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Research article

Evolving to stay the same: life history evolution and trade-offs in response to high and low total food

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Food drives ecology and evolution, but few studies have directly investigated the impacts of the total amount of food on life history evolution within-species. Among the limited number of available case studies that do directly test total food effects on life history evolution we still lack consensus, partially owing to incompletely described life histories. We explored life history trade-offs across the whole life cycle, and the consequences for trait and population dynamics, in a marine copepod evolved under high and low total food using an integral projection model (IPM). Populations were subjected to high- and low-food regimes and a common garden experiment after 30 generations of evolution. We then sampled and measured individual vital rates (growth, reproduction, and survival) from hatching until death, which were used to parameterise IPMs. Food regime had a significant but slight effect on life histories, which appeared 'slow' and 'fast' in low-food and high-food lineages, respectively. Low-food lineages grew bigger and produced larger offspring to genetically compensate for their environment, but this compensation came with costs; notably shorter lifespans and less chance of producing clutches of eggs. Despite these differences, population ecology and fitness were similar in high- and low-food lineages as anticipated by per-capita rather than total food effects. Consequently, though natural planktonic populations may genetically mitigate the effects of climate-induced food scarcity, there are limits to this compensation and likely unforeseen impacts effects for wider food webs.

Keywords: experimental evolution, food, genetic compensation, integral projection models (IPMs), life history evolution, trade-offs

Introduction

Life histories evolve as a function of when and how selection acts on the life cycle (Stearns 1992). A venerable line of theory has explored the role of food as an agent of selection in life history evolution, from classic r/K and competitive-stress tolerant-ruderal (C-S-R) life history strategies (Pianka 1970, Grime 1974) to contemporary demographic models (Parker and Begon 1986, Winemiller and Rose 1993, Day and Rowe 2002, Coulson et al. 2022). Older models such as r/K selection emphasised the

role of per-capita (or relative) food abundance in life history evolution, while the effects of total (at the population-level) food abundance have received limited theoretical attention (Grether et al. 2001, Reznick et al. 2002). This lack of theory may be due to too few case studies that show effects of total food on life history evolution and the subsequent ecological consequences – we seek to address this.

Though we have extensive macroecological evidence for life history evolution along primary productivity gradients (Huston and Wolverton 2011, Moatt et al. 2016, Marshall et al. 2018), the degree to which these patterns reflect microevolutionary processes remains unclear. For example, species in low-food environments often produce smaller offspring (Marshall et al. 2018), but when tested within-species low-food environments select for larger offspring (Allen et al. 2008). Macroecological patterns can be inconsistent – body size is often positively correlated with primary productivity across species (Huston and Wolverton 2011), but predation flips this relationship in marine copepods (Brun et al. 2016).

Short-term (plastic) effects of food on life histories have been widely reported. Individuals in food-rich conditions typically grow faster, larger, and exhibit higher fecundity than those from food-scarce environments (Berggreen et al. 1988, Lynch 1989, McCauley et al. 1996, Lindström 1999, Rinke and Vijverberg 2005, Gangur and Marshall 2020). Food restriction can reduce size-specific net energy intake, with knock-on effects such as smaller adult size and egg volumes (Lynch 1989). But such short-term responses are not necessarily indicative of, and can even obscure, longer-term life history evolution e.g. due to transgenerational plasticity (Burgess and Marshall 2014) and countergradient variation (Conover and Schultz 1995). Direct empirical tests of life history evolution under different food regimes are rare. Apart from a few canonical examples (Reznick and Travis 2019), we lack a detailed understanding of how life history traits evolve and trade-off against each other under different food regimes.

How total food levels shape life history evolution within-species has been experimentally tested in a few key study systems, but consensus is still lacking. For example, restoration ecology was used in *Daphnia* to show shifts from 'thrifty' higher growth efficiency and flatter reaction norms in ancient low phosphorus (P) environments to 'opportunistic' lower growth efficiency modern genotypes with greater plasticity to P supply (Frisch et al. 2014). High-food regimes can select for either larger (in mosquitofish) or smaller (in copepods and guppies) offspring relative to low-food regimes (Hulthén et al. 2021, Felmy et al. 2022, Blake and Marshall 2023). In copepods, egg size-fecundity trade-offs are hidden by countergradient variation, while in guppies they are not (Felmy et al. 2022). Nonetheless, there is evidence from guppies that high- and low-food environments may select for 'fast' and 'slow' life histories, respectively (Felmy et al. 2022). Theory generally describes 'fast' life histories as favouring current over future reproduction relative to 'slow' life histories. Relative to slow life histories, fast ones exhibit: faster growth, earlier maturity, more frequent litters of offspring with lower parental investment, higher mortality, and shorter lifespans

(Stearns 1992). These patterns have been widely observed across taxa (Sæther 1987, Bauwens and Diaz-Uriarte 1997, Bielby et al. 2007, Salguero-Gómez et al. 2016), and are classically attributed to extrinsic mortality and environmental stochasticity (Charnov 1991, Charlesworth 1994, Kozłowski and Weiner 1997). However, our understanding of what drives 'fast' and 'slow' life histories remains incomplete (Del Giudice 2020), and without a clear role for food. Overall, while experimental evolution studies (Hulthén et al. 2021, Felmy et al. 2022, Blake and Marshall 2023) do show life history evolution under different levels of total food – reiterating that the focus on relative (per-capita) food in classic r/K theory is insufficient – generalising remains a challenge.

The different life history responses to total food reported among experimental evolution studies may arise from taxa-specific trade-offs. Trade-offs must arise in these studies because populations evolving at carrying capacity under different total levels of food can experience similar levels of per-capita food and density dependence (Reznick et al. 2002). Consequently, life history responses to food in these systems are likely to be zero-sum – individuals with finite resources cannot simultaneously maximise all components of fitness (van Noordwijk and de Jong 1986). Understanding different trade-offs among taxa can therefore help us to make broader generalizations about life history responses to total food. To identify potential trade-offs, we can characterise the relationships between food availability and stage-specific survival and fecundity, life history traits, and ecological dynamics. Integral projection models (IPMs) provide a powerful framework to evaluate joint change in vital rates (e.g. growth, survival, and fecundity) and trait and population dynamics across different environments (Coulson et al. 2010). With IPMs, we can calculate ecological and life history descriptors such as population structure, growth rates, and generation time from phenotypic-trait-vital-rate associations. We can then use these descriptors to evaluate the consequences of food regime, including life history trade-offs (Travis et al. 2014). Unlike common depictions of simple spectra (such as r/K), life history trade-offs along food gradients can be complex and non-uniform (Felmy et al. 2022). IPMs can also identify such nuances, for example by perturbing trait values and evaluating which life history components show the highest sensitivities of fitness (Coulson et al. 2022). Using these tools, we dig deeper into previous work in copepods (Blake and Marshall 2023) to obtain a fuller picture of life history trade-offs under different food regimes across the whole life cycle.

