evidence for their occurrence remains scarce. Here, we assess the consistency of the theory of GC with the results from a two-year field survey on medaka *Oryzias latipes* in Japan. We complement this field work with an analysis of literature data on the cost of reproduction in medaka and other small-sized fish species. Overall, our results support the view that intercohort exploitative competition may increase the mortality cost of reproduction, result in GC, and potentially favour the emergence of semelparity.

Materials and methods

Model fish species

The medaka belongs to Beloniformes (family Adrianichthyidae), a sister order of Cyprinodontiformes (Poeciliids, killifishes). The medaka is a small fish (25-35 mm as adult) inhabiting shallow, still and slow-flowing fresh or brackish-waters of Japan, Korea and China (Yamamoto 1975). The medaka is omnivorous and, although showing a marked preference for zooplankton, also feeds on diatoms,

filamentous algae, or aquatic insects (Terao 1985). Due to its high tolerance to thermal and saline variation, its short generation time and general ease of maintenance and manipulation, the medaka has long been a laboratory model in genetics and developmental biology (Kinoshita et al 2009; Naruse et al 105 2011). The medaka is currently considered as endangered in its natural habitats, and gaining knowledge on its ecology may be useful for building conservation plans.

Sampling sites and fish communities

We sampled two sites at Inba-numa (Chiba Prefecture near Tokyo): an irrigation ditch (0.5-1 m wide) 110 in a paddy field, and the shore of Lake Inba (11.55 km², mean depth = 1.7 m, see Fig. 1). The irrigation ditch was distant from the lake by more than 2 km (Fig. 1), and we therefore assumed that we sampled two separate (sub)populations.

The catchment of Lake Inba is intensively cultivated (Nakamura et al 2009), and the two sampling sites 115 were eutrophic with average dissolved phosphorus (P₀₄³⁻) concentrations of 0.64 (± 0.34 SD) and 0.48 (± 0.20 SD) mg l⁻¹ in the ditch and lake, respectively. The irrigation ditch had a muddy bottom, and water level varied due to frequent pumping and flushing to and from rice fields. The lake shore had a sandy bottom and constituted a more stable habitat. In the ditch, medaka co-occurred with the following fish species: field gudgeon *Gnathopogon elongatus*, topmouth gudgeon *Pseudorasbora parva*, common 120 carp *Carassius carassius*, pond loach *Misgurnus anguillicaudatus*, rosy bitterling *Rhodeus ocellatus*, Amur goby *Rhinogobius brunneus*, and Amur catfish *Silurus asotus*. All these species are bottom-dwelling (although carp may also feed in the pelagic), in contrast with medaka that is pelagic. At the lake shore, we could not capture other species than medaka but a number of species are known to occur into the lake (http://wldb.ilec.or.jp/data/databook_html/asi/asi-29.html).

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Medaka sampling and phenotyping

Medaka were sampled between 12:00 and 14:00 with a hand net, monthly or bimonthly from October 1983 to October 1984, and from April to September 1985. To representatively sample each site, we fished a stretch of 300 m in the irrigation ditch and of 500 m along lake shore. All captured fish (N = 4,571) were immediately killed in concentrated formalin to prevent vomiting, and fixed in a 10% formalin solution followed by 70% ethanol. At the laboratory, fish were measured for standard length (*SL*, from the snout to the base of the caudal fin) to the nearest mm (ranged from 9 to 33 mm), and their maturity status (juvenile vs. adult) and sex were determined from secondary sexual characters under a binocular microscope (Yamamoto 1975). The 50% maturation probability occurred at 16.2 mm *SL*. The age of each fish was determined from counting opaque rings in otoliths (Terao 1985). The spring and summer growth period is associated with formation of a clear, translucent zone in medaka otoliths, while arrested growth in winter is associated with an opaque zone (winter check). Otoliths with no winter check indicated a 0+ individual, with one winter check indicated a 1+ individual, and so on.

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Ectoparasites

In 1985, prevalence of the ectoparasite anchor worm (*Lernea cyprinacea*, copepod crustacean) was recorded on a subset of 216 adults sampled on May 27th (N = 136), June 15th (N = 67) and July 9th (N = 13) at Inba-numa. This decreased number of sampled fish through time is not due to a decreasing sampling effort, but reflects the fact that adults were progressively disappearing (see Results). To this data we added in our analysis data from Egami et al (1988) reporting prevalence of *L. cyprinacea* and *Argulus japonicus* in adult medaka from a pond in Yamagushi city on May 8th (N = 40) and June 15th

1985 (N = 48).

Medaka diet and prey availability

On three dates in 1984 (April 25th, June 16th and July 2nd), we dissected guts from fish caught in the irrigation ditch under a binocular microscope (N = 354 fish). We analysed food items present in the anterior part of the gut before it turns 180° (hereafter “stomach”). We identified food items at the most inclusive taxonomic level possible, and classified them into five items: cladocerans (mainly *Moina rectirostris*, *Bosmina longirostris* and unidentified Daphniidae), nauplius larvae of copepods, copepodite stage (adult) of cyclopoid copepods, zoobenthos (mainly annelida, chironomid larvae, and larvae of other dipterans), and algae (mainly *Closterium* sp.) and plant debris (hereafter “algae”). Noticeably, we did not find any medaka larvae in stomach contents, indicating absence of cannibalism. Finally, we visually evaluated the degree of stomach fullness (ranging from 0 to 100%).

We tracked seasonal changes in environmental abundances of zooplankton and zoobenthos – the most energetically-profitable food resources for medaka – both in the irrigation ditch and at lake shore. Zooplankton was collected by hauling a plankton net over 5 meters, while zoobenthos was collected with a hand net (0.5 mm mesh size) from 20 × 20 cm squares (4 replicates, pooled for a given date), yielding a total sample size of N = 82 observations. All captured organisms were preserved in formalin and enumerated under a binocular microscope.

Literature data on the mortality cost of reproduction

In order to complement our field data, we used data on the mortality cost of reproduction in female medaka under laboratory conditions. Hirshfield (1980) kept 381 female medaka in individual tanks

(i.e., with no competition) during 25 days and elicited daily spawning by adding a male in their aquarium. Females were maintained under three temperatures (25, 27 and 29°C) and three feeding regimes (18.68, 12.4 or 8.86 mg Tetramin fish⁻¹ day⁻¹) in a factorial design, yielding a total of 9 experimental treatments. These three feeding regime were chosen to “range from near maintenance levels (minimal amount necessary to keep fish alive) to near *ad libitum*” (Hirshfield 1980). At the end of the 25-day period, Hirshfield then recorded health status, fecundity and energy budgets for each individual fish. Here, we have specifically analysed count data on moribund or dead vs. healthy fish in each of the 9 treatments (as reported in Hirshfield's Table 2, page 286) in a binomial model (see below). Hirshfield did not provide any statistical treatment of this data, and our analysis is not a duplication of Hirshfield's results but instead represents an add-on.

Data analysis

Prevalence of ectoparasites. We modelled probability for presence of at least one ectoparasite on adult medaka in a binomial regression (GLM):

$$C_{jk} \sim \text{Bin}(N_{jk}, p_{jk})$$

$$\ln\left(\frac{p_{jk}}{1-p_{jk}}\right) = \beta_{0,j} + \beta_1 D_k \quad (1),$$

where \sim = “is distributed as”, C_{jk} = count of infected fish of sex j on date k , Bin = binomial distribution, N_{jk} = total number of fish of sex j examined on date k (304 fish examined), p_{jk} = probability for a fish of sex j examined on date k to be infected, $\beta_{0,j}$ = sex-specific intercept, β_1 = regression slope for the effect of date, D_k = date scaled to zero mean

and unity standard deviation to avoid spurious correlations between intercept and slope. Sex-specific data was available only at Inba-numa, and we thus treated sex as a random variable following a categorical distribution (Royle and Dorazio 2008). By doing so, we assumed that the sex-ratio was the
 195 same at Inba-numa and Yamagushi.

