



Empirical evidence for competition-driven semelparity in wild medaka

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Abstract 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 resource competition, resulting in apparent semelparous life histories and non-overlapping generations. However, empirical support for such a competition-driven semelparity (CDS) remains scarce. Here, we report a high consistency of cohort dynamics with CDS in wild medaka (*Oryzias latipes*). As predicted by the theory, there was a strong juvenile-adult diet overlap, and all individuals died after reproduction as semelparous age-1 adults, synchronous with a rapid somatic growth of age-0 juveniles into the adult stage and with dropping abundances of zooplankton food resources. In addition to the theory, we found evidence for increased reproductive allocation under

food stress, translating into immune depression and elevated parasite prevalence. Therefore, CDS in medaka emerges both from intercohort competitive exclusion and from food-dependent energy reallocation from maintenance to reproduction, the later presumably representing an adaptive response to the former. The literature data show that the strengths of both intercohort competition and reproductive allocation increase at higher temperatures in many ectotherms, pointing to climate warming as a potentially powerful magnifier of CDS in the wild.

Keywords Body size · Longevity · r and K strategies · Recruit-driven generation cycles · Resource competition · Semelparity

Introduction

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). A high mortality cost of reproduction is expected to favour the evolutionary emergence of semelparity (Charnov and Schaffer 1973), a “suicidal” reproductive strategy in which individuals invest all of their energy in their first reproduction at the cost of somatic deterioration and death. A high mortality cost of reproduction is often considered to proximally result from increased predation risk (Magnhagen 1991) and from immune depression due to conflicting energy demands between reproduction and immunity (Zuk and Stoehr 2002; Harshman and Zera 2007). Here, we suggest that intercohort exploitative competition, i.e., the competition for resources between adults and their juveniles, should also be considered among the sources of adult mortality that may select toward semelparity.

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The size-scaling of intake and metabolic rates are key to determine the relative dominance of different life-history stages in exploitative competition. 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 deplete resources at resource levels at which large-sized adults cannot meet their maintenance requirements and starve to death. In terms of life history, this competitive exclusion of adults by their juveniles thus results in a "competition-driven semelparity" (CDS). At the population level, CDS is predicted to translate into so-called recruit-driven generation cycles, a type of population dynamics in which both consumer and resource densities oscillate on a period determined by the age at maturity of the consumer (Persson et al. 1998). CDS is expected to occur in all organisms in which (a) R^* increases with body size, (b) resources substantially overlap between juveniles and adults, and (c) adults can not offset the effects of exploitative competition through interference competition or cannibalism (Claessen et al. 2000; Le Bourlot et al. 2014).

Cohort dynamics consistent with CDS 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 CDS have also been reported in the yellow perch *Perca flavescens* (Persson et al. 2004). However, despite the large scope for CDS in animal populations (e.g., non-overlapping generations) empirical evidence for its occurrence remains scarce. Here, we assess the consistency of the theory of CDS with the results from a 2-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.

Materials and methods

Model fish species

The medaka belongs to Beloniformes (family Adrianchthyidae), a sister order of Cyprinodontiformes (Poeciliids, killifishes). The medaka is a small fish (25.0–35.0 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. 2011). Recently, it was shown experimentally that medaka standard body length is a strong predictor of medaka capacity to prey on large-sized cladocerans (large individuals of *Daphnia pulex*), which in turn controlled algal concentrations through grazing (Renneville et al. 2015). However, less or little is known on medaka ecology in the wild, where the species is currently considered as endangered due to habitats loss. The construction or development of future conservation plans will be fostered if we increase our basic knowledge on medaka ecology.

Sampling sites and fish communities

We sampled two sites at Inba-numa (Chiba Prefecture near Tokyo) in 1983, 1984 and 1985: an irrigation ditch (0.5–1.0 m wide) in a paddy field, and the shore of Lake Inba (11.55 km², mean depth is 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 were eutrophic with average dissolved phosphorus (PO_4^{3-}) 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



Fig. 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

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 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).

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 December 1985. Our sampling method allowed us to capture fish from 6.0 mm standard length (*SL*: from the snout to the base of the caudal fin). To representatively sample each site, we fished a stretch of 300 m in the irrigation ditch and of 500 m along lake shore. Sampling effort was adjusted (but not recorded) to capture a representative number of individuals. All captured fish ($n = 4571$) 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 *SL* to the nearest mm (ranged from 6.0 to 34.0 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. Unfortunately, the raw body mass data were lost. We thus used the Figure_Calibration plugin in ImageJ (http://www.astro.physik.uni-goettingen.de/~hessman/ImageJ/Figure_Calibration/) to calculate the mean body mass of each cohort and sex group from Fig. 5 in Terao (1985).

Ectoparasites

In 1985, prevalence of the ectoparasite anchor worm (*Lernaea cyprinacea*, copepod crustacean) was recorded on a subset of 216 adults sampled on May 27 ($n = 136$), June 15 ($n = 67$) and July 9 ($n = 13$) at Inba-numa. This lower

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 Yamaguchi City on May 8 ($n = 40$) and June 15, 1985 ($n = 48$).