Marine copepods play a critical role in marine communities and the ocean carbon pump (Turner 2015). They comprise the major (> 75%) component of zooplankton biomass, facilitating the flow of nutrients and energy through ocean food chains as a vital source of food for consumers (Conover and Huntley 1991, Pakhomov et al. 2002). Ocean primary productivity is expected to decline as a result of climate change (Fu et al. 2016). Warming increases upper ocean stratification, impacting nutrient fluxes and light availability for photosynthesis (Hannon et al. 2001). The effects of stratification are compounded as higher temperatures select

for smaller phytoplankton cell size, which yield a lower total biovolume relative to larger cells at a given nutrient flux (Malerba et al. 2018). And higher temperatures reduce the efficiency of energy transfer from phytoplankton to copepod grazers (Barneche et al. 2021). As model organisms, marine copepods have been used in previous experimental evolution studies (Kelly et al. 2012, Blake and Marshall 2023), but the indirect effects of changing food regimes, for example due to climate change, have remained largely unexplored. Copepods are highly suitable for parameterising IPMs due to their short life cycles (for measuring lifetime reproductive output) and established protocols for vital-rate measurement (Coulson 2012). In this study we built on work by Blake and Marshall (2023) and evaluated how the total amount of food influenced life history evolution in a marine copepod. We did so by investigating the joint life history and ecological effects of food regime, including trade-offs, using IPMs and an experimental evolution approach. We found slight but significant divergence in life histories after approximately 30 generations of evolution under high- and low-food regimes, resulting in 'faster' and 'slower' ecotypes, respectively, but little difference in fitness or population ecology. In doing so we lay the groundwork for future experimentation to ascertain exact mechanisms driving these changes, such as competitive interactions.

Material and methods

Study system

Tisbe sp. is a littoral marine copepod from the Tisbidae family (Arthropoda: Harpacticoida) that has not been resolved to species level in the Southern Ocean (McKinnon pers. comm.). Our laboratory cultures were originally sampled in 2017 from wild populations in Port Phillip Bay, Victoria, Australia, and have been reared on a marine microalga *Dunaliella tertiolecta*.

In a previous study, we subjected populations of *Tisbe* sp. to experimental evolution under high and low levels of total food for approximately 30 generations (Blake and Marshall 2023). Mothers from these populations (G0) were sampled to initiate a common garden experiment. Common gardening was conducted at an intermediate level of food for two generations (G1–2) to disentangle evolutionary responses to food from developmental and cross-generational plastic effects of food. Copepods are translucent and *Tisbe* sp. externally brood their eggs, which remain on the mother until they hatch and the larval offspring are born, permitting easy measurement of reproductive traits.

Copepods were reared in cohorts of approximately 25 and life histories were primarily measured at maturity, rather than throughout the whole life cycle. In this study, we continued this work using G3 individuals (section 'Summary of experimental evolution and common gardens (G0–2)'), rearing copepods individually through development then in breeding pairs after maturity, collecting more granular

vital rate data from hatching until death to parameterise IPMs (section 'G3 vital rate measurements'). The relationship between the two studies is illustrated in Supporting information. Of note was that population densities at equilibrium were estimated at approximately 5000 copepods in low-food lineages and 20 000 copepods in high-food lineages (Blake and Marshall 2023). But while we suspected that densities were likely a driver of evolution, we did not attempt to disentangle the effects of density and food concentration in the present study – we address this further in the discussion.

Summary of experimental evolution and common gardens (G0–2)

Here we summarise the experimental evolution and common garden experiments that were performed prior to collecting individual vital rates. Detailed methods for experimental evolution and common gardening (G0–2) are provided by Blake and Marshall (2023).

Experimental evolution commenced on 13 October 2018. Ancestral stocks were divided between two treatments – high-food and low-food environments – differing in their rate of food supply (of *D. tertiolecta* cells) by an order of magnitude. Food dosing was semicontinuous and automated every 2 h on weekdays using peristaltic pumps, with high-food treatments receiving approximately 4.5×10^9 algae cells per litre of culture per week and low-food treatments receiving approximately 4.5×10^8 algae cells per litre of culture per week. Laboratory temperature was set at 21°C with a light:dark photoperiod of 12:12 h, and salinity was maintained at 37 ppt with monthly monitoring. In total, 20 copepod cultures were subjected to experimental evolution, consisting of 10 high-food and 10 low-food lineages reared in 1-l glass pressure equalising dropping funnels, in five feeding blocks of two high-food and two low-food cultures. However, one low-food lineage went extinct in October 2019 due to bacterial contamination.

To eliminate plastic responses to experimental food treatments, individuals were sampled from the high- and low-food lineages and reared in a common environment (or 'common garden') over multiple generations. Copepods were sampled from evolutionary cultures (G0) and their descendants were reared under intermediate conditions over two generations (G1 and G2) to eliminate cross-generational effects on phenotypes (Burgess and Marshall 2014). With an estimated generation time of 17 days, our *Tisbe* sp. cultures had undergone approximately 30 generations of evolution prior to common gardening, which commenced on 18 February 2020. G1 copepods and their G2 offspring were reared (separately) in cohorts of 20–30 individuals and provisioned an intermediate food supply of approximately 2.475×10^9 *D. tertiolecta* cells per litre per week. Cohorts were reared in sterile plastic culture trays containing 4 ml freshly pasteurised sea water (FSW) with the same temperature and photoperiod as evolutionary cultures. Salinity was maintained at 37 ppt by initially weighing culture trays and then weighing twice a week to restore mass lost to evaporation with reverse osmosis

water. Vital rate data collection commenced once G2 individuals began producing G3 larvae in March 2020.

G3 vital rate measurements

G3 larvae were collected opportunistically, between 27 March and 19 May 2020, from 4–10 G2 mothers per lineage. Mothers from different lineages had been kept separate from G0–G2. This approach was required as variation in development time between lineages across two generations of common gardening resulted in staggered production of G3 larvae. Variation in reproductive output during common gardening also resulted in a scarcity of G2 mothers in some lineages. Larvae were collected from first clutches only, and 2–4 larvae were collected per clutch depending on the availability of G2 mothers. In total we collected at least 20 individual larvae per lineage, with excess larvae collected in some lineages for redundancy where the expected number of G2 mothers was initially uncertain.

Throughout the experiment, individual copepods were fed every two days based on the per-capita food provisioning experienced by their G1 and G2 ancestors in intermediate-food environments. Since it was impractical to rear adult copepods in sub-1 ml volumes, this resulted in different cell provisioning per litre of copepod culture per week from G1–2 to G3, but constant per-capita feeding at approximately 495 000 cells per copepod per week (Table 1). We erred on the upper range of food supply to maximise survival to maturity and ensure acceptable replication of reproduction data.

Gravid G2 mothers were moved from their cohorts to sterile plastic culture trays with 4 ml FSW and food. Eggs were checked daily until they had hatched. G3 larvae were then collected when 0–24 h old and pipetted into separate wells in a sterile 96 well plastic culture tray with 280 μl FSW and food. At metamorphosis (generally 1–3 days after hatching) juveniles were transferred to separate wells in a new sterile 24 well plate plastic culture tray with 2 ml FSW and food. Adulthood was determined by counting moults, with five moults between the first juvenile stage and the adult stage (Gangur and Marshall 2020). Sex was then determined morphologically, and adult males and females (within the same lineage) were randomly paired and transferred to new wells in a sterile 24 well plate plastic culture tray with 2 ml FSW and food. Where the sex ratio was skewed in favour of females, mature males were randomly selected and allocated to the oldest unmated mature female until mating or eggs were observed. Males were then continuously cycled to non-gravid females with the longest time since their last clutch. Copepods can also store sperm (Hutchinson et al. 1999), which we have observed in *Tisbe* sp., and as such we assumed that females were not sperm limited. The experiment was conducted at the same temperature and with the same photoperiod as experimental evolution and common gardens (21°C with a light:dark photoperiod of 12:00:12:00 h). The larval and juvenile stages were sufficiently short that we assumed salinity remained close to 37 ppt with lids on the culture trays to minimize evaporation, while adults were moved to new culture trays with FSW at 37 ppt salinity each week.