Stomach fullness. A critical assumption for the emergence of GC is that R^* increases with body size. We could not measure directly the relationship between R^* and body size in medaka at Inba-numa, and we tested this hypothesis only indirectly by measuring the relationship between stomach
 200 fullness and body size. Degree of stomach fullness reflects the difference between willingness to forage (appetite reflecting maintenance rate), and body capacity to digest and assimilate the ingested food. We reasoned that a low R^* should be associated a high capacity to digest food relative to appetite, translating into a relatively empty stomach. In contrast, a high R^* should be reflected by a relatively full stomach. Preliminary analyses showed that there was no effect of sampling date on mean
 205 stomach fullness, or on the slope of the relationship between stomach fullness and body size. Hence, we modelled the relationship between stomach fullness and body length using an overdispersed binomial regression:

$$Y_i \sim \text{Bin}(N_i, pf_i)$$

$$\ln\left(\frac{pf_i}{1-pf_i}\right) = \beta_0 + \beta_1 SL_i + \epsilon_i \quad (2),$$

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where Y_i = integer varying between 0 and 100 and reflecting percentage of stomach fullness in fish
 i (354 observations), $N_i = 100$ = constant number of observations for fish i , $pf_i =$

proportion of stomach fullness in fish i , β_0 = intercept, β_1 = regression slope, SL_i =
 standard length for fish i scaled to zero mean and unity standard deviation, and ϵ_i = normally-
 215 distributed random overdispersion term. To account for 1 missing length observation, we treated SL
 as a normally-distributed random variable.

Size-dependency of predatory behaviour. Another critical assumption for the emergence of GC is
 that there is a strong resource overlap among small (juvenile) and large (adult) individuals. We tested
 220 this hypothesis using stomach content data. We first examined finely the size-dependency of medaka
 predatory behaviour on specific prey items, and then measured overall diet overlap among juvenile and
 adult medaka (adult $SL > 16.2$ mm) using Schoener's similarity index (Schoener 1968, see below).

To gain a fine understanding of the size-dependency of medaka predatory behaviour we modelled the
 225 effect of medaka body length on the probability of eating a given prey item using a Bernoulli mixed-
 effects model:

$$P_{ijk} \sim \text{Bern}(p_{ijk})$$

$$\ln\left(\frac{p_{ijk}}{1-p_{ijk}}\right) = \beta_{0,jk} + \beta_{1,k} SL_{ijk} \quad (3),$$

230 where P_{ijk} = presence or absence of food item k on date j in stomach of fish i (1,765
 observations), Bern = Bernoulli distribution, $\beta_{0,kj}$ = normally-distributed random intercept
 varying depending on prey item k at each date j (yielding 15 intercepts), $\beta_{1,k}$ = normally-
 distributed random slope varying depending on prey item k (yielding 5 slopes), SL = as in

model 2. We used this random effects structure because fitting various models revealed that the prevalence of each food item in medaka stomachs changed among each sampling date (as probably influenced by fluctuations in prey availability in the environment), but that the size-dependency of medaka predatory behaviour was influenced only by the type of food item and not by the sampling date.

To further explore the potential for interstage competition in medaka, we computed diet overlap among juveniles and adults using Schoener's similarity index (Schoener 1968):

$$S = 1 - 0.5 \sum_k |p_{J,k} - p_{A,k}|$$

where $p_{J,k}$ and $p_{A,k}$ = frequency of food item k in the diets of juveniles (J) and adults (A), respectively. We computed S separately for April 25th and July 7th, and estimated standard deviation for each S using a bootstrap procedure (random sampling of half the data and computation of S , repeated 1,000 times).

Literature data on the mortality cost of reproduction. We modelled the effects of temperature and food regime on female medaka reproductive mortality with a binomial model:

$$C_i \sim \text{Bin}(N_i, p_i)$$

$$\ln\left(\frac{p_i}{1-p_i}\right) = \beta_{0,f} + \beta_1 T_i \quad (4),$$

255 where C_i = count of moribund or dead fish in treatment i (combination of feeding regime and temperature), N_i = total number of fish in treatment i (351 fish in all treatments), p_i = mortality probability in treatment i , $\beta_{0,f}$ = intercept specific to each food regime (3 different intercepts), β_1 = regression slope, T_i = temperature in treatment i , scaled to zero mean and unity standard deviation to avoid spurious correlations between intercept and slope. We used this model
 260 with a single slope β_1 because preliminary analyses showed that the temperature effect did not vary significantly among feeding regimes.

Model fitting and tests of significance. We estimated parameters in models (1-4) using JAGS v. 3.4 (Plummer 2003) in R v. 3.2.1 through the package `jagsUI`, which itself relies on packages `rjags`
 265 and `CODA` (Plummer et al 2006). We ran three independent MCMC chains of 50,000 (model 1 and 4), 1,000,000 (model 2), and 200,000 (model 3) iterations each with a burn-in period of 40,000 (model 1 and 4), 900,000 (model 2) and 190,000 (model 3), and thinned chains at a period of 5 (model 1, 3 and 4) and 25 (model 2) iterations. Uninformative priors for regression parameters were defined as normal distributions with zero mean and 100 standard deviation, and for variance parameters as a uniform
 270 distribution between 0 and 100. Convergence was assessed using the Gelman–Rubin statistic (R-hat, Gelman and Rubin 1992).

We further assessed goodness of fit of our models by using a Bayesian p-value (Gelman et al 1996). Briefly, we computed residuals for the actual data as well as for synthetic data simulated from
 275 estimated model parameters (i.e., residuals for ideal data). Then, we plotted synthetic (“ideal”) residuals against true residuals and drawn the 1:1 line. If the model fitted, about half of the points lied

above the line. The exact proportion is given by the Bayesian p-value. Bayesian p-values for model (1) to (4) were 0.37, 0.27, 0.49 and 0.53, respectively, indicating reasonably good to excellent model fit. Data, model code and goodness of fit graphics are provided as Electronic Supplementary Material.

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We tested the significance of effects from posterior parameter distributions in a test equivalent to a bilateral t-test. Specifically, the MCMC p-value was twice the proportion of the posterior which sign was opposite to the sign of the mean posterior value.

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Results

Medaka cohort dynamics

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Cohort dynamics were highly consistent at the two sampling sites (Fig. 2). Spawning occurred in May-June, and newly-hatched fry (about 4 mm *SL*) were first seen from late May to mid-June (stars in Fig. 2). 0+ juveniles grew very rapidly and reached sexual maturity (length at 50% maturation probability) roughly synchronous with the disappearance of their 1+ parents (Fig. 2). Coexistence of adults and juveniles lasted for about two weeks in 1984 and three weeks in 1985. Fish stopped growing during winter. In the following May, medaka resumed growth, started reproducing and died. No individual wintered a second time (i.e., not a single 2+ individual was caught).

295

Seasonal dynamics of prey

Abundances of zooplankton and zoobenthos prey were highly variable (Fig. 3). They peaked in April in the irrigation ditch and around May at the lake shore, before rapidly dropping in June (ditch) and July (lake).

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Prevalence of ectoparasites (model 1)

Prevalence of ectoparasites on adults was significantly higher on females (MCMC p-value of the male-female difference < 0.0001), and increased significantly during the spawning season (significant slope of the *Date* effect in model 1, Table 1).

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Stomach fullness (model 2) and diet (model 3)

Stomach fullness significantly increased with increasing standard length (significant slope of the *SL* effect in model 2, Table 1). However, predation probability on an average food item did not significantly increase with increasing *SL* (non significant slope of the *SL* effect in model 3, Table 1). The finding that *SL* did not significantly influence overall resource use was also supported by calculation of Schoener's indices, which show a very strong diet overlap among juveniles and adults of 0.95 on both 25th April ($\pm 6.4 \cdot 10^{-3}$ SD) and 7th July ($\pm 1.1 \cdot 10^{-2}$ SD).

Although overall resource use was not size- or stage-dependent, the size-dependency of medaka predatory behaviour varied with each prey item. Probability to eat cladocerans increased with increasing medaka *SL* (positive slope for the “Cladocera” food item, Table 2). In contrast, probability to eat benthic prey or copepods of both stages decreased with increasing medaka *SL* (negative slopes for “Benthic”, “Copepodite” and “Nauplius” food items in Table 2). Probability to eat algae was not size-dependent (slope for the “Algae” food item not significantly different from 0, Table 2).

Mortality cost of reproduction in the laboratory (model 4)

Mortality probability of reproducing female medaka significantly increased with increasing
 325 temperature (slope of the *Temperature* effect significantly different from 0, model 4, Table 1, Fig. 4).
 We tested for the differences among model intercepts (evaluated at a mean temperature of 27°C due to
 temperature scaling), and found that mortality was significantly higher under the low food regime
 compared with the high food regime (MCMC p-value of the difference = 0.0447, Fig. 4). The positive
 effect of the low food regime on mortality was even larger at 29°C (Fig. 4).