Medaka diet and prey availability

On three dates in 1984 (April 25, June 16, and July 2), 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 rectoris* 557.7 $\mu\text{m} \pm 120.6$ SD, *Bosmina longirostris* 402.0 $\mu\text{m} \pm 145.7$ SD and unidentified Daphniidae), nauplius larvae of copepods (181.7 $\mu\text{m} \pm 36.0$ SD), copepodite stage (adult) of cyclopoid copepods (797.2 $\mu\text{m} \pm 152.0$ SD), 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. Because the range of body sizes within each taxa of zooplankton was relatively limited (as compared with the between-taxa range), we considered that each zooplankton taxa represented a distinct resource for medaka and applied a similar approach to zoobenthos.

From October 1983 to October 1984, we tracked seasonal changes in environmental abundances of zooplankton and zoobenthos—presumably the most energetically-profitable food resources for medaka—both in the irrigation ditch and at the 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 (44 for zooplankton and 38 for zoobenthos). 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 effects of temperature and food ration on reproductive investment and mortality 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, 12.40, 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 thus not a duplication of Hirshfield’s results but instead represents an add-on.

Data analysis

Prevalence of ectoparasites

We partitioned adult medaka among two infection categories (infected or non-infected) and thus modelled the infection probability p of this binary outcome in a binomial generalized linear model (GLM) of the form:

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

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

where \sim is “is distributed as”; C_{jk} is count of infected fish of sex j on date k ; Bin is binomial distribution; N_{jk} is total number of fish of sex j examined on date k (304 fish examined in total); p_{jk} is probability for a fish of sex j examined on date k to be infected; \ln is the natural logarithm; $\beta_{0,j}$ is sex-specific intercept; β_1 is regression slope for the effect of date; D_k is 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, see also Electronic Supplementary Material (ESM)). By doing so, we assumed that the sex-ratio was the same at Inba-numa and Yamaguchi.

Size-dependency of predatory behaviour

A critical assumption for the emergence of CDS is that there is a strong resource overlap among small (juvenile) and large (adult) individuals. We tested this hypothesis using stomach content data. First, to gain a fine understanding of the size-dependency of medaka predatory behaviour we modelled the effect of medaka body length

on the probability p of eating a given prey item using a Bernoulli mixed-effects GLM:

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

$$\ln\left(\frac{p_{ijk}}{1 - p_{ijk}}\right) = \beta_{0,jk} + \beta_{1,k} SL_i \quad (2)$$

where P_{ijk} is presence or absence of food item k on date j in stomach of fish i (1765 observations); Bern is Bernoulli distribution; $\beta_{0,jk}$ is normally-distributed random intercept varying depending on prey item k at each date j (yielding 15 intercepts); $\beta_{1,k}$ is normally-distributed random slope varying depending on prey item k (yielding 5 slopes); SL_i is individual standard length scaled to zero mean and unity standard deviation. 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. This hierarchical structure for intercepts and slopes thus considered the high-level, overall resource use to be informed from lower-level, item-specific intercepts and slopes, which in turn were mutually-informed through their common, higher-level normal distribution (Royle and Dorazio 2008). Parameters for overall resource use (reported in Table 1) were provided by the mean and standard deviations of the normal distributions for the intercept and slope, while date- and item-specific parameter values that made up the normal distributions are reported in Table 2.

Second, to accurately quantify the potential for inter-cohort competition in medaka, we computed diet overlap among juveniles ($9.0 \text{ mm} \leq SL < 16.2 \text{ mm}$) and adults ($16.2 \text{ mm} \leq SL \leq 33.0 \text{ mm}$) using Schoener’s similarity index S (Schoener 1968), which has been suggested to be one of the best niche overlap measures (Abrams 1980): $S = 1 - 0.5 \sum_k |p_{J,k} - p_{A,k}|$, where $p_{J,k}$ and $p_{A,k}$ are frequency of food item k in the diets of juveniles (J) and adults (A); respectively. We computed S separately for April 25 and July 2, and estimated standard deviation for each S using a bootstrap procedure (random sampling of one-third of the data and computation of S , repeated 5000 times).

Literature data on the mortality cost of reproduction

As for model (1), Hirshfield’s (1980) data consists of a binomial outcome, specifically counts of moribund or dead vs. healthy fish in each of the 9 temperature and food treatments. We modelled this data with a binomial GLM:

Table 1 Summary statistics for the main effects in models 1-3

Model	Response	Predictor	Distribution	Link	Fixed-effect parameter	R-hat	Mean estimate	SD of the estimate	MCMC <i>P</i> value
1	Prevalence of ectoparasites	Sex	Binomial	Logit	$\beta_{0, F}$	1.008	0.361	0.245	0.135
					$\beta_{0, M}$	1.021	-3.007	0.538	<0.0001
					β_1	1.020	2.296	0.316	<0.0001
2	Probability of eating a given food item	SL	Bernoulli	Logit	* β_0	1.013	-5.044	2.093	<0.0001
					* β_1	1.001	-5.311	2.896	0.3700
3	Mortality probability	Feeding regime	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
		Temperature	β_1	1.009	1.127	0.202	<0.0001		

R-hat is the Gelman–Rubin statistic. Values of R-hat below 1.1 indicate convergence for the estimated parameter

SL is medaka standard length

* Estimate is the mean of the normal distribution of a random effect (see “Materials and methods” for more details)