To measure vital rates (growth, survival and reproduction) of our G3 individuals, copepods were checked every day from hatching to death until the final copepod died. The experiment ended on 21 July 2020. For growth, size data at hatching and metamorphosis (in addition to adulthood) were collected from 10 randomly selected individuals per lineage. Length measurements were collected from photographs taken at $t0$ (within 24 h of hatching), at metamorphosis, and at death (whether before or after reaching adulthood). For reproduction, gravid females and their eggs were photographed (within 24 h of developing eggs) and then transferred to separate wells in sterile 24 well plate culture trays with 2 ml FSW and food. Gravid females were checked daily until their eggs had hatched, at which point they were immediately returned to their original wells with their mates. G4 larvae in each well were euthanised with 100 μl of 40% formaldehyde solution (Sigma-Aldrich) and photographed for counting to obtain the lifetime reproductive output of each female. Size at $t0$ and gravid mothers (to obtain egg size) were photographed using a Motic Moticam 1080 camera mounted on an Olympus SZ61 dissecting microscope. Size at metamorphosis, size at death, and euthanised offspring were photographed using an Olympus IX73 inverted compound microscope system. Measurements and counts were taken digitally using FIJI ver. 1.53c (Schindelin et al. 2012).

Integral projection models

To explore how life history evolution in response to differential food regime affected asymptotic population growth

Table 1. Summary of culture volumes, food quantities (in algae cells per litre per week), and group sizes from G0 (evolutionary lines), through G1–2 (common gardens), to G3 (present study). Food quantity and group size in G0 are specified as low-food treatments/high-food treatments. G1 and G2 food quantities were equivalent to the average (intermediate) ambient food density experienced by G0 copepods. Per-capita food was kept the same between G1–2 and G3 copepods.

Generation	Culture volume (ml)	Food quantity (algae cells per litre per week)	Group size
G0	1000	$4.5 \times 10^8 / 4.5 \times 10^9$	~5000/~20 000
G1	4	2.475×10^9	20–30
G2	4	2.475×10^9	20–30
G3			
Larvae	0.28	2.475×10^8 (once only)	1
Juveniles	2	2.475×10^8	1
Adults	2	4.950×10^8	2 (mating pairs)

rate (λ), we developed single-sex (female-only) deterministic IPMs parameterised with our experimental data. We did not include density-dependence in our models as per-capita food was held relatively constant throughout the common garden experiment. Consequently, there was little variance in per-capita food availability at the lineage level, and we were unable to characterise density dependence. Measuring λ allowed us to verify that our models had correctly described our study system. Our copepods had persisted in both low and high food environments for approximately 18 months fluctuating around carrying capacity – approximately 30 generations, with a 17 day generation time (Blake and Marshall 2023). Consequently, there was no expected trend in population sizes over the course of the study, but densities will have fluctuated day-to-day. Thus, the long-run stochastic growth rates would have been 0 (no temporal trend in population density), but our estimate of λ from a deterministic average matrix is expected to be a little greater than 1, simply because the long-run stochastic growth rate is a geometric mean while λ is the growth rate from a matrix based on arithmetic mean rates. Therefore, we predicted that λ should be close to, but slightly higher than, 1.

Following the approach by Ellner and Rees (2006), we two constructed separate size- and age-structured IPMs, one for females for high- and one for females in low-food lineages. Each IPM was of the form:

$$N_0\left(z',t+1\right)=\sum_a^M \int_L^U F_a\left(z',z\right)N_a\left(z,t\right)dz, \qquad (1a)$$

$$N_a\left(z',t+1\right)=\int_L^U P_{a-1}\left(z',z\right)N_{a-1}\left(z,t\right)dz \qquad (1b)$$

where $N_a(z', t+1)$ is the distribution of size z for age a individuals in time-step $t+1$; $F_a(z', z)$ is the fecundity kernel; $P_{a-1}(z', z)$ is the survival-growth kernel; M is the maximum age; and U and L are the maximum and minimum possible values of z (size), respectively. Equation 1a represents production of new recruits, and Eq. 1b represents individuals of size z living to age a and growing to new size z'.

The fecundity and growth-survival kernels F and P can be further decomposed into functions of growth (g), survival (s), reproduction (f and b), and inheritance (d):

$$F_a\left(z',z\right)=f\left(z,a\right)b\left(z,a\right)d\left(z',z\right)s\left(z,a\right)\times 0.5 \qquad (2)$$

$$P_a\left(z',z\right)=g\left(z',z\right)s\left(z,a\right) \qquad (3)$$

The full models for the individual vital rate functions are: $f(z, a)$ is the probability of producing a viable clutch of eggs, and is the product of the probabilities of clutch production, $f_c(z, a)$; and of those eggs yielding offspring – henceforth 'offspring production', $f_v(z, a)$ for a mother of size z and age a

that survives time-step t. $b(z, a)$ is the mean number of offspring produced by reproducing mothers of size z and age a that survive time-step t. $d(z', z)$ is the conditional Gaussian size distribution of eggs at age 0 (just before hatching) produced by a mother of size z and age a, modelled with constant variance σ_d^2. We used egg size rather than larvae size at age 0 as we found in a pilot study that they are highly correlated, and because *Tisbe* sp. larvae rapidly moult through the initial larval stages within hours of hatching, making them impractical to measure. $s(z, a)$ is the probability an individual of size z and age a survives time-step t. And $g(z', z)$ is the conditional Gaussian probability density function governing transitions from size z at age a to size z' for survivors of time-step t, modelled with constant variance σ_g^2.

Our models were parameterised with vital rate models fitted to daily data and were iterated on a daily time-step. As we performed post-reproductive censuses of our copepods, mothers in our model must survive to reproduce. Accordingly, $s(z, a)$ was included in both the reproduction and growth-survival kernels as both growth and reproduction are conditional on survival (Ellner et al. 2016). The fecundity kernel $F_a(z', z)$ was multiplied by 0.5 as we only considered females and assumed an equal sex ratio. We also assumed no brood-time for viable eggs, to simplify model structure, as accounting for brood time would only have a minor effect on reducing the asymptotic growth rate λ (Supporting information). IPM and vital rate functions and parameters are summarised in Table 2.

We implemented our IPMs by discretising the distribution of size z individuals at age a N_a using the midpoint rule, approximating the per-time-step dynamics with an age- and size-structured matrix (Ellner et al. 2016). Copepod size was split into 100 classes that ranged from 0 to 1 mm, and copepod age ranged from 0 to 80 days in increments of 1 day. Model projections were checked to ensure there were no evictions from the model (Williams et al. 2012). Asymptotic population growth rate (λ) was calculated using the dominant right eigenvectors from our IPMs at equilibrium – once the models had reached stable population structure and population growth.