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Discussion

Theory predicts that the critical resource density R^* at which food intake exactly covers
 maintenance requirements increases with body size, such that adults may be competitively excluded by
 their juveniles (Persson et al 1998; De Roos et al 2003; Kooijman 2010). This positive size-scaling of
 335 R^* should result in an apparent semelparity of life histories, and translate into recruit-driven
 generation cycles (GC) at the population level (Persson et al 1998). However, to date empirical
 evidence for competition-mediated semelparity and GC in wild populations remains scarce.

Medaka cohort dynamics at Inba-numa revealed a high consistency with GC, in which all adults died
 340 shortly after their juveniles have reached a SL of about 10 mm. A similar pattern with adults dying
 as post-reproducing, age 1+ was reported for medaka in irrigation canals of ricefields near Ushikunuma
 pond (Ibaraki Pref., Japan, Awaji and Hanyu 1987) and in a small pond in Yamaguchi City (Yamaguchi
 Pref., Japan, Egami et al 1988). Therefore, semelparity and GC seem to be the norm in wild medaka in
 Japan. However, GC require by definition that the mortality cost of reproduction operates through food
 345 shortage due to competition from juveniles. We will now critically assess empirical evidence for this

hypothesis in medaka.

Competition-mediated cost of reproduction

Egami et al (1988) have shown that transferring wild, reproducing (age 1+) medaka to captive
 350 conditions with unrestricted food prolonged their lifespan by several months and up to 2 years. They
 also report that mean lifespan under fully captive conditions is 2.7 years, and concluded that medaka
 longevity is markedly reduced under wild conditions. Similarly, Hirshfield (1980) found in the
 laboratory that, on near-maintenance food levels (“low food” regime), the mortality rate after 25 days
 of reproduction in female medaka ranged from 0% at 25°C to 31 % at 29°C (Fig. 4). In contrast, in the
 355 wild in Japan 100% of both female and male die, indicating that the cost of reproduction severely
 increases for both sexes under natural conditions. We suggest that food shortage linked to intercohort
 exploitative competition plays an important role in restricting longevity in wild medaka.

Indeed, the energy brought by Hirshfield's near-maintenance, “low food” regime (8.86 mg Tetramin
 360 fish⁻¹ day⁻¹) was probably way higher than the energy taken by an adult medaka in the wild. An
 individual zooplankter's dry weight is just a few micrograms (Watkins et al 2011). The largest
 zooplankter at Inba-Numa (*Moina rectirostris*, 0.55 mm average length) has a dry weight of about 1.8
 micrograms. Almost 5,000 *Moina rectirostris* are needed to amount 8.86 mg. Additionally, Tetramin is
 arguably more energetic than dry zooplankton. Hence, although we can not safely estimate energy
 365 intake by medaka at Inba-numa, we can still presume that adult medaka were under severe starvation
 and intensive competition for food with their juveniles.

Accordingly, overall medaka predation efficiency was not size-dependent (Model 3, Table 1), and

Schoener's index showed a very strong diet overlap among juveniles and adults (at least in the 9-33 mm
 370 *SL* range), demonstrating that juvenile and adult medaka were competing for common food
 resources. A summer drop in the abundance of zooplankton (especially cladocerans), as observed at
 Inba-numa, is a classical feature of aquatic ecosystems and is generally driven by fish predation
 (Sommer et al 2012). Although medaka was by far the dominant fish species in irrigation ditches and
 around the lake (at least in the areas that we sampled), other fish species might have also participated in
 375 consuming zoobenthos and zooplankton. Hence, we can not rule out possible effects of interspecific
 competition in resource depletion.

Probably, adult medaka were competitively dominated by their juveniles. We found that stomach
 fullness increased in parallel with body size, in line with the classical observation that both energy
 380 demands and R^* increase with body size in fish (Persson and De Roos 2006). Additionally, female
 medaka lay 4 to 30 eggs daily during the May-June reproductive period (Terao 1985; Kinoshita et al
 2009), while male spend much energy in courtship, displaying and fighting to gain access to females
 (Clark and Grant 2010). Undoubtedly, these energetic demands strongly increased adult R^* and
 played an important role in mediating the competitive exclusion of adults.

385 Finally, this competition-mediated semelparity and resultant GC in medaka are probably favoured by
 high summer temperatures (May-July average of $27.6^{\circ}\text{C} \pm 3.1$ SD at Inba-numa). Recent studies
 suggest that higher temperatures shift R^* differently for small and large individuals, such that the
 competitive asymmetry in favour of small-sized individuals increases (Ohlberger et al 2011; Edeline et
 390 al 2013; Vindenes et al 2014) and the prevalence of GC is enhanced (Ohlberger et al 2011).

Cost of reproduction through energy-allocation conflicts

Although our study supports the hypothesis of a competition-mediated cost of reproduction, there is
 395 further evidence that reproductive mortality in medaka was also caused by a decreased somatic
 maintenance. At Inba-numa, we found an increasing parasite prevalence on adult medaka through the
 spawning season, suggesting that the cumulated energy costs of reproduction translated into decreased
 immune investment. Accordingly, reproduction generally reduces immune investment and increases
 sensitivity to parasites and pathogens in animals (Zuk and Stoehr 2002; Harshman and Zera 2007;
 400 Edeline et al 2008). *Lernaea cyprinacea*, one of the monitored parasites on medaka, is notoriously
 thermophilic and its increased prevalence was thus probably caused not only by immune depression in
 their hosts, but also directly favoured by warming summer temperatures. However, females arguably
 invest more than males in reproduction, and we indeed found a female-biased prevalence of parasites in
 medaka (Model 1, Table 1). This result provides convincing evidence that reproduction competed with
 405 immunity for energy allocation in medaka.

Often, theoretical models of energy allocation assume that reproductive investment, i.e., the fraction of
 assimilated energy allocated to reproduction, is constant, such that lower food resources should
 decrease in parallel both reproduction and maintenance (Persson et al 1998; Kooijman 2010). However,
 410 this assumption does not fit with experimental data on medaka. Hirshfield (1980) showed that female
 medaka tend to maintain a constant reproductive output under reduced food rations, such that
 reproductive investment *increases* under food stress. The same response to food stress is observed in
 female stickleback, that subsidize egg production from body tissue (Wootton 1977; Wootton 1984).
 This priority given to reproduction over somatic maintenance under food stress may induce a positive,

415 food-dependent feedback in which reproduction induces intercohort competition and food stress, which
in turn stimulates increased reproductive allocation. Such a positive feedback might explain why adult
medaka at Inba-numa and elsewhere in Japan disappear so abruptly in July.

Many ectotherms conform to the so-called temperature-size “rule” (Angilletta 2009), i.e., to an
420 increased energy allocation to reproduction at the cost of reduced somatic growth and investment under
higher temperatures. In line with the temperature-size rule, higher temperatures increased the mortality
cost of reproduction at all ration levels in Hirshfield's experiment (Model 1, Table 1, Fig. 4). Hirshfield
(1980) further showed that the increase in reproductive investment under food stress (as mentioned
above) was apparent only at temperatures above 25°C. Hence, high summer temperatures at Inba-numa
425 probably also increased energy reallocation from the soma to reproduction, and thus further increased
the potency of intercohort competition to cause adult death and GC.

Generality of our results

Literature data in other fish species than medaka further point to a positive link between intensive
430 reproductive investment and a high mortality cost of reproduction, translating into semelparity and
apparent GC. In seasonal environments, relatively short breeding periods impose pulsed breeding,
which is associated both with a strong recruitment of juveniles (and potentially strong intercohort
competition) and with a high energetic investment into reproduction.

435 For instance, in seasonal environments in Europe, females of the invasive mosquito fish *Gambusia*
holbrooki (adult *SL* range = 20-40 mm) produce multiple clutches of 15 to 86 embryos from May to
August, a period during which recruitment of newborns is intensive and continuous (Fernandez-

Delgado 1989; Vargas and de Sostoa 1996; Specziár 2004; Gkenas et al 2012). This breeding pattern is very similar to that of medaka, similarly results in an annual life cycle in which mosquito fish die as
 440 semelparous 1+ adults (Fernandez-Delgado 1989; Vargas and de Sostoa 1996; Gkenas et al 2012), and is associated with cohort dynamics consistent with GC (Cabral and Marques 1999).

The threespined stickleback (*Gasterosteus aculeatus*, adult *SL* range = 35-65 mm) occurs exclusively in seasonal environments. Females lay on average 93 eggs per clutch (SD = 43) and spawn
 445 15 to 20 clutches during a 1 to 3 months breeding season (Baker 1994; Baker et al 2008). Throughout their circumboreal coastal distribution, sticklebacks die as semelparous 1+ or 2+ adults (Bertin 1925; Baker 1994). However, in a few populations large-bodied (adult *SL* > 75 mm) sticklebacks have prolonged lifespans and enjoy iteroparity (Gambling and Reimchen 2012). It would be interesting to examine whether patterns of intercohort resource competition (or counteracting cannibalism) differ
 450 among these short- and long-lived stickleback populations.

