1   **Title:** Temperature variability alters the stability and thresholds for collapse of interacting

2   species

3   **Authors:** Laura E. Dee[1*], Daniel Okamtoto[2], Anna Gårdmark[3], Jose M. Montoya[4], and Steve J.

4   Miller[5]

5   **Affiliations:**

6   [1]Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado

7   80309 USA.

8   [2]Department of Biological Science, Florida State University, Tallahassee, Florida 32303 USA.

9   [3] Department of Aquatic Resources, Swedish University of Agricultural Sciences, Öregrund,

10   Sweden.

11   [4] Theoretical and Experimental Ecology Station, CNRS and Paul Sabatier University, Moulis,

12   France

13   [5] Environmental Studies Program, University of Colorado, Boulder, Colorado

14   80309 USA.

15   *Corresponding Author:* Laura.Dee@colorado.edu

16   **Keywords:** temperature variability, thermal performance curves, predator-prey interactions,

17   climate change, climate variability, climate extremes, stability.

18   **Abstract**

19   Temperature variability and extremes can have profound impacts on populations and ecological

20   communities. Predicting impacts of thermal variability poses a challenge because it has both

21   direct physiological effects and indirect effects through species interactions. In addition,

22   differences in thermal performance between predators and prey and non-linear averaging of

23   temperature-dependent performance can result in complex and counterintuitive population

1

24   dynamics in response to climate change. Yet the combined consequences of these effects remain

25   underexplored. Here, modeling temperature-dependent predator-prey dynamics, we study how

26   changes in temperature variability affect population size, collapse, and stable coexistence of both

27   predator and prey, relative to under constant environments or warming alone. We find that the

28   effects of temperature variation on interacting species can lead to a diversity of outcomes, from

29   predator collapse to stable coexistence, depending on interaction strengths and differences in

30   species' thermal performance. Temperature variability also alters predictions about population

31   collapse – in some cases allowing predators to persist for longer than predicted when considering

32   warming alone, and in others accelerating collapse. To inform management responses that are

33   robust to future climates with increasing temperature variability and extremes, we need to

34   incorporate the consequences of temperature variation in complex ecosystems.

35

36   **<u>Introduction</u>**

37   Climate change is altering climate extremes and variability of environmental conditions

38   [1], yet much of the focus on the impacts of climate change on wild populations remains on how

39   shifts in average conditions will affect dynamics and distributions [2,3]. Yet as average

40   temperatures shift, both temperature variability and the frequency of extreme events, such as

41   marine heat waves, are changing [1,4–6]. Changes in temperature variation and extremes can

42   have profound impacts on individuals and populations, as temperature affects their rates of

43   metabolism, consumption, somatic growth, reproduction, and survival [7,8]. These processes

44   underpin the productivity and resilience of populations and ecosystems [9], on which ecosystem

45   services, such as fisheries yields [10], and population resilience depend. While the potential

46   impacts of temperature variability and extremes have been demonstrated, and in some cases pose

47   a greater risk to species than increases in mean temperature [7,8,11], predicting the importance

48   of temperature variability and extremes for populations, communities, and the ecosystem

49   functions and services they support remains challenging. First, temperature can have both direct

50   and indirect effects that create complex feedbacks and dynamics [12]. Directly, temperature

51   affects species through physiological performance. But temperature can also impact species

52   indirectly, as shown for warming [13,14], by increasing or decreasing important resources or

53   prey species (in turn affecting consumers and predators), changing competitive abilities (altering

54   prey abundance distributions), and altering feeding rates and top-down control (affecting prey)

55   [15–18]. Second, even without shifts in mean temperatures, temperature variability can alter

56   mean vital rates because of non-linear relationships between temperature and processes including

57   growth, reproduction, and mortality (Fig 1; [19]). As a result, the responses of populations to

58   increasing temperature variability and extremes induced by climate change, especially in a

59   community context, remains a key research frontier in marine population dynamics, community

60   ecology, and fisheries science.