Parameterising the vital rate functions with experimental data

All vital rate functions were fitted using mixed effects models, except for growth which was determined after fitting data to a Gompertz growth curve. Analyses were performed with R ver. 4.1.2 (www.r-project.org) and RStudio ver. 2021.09.1 (RStudio Team 2021), using 'dplyr' (Wickham et al. 2021) to prepare the data. Linear mixed effect models were fitted with 'lme4' (Bates et al. 2015). The 'lmerTest' package (Kuznetsova et al. 2017) was used to perform post-hoc tests and likelihood ratio tests on random effects in order to find the single best model for each vital rate. Akaike information criterion (AIC) tables were obtained with the 'MuMIn' package (Barton 2022), and mixed effect model diagnostics were visually assessed using 'DHARMa' (Hartig 2022). Figures

Table 2. Summary of IPM and vital rate functions and parameters used to construct high- and low-food integral projection models (IPMs). Function parameters refer to the full functions – after parameter fitting via model selection, some functions were dropped ().

Parameter	Description
Z	Size at time-step t
z'	Size at time-step $t+1$
a	Age at time-step t
M	Maximum age
U/L	Maximum and minimum possible values for size (z), respectively
Function	**Description**
$N_0(z', t+1)$	IPM function for individuals of size z producing new recruits of size z' and age 0 (Eq. 1a)
$N_a(z', t+1)$	IPM function for individuals of size z producing growing to size z' and age a (Eq. 1b)
$F_a(z', z)$	Fecundity-survival kernel (Eq. 2)
$P_a(z', z)$	Growth-survival kernel (Eq. 3)
$f(z, a)$	Probability of an individual of size z and age a producing a a viable clutch of eggs (Eq. 2). Product of f_e and f_v
$f_e(z, a)$	Probability of clutch production, empirically derived from daily presence/absence of eggs in mature female copepods
$f_v(z, a)$	Probability of a clutch of eggs yielding offspring, empirically derived from clutch success/failure
$b(z, a)$	Mean number of offspring produced by reproducing mothers of size z and age a that survive time-step t (Eq. 2). Empirically derived from measurements of mother size and age and offspring counts per clutch
$d(z', z)$	Conditional Gaussian size distribution of eggs at age 0 (just before hatching) produced by a mother of size z and age a (Eq. 2). Empirically derived from photographs of egg sacs prior to hatching
$s(z, a)$	Probability an individual of size z and age a survives time-step t (Eq. 2, 3). Empirically derived from daily counts of live and dead individuals
$g(z', z)$	Conditional Gaussian probability density function governing transitions from size z at age a to size z' for survivors of time-step t (Eq. 3). Derived from Gompertz functions fitted to size measurements on individual copepods at hatching, metamorphosis, and maturity

were made using 'ggplot2' (Wickham 2016). Diagnostic residuals versus predicted values and QQ plots were visually assessed as per Quinn and Keough (2002).

Growth curve interpolation

To model growth (g) – size at time $t+1(z')$ as a function of size at time $t(z)$ – we required individual size at each time-step (day). We did so by fitting growth curves to copepod size data collected at key points in the life cycle (hatching, metamorphosis, adulthood), and interpolating these growth curves to obtain estimates of size at each age (time-step) for each copepod, from hatching to the maximum age in the model (80 days). The growth function (g) was derived with exact fits of log z' (size at time $t + 1$) as a linear function of log z (size at time t) at the population level for each of the two food-level treatments.

Gompertz models have been previously used to model growth in crustaceans (Piscart et al. 2003), and pilot work suggested that a Gompertz curve was better suited to *Tisbe* sp. than a von Bertalanffy curve owing to their determinate growth, with growth stopping at maturity or approximately 17 days (Maszczyk and Brzezinski 2018). As such, copepod size and age data collected from a subset of individuals with measurements at hatching, metamorphosis, and adulthood ($n_{high\text{-}food} = 19$, $n_{low\text{-}food} = 24$) were fitted to a Ricker parameterisation of the Gompertz model (Tjørve and Tjørve 2017). Gompertz models were fitted using non-linear least squares parameter estimation with the nls() function:

$$W(t) = W_0 e^{m\left(1-e^{-kGt}\right)} \tag{4a}$$

$$A = W_0 e^{m} \tag{4b}$$

where $W(t)$ is size at time t, W_0 is size at hatching, k_G is a growth parameter, and m is a scale parameter related to the upper asymptote of the growth curve A (size at adulthood in determinate growers) by Eq. 4b. Using values for W_0, $W(t)$ at metamorphosis, and A from individuals that lived to adulthood, we obtained population level estimates of k_G, W_0, and A for high- and low-food treatments (Supporting information). As the data were too sparse to include a random effects structure based on individual ID, the total number of data points was 57 for high-food and 72 for low-food.

Other vital rate functions

Following standard IPM conventions (Coulson 2012), vital rate functions were fitted using mixed effects models, and model reduction was performed based on AIC for all subsets of the full models. As we sought to use the single best model rather than model averaging, when the best-fit model for each function was not also the simplest (fewest terms) it was compared to the simplest model that had ΔAIC of less than two using post-hoc likelihood tests for final model selection.

Model sets and random effects

As per Coulson (2012), inheritance was fitted using a linear mixed effects model; probability of survival, probability of clutch production, and probability of offspring production were fitted using binomial generalised linear mixed effects models; and clutch size was modelled using a Poisson generalised linear mixed effects model. All models included individual copepod ID as a random effect with random intercepts only, as the data were too sparse to support more complex

random effects structures. All full models included body size, age, and age^2 as fixed effect terms. Food regime (treatment) was also included as a fixed effect term in all models, as well as its interactions with size and age. The interaction between size and age was only included in the full models for the probability of offspring production, clutch size, and inheritance where they exhibited a bivariate normal distribution. Model sets used for model selection included all subsets of the full models. Following Coulson (2012), variance was modelled for growth and inheritance only, and was obtained by fitting linear models to the squared residuals extracted from the nonlinear least-squares models (for growth) or mixed model (for inheritance).

Post-hoc analyses

Life table response experiments (LTREs) were performed following Ellner et al. (2016) to evaluate how each vital rate parameter contributed to differences in asymptotic population growth rate (λ) between high- and low-food IPMs. Variation in λ was approximated as a function of vital rate parameters using a first-order Taylor series:

$$\text{Var}(\lambda) \approx \sum_{i=1}^{n} \sum_{j=1}^{n} \text{Cov}(\theta_i \theta_j) s_i s_j \qquad (5)$$

where i and j indicate the ith and jth parameters from the high- and low-food IPMs, respectively, θ is the parameter vector, and s is the eigenvalue sensitivity $\partial\lambda/\partial\theta_i$ in the mean kernel. Eigenvalue sensitivities were estimated using finite differences. The relative contribution of each parameter to Var(λ) was then indicated by the sign and magnitude of its Taylor coefficient.

We also obtained survivorship and fertility schedules, from which we obtained estimates for generation time following Steiner et al. (2014). Survivorship schedules were obtained by initiating a new cohort of age 0 offspring from the IPM stable distributions and iterating them until extinction to obtain survival to each age. Fertility schedules were obtained by normalising the IPM stable size distribution at each age to evaluate reproduction at each age by the average individual. Using survivorship and fertility schedules we then obtained the mean age of reproduction T_c:

$$T_c = \sum_a a\varphi_a \qquad (6a)$$

$$\varphi_a = \frac{f_a l_a}{R_0} \qquad (6b)$$

$$R_0 = \sum_a l_a f_a \qquad (6c)$$

where φ_a is the fraction of total reproduction at age a produced by a stable cohort with survivorship l_a and fertility f_a and net reproductive rate R_0.