In contrast to seasonal environments, weakly seasonal environments allow the spread of reproductive investment across longer periods, which is expected to favour increased longevity. For instance, each female guppy (*Poecilia reticulata*, adult *SL* range = 14-35 mm) or least killifish (*Heterandria formosa*,
 455 adult *SL* range = 11-35 mm) gives birth to small litters of 5 to 20 juveniles at intervals of a few days or weeks across their whole reproductive life, which lasts for several years (Turner 1937; Travis et al 1987; Reznick et al 2004). This prolonged coexistence of adults and juveniles demonstrates the absence of any severe mortality cost of reproduction, and also suggests the absence of GC in these species.

Conclusions

Taken together, our results and the literature data provide a coherent picture of GC as resulting both from indirect costs of reproduction due to intercohort exploitative competition and from direct costs due to energy reallocation from somatic maintenance to reproduction. The two sources of reproductive mortality are tightly intertwined, because intercohort competition is expected to induce selection towards semelparous energy-allocation strategies. Furthermore, by increasing in parallel the asymmetry of competition in favour of small-sized individuals and the fraction of energy allocated to reproduction, high temperatures increase the potential for – and adaptive nature of – semelparity and resultant GC.

In evolutionary biology, senescence and lifespans remain dominantly considered to evolve in response to variations in predation mortality (Abrams 1991; Reznick et al 2004). In particular, semelparity is often considered to have evolved in small-sized species due to high predation mortality on their adults, which makes individuals unlikely to reproduce more than once (Pianka 1970; Charnov and Schaffer 1973). It is interesting to note that small-sized species are also at a higher risk of intercohort competition, because similarity of juvenile and adult body sizes also entails a high niche overlap (Woodward et al 2005). Hence, although predation undoubtedly plays an important role in life-history evolution, it seems reasonable to also consider intercohort exploitative competition among the extrinsic mortality factors that potentially mould life histories in the wild.

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Table. 1. Summary statistics for fixed effects in models 1-4. *SL* = medaka standard length.

*indicates that the estimate is the mean value of the normal distribution of random effects. R-hat is the Gelman–Rubin statistic. Values of R-hat below 1.1 indicate convergence for the estimated parameter.

600 The MCMC p-value is twice the proportion of the posterior which sign is opposite to the sign of the mean posterior value (equivalent to a bilateral t-test).

Model	Response	Predictor	Distribution	Link	Fixed-effect parameter	R-hat	Mean estimate	SD of the estimate	MCMC p-value
1	Prevalence of ectoparasites	<i>Sex</i>	Binomial	Logit	$\beta_{0, F}$	1.008	0.361	0.245	0.135
					$\beta_{0, M}$	1.021	-3.007	0.538	<0.0001
		<i>Date</i>			β_1	1.020	2.296	0.316	<0.0001
2	Proportion of gut fullness	<i>SL</i>	Binomial	Logit	β_0	1.014	-0.146	0.473	0.770
					β_1	1.006	2.054	0.477	<0.0001
3	Probability of eating a given food item	<i>SL</i>	Bernoulli	Logit	* β_0	1.013	-5.044	2.093	<0.0001
					* β_1	1.001	-5.311	2.896	0.3700
4	Mortality probability	<i>Feeding regime</i>	Binomial	Logit	$\beta_{0, H}$	1.009	-2.755	0.338	<0.0001
					$\beta_{0, Med}$	1.011	-2.182	0.280	<0.0001
					$\beta_{0, Low}$	1.004	-1.999	0.273	<0.0001
		<i>Temperature</i>			β_1	1.009	1.127	0.202	<0.0001

Table. 2. Random effects in model 3. Intercept and slope are for the effect of individual standard length (SL) on probability of finding a given food item in medaka stomach on a given date (as indicated in the random effect column), on a logit scale. See Table 1 legend for further details.

Intercept					Slope				
Random effect parameter	R-hat	Mean estimate	SD of the estimate	MCMC p-value	Random effect parameter	R-hat	Mean estimate	SD of the estimate	MCMC p-value
$\beta_{0, \text{July 2nd 84 Algae}}$	1.001	-1.01	0.223	<0.0001	$\beta_{1, \text{Algae}}$	1.000	-0.150	0.180	4.04E-01
$\beta_{0, \text{July 2nd 84 Benthic}}$	1.000	-1.374	0.263	<0.0001	$\beta_{1, \text{Benthic}}$	1.001	-0.730	0.211	<0.0001
$\beta_{0, \text{July 2nd 84 Cladocera}}$	1.002	-1.683	0.283	<0.0001	$\beta_{1, \text{Cladocera}}$	1.000	1.104	0.231	<0.0001
$\beta_{0, \text{July 2nd 84 Copepodite}}$	1.244	-11.499	4.522	<0.0001	$\beta_{1, \text{Copepodite}}$	1.002	-1.649	0.502	2.00E-03
$\beta_{0, \text{July 2nd 84 Nauplius}}$	1.019	-16.048	3.130	<0.0001	$\beta_{1, \text{Nauplius}}$	1.014	-5.497	1.148	<0.0001
$\beta_{0, \text{June 16th 84 Algae}}$	1.027	-9.836	4.165	<0.0001					
$\beta_{0, \text{June 16th 84 Benthic}}$	1.044	-9.666	4.296	<0.0001					
$\beta_{0, \text{June 16th 84 Cladocera}}$	1.000	-1.127	0.354	<0.0002					
$\beta_{0, \text{June 16th 84 Copepodite}}$	1.090	-8.731	4.223	<0.0003					
$\beta_{0, \text{June 16th 84 Nauplius}}$	1.076	-6.859	3.930	2.80E-02					
$\beta_{0, \text{April 25th 84 Algae}}$	1.000	0.267	0.182	1.36E-01					
$\beta_{0, \text{April 25th 84 Benthic}}$	1.001	-0.448	0.188	7.93E-03					
$\beta_{0, \text{April 25th 84 Cladocera}}$	1.025	-5.528	1.308	<0.0001					
$\beta_{0, \text{April 25th 84 Copepodite}}$	1.001	1.084	0.224	<0.0001					
$\beta_{0, \text{April 25th 84 Nauplius}}$	1.010	-3.988	0.725	<0.0001					

610

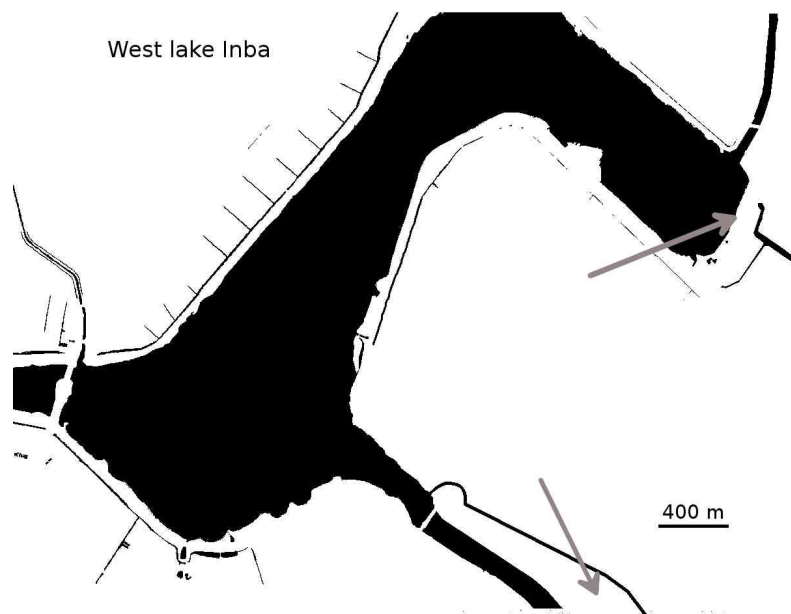


Figure 1. Map of Lake Inba-numa and of main drainage canals. Grey arrows show the locations of sampling sites at lake shore and in an irrigation ditch connected to a canal.