Table 2 Random effects in model 2

Random effect parameter	R-hat	Mean estimate	SD of the estimate	MCMC <i>P</i> value
β_0 , July 2nd 84 Algae	1.001	-1.010	0.223	<0.0001
β_0 , July 2nd 84 Benthic	1.000	-1.374	0.263	<0.0001
β_0 , July 2nd 84 Cladocera	1.002	-1.683	0.283	<0.0001
β_0 , July 2nd 84 Copepodite	1.244	-11.499	4.522	<0.0001
β_0 , July 2nd 84 Nauplius	1.019	-16.048	3.130	<0.0001
β_0 , June 16th 84 Algae	1.027	-9.836	4.165	<0.0001
β_0 , June 16th 84 Benthic	1.044	-9.666	4.296	<0.0001
β_0 , June 16th 84 Cladocera	1.000	-1.127	0.354	<0.0002
β_0 , June 16th 84 Copepodite	1.090	-8.731	4.223	<0.0003
β_0 , June 16th 84 Nauplius	1.076	-6.859	3.930	0.0280
β_0 , April 25th 84 Algae	1.000	0.267	0.182	0.1360
β_0 , April 25th 84 Benthic	1.001	-0.448	0.188	0.0079
β_0 , April 25th 84 Cladocera	1.025	-5.528	1.308	<0.0001
β_0 , April 25th 84 Copepodite	1.001	1.084	0.224	<0.0001
β_0 , April 25th 84 Nauplius	1.010	-3.988	0.725	<0.0001
β_1 , Algae	1.000	-0.150	0.180	0.4040
β_1 , Benthic	1.001	-0.730	0.211	<0.0001
β_1 , Cladocera	1.000	1.104	0.231	<0.0001
β_1 , Copepodite	1.002	-1.649	0.502	0.0020
β_1 , Nauplius	1.014	-5.497	1.148	<0.0001

Normally-distributed intercepts (β_0) and slopes (β_1) for the effect of individual standard length (SL) on the probability of finding a given food item in a medaka stomach on a given date (as indicated in the random effect column), on a logit scale

See Table 1 legend for further details

$$C_i \sim Bin(N_i, p_i)$$

$$\ln\left(\frac{p_i}{1-p_i}\right) = \beta_{0,fi} + \beta_1 T_i \tag{3}$$

where C_i is count of moribund or dead fish in treatment i ; N_i is total number of fish in treatment i (351 fish in all treatments); p_i is mortality probability in treatment i ; $\beta_{0,fi}$

is intercept specific to each food regime (3 different intercepts); β_1 is regression slope; T_i is temperature in treatment i ; scaled to zero mean and unity standard deviation. We used this model 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 (1–3) using JAGS v. 3.4 (Plummer 2003) in R v. 3.2.3 through the package jagsUI, which itself relies on packages rjags and CODA (Plummer et al. 2006). We ran three independent Markov chain Monte Carlo (MCMC) chains of 50,000 (models 1 and 3) and 200,000 (model 2) iterations each with a burn-in period of 40,000 (models 1 and 3) and 190,000 (model 2), and thinned chains at a period of 5 (models 1, 2, and 3) 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 distribution between 0 and 100. Convergence was assessed using the Gelman–Rubin statistic (Gelman and Rubin 1992). 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 for which the sign was opposite to that of the mean posterior value.

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 estimated model parameters

(i.e., residuals from fitting the model to “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 laid above the line. The exact proportion is given by the Bayesian P value. Bayesian P values for model (1) to (3) were 0.37, 0.49, and 0.53, respectively, indicating reasonably good to excellent model fit. Data, model code and goodness of fit graphics are provided as ESM.

Results

Medaka cohort dynamics

Cohort dynamics were highly consistent at the two sampling sites (Fig. 2a). Newly-hatched fry (about 4.0 mm SL) were first seen in mid-June in 1984 and late May in 1985 (stars in Fig. 2a). This mismatch was presumably due to cooler mean water temperatures in April and May 1984 (12.2 °C) compared to the same months in 1985 (16.0 °C). Newly-hatched juveniles grew very rapidly to reach about 10.0 mm SL roughly in 2 weeks, yielding an average growth rate of $(10 - 4)/14 \approx 0.4$ mm day⁻¹.

Fig. 2 Medaka cohort dynamics. **a** Time series of mean (\pm SD) medaka standard body length in the irrigation ditch (*open circles*), and lake shore (*filled circles*) at Inbanuma. 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. **b** Time series for the proportion of age-1 fish in the catch. Numbers indicate the total size of the catch, pooling among the two sampling sites and among sampling dates that were less than 5 days apart