Results

Vital rate functions

We observed slight but significant systemic differences between high- and low-food lineages across multiple vital rates. Growth, clutch size, probability of clutch production, and egg size (inheritance) all evolved in response to food regime with treatment effects retained in the final models, consistent with prior work in *Tisbe* sp. (Blake and Marshall 2023). Vital rate models and sample sizes (pooled within food regimes for growth, and at the subject/individual copepod level for other models) are presented in Fig. 1 following standard IPM convention (Coulson 2012). Final models and parameter values used in IPMs are presented in Table 3, and the Supporting information contains tables from the model selection process.

Growth (*g*)

Growth rates evolved in response to food regime, resulting in different parameterisations of Gompertz growth models. As such the final models were of the form: $g \sim z$, with separate models fitted for each treatment. Copepods from high-food lineages grew slightly faster relative to low-food lineages when young, but copepods from low-food lineages matured at a later age and larger size (Fig. 1a). However, there was considerable individual variation around the population-level growth functions. Figures for log size$_{t+1}$ as a function of log size$_t$ for each food regime are provided in the Supporting information.

Survival (*s*)

Survival was influenced by age and size, but not food regime, resulting in the final model: $s \sim z + a + a^2$. Copepod survival declined with age. But the impact of senescence on survival was offset by size such that, at any given age, larger individuals were more likely to survive to the next day (Fig. 1b, Supporting information).

Reproduction (*f*)

Food regime and maternal size and age dictated the probability of producing a clutch of eggs, as well as the interaction of food regime and age, yielding the final model: $f_e \sim z + \text{treatment} \times (a + a^2)$. Larger mothers were always more likely to brood eggs. The probability of clutch production increased with age to a peak at 28.3 days old in low-food lineages (Fig. 1c) and 23.4 days old in high-food lineages (Fig. 1d), after which senescence caused the probability of clutch production to rapidly decline (Supporting information). Once a clutch of eggs was produced, they were more likely to fail for larger mothers (Fig. 1e, Supporting information), with the final model: $f_v \sim z$.

Clutch size (*b*)

Clutch size evolved in response to food regime, as well as maternal age and the interaction of food regime and age, yielding the final model: $b \sim \text{treatment} \times a + a^2$. In general,
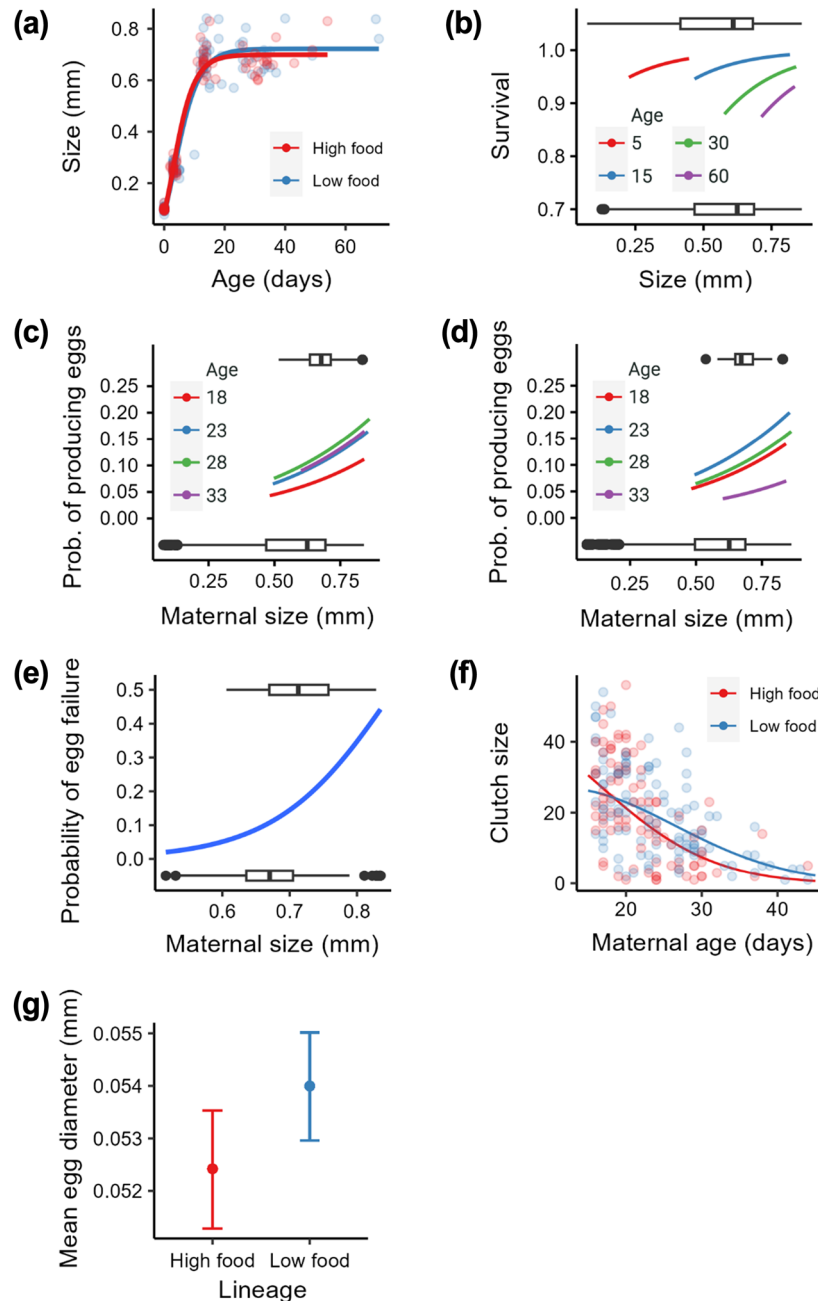
Figure 1. Vital rate models for growth (a), survival (b), probability of egg production in low (c) and high (d) food lineages, probability of offspring production (as egg failure) (e), clutch size (f), and inheritance (g). In panels for growth, clutch size, and egg size, high-food and low-food lineages are represented by red and blue, respectively. Raw data are shown as points in panels for growth and clutch size, and as box-and-whisker plots (across all ages) in panels for survival, probability of egg production, and probability of offspring production (egg failure). Box-and-whisker plots indicate distribution of successes (upper box) and failures (lower box). (a) Non-linear least square curves of copepod size (length in millimetres) at age t (days) with data pooled within each food-regime ($n_{high-food} = 57$, $n_{low-food} = 72$). (b) Probability of copepod survival to next time-step (day) $t+1$ as a function of size in millimetres ($n_{high-food} = 95$, $n_{low-food} = 110$), shown at four ages (5 days old in red; 15 days old in blue; 30 days old in green; 60 days old in purple). (c, d) Probability of clutch production, conditional on survival, as a function of maternal size in millimetres in low-food (c) and high-food (d) regimes ($n_{high-food} = 63$, $n_{low-food} = 61$). We show four different ages (18 days in red, 23 days in blue, 28 days in green, 33 days in purple) to illustrate the parabolic relationship with age–peak clutch production occurs at 23.4 days old in high-food lineages and 28.3 days old in low-food lineages. (e) Probability of offspring production (as egg failure) as a function of maternal size in millimetres ($n_{high-food} = 46$, $n_{low-food} = 44$). Eggs were more likely to fail for larger mothers. (f) Mean clutch size as a function of maternal age in high-food (red) and low-food (blue) lineages ($n_{high-food} = 40$, $n_{low-food} = 41$). Clutch size is larger in low-food lineages after 18.4 days. (g) Inheritance based on mean egg size in high-food (red) and low-food (blue) lineages ($n_{high-food} = 37$, $n_{low-food} = 49$). Error bars show bootstrapped 95% confidence intervals.