61   Directly, temperature variability can impact populations of species in a variety of ways,

62   including by altering the rates of fundamental processes that determine population size,

63   extinction risk, and productivity. Increases in the frequency or duration of exposure to extreme

64   temperatures can induce physiological shock leading to depressed somatic growth or lower

65   survival [20,21]. Temperature variability and extremes above cold or warm events, in contrast to

66   mean temperature conditions, can also alter environmental cues that induce or suppress

67   reproductive cycles leading to skip spawning [22], development [23,24], or hatching [23] that

68   change the number of offspring (i.e. recruitment in fish) or cause reproductive failure. Theory

69   and empirical work shows species' performance responds non-linearly and asymmetrically to

3

70 environmental temperature, including intrinsic growth rates and other fitness proxies. This

71 relationship is known as a thermal performance curve (TPC) [8,25,26]. Because of this non-

72 linearity, changes in temperature variance can affect demographic rates differently than changes

73 in mean temperature alone, due to non-linear averaging and Jensen's inequality (i.e., that the

74 mean of a concave function is smaller than the concave function of a mean, and vice versa for

75 convex functions, see Fig. 1; put in an ecological context *reviewed in* [19]). This also means that

76 if species are well-adapted to the mean conditions, such that their thermal optimum is close to

77 the average environmental temperature (i.e., in the concave part of the thermal performance

78 curve), then increases in temperature variation around the mean are predicted to reduce a

79 species' performance (e.g., growth rate) [20,27,28]. These impacts scale from individuals to

80 population growth rates [29,30]. Similarly, nonlinear TPCs suggest that higher frequency or

81 duration of exposure to temperature extremes, rather than longer-term temperature averages,

82 shape growth and mortality [31] due to species' asymmetric responses to higher temperatures

83 and extremes [20]. Collectively, these nonlinear responses and intermittent exposures to thermal

84 extremes suggest that temperature variability can alter population dynamics in complex ways not

85 explained by warming of average temperatures alone [7,30,32].

86   Simultaneously, temperature can indirectly affect populations through species interactions,

87 thus community and ecosystem responses to temperature variability are complex to predict.

88 Species interactions mediate how temperature impacts a population's growth, biomass, and

89 dynamics. Because species that interact can respond differently to temperature [33,34], species-

90 specific thermal performances can alter interspecific interactions and resulting population

91 dynamics. For instance, if temperature increases prey growth while predators net growth increase

92 less (e.g., due to increased metabolism for larger bodied-species,[35,36]), prey can outgrow

93   predation windows raising survival [37]. This suggests that if prey thrive directly in response to

94   temperature variation when predators are heat suppressed, prey may flourish in response to

95   heatwaves, and *vice versa.* Understanding the consequences of temperature variability for marine

96   communities therefore requires considering species interactions, because some species benefit

97   from variable temperatures while others lose (Fig. 1).

98   However, the effects of both temperature variability (or extremes) and species

99   interactions are rarely accounted for in studies of how climate change impacts community

100   dynamics and ecosystem functioning. On one hand, lab studies that quantify the impacts of

101   temperature variability on individuals and populations often focus on the direct physiological

102   effects on performance (e.g., [8,30,32]), with few considering both variation and interactions (*but*

103   *see* [7,38,39]). On the other hand, most experimental and theoretical studies investigating

104   warming effects on species interactions and their indirect effects do so under different levels of

105   average temperature conditions (e.g.,[15,37]), with less emphasis on variability and extremes

106   (*but see* e.g., [7]). However, when demographic rates depend non-linearly on temperature and

107   interacting species differ in their thermal responses, we anticipate that the net effect of these

108   processes can lead to unexpected outcomes for population dynamics and stability. Indeed, the net

109   effect of temperature variability could be more positive or negative than considering either effect

110   in isolation.

111   In this paper, we examine how different temperature regimes impact the dynamics of

112   interacting predators and prey, with a focus on multiple types of temperature variability,

113   including increases in temperature variability associated with climate change. We theoretically

114   investigate when considering the combined direct and indirect effects of temperature variability

115   ("net effect") alters predictions for population productivity, stability, and trajectories through

116   time, relative to considering a constant environment and/or warming average temperatures alone.