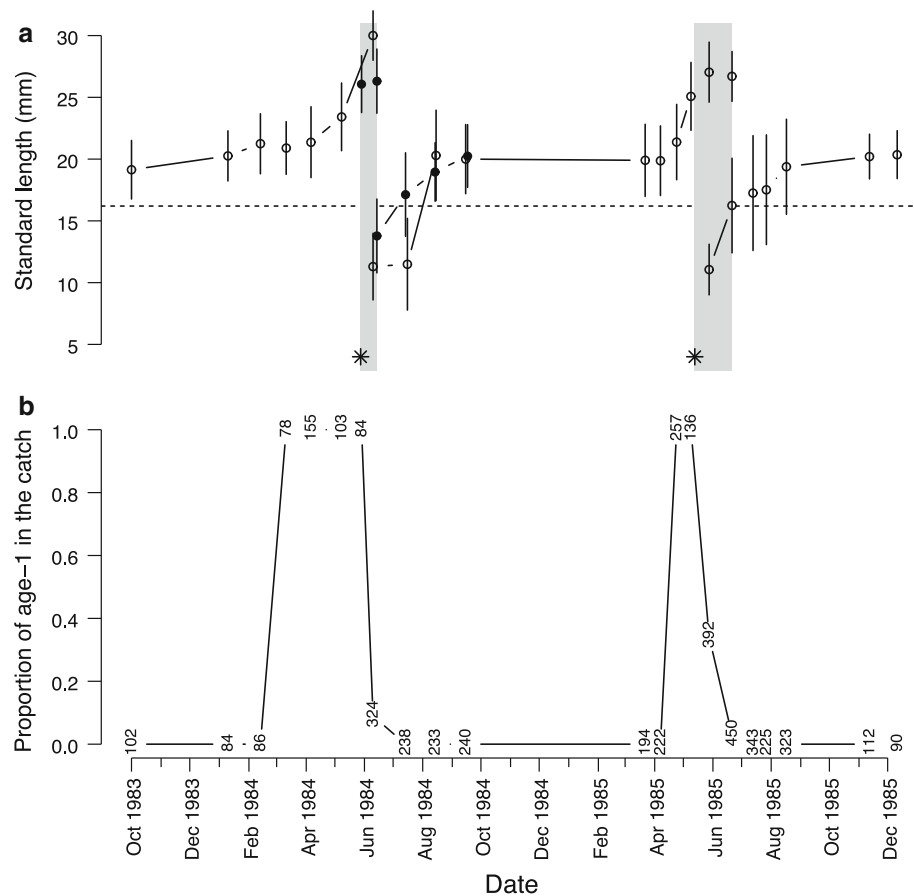
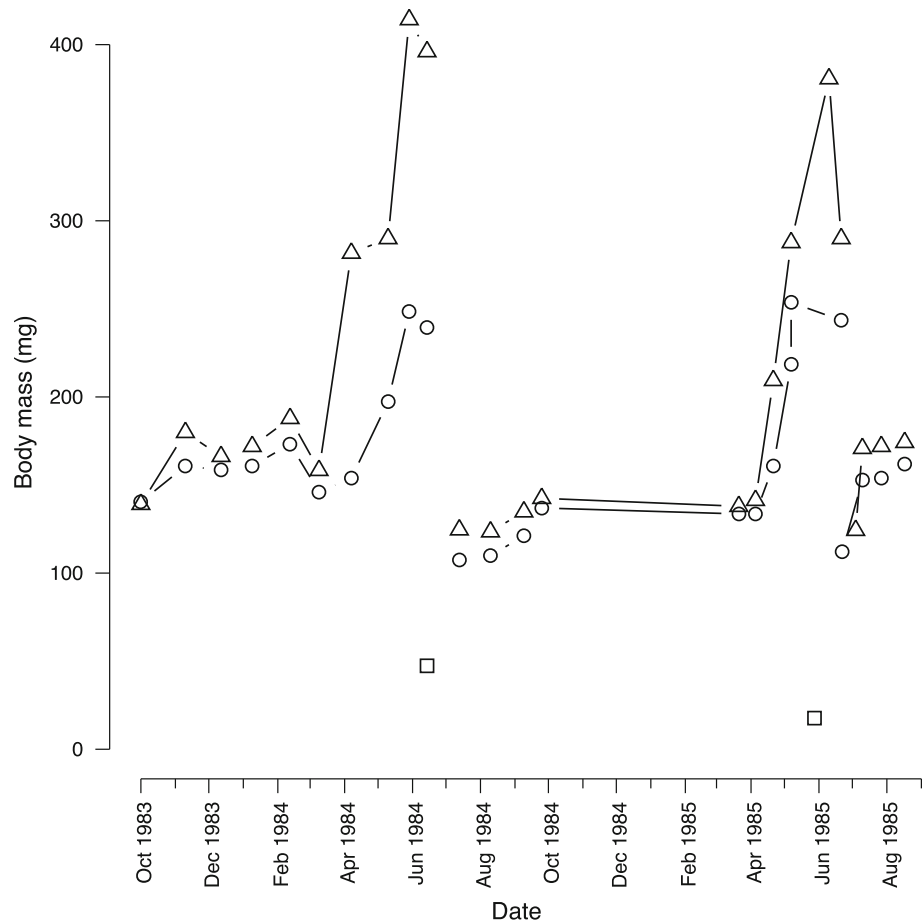


Fig. 3 Medaka body mass dynamics. Time series for mean body mass in immature (squares), female (triangles) and male (circles) medaka at Inba-numa. Dynamics were similar in the irrigation ditch and at lake shore, therefore data were pooled among the two sampling sites



In both years, juvenile recruitment into the 10.0–15.0 mm size class was synchronous with a drop in the proportion of age-1 adults in the catch (Fig. 2b), and adults ran extinct almost exactly when juveniles reached the *SL* at 50 % maturation probability (horizontal dashed line in Fig. 2a) such that generation overlap was reduced to about 2 weeks in 1984 (from June 15 to July 1) and 5 weeks in 1985 (from May 31 to July 9). Specifically, samples included a mixture of adults and juveniles on a single date in 1984 ($n = 324$ fish including 29 adults on June 28, Fig. 2b) and on two dates in 1985 ($n = 392$ fish including 134 adults on June 15, $n = 450$ fish including 13 adults on July 9, Fig. 2b). In all of the other samples, adults constituted either the entire catch (not a single juvenile caught, proportion of 1) or were totally absent from the catch (proportion of 0). Fish stopped growing during winter, resumed growth during the following May, reproduced and died. No individual wintered a second time (i.e., not a single age-2 + individual was caught).