Table 3. Parameter estimates for vital rate functions for the final integral projection models (IPMs) and their standard errors. Treatment was coded as a factor (1 = low food, 0 = high food). Intercept (σ^2) specifies the variance around the growth and inheritance functions as a constant. All models included individual copepod ID (subject) as a random effect with random intercepts only, as the data were too sparse to support more complex random effect structures.

Functions/Parameters	High-food IPM		Low-food IPM	
	Value	SE	Value	SE
Growth – $g(z', z)$				
Intercept (log)	-3.67×10^{-2}		-2.76×10^{-2}	
Size$_t$ (log)	7.65×10^{-1}		8.05×10^{-1}	
Intercept (σ^2)	5.76×10^{-3}	9.94×10^{-4}	1.01×10^{-2}	1.71×10^{-3}
Survival – $s(z, a)$				
Intercept	2.49	2.37×10^{-1}	2.49	2.37×10^{-1}
Size	5.48	8.70×10^{-1}	5.48	8.70×10^{-1}
Age	-1.70×10^{-1}	2.55×10^{-2}	-1.70×10^{-1}	2.55×10^{-2}
Age^2	1.60×10^{-3}	3.32×10^{-4}	1.60×10^{-3}	3.32×10^{-4}
Probability of reproducing – $f(z, a)$				
Probability of clutch production – $f_e(z, a)$				
Intercept	-10.93	1.26	-10.93	1.26
Treatment			2.88	1.32
Size	2.87	1.15	2.87	1.15
Age	6.04×10^{-1}	1.05×10^{-1}	6.04×10^{-1}	1.05×10^{-1}
Age^2	-1.29×10^{-2}	2.32×10^{-3}	-1.29×10^{-2}	2.32×10^{-3}
Age:Treatment			-3.14×10^{-1}	1.16×10^{-1}
Age^2:Treatment			7.77×10^{-3}	2.50×10^{-3}
Probability eggs produce offspring – $f_v(a)$				
Intercept	-13.05	5.07	-13.05	5.07
Size	15.54	7.31	15.54	7.31
Clutch size – $b(a)$				
Intercept	3.84	3.17×10^{-1}	3.84	3.17×10^{-1}
Treatment			-8.34×10^{-1}	2.22×10^{-1}
Age	5.27×10^{-3}	2.56×10^{-2}	5.27×10^{-3}	2.56×10^{-2}
Age^2	-2.21×10^{-3}	5.35×10^{-4}	-2.21×10^{-3}	5.35×10^{-4}
Age:Treatment			4.54×10^{-2}	9.09×10^{-3}
Inheritance – d				
Intercept	5.24×10^{-2}	5.80×10^{-4}	5.24×10^{-2}	5.80×10^{-4}
Treatment			1.58×10^{-3}	7.86×10^{-4}
Intercept (σ^2)	2.61×10^{-5}	4.03×10^{-4}	2.61×10^{-5}	4.03×10^{-4}

older mothers produced fewer eggs per clutch. Mothers from high-food lineages produced larger clutches when young (< 18.4 days old) relative to mothers from low-food lineages, while older (> 18.4 days old) mothers from low-food lineages produced larger clutches relative to those from high-food lineages (Fig. 1f, Supporting information). Clutch size was essentially 0 beyond 42.9 days old in high-food lineages and 50.1 days old in low-food lineages.

Inheritance (*d*)
We found that egg size evolved in response to food regime but was unaffected by either maternal size or age. As such the final model was: *d* ~ treatment. Mothers from low-food lineages produced slightly larger eggs than mothers from high-food lineages (Fig. 1g, Supporting information).

IPM model analysis
We found that asymptotic population growth rate (λ) was slightly above one in both lineages, and only slightly higher in the high-food IPM relative to the low-food IPM. The difference in λ between the two food regimes was mainly driven by the probability of clutch production and by clutch size to a lesser extent (Table 4). Separate sensitivity analyses were also performed on the high- and low-food regime models (Supporting information). Copepods from low-food lineages were slightly less likely to survive to any given age, but reached peak reproduction at a slightly older age, relative to high-food lineages (Fig. 2). Copepods from low-food lineages also exhibited slightly later estimates for generation time, and lower net reproductive rates (Table 4). We found only subtle differences in stable size and age distributions, and reproductive values, between the high- and low-food regimes (Supporting information).

Discussion

We combined experimental evolution with formal demographic models to identify life history trade-offs under different food regimes, and how life history evolution affected population-level ecological parameters. Total food levels shaped copepod vital rates, causing slight divergence in life histories between high- and low-food regimes. We found that total food drove differences in growth, probability of clutch

Table 4. Integral projection model (IPM) analyses, showing asymptotic population growth rate (λ) for high- and low-food IPMs, life table response experiment (LTRE) results, and results from survivorship and fertility schedules (net reproductive rate and estimated generation time). LTRE values are coefficients for the first-order Taylor series estimating var(λ) between the two food regimes, where the magnitude of the coefficient indicates relative importance, and the sign of the coefficient, indicates positive or negative covariance with $\lambda_{high-food}$ relative to $\lambda_{low-food}$. LTRE results are ordered from most positive to most negative with vital rate functions specified first and parameter second in parentheses.

Model analysis output	Value
Asymptotic population growth rate (λ)	
High-food IPM	1.120
Low-food IPM	1.102
LTRE Taylor coefficients	
Probability of clutch production (Treatment:Age)	17.70
Clutch size (Treatment)	3.17
log size$_{t+1}$ (Slope)	1.01
σ^2 log size$_{t+1}$ (Slope)	0.40
Egg size (Treatment)	−0.05
log size$_{t+1}$ (Intercept)	−0.42
Clutch size (Treatment:Age)	−2.77
Probability of clutch production (Treatment:Age^2)	−7.79
Probability of clutch production (Treatment)	−10.26
Net reproductive rate (R_0)	
High-food IPM	7.37
Low-food IPM	5.80
Estimated generation time (days)	
High-food IPM	19.15
Low-food IPM	20.22

production (interacting with maternal age), clutch size (also interacting with age), and egg size. Consequently, based on post-hoc analyses of IPMs, copepods from high-food lineages grew slightly faster to a smaller adult size, reached peak egg production younger, and produced smaller eggs relative to low-food lineages. Relative to low-food, high-food lineages also had a slightly shorter generation time and were longer-lived. Despite these phenotypic responses to total food, we found little difference between food regimes in population-level ecological parameters. Differences in asymptotic population growth rates (λ) and stable age and size distributions were slight, suggesting that high- and low-food lineages performed similarly in a common environment. We found mixed agreement with previous studies: we identified that the likelihood of a clutch trades-off against the early adulthood performance previously reported in low-food lineages, but overall life history responses were muted compared to prior work in *Tisbe* (Blake and Marshall 2023). And while we found that life history changes broadly fell along the fast-slow spectrum, longevity did not evolve in the direction anticipated by theory (Del Giudice 2020). But unsurprisingly λ was slightly above one in both treatments, suggesting that despite our unexpected results, our models likely predicted the behaviour of our study system well.