117   Specifically, we ask:

118   1) How does increasing temperature variability affect population size through time,

119   occurrence of collapse, and stable coexistence of both predator and prey, relative to a

120   constant environment?

121   2) How do these effects depend on the predator's and prey's TPCs relative to the

122   temperature variability regime, and relative to one another?

123   3) What are the net *versus* direct effects of temperature variability on these properties when

124   species interact, and when are direct versus net effects acting in opposite directions?

125   4) How do effects of temperature variability compare to and/or modify the effects of

126   increasing mean temperatures?

127   We hypothesize that the extent to which the effects of temperature variability shift predictions

128   about population growth, size, and stable coexistence beyond warming average conditions will

129   depend on the 1) thermal variability regime, 2) strength in species interactions, and 3) overlap in

130   TPCs of interacting species (Fig. 1). We motivate our theoretical investigation with a marine

131   predator-prey system, though the model applies more generally to predator-prey systems

132   experiencing both temperature variability and rising temperatures.

133   **Methods**

134   *Model*

135   We model a predator-prey system in which a subset of key parameters depend upon

136   temperature. In line with prior investigations of how temperature affects community dynamics

137   [40–43], we use a Rosenzweig-MacArthur model with a prey population $x(t)$ and predator

138   population $y(t)$ changing as a function of time t:

139
$$\frac{dx(t)}{dt} = r\big(T(t)\big)x(t)\left(1 - \frac{x(t)}{K}\right) - y(t)f\big(x(t), y(t), T(t)\big), \tag{1}$$

140
$$\frac{dy(t)}{dt} = \big(cf\big(x(t), y(t), T(t)\big) - m\big)y(t). \tag{2}$$

141   Here, r is the temperature-dependent intrinsic growth rate of the prey population, K their

142   carrying capacity, $T(t)$ is temperature at time t, m the density-independent mortality in the

143   predator, and f denotes the Holling type II functional response of the predator:

144
$$f\big(x(t), y(t), T(t)\big) = \frac{a\big(T(t)\big)x(t)}{a\big(T(t)\big)hx(t)+1}. \tag{3}$$

145   Here a denotes attack rate, which depends on temperature; h is handling time; and c is

146   conversion efficiency.

147   In the absence of temperature effects, this Rosenzweig-MacArthur model has three

148   equilibria: joint extinction, extinction of the predator with the prey at carrying capacity, and a

149   coexistence equilibrium. The coexistence equilibrium is defined by:

150
$$x^* = \frac{m}{a(c-mh)}, \quad y^* = \frac{r}{a}\left(1 - \frac{x^*}{K}\right)(ahx^* + 1), \tag{4}$$

151   which requires that $aK(c - mh) > m$. We use this equilibrium to set the starting conditions, in

152   terms of the populations levels (abundances), to provide consistent initial conditions under which

153   there are no transitory dynamics in the absence of temperature-dependence.

154   We focus on understanding how temperature variability influences population dynamics

155   via impacts to the predator and the prey species. Particularly, we model how both the attack rate

156   (a) of the predator [44] and the intrinsic growth (r) of the prey [8] depend on temperature.

157   Following current theory and empirical studies, we assume $r(T)$ and $a(T)$ follow unimodal non-

158   linear relationships, with maxima at T_r^* and T_a^*, respectively (Fig. 1). Although the shape of

159   thermal performance curves (TPCs) will vary among species, populations, and life stages, TPCs

160   are generally considered to have a steep, negative drop-off in performance above optimal

7

161   temperatures, but rapid gains in performance at lower temperatures (Fig. 1) [33,45,46]. In our

162   model, we use species-specific asymmetric hump-shaped TPC following Gårdmark et al. (in

163   prep) and [47,48]; see SI for details.