The dynamics of mean cohort body mass show that adult extinction in July was preceded by a mass loss in both years (Fig. 3). In 1985, this mass loss was steeper in females than in males, which also generally grew less fast than females in both years (Fig. 3).

Seasonal dynamics of prey

Abundances of zooplankton and zoobenthos peaked in early May for zoobenthos and early June in zooplankton (Fig. 4). The rapid decrease of zooplankton abundance in June and July was tightly paralleled by a rapid decline in the proportion of reproducing, age-1+ medaka in the catch (Fig. 4).

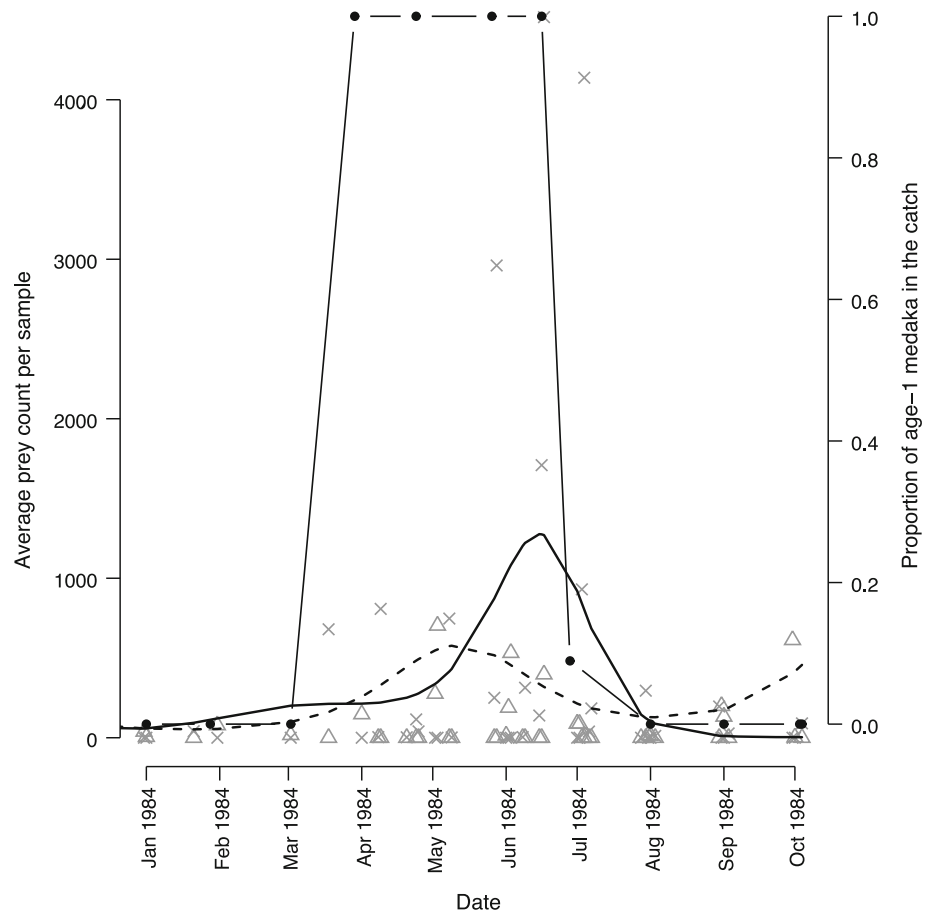
Prevalence of ectoparasites (model 1)

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

Size-dependency of medaka diet (model 2)

The mean slope of the predation probability–size relationship in the 9.0–33.0 mm *SL* range was not significantly different from 0 (average slope in model 2, Table 1), indicating that overall resource use (i.e., predation on an average food item) by medaka was size-independent. This

Fig. 4 Seasonal variation in prey abundance. *Gray crosses* and *triangles* represent mean counts (pooled among sampling sites) of zooplankton and zoobenthos, respectively. The *smoothed lines* show natural cubic splines fitted to the zooplankton (*solid*) and zoobenthos (*dashed*) data, respectively, using the gam function of the mgcv library of R (Wood 2006). The *line and dots* represent the proportion of age-1 medaka in the catch (pooled among sampling sites)



overall size-independence of resource use was in fact driven by contrasted size-dependencies of predation probability on particular food items. Indeed, item-specific slopes (random slopes in Table 2) revealed that the relationship was sometimes positive (cladocerans), sometimes negative (benthic prey or copepods of both stages) or sometimes not significantly different from 0 (algae).