We found that high and low food levels elicited phenotypic responses resembling 'fast' and 'slow' life histories,

respectively. Divergent patterns of growth, fecundity, clutch production, and offspring size in the different food treatments were consistent with predictions on the fast-slow continuum (Stearns 1992). However, we also found that survivorship and longevity (based on post-hoc analyses) were lower in the 'slow' low-food lineages than the 'fast' high-food lineages. Classic models of fast-slow life histories based on extrinsic mortality typically predict that the opposite should occur (Del Giudice 2020), though with some notable empirical exceptions (Reznick et al. 2004, Chen and Maklakov 2012). But the disagreement between our results and expectations may simply be an artefact of definitions. A number of life history measures can be used to identify 'fast' and 'slow' strategies including lifespan and time to maturity (Araya-Ajoy et al. 2018); generation time – which we used in our study – is another (Gaillard et al. 2005). By doing so we were able to examine how survivorship (l_a), fertility (f_a), and net reproductive rate (R_0) each contributed to the placement of high- and low-food lineages on the fast-slow spectrum. With this framework it was evident that low-food lineages were paradoxically classified as 'slow' despite lower survivorship across the life cycle. Instead, delayed reproduction drove an increase in generation length and a slowing of the life history. In other words, the components of generation time help to highlight that the co-occurrence of shorter lifespan and delayed maturity in low-food lineages was of greater relevance than the classification as 'slow' as such.

Characterising high- and low-food lineages as 'fast' and 'slow, respectively, our findings contradict expected 'fast' and 'slow' patterns of maturation and longevity from both theory and empirical evidence (Del Giudice 2020). However, 'non-classical' models as well as other empirical exceptions to classical predictions, offer possible explanations for the patterns we observed. First, an apparent lack of trade-offs between current and future reproduction (in our study, for the 'fast' high-food lineages) has been previously reported in *Daphnia*, and can arise due to costs associated with acquisition that can only be sustained at higher resource levels (Reznick et al. 2000). Such a scenario could be tested for using reciprocal transplant experiments, where we would expect that high-food lineages should underperform relative to low-food lineages in a low-food environment. Alternatively, adult size and early reproduction may trade-off independently of longevity, mediated by the benefits of larger size at sexual maturity for adults against the costs of delayed maturity for juveniles (Coulson et al. 2022). That is, delayed reproduction in low-food lineages may have some mitigating effect such that fitness would have been lower if maturation happened earlier at the expense of adult size or condition. Such an effect could be a consequence of genetic drift (Lynch 2007), or nutritional constraints. Indeed, mothers in low-food environments may be constrained by lower rates of fatty acid synthesis – reserves of fatty acids have been shown to be essential for reproduction in conspecifics (Norsker and Støttrup 1994, Arndt and Sommer 2014). Work in *Drosophila* evolved under different levels of total larval food also suggests that life history correlates of starvation resistance (such as larger adult mass
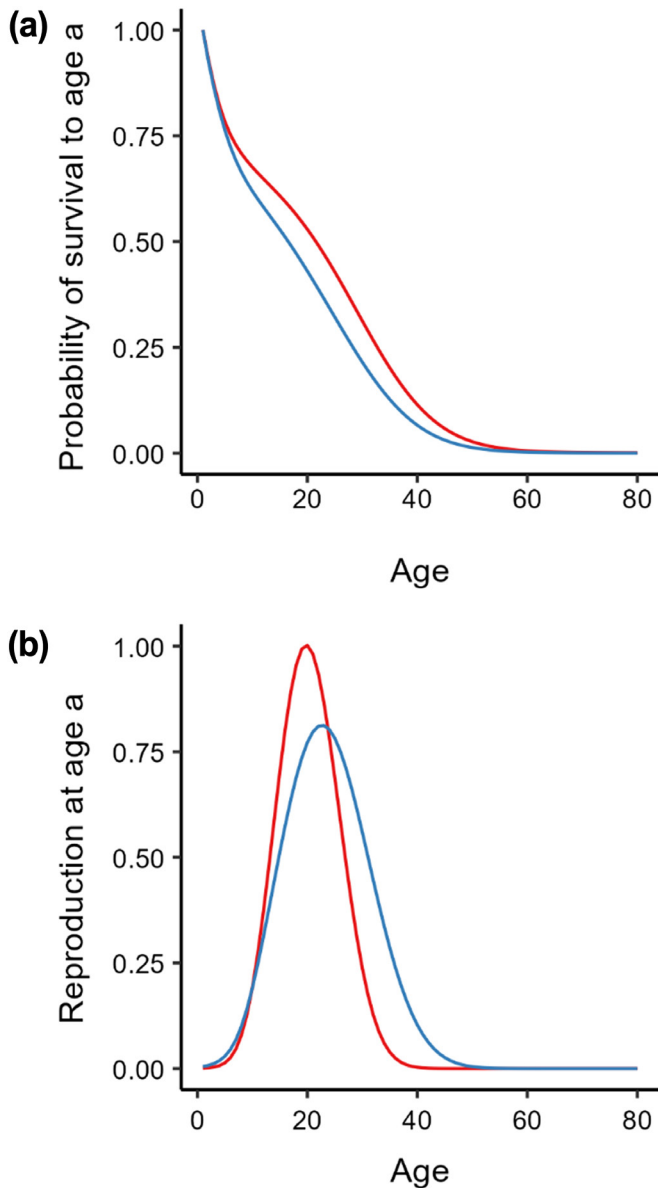
Figure 2. Survivorship schedules (a) showing probability of survival to a given age, and fertility schedules (b) showing mean reproduction at a given age in high (red) and low (blue) food lineages. Survivorship and fertility schedules are derived from posthoc analyses.

and lower fecundity – similar to 'slow' life histories) may be independent of longevity, or even antagonistic (Rion and Kawecki 2007). Finally, mechanisms of density dependence can generate unexpected responses along the fast-slow continuum. For example, Vries et al. (2022) showed how extrinsic mortality can favour 'slow' rather than 'fast' life histories if density dependence selectively harms juveniles. Similarly, modelling by Dańko et al. (2017) showed how when density dependence acts on production rate (a measure of metabolic efficiency), higher mortality can instead lead to later maturity and larger adult size. Ultimately however, we lack a sufficiently detailed description of conditions in our evolutionary environments to explain why we observed both delayed

reproduction and short longevity in low-food copepods. The high computational demands of bootstrapping for IPM outputs and their post-hoc analyses also precluded estimates of confidence. Though not unusual for IPMs that incorporate complex demography (Ellner and Rees 2006), this also motivates follow-up study.