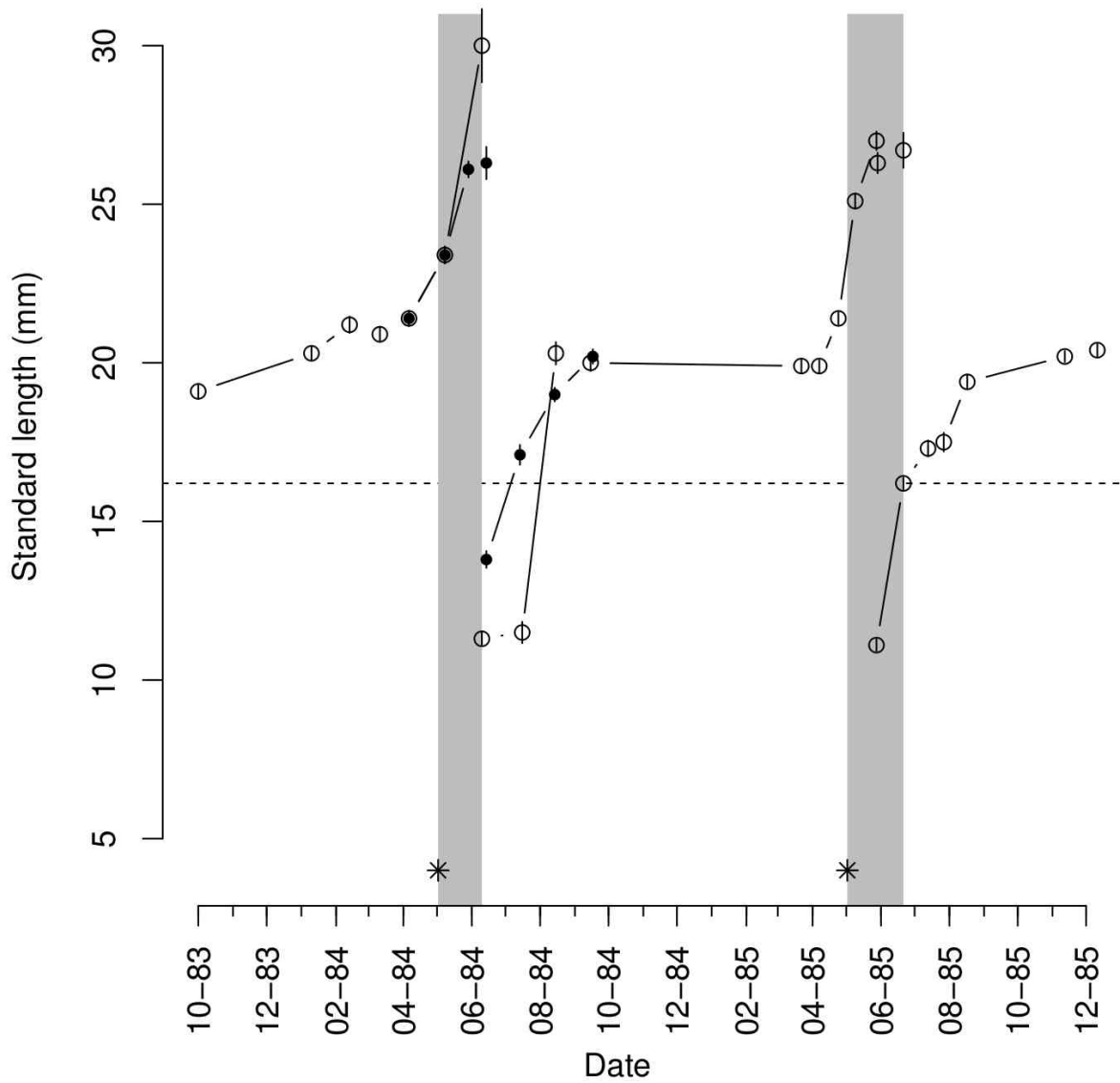
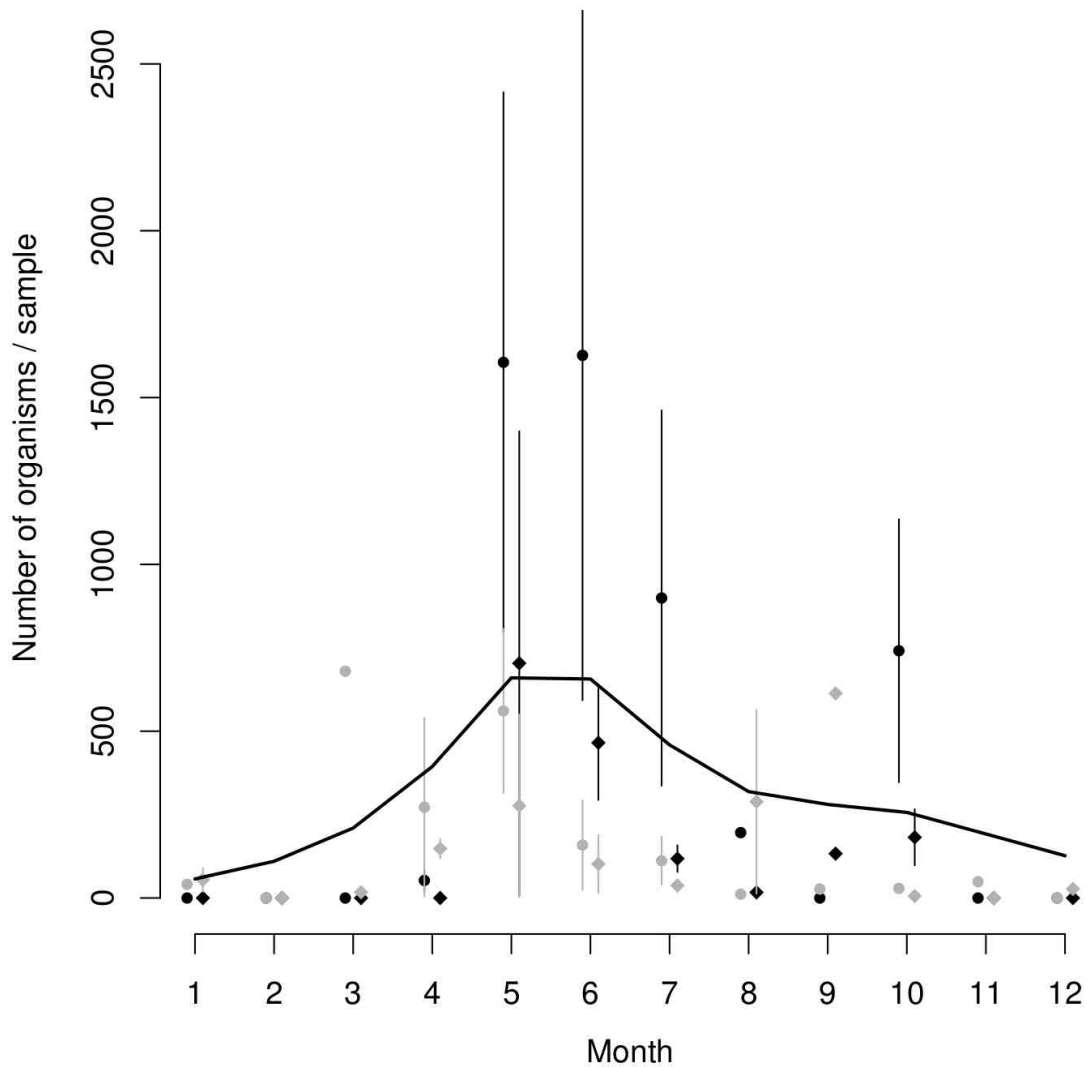
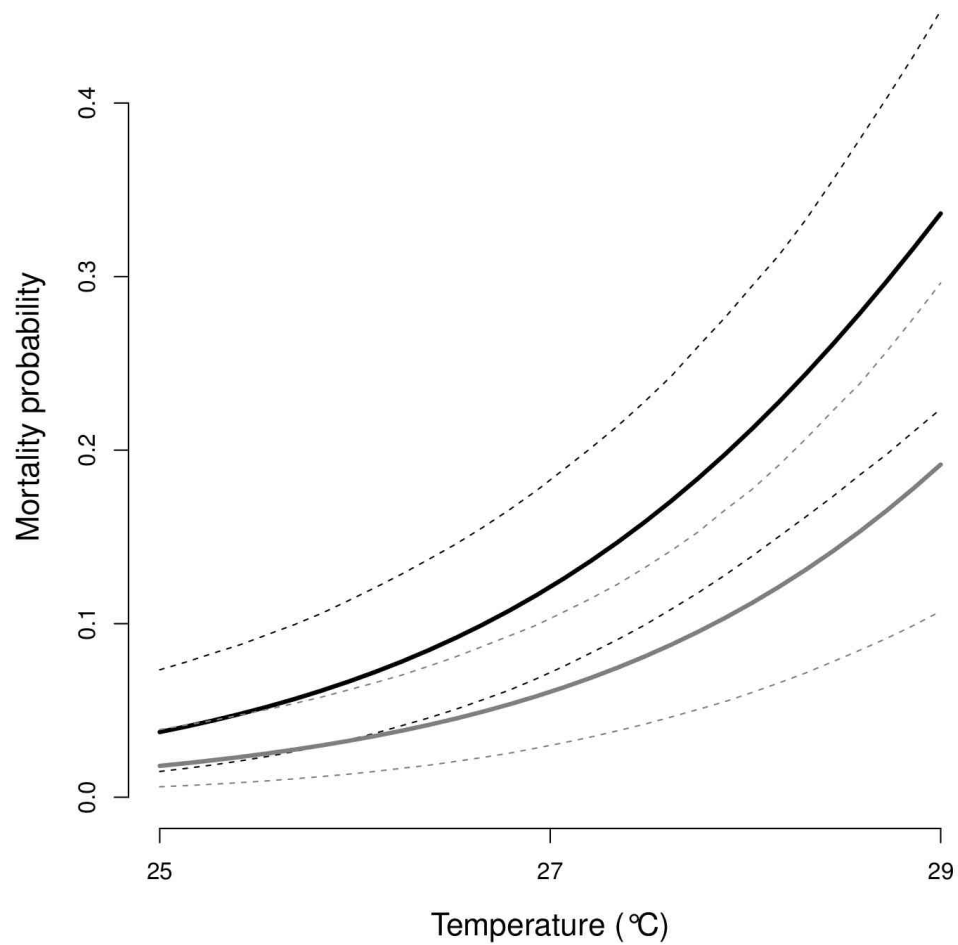