The size-dependency of medaka item-specific predation behaviour, however, was not strong enough to induce a niche separation between juveniles and adults. Indeed, Schoener's indices (Fig. 5), which calculate the sum of all item-specific overlaps (see Methods), showed a very high diet overlap among juveniles ($9.0 \text{ mm} \leq SL < 16.2 \text{ mm}$) and adults ($16.2 \text{ mm} \leq SL \leq 33.0 \text{ mm}$) of 0.95 on both April 25 ($\pm 1.6 \cdot 10^{-2}$ SD) and July 2 ($\pm 1.4 \cdot 10^{-2}$ SD, see also Fig. 5).

Mortality cost of reproduction in the laboratory (model 3)

Mortality probability of reproducing female medaka significantly increased with increasing temperature (slope of the temperature effect was significantly different from 0,

model 3, Table 1; Fig. 6). We tested for the differences among model intercepts, and found that mortality was significantly higher under the low food regime compared to the high food regime (MCMC P value of the difference = 0.0447, Fig. 6).

Discussion

Theory, supported by empirical data in fish (Persson and De Roos 2006), predicts that the critical resource density R^* at which food intake exactly covers maintenance requirements often increases with body size (De Roos et al. 2003; Kooijman 2010). Hence, if resources substantially overlap between juveniles and adults and adults can not offset the effects of exploitative competition through interference competition or cannibalism, then adults should be competitively excluded by their juveniles (Persson et al. 1998). Adults should thus realize an apparent competition-driven semelparity (CDS). However, empirical support for such a theoretically-predicted CDS remains scarce. Here, we have evaluated the empirical evidence for CDS in wild medaka at two sites at Inba-numa, Japan.

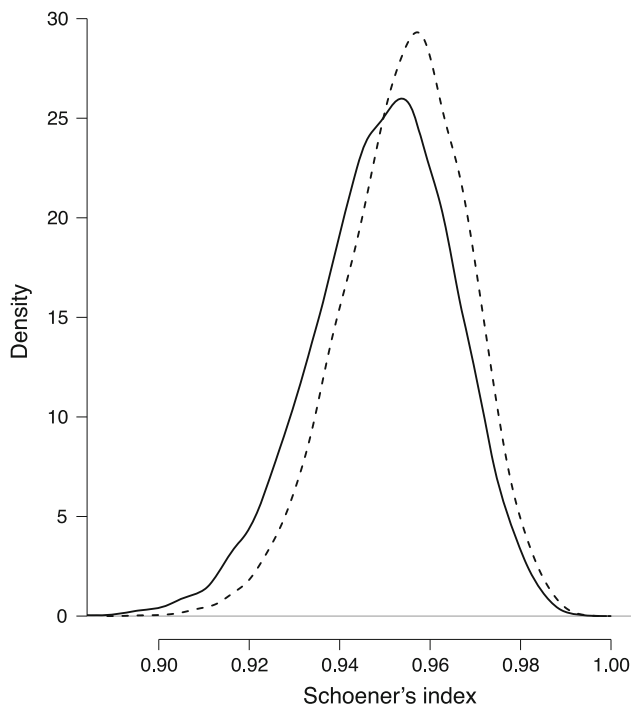


Fig. 5 Distribution of diet overlap among juvenile and adult medaka at Inba-numa. *Solid line* April 25, 1984, *dashed line* July 2, 1984. Schoener's index was computed in a bootstrap procedure yielding for each date 5000 indices. Densities were plotted using a Gaussian smoothing kernel with a standard deviation of $2.5 \cdot 10^{-3}$

Medaka cohort dynamics at Inba-numa were highly consistent with CDS. All individuals matured at age-1+, reproduced and died when their juveniles reached a *SL* of about 16.0 mm, which corresponds to the size at 50 % maturation probability. A similar pattern with adults abruptly 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 seems to be the norm in wild medaka in Japan. For this observed semelparity to be CDS, the mortality cost of reproduction should operate through food shortage due to exploitative competition from juveniles. We now critically assess the consistency of our empirical data with this hypothesis.

Competition-driven cost of reproduction

Our CDS hypothesis is supported by the fact that medaka are semelparous in the wild but iteroparous in captivity. Under fully captive conditions (i.e., in the absence of exploitative competition), lifespan of medaka is on average 2.7 years and can reach up to 5 years (Egami 1971). Similarly, Hirshfield (1980) found in the laboratory in

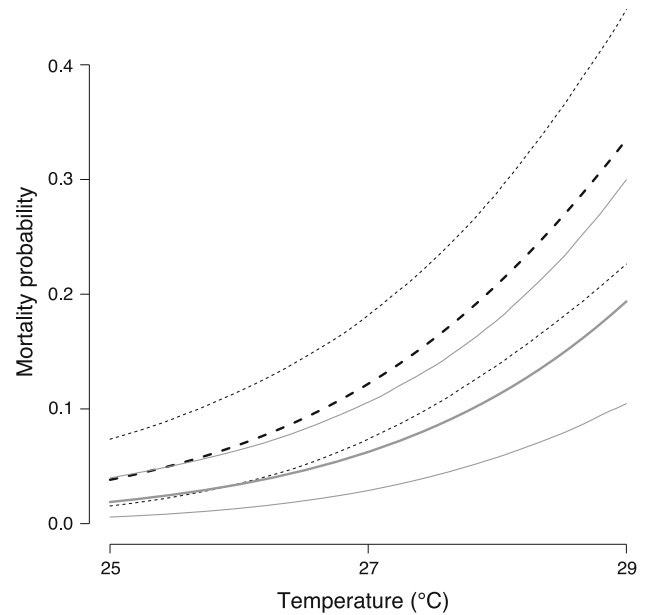


Fig. 6 Mortality cost of reproduction in female medaka at three temperatures in the laboratory. *Solid, gray lines* high food regime. *Dashed, black lines* low food regime. *Thick lines* represent mean probability and *thin lines* represent 95 % credible intervals. We do not represent the medium food regime for which the mortality probability lies in between the high and low regimes