164   We focus on the temperature-dependence of these two parameters, attack rate *a* and prey

165   growth rate *r*, but recognize that temperature also could influence other parameters in our model

166   (e.g., carrying capacity *K*, handling time *h*, and mortality rate *m*) [44,49]. We choose to examine

167   the temperature dependence of *a* and *r* because these are the parameters for which we have the

168   most unequivocal information (*see* [50]). For example, carrying capacity may also vary with

169   temperature [49], but that parameter is not mechanistic in the Rosenzweig-MacArthur model.

170   That is, *K* may be determined by many factors including primary productivity, nutrient supply,

171   and habitat availability, and temperature may affect each of these in different and complex ways

172   that are more likely linked to exogenous factors that this model does not incorporate.

173

174   ***Simulations***

175   The way in which temperature variability affects growth and attack rates depends on the

176   distribution of temperatures to which species are exposed and the species' TPCs. Because TPCs

177   for a prey and its predator are likely to differ (Fig. 1), we explore how overlap of TPCs and their

178   relation to temperature distributions affect population dynamics for both species. Thus, we

179   conduct several simulations that combine and vary both: the temperature regime and how

180   species' TPCs relate to one another. For each simulation, we examine how the temperature

181   regime influences average temperature-dependent demographic rates (*r* and *a*), long-run

182   population means for both predator and prey, and the equilibrium type (either extinction or

183   coexistence with either fixed densities or cycling dynamics). Here, we define '*long-run*' predator

184   and prey populations based on the last 10% of the simulated time steps (final 200 out of the 2000

185   time steps), which provides time required to reach a stationary distribution (Fig. S1), if one

186   exists.

187

188   **Temperature regimes**

189   *Scenarios of temperature regimes for means and variability*

190   The temperature regimes we consider are (1) temperature variability of different

191   amplitudes, but constant mean temperature ('variability-only'), (2) increasing mean temperature,

192   but no variability ('warming-only'), (3) increasing mean temperatures and constant temperature

193   variability of different amplitudes ('warming-and-constant variability') and (4) both increasing

194   mean temperatures and increasing temperature variability ('warming-and-increasing variability').

195   We generate the temperature variability and warming regimes as follows. In the

196   variability-only regime, temperatures oscillate linearly between a maximum T_{max} and minimum

197   T_{min} , completing one cycle per time period (see SI) to reflect seasonality. In this scenario,

198   increases in temperature variability do not affect the mean temperature $\bar{T}$. In the warming-only

199   regime, temperatures increase linearly from T_{min} to T_{max} over the course of the simulation. To

200   facilitate comparison, all warming-only scenarios share the same $\bar{\bar{T}}$, such that the variability-only

201   and warming-only regimes have the same overall distribution of temperatures for a given T_{min}

202   and T_{max}. We generate these regimes for different sets of T_{min} and T_{max}, which we refer to as

203   "amplitudes." Finally, the warming-and-variability scenarios combine the linear warming and

204   linear oscillation effects with different amplitudes, where both warming and variability share a

205   specified amplitude (see SI).

206

207 *Scenarios with stochastic events driving temperature variability*

208   In addition to the deterministic temperature changes in the form of seasonal variation,

209 warming, or both, <u>we also simulate temperature variability that is stochastic, to test the</u>

210 <u>sensitivity of our results.</u> We examine two types of stochastic temperature changes (see SI

211 section 1.2). First, we examine major "events" modeled after El Niño; when such an event

212 occurs, the temperature shifts up during a given year. Second, we examine smoother stochastic

213 variability in the form of a Gaussian process with squared exponential covariance function,

214 allowing for both variance and autocorrelation to increase through time. In both cases, we add

215 these stochastic temperature deviations on top of our baseline scenario of oscillating (seasonal)

216 temperatures – enabling us to focus solely on the two types of variability rather than the

217 combination of variability and warming.