Figure 2. Medaka cohort dynamics. Time series for mean (± SEM) medaka standard body length in the irrigation ditch (open circles), and lake shore (filled circles) at Inba-numa. Stars represent newborns, and the darkened area represents the putative period of adult-juvenile overlap. The horizontal dashed line represents length at 50% maturation probability. X-axis labels indicate month and year.



625 **Figure 3. Seasonal variation prey abundance for medaka.** Mean abundances (\pm SEM) for each month, separated among zooplankton and zoobenthos in the irrigation ditch (gray), and at lake shore (black). The smoothed line illustrates the seasonal cycle and was fitted using a natural cubic spline with the `gam` function of the `mgcv` library of R (Wood 2006).



630 **Fig. 4. Mortality cost of reproduction in female medaka at three temperatures in the laboratory.**

Gray lines: high food regime. Black lines: low food regime. Solid lines represent mean probability and dashed lines represent 95% credible intervals. We did not represent the medium food regime, which mortality probability lied in between the two others.

ELECTRONIC SUPPLEMENTARY MATERIAL for

Recruit-driven generation cycles and the cost of reproduction in wild medaka

Eric Edeline, Osamu Terao, Kiyoshi Naruse

Data, model codes and graphical diagnostics

Model 1 for prevalence of ectoparasites: a binomial ANCOVA

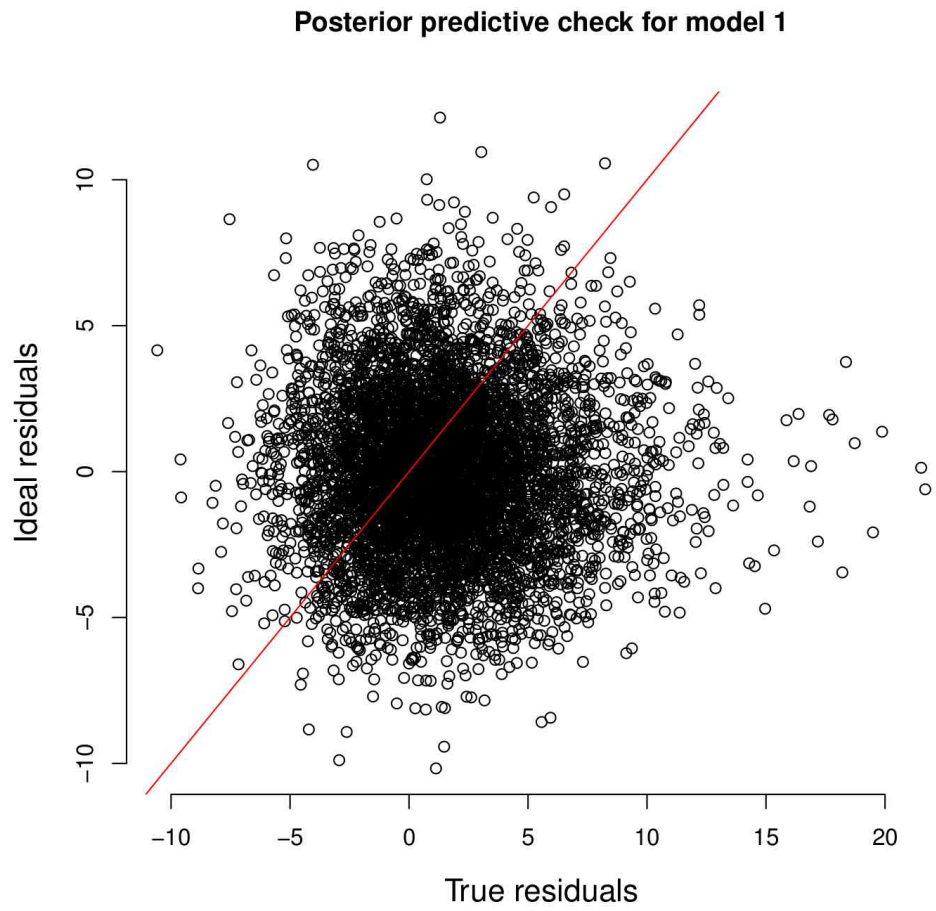
```
## THE MODEL
model{
645 ## priors
    #sex and intercept
    for(j in 1:q){
        sexprob[j] ~ dunif(0, 1)
        alpha[j] ~ dnorm(0, 0.01)
650 }
    #slope
    beta ~ dnorm(0, 0.01)
    ##likelihood
    for ( i in 1 : n){
655 C[i] ~ dbin(p[i], N[i])
        logit(p[i]) <- alpha[sex[i]] + beta*x[i]
        sex[i] ~ dcat(sexprob[]) #distribution for the sex variable
    }

660 ##fit assessment
    for (i in 1:n){
        predicted[i] <- N[i]*p[i]
        resid[i] <- (C[i]-N[i]*p[i])/sqrt(N[i]*p[i]*(1-p[i])) #Pearson
        residuals for the real data
665 C.new[i] ~ dbin(p[i], N[i]) #create replicate dataset, ideal
        because created from model parameters
        resid.new[i] <- (C.new[i]-N[i]*p[i])/sqrt(N[i]*p[i]*(1-p[i]))
        #Pearson residuals for the replicate (ideal) data
        D[i] <- pow(resid[i],2) #squared Pearson residuals
670 D.new[i] <- pow(resid.new[i], 2)
    }
    #discrepancy measures
    fit <- sum(resid[])
    fit.new <- sum(resid.new[])
675 }"

## THE DATA
```

Recruit-driven generation cycles in wild medaka

```
680 C<- c(1,3,1,0,5,5,28,35)#Number of infected fish, two last values for  
Yamagushi  
N <- c(68,35,7,68,32,6,40,48)#total number of fish examined  
Date <- c("1985-05-27","1985-06-15","1985-07-09","1985-05-27","1985-  
06-15" ,"1985-07-09","1985-08-05","1985-06-15")  
sex <- as.factor(c("M","M","M","F","F","F",NA,NA))  
685  
  
## POSTERIOR PREDICTIVE CHECK
```