In sum, our findings suggest that adaptation to total food differences does occur, but these responses are muted. We observed that copepods exhibited different life histories yet converged to similar population growth rates (λ). But despite being subjected to approximately 30 generations of selection and an order of magnitude difference in food provisioning, divergence between experimental treatments was slight. For example, low-food adults were only 3.3% larger than high-food adults on average. By comparison, predation in particular can have a markedly higher impact on body size – as much as a 16.6% in under 20 generations in the preeminent Trinidadian guppy system (Reznick et al. 1997), or 13% in *Daphnia* (Fisk et al. 2007), for example. On the other hand, the weak effect we report of food on life history evolution is broadly consistent with recent synthesis suggesting that other major agents of selection (warming, competition, as well as predation) also show only weak effects on life history trait evolution among study systems (Grainger and Levine 2022).

In conjunction with our preceding work in *Tisbe*, our results round out a nuanced picture of life history responses to total food in this study system. In the previous study, Blake and Marshall (2023) focused on cohort-level responses in G1 and G2 of common gardening and found a similarly modest divergence in body size between high- and low-food lineages, but overall the effect of total food was complex and systemic. They reported that low-food adult females were 1.84% larger after two generations of common gardening. But total food effects on body size reported in G2 were obscured by opposing environmental responses in G0, where low-food adult females were 1.89% smaller than their high-food counterparts. Blake and Marshall (2023) concluded that this 'cryptic evolution' was likely the result of genetic compensation, whereby a maladaptive plastic response induced by a harsh environment elicited a counteracting genetic response (sensu Grether 2005). Similarly, reproductive scaling with size was steeper in low-food mothers, and there were clear differences in reproductive allocation between high- and low-food lineages in G2 individuals (Blake and Marshall, 2023). These responses to total food in reproductive traits were also cryptic and obscured in G0. In the present study, we focused on the individual-level responses of G3 offspring of the G1 and G2 copepods reared in common gardens by Blake and Marshall (2023). And our present results suggest that the cost of this genetic compensation in low-food lineages is likely a shorter lifespan and less chance of producing clutches of eggs.

Nonetheless, total food effects in the present study were mild and we failed to detect the same size-reproductive scaling trade-offs reported in previous work by Blake and Marshall (2023) – methodological issues may be partially responsible. By conducting our experiment on G3 individuals we were able to account for potentially confounding

cross-generational plasticity (Burgess and Marshall 2014), but the evolutionary signal may have also eroded due to release from the original food treatments while individuals simultaneously adapted to a new (intermediate-food) environment (Huey and Rosenzweig 2009). Lower population densities in low-food environments may have sufficiently impacted genetic variation to constrain trait evolution (Chevin et al. 2010). Finally, replication in some lineages was also low due to high attrition in obtaining mature, reproductive females for data collection from an initial cohort of unsexed larvae. Though mortality was not particularly high, only approximately half of the individuals we initially collected were suitable for data collection (i.e. female). And of those females, not all were reproductive. Sample sizes for fitting growth curves were particularly low due to the delicacy of the initial larval stage when photographing for size at $t0$ – logistically, it was only feasible to measure a fraction of individuals in the larval stage. Low replication was particularly likely to be responsible for failing to detect nuanced patterns in size-reproduction scaling and reproductive allocation strategies previously found in *Tisbe* (Blake and Marshall 2023). Together, replication and logistical issues that necessitated sampling multiple G3 individuals from single G2 mothers may have resulting in inbreeding events in the present study. Full-sib mating may have occurred for one generation (G4), and can cause inbreeding depression in other copepods (e.g. *Tigriopus*: Palmer and Edmands 2000). That said, we assume similar rates of inbreeding in both high- and low-food lineages, so that inbreeding should have a minimal impact when contrasting these treatments.

On the other hand, macroecological patterns of copepod life histories along productivity gradients may broadly support our finding of weak food effects on life history evolution. Mean body size in copepod communities declines with higher primary productivity (Brun et al. 2016), though in other taxa the reverse is generally true (Huston and Wolverton 2011). Brun et al. (2016) speculated that copepods may be pressured by size-selective predation (Brucet et al. 2010), which is higher in more productive upwelling regions (Cury et al. 2000). Previous work in *Tisbe* showed that unreported countergradient variation could mask an underlying evolutionary response more consistent with patterns observed in other taxa (Blake and Marshall, 2023). But our study suggests that total food effects in copepods may also simply be relatively weak, reflecting the relative importance of top-down versus bottom-up processes in natural systems.

Future work should investigate the mechanisms by which food drives life history evolution in *Tisbe* to understand how a low-food environment favours delayed reproduction with a short lifespan. From our current results we speculate that, in low-food lineages, shorter lifespan and slower reproductive output may trade-off against larger body size and the steeper size-reproduction scaling reported by Blake and Marshall (2023). But a limitation of our studies is that we did not initially set out to identify exact mechanisms driving evolution, but simply to evaluate whether total food would drive live history evolution at all. Logistical constraints meant that some potentially important environmental and population parameters could not be controlled, including population densities and pH. However, informal monitoring of densities suggested that, after experimental evolution began, high- and low-food populations rapidly reached equilibria around 20 000 and 5000 individuals, respectively (Blake and Marshall 2023). In particular, future work needs to disentangle the effects of crowding from those of total food quantity. Studies in conspecifics suggest that total food may influence copepod life history due to crowding in a variety of ways, including accumulation of secondary metabolites, impacts on female fertility and mating incidence, and rates of egg cannibalism and collisions (Walker 1979, Miralto et al. 1996). Future empirical work could also evaluate whether life history evolution was actually adaptive, and not simply the product of non-adaptive forces such as drift (Lynch 2007). Reciprocal transplant experiments represent the gold standard for addressing such questions by identifying local adaptation to distinguish adaptive and non-adaptive evolution (Kawecki and Ebert 2004, Blanquart et al. 2013). IPMs are a powerful tool for investigating eco-evolutionary feedback loops, which have attracted growing interest in the wider literature (Coulson et al. 2011, Coulson 2012). Preliminarily we found no evidence for such feedbacks, but reciprocal transplant experiments would provide the necessary data for a formal test of eco-evo dynamics under different total food regimes.

Conclusions

Ocean primary productivity is expected to decline due to climate change (Fu et al. 2016), driven by upper ocean stratification (Hannon et al. 2001), primary producer adaptations to higher temperatures (Malerba et al. 2018), and the impact of higher temperatures on energy transfer between trophic levels (Barneche et al. 2021). Our results support previous work suggesting that copepod grazers can mitigate these impacts to some extent by genetically compensating for increasingly harsh environments – a silver lining for marine food webs in the face of anthropogenic change. However, we also show that this mitigation has costs for copepods, the consequences of which remain unclear. Changes in copepod body size and reproductive output in particular may have knock on effects for consumers – feeding rates of many planktivores are sensitive to copepod size (van Deurs et al. 2014), particularly in fish fry (Jackson and Lenz 2016). Given the outsized role that copepods play in marine systems, comprising most of the zooplankton biomass (Conover and Huntley 1991, Pakhomov et al. 2002), future studies should continue peeling back the mechanisms driving copepod responses to total food, as well as their potential impacts on broader food webs.

Author contributions

Alexander Blake: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Methodology (equal); Project administration (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Tim Coulson**: Conceptualization (equal); Formal analysis (supporting); Methodology (supporting); Supervision (lead); Validation (supporting); Writing – review and editing (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.5hqbzkhbq (Blake and Coulson 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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