individual tanks that the mortality rate after 25 days of reproduction in female medaka reached a maximum of 31 % at 29 °C on a “low food” regime (Fig. 5). In contrast, in the wild in Japan 100 % of both female and male die in the weeks following juvenile hatching, indicating that the cost of reproduction severely increases for both sexes under natural conditions. Egami et al. (1988) have further shown that optimal conditions in captivity can even increase the longevity of wild medaka that have already reproduced in the wild. Specifically, from 25 adults transferred from a small pond in Yamaguchi City to captivity and treated for parasites on May 21 and June 15 1985, 11 died within a week and 14 were still alive and healthy on September 18 (their wild counterparts were all dead since early July). Two of these fish were still alive in September 1986 (Egami et al. 1988). Taken together, these data demonstrate that environmental conditions in the wild severely shorten medaka longevity.

Most likely, a key longevity-setting factor for wild medaka is food availability. Hirshfield's (1980) data show that a “low food” regime ($8.86 \text{ mg Tetramin fish}^{-1} \text{ day}^{-1}$) that covers “near-maintenance” needs increases significantly the mortality rate of reproducing females compared to a “high-food” regime ($18.68 \text{ mg Tetramin fish}^{-1} \text{ day}^{-1}$, Fig. 6). This result demonstrates that, even when food intake covers maintenance requirements, a food reduction does increase mortality in reproducing medaka. At Inba-

numa, food shortage was probably much more severe than in Hirshfield's low-food regime, and adult medaka were probably unable to meet their maintenance requirements. The largest zooplankter at Inba-numa (*Moina rectirostris*, 550.0 μm average length) has a dry weight of about 1.8 micrograms (Watkins et al. 2011). Hence, almost 5000 *Moina rectirostris* are needed to amount 8.86 mg Tetramin, which represents an enormous number of prey to capture and digest daily for a medaka. Additionally, Tetramin is arguably more energetic than dry zooplankton and probably more than 5000 zooplankters are in fact needed to reach the food value of 8.86 mg Tetramin.

Comparison of trajectories for mean body length (Fig. 2a) and mean body mass (Fig. 3) suggest that adult extinction was preceded by a decrease in mean body condition and possibly also by a selective mortality of the largest individuals. Accordingly, mean adult body mass neatly decreased during the last occurrence of adults in both 1984 and 1985, while mean body length either did not decrease (1984) or showed a slight decrease (1985). Pre-extinction mass loss tended to be sharper in females than in males (Fig. 3, 1985), possibly because females invest more energy than males into reproduction and thus suffered from more severe starvation. Finally, the tight parallelism between zooplankton crash in July and massive death of adults at Inba-numa (Fig. 4) brings further support to the hypothesis that reproducing adults were facing a severe food shortage and died from starvation.

Together with limiting resources, niche overlap is the other necessary and sufficient ingredient for exploitative competition to emerge. At Inba-numa, adults and juveniles of medaka were strongly overlapping for food resources, thus setting the stage for intercohort competition. Our stomach content data show that medaka body size did influence their predation efficiency on cladocerans (preferred by large medaka), as well as on copepods and benthic prey (preferred by small medaka). However, these size-dependent preferences were not strong enough to induce a niche separation, and Schoener's indices among juveniles and adults were very high (Fig. 5). Importantly, despite substantial variation in resource availability in between late April and early July (Fig. 4), diet overlap remained high, suggesting that adults were unable to adjust to resource variation by shifting to alternative food resources. In sum, our results, showing that juvenile medaka were still thriving while their parents were starving to death are in line with the size-dependent R^* theory (Persson et al. 1998; Kooijman 2010) and with empirical data in fish (Persson and De Roos 2006) that show that R^* increases with body size.

Finally, for all of the assumptions of CDS to be fulfilled, it is also necessary for resource limitation to result from a joint consumption from adults and juveniles.

Unfortunately, a robust separation of the relative contributions of bottom-up (food limitation) and top-down (fish predation) effects on zooplankton dynamics at Inba-numa cannot be achieved by empirical data such as ours, and we here have to rely on the literature data to propose a most likely mechanism for zooplankton drop. The global knowledge on successional dynamics of plankton communities has been synthesized and formalized in the so-called Plankton Ecology Group (PEG) model, which was originally developed for lakes, reservoirs and pond ecosystems. The PEG model predicts that zooplankton abundances in summer are mainly controlled by predation from fish, especially in eutrophic water bodies such as our two sampling sites (Sommer et al. 1986, 2012). Medaka was by far the dominant fish species in irrigation ditches and at the lake shore in the sites that we sampled. Hence, based on predictions from the PEG model, we suggest that predation from medaka was probably a major driver of the summer decline in the local zooplankton abundances at Inba-numa, and we conclude that our study therefore provides good empirical evidence for CDS in wild medaka.