Model 2 for stomach fullness: an overdispersed binomial GLM

```

695  ## THE MODEL
      model{
      ##likelihood
      for ( i in 1 : n){
      C[i] ~ dbin(p[i], N[i])
700  logit(p[i]) <- alpha + beta*x[i] + eps[i]
      eps[i] ~ dnorm(0, tau.eps)
      x[i] ~ dnorm(mu.x, tau.x) #Treat SL as a random variable to account
      for one NA
      }

705  ##priors
      alpha ~ dnorm(0, 0.01)
      beta ~ dnorm(0, 0.01)
      tau.eps <- pow(sigma.eps, -2)
710  sigma.eps ~ dunif(0, 10)
      mu.x ~ dnorm(0, 0.01)
      tau.x <- pow(sigma.x, -2)
      sigma.x ~ dunif(0,10)
      ##fit assessment
715  for (i in 1:n){
      resid[i] <- (C[i]-N[i]*p[i])/sqrt(N[i]*p[i]*(1-p[i] + 0.5))
      C.new[i] ~ dbin(p[i], N[i])
      resid.new[i] <- (C.new[i]-N[i]*p[i])/sqrt(N[i]*p[i]*(1-p[i] + 0.5))
      }

720  #discrepancy measures
      fit <- sum(resid[])
      fit.new <- sum(resid.new[])
      }"

725  ## THE DATA
      C <-
      c(0,50,100,50,100,50,0,100,12,50,100,50,50,50,100,100,100,12,100,100,
      25,25,100,50,100,50,50,100,12,100,25,100,25,100,100,100,0,50,25,100,5
      0,100,25,25,50,100,100,50,50,100,100,100,100,50,50,50,100,25,25,50,10
730  0,100,100,50,100,100,100,100,100,100,100,100,50,25,100,50,50,100,50,5
      0,50,50,50,25,100,50,0,50,50,50,50,100,100,50,50,25,6,0,100,100,100,1
      00,6,100,100,50,50,100,50,50,50,50,50,100,100,100,50,100,100,25,100,1
      00,100,100,100,75,100,100,50,50,0,100,75,33,100,12,25,100,50,100,0,0,
      100,100,50,100,100,12,100,0,50,25,0,50,50,25,0,25,25,100,0,50,25,NA,N
735  A,100,NA,0,NA,25,0,25,50,50,12,50,12,25,NA,NA,NA,NA,NA,NA,NA,NA,NA,
      ,NA,0,50,0,25,NA,NA,NA,100,75,0,0,NA,NA,NA,NA,50,0,100,50,50,25,100,1
      00,50,100,0,0,25,50,100,100,0,100,100,0,0,0,0,0,50,0,0,100,100,0,0,6,

```

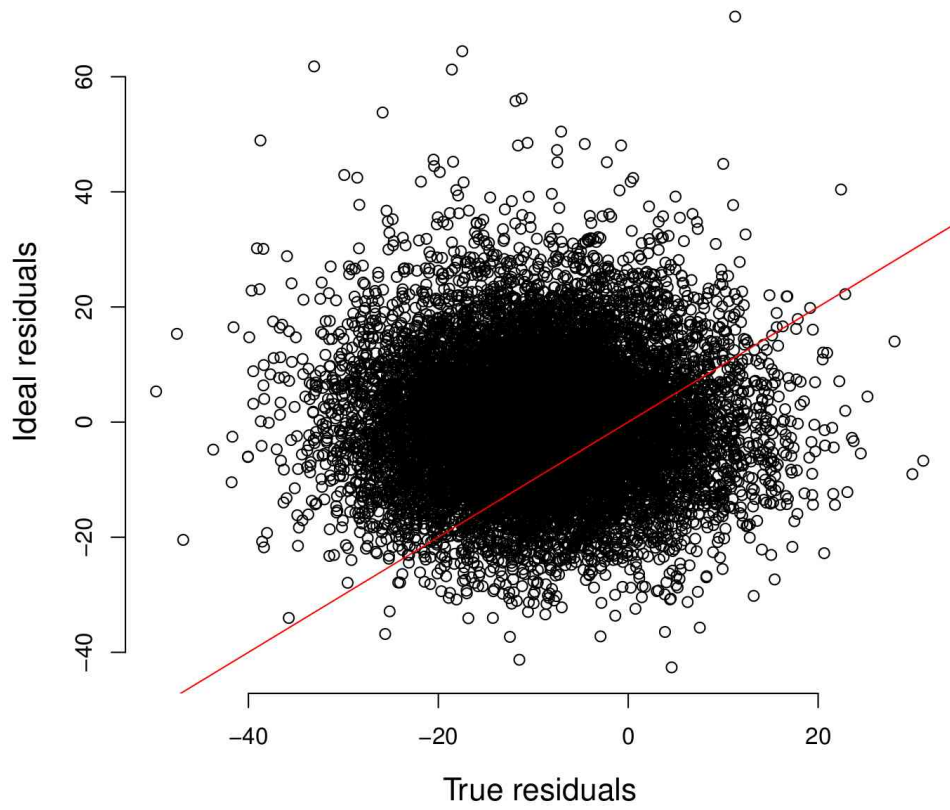
Recruit-driven generation cycles in wild medaka

```

50,0,50,0,50,0,25,0,100,100,0,0,50,0,100,0,50,50,0,25,50,6,0,0,0,10
0,100,0,0,0,0,50,0,0,50,0,0,50,100,0,0,25,0,50,0,25,12,0,25,25,25,0,0
740 ,0,25,0,0,0,50,0,50,25,0,0,50,0,6,0,0,100,12,50,25,25,0,0,0,25,25,100
,0,12,12,0,0,0,6,12,3,100,25,12,25,0,0,100,0,50,0,0,25,25,25,12,0,50,
0,0,0,0,0,0,0,0,0,0,25) #proportion of stomach fullness
N <- rep(100, times = length(C)) #total space in a stomach
x <-
745 c(26,25,25,24,24,24,24,24,24,24,24,23,23,23,23,23,23,23,23,23,23,23,2
3,23,22,22,22,22,22,22,22,22,22,22,22,22,21,21,21,21,21,21,21,21,2
1,21,21,21,21,21,21,21,21,21,21,21,20,20,20,20,20,20,20,20,20,20,2
0,20,20,20,19,19,19,19,19,19,19,19,19,19,19,19,19,19,19,19,19,18,18,1
8,18,18,18,18,18,18,18,18,17,17,17,17,17,17,17,17,17,16,16,16,16,16,1
750 5,15,15,14,14,14,14,14,13,13,13,30,29,31,31,29,31,32,30,30,30,31,31,N
A,29,30,31,28,29,29,29,29,29,30,29,29,30,27,27,29,30,29,29,29,27,29,2
8,26,27,27,28,26,26,27,27,28,24,25,26,27,25,27,26,25,26,25,24,25,27,2
5,25,25,25,25,26,24,24,24,24,24,24,23,23,23,24,25,26,23,23,24,23,23,2
4,23,21,33,31,30,29,29,28,28,27,27,27,27,27,26,26,25,25,25,25,24,24,2
755 4,24,24,23,23,23,20,20,19,19,18,18,18,18,18,18,18,18,17,17,17,17,17,1
7,17,17,17,17,17,17,17,16,16,16,16,16,16,16,16,16,16,16,15,15,15,1
5,15,15,15,15,15,15,15,15,15,15,15,15,14,14,14,14,14,14,14,14,14,1
4,14,14,14,14,14,14,14,14,14,14,14,13,13,13,13,13,13,13,13,13,13,1
3,13,13,13,13,13,13,13,13,13,12,12,12,12,12,12,12,12,11,11,11,10,10,9
760 ,9,9,9,9,9,9,9,9,9) #standard length

```

Posterior predictive check for model 2



765 Model 3 for predatory behaviour: a bernoulli GLMM

```

## THE MODEL
model{
#likelihood
770 for ( i in 1 : n){
y[i] ~ dbern(p[i])
logit(p[i]) <- alpha[alpha.indx[i]] + beta[beta.indx[i]]*x[i]
}
#priors
775 for(i in 1:q){
alpha[i] ~ dnorm(mu.int, tau.int) #random intercept; varied for each
prey item and date
}
mu.int ~ dnorm(0, 0.01)           #hyperprior for mean of each random
780 effect
sd.int ~ dunif(0, 100)           #hyperprior for SD of each random
effect
tau.int <- pow(sd.int, -2)
#
785 for(i in 1:l){
beta[i] ~ dnorm(mu.slope, tau.slope) #random slope; varied by prey
item
}
mu.slope ~ dnorm(0, 0.01)         #hyperprior for mean of each random
790 effect
sd.slope ~ dunif(0, 100)         #hyperprior for SD of each random
effect
tau.slope <- pow(sd.slope, -2)
##fit assessment
795 for (i in 1:n){
resid[i] <- (y[i]-p[i])           #raw residuals
y.new[i] ~ dbern(p[i]);           #create replicate dataset
ideal because created from model parameters
resid.new[i] <- (y.new[i]-p[i])
800 }
#discrepancy measures
fit <- sum(resid[]);
fit.new <- sum(resid.new[]);
}
805 ## THE DATA

y <-
c(0,1,1,1,0,1,0,0,1,1,1,1,1,1,0,1,1,1,1,1,0,0,1,1,0,0,1,0,1

```

Recruit-driven generation cycles in wild medaka

810 ,1,1,0,1,1,1,1,1,0,1,0,0,1,1,0,1,0,1,0,1,0,0,1,0,1,1,1,1,1,1,1,1,
1,1,0,1,0,1,0,0,0,0,1,0,1,0,0,0,0,1,0,0,1,1,0,0,0,0,1,0,1,0,1,0,1,0,0,
,1,0,1,0,0,0,0,0,1,1,1,1,1,0,0,1,1,0,1,0,1,1,0,0,0,0,0,0,0,0,0,0,0,
0,
,0,
815 0,0,0,0,1,0,0,0,0,0,0,0,0,0,0,1,1,0,0,0,0,0,0,0,0,0,0,0,0,0,1,0,0,0,0,0,0,
,1,0,1,0,0,0,0,0,0,0,0,0,0,1,0,1,1,1,0,0,0,0,0,1,1,0,0,0,0,0,0,0,0,0,1,
0,0,1,0,0,0,1,1,0,1,1,0,0,0,0,1,0,0,0,1,0,1,0,0,0,1,0,1,0,0,1,1,1,1,1,
,0,0,0,1,1,1,0,1,0,0,0,0,1,1,0,1,0,1,1,0,0,1,0,1,0,0,1,1,0,0,0,0,0,0,
0,0,0,0,0,0,0,0,0,1,0,
820 ,0,
0,
,0,
0,0,1,1,1,1,1,1,1,1,0,0,1,1,1,1,0,1,1,0,1,1,1,0,1,1,1,0,1,1,0,0,
,1,0,0,0,1,0,1,1,1,1,1,1,1,0,
825 0,0,0,0,0,1,0,1,1,1,1,0,1,0,1,0,0,1,1,1,1,0,0,1,0,0,0,0,0,1,0,0,0,1,0,
,0,0,1,0,
0,
,0,0,0,1,0,
0,0,1,1,0,
830 ,0,1,1,0,0,0,0,1,1,0,0,1,1,1,1,1,1,1,0,1,0,1,0,1,1,1,1,1,0,1,0,1,1,
1,0,1,1,1,1,1,1,1,1,1,1,1,1,1,1,0,0,1,1,0,0,0,1,1,1,1,1,1,1,1,1,1,0,
,1,1,1,1,1,0,1,1,1,1,0,1,1,1,1,0,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,
1,1,1,0,
,0,
835 0,
,0,
0,
,0,
0,
840 ,0,
0,
,0,
0,1,1,1,1,1,0,1,1,1,1,1,0,
,0,
845 0,
,0,
0,
,0,
0,
850 ,0,0,0,1,0,1,0,1,0,0,0,0,0,0,0,1,0,0,1,0,0,0,0,0,0,1,0,0,1,0,1,0,0,0,
0,0,0,0,1,0,0,0,0,0,0,0,0,0,0,0,0,0,1,0,0,1,0,0,1,1,0,1,0,0,0,0,1,0,0,1,
,0,1,0,1,0,1,1,0,1,0,0,1,1,0,1,0,1,0,0,0,1,1,1,1,1,0,0,1,1,0,1,1,0,1,
1,1,1,1,1,1,0,0,0,1,1,1,0,1,0,1,0,1,1,1,0,0,0,0,0,0,0,0,0,0,0,0,0,
,0,

Recruit-driven generation cycles in wild medaka

[illegible]

Recruit-driven generation cycles in wild medaka

```

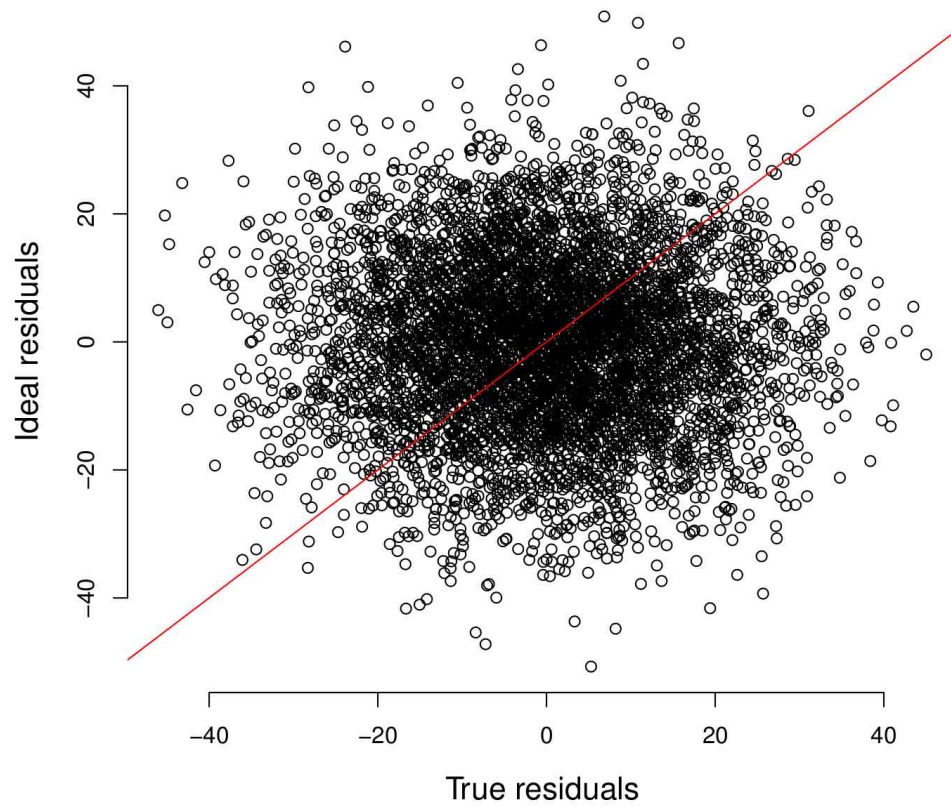
900 6/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/8
    4,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/0
    6/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,1
    6/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/8
    4,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/0
905 6/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,1
    6/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/8
    4,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/0
    6/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,1
    6/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/84,16/06/8
910 4,16/06/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/0
    7/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,0
    2/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/8
    4,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/0
    7/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,0
915 2/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/8
    4,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/0
    7/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,0
    2/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/8
    4,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/0
920 7/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,0
    2/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/8
    4,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/0
    7/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,0
    2/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/8
925 4,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/0
    7/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,0
    2/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/8
    4,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/07/84,02/0
    7/84) #sampling dates for individual fish
930
    Date <- rep(Dateshort, times = 5) #date of capture data

    Tax <- as.factor(c(rep("Algae", times=354), rep("Cladocera",
    times=354), rep("Copepodite", times=354), rep("Nauplius", times=354),
935 rep("Benthic", times=354))) #identity of prey

    alpha.indx <- as.numeric(as.factor(paste(Date, Tax)) ) #index for
    random intercept
    beta.indx <- as.numeric(Tax) #index for random slope
940 n <- length(y)
    q = length(levels(as.factor(paste(Date, Tax))))
    l = length(levels(Tax))

```

Posterior predictive check for model 3



950 Model 4 for mortality probability in female medaka: a binomial ANCOVA

```

## THE MODEL

model{
955  ## priors
  #intercept
  for(j in 1:3){
    alpha[j] ~ dnorm(0, 0.01)
  }
960  beta ~ dnorm(0, 0.01)
  ##likelihood
  for ( i in 1 : n){
    C[i] ~ dbin(p[i], N[i])
    logit(p[i]) <- alpha[food[i]] + beta*x[i]
965  }

  ##fit assessment
  for (i in 1:n){
    resid[i] <- (C[i]-N[i]*p[i])/sqrt(N[i]*p[i]*(1-p[i]))
970    C.new[i] ~ dbin(p[i], N[i])
    resid.new[i] <- (C.new[i]-N[i]*p[i])/sqrt(N[i]*p[i]*(1-p[i]))
  }
  #discrepancy measures
  fit <- sum(resid[])
975  fit.new <- sum(resid.new[])
}

## THE DATA

980  C <- c(0,0,1,5,7,8,9,13,15) #count of moribund or dead female
  N <- c(48,46,48,48,48,47,48,48,48) #total count of female
  x <- c(25,25,25,27,27,29,27,29,29) #non-scaled temperature data
  food <- c(L,H,M,H,M,H,L,M,L) #feeding regimes
  n <- length(C)
985

```