Cost of reproduction through energy-allocation conflicts

Although our study supports the CDS hypothesis, there is also evidence that reproductive mortality in medaka was further caused by a decreased somatic maintenance. At Inba-numa, we found an increasing parasite prevalence on adult medaka during the spawning season. This result suggests that, as often observed in animals (Zuk and Stoehr 2002; Harshman and Zera 2007; Edeline et al. 2008), the cumulated energy costs of reproduction translate into decreased immune investment in medaka. *Lernaea cyprinacea*, one of the monitored parasites on medaka, is notoriously thermophilic, and its increased prevalence was thus probably directly favoured by warming summer temperatures. However, female medaka arguably invest more energy than males in reproduction, and we indeed found a female-biased prevalence of parasites in medaka (Model 1, Table 1). This result suggests that increased prevalence of *Lernaea cyprinacea* was also caused by fish immune depression, and thus provides convincing evidence that reproduction competed with 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, 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 (*Gasterosteus aculeatus*), that subsidize egg production from body tissue (Wootton 1977, 1984).

Importantly, this suicidal strategy of energy reallocation from maintenance to reproduction under food stress is not a mechanism competing with resource competition in explaining semelparity. Instead, the two mechanisms are intertwined and give rise to a positive, food-dependent feedback in which reproduction induces intercohort competition and food stress, which in turn stimulates increased reproduction and somatic deterioration. Such a positive feedback may explain why adult medaka at Inba-numa and elsewhere in Japan disappear so abruptly in July in parallel with dropping food densities (Fig. 4). Ultimately, this mechanism of energy reallocation from maintenance to reproduction under food stress might possibly reflect a conditional, food-dependent reproductive strategy that was evolved by medaka in response to competition-induced reproductive mortality.

Thermal facilitation of medaka CDS

Apparent CDS in medaka at Inba-numa was probably favoured by high summer temperatures (May–July average of $27.6\text{ }^{\circ}\text{C} \pm 3.1\text{ SD}$), which may operate by (a) increasing the competitive asymmetry in favour of small individuals and (b) increasing energy reallocation from maintenance to reproduction.

Accordingly, 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 al. 2013; Vindenes et al. 2014) and the prevalence of CDS is thus enhanced (Ohlberger et al. 2011). In parallel, many ectotherms conform to the so-called temperature-size “rule” (Angilletta 2009), i.e., to an increased energy allocation to reproduction at the cost of reductions in both somatic growth and maintenance 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 3, Table 1; Fig. 5). Hence, high summer temperatures at Inba-numa probably also increased energy reallocation from the soma to reproduction, and thus further increased the potency of intercohort competition to cause the above-mentioned positive feedback mechanism that resulted in apparent CDS.

Generality of our results

In seasonal environments, relatively short breeding periods impose pulsed breeding, i.e., an intensive reproductive

effort associated both with a strong recruitment of juveniles, and potentially with strong intercohort competition. For instance, in seasonal environments in Europe, females of the invasive mosquito fish *Gambusia holbrooki* (adult SL range = 20.0–40.0 mm) produce multiple clutches of 15–86 embryos from May to August, a period during which recruitment of newborns is intensive and continuous (Fernandez-delgado 1989; Vargas and 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 semelparous 1+ adults (Fernandez-delgado 1989; Vargas and Sostoa 1996; Gkenas et al. 2012), and is also associated with cohort dynamics consistent with CDS (Cabral and Marques 1999).

In the threespined stickleback (adult SL range = 35.0–65.0 mm), which occurs exclusively in seasonal environments, females lay on average 93 eggs per clutch ($SD = 43$) and spawn 15–20 clutches during a 1–3 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), also suggesting CDS. Interestingly, there is a tendency for low-latitude stickleback populations to have shorter lifespans than northern populations (Baker 1994; DeFaveri and Merilä 2013), which might possibly reflect a thermal facilitation of CDS.

In contrast to seasonal environments, weakly seasonal environments allow the spread of reproductive investment across longer periods. This absence of any reproductive pulse is expected to prevent strong juvenile-adult competition and to favour increased longevity. For instance, in tropical habitats each female guppy (*Poecilia reticulata*, adult SL range = 14.0–35.0 mm) or least killifish (*Heterandria formosa*, adult SL range = 11.0–35.0 mm) gives birth to small litters of 5–20 juveniles. This occurs 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 CDS in these species.

Conclusions

Taken together, our results and the literature data provide a coherent picture of CDS as resulting from intercohort exploitative competition, but also from energy reallocation from somatic maintenance to reproduction. The two sources of reproductive mortality are tightly intertwined, because intercohort exploitative competition is expected to induce natural 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.

In evolutionary biology, semelparity is often considered to have evolved in small-sized species (*r*-strategists) due to high predation mortality on the adults, which makes individuals unlikely to reproduce more than once (Pianka 1970; Charnov and Schaffer 1973; Magnhagen 1991). It is interesting to note that small-sized, *r*-strategists are also at a higher risk of intercohort competition, because the similarity of juvenile and adult body sizes also entails a high niche overlap. 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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