218

219 *Examining how predator-prey TPC overlap and trophic structure modulates effects of*

220 *temperature*

221   To investigate the extent that TPC overlap between predator and prey species determines

222 the impact of temperature on each population and their coexistence, we systematically vary the

223 extent of TPC overlap between predator and prey species for each temperature scenario. For each

224 temperature regime, we consider a range of configurations of species' TPCs, defined by the

225 offset $T^* - \bar{T}$ (in degrees Celsius) between each species' optimal temperature and the mean

226 environmental temperature (see Fig. 1). Specifically, we consider cases where the TPCs for the

227 predator and prey have offsets of the same magnitude but opposite sign, so that the location of

228 both TPCs is defined in terms of the prey offset (as in Fig 1). When that offset is zero, the

229 predator and prey TPCs overlap exactly. Table S1 defines parameters for these simulations.

10

230   Finally, we conduct an additional set of analyses in which we introduce a second prey

231   species with different thermal affinities than the first prey. To do so, we use a multispecies

232   Holling type II functional response [51], to maintain the same functional form assumptions as

233   above, in order to isolate the effect of adding an additional prey on stable coexistence. To test the

234   influence of multiple prey species with different TPCs on co-existence of predator and prey

235   species, we shifted the first prey TPC and the predator TPC in opposite directions as before, but

236   fixed the second prey TPC at the environmental mean, to facilitate comparison with the single

237   prey case.

238

239   *Calculating direct effects versus net effects of temperature via species interactions*

240   To quantify the importance of accounting for species interactions when studying the

241   effects of temperature variability, we contrast the direct and net effects (direct plus indirect) of

242   temperature variability on the predator population. For each combination of temperature regime

243   and species' TPCs, we track the predator population for three simulations, with growth and

244   attack rates set to (*i*) $r(\bar{T})$ and $a(\bar{T})$; (*ii*) $r(\bar{T})$ and $a(T)$; and (*iii*) $r(T)$ and $a(T)$; rates defined

245   either at the actual temperature T or at the mean temperature $\bar{T}$ ignoring variability. Thus,

246   simulation (1) ignores all effects of temperature variability, simulation (2) ignores the effects of

247   variability on prey growth, and simulation (3) examines the effects of temperature variability on

248   both species. We define the net effect of temperature variability as the difference in long-run

249   predator population between simulations (3) and (1), while the direct effect is defined by the

250   difference between simulations (2) and (1).

251

252   **Results**

11

253   *Effects of temperature variability on long-run populations*

254   Increases in temperature variability produce either stable coexistence, predator-prey cycles,

255   or extinctions (Fig. 2), depending on the difference in predator and prey TPCs and parameters

256   relating to species interactions (predator conversion efficiency and attack rate) (Figure 1; Figure

257   S1). When TPCs for predator and prey coincide (i.e., are identical), variable temperatures can

258   drive the predator extinct from an equilibrium that is stable under conditions without temperature

259   variability (Figure 2b; Fig S1). For higher parameter values of predator conversion efficiency

260   ($c = 0.3$ in Fig. 2a versus $c = 0.1$ in Fig. 2b), however, increasing temperature variability can

261   stabilize the system, causing a shift from cyclic dynamics (limit cycle) to a stable equilibrium

262   point (fixed point) (Fig 2a). The opposite effects can arise when the TPCs for the two species are

263   offset so that the prey's temperature optimum is higher. Specifically, when peak attack rates are

264   high, variability can save the predator from extinction, if the prey has a much higher optimum

265   temperature than the predator, or destabilize an otherwise stable equilibrium by inducing cyclic

266   dynamics when the difference in TPCs between predator and prey is less (Fig. 2c). Even when

267   variability does alter the type of equilibrium that arises, equilibrium population levels can be

268   driven up or down.

269   The presence of a second prey species with different thermal affinities from the first prey

270   increases the parameter space with stable coexistence (Fig. S5). Predator feeding on an

271   alternative prey with TPC at mean temperature stabilizes dynamics and prevents extinction,

272   especially when the original prey has a much lower optimal temperature than its predator

273   (negative prey TPC offsets, cf. Fig. 2 and Fig. S5) and for predators with low conversion

274   efficiency (Fig. S5).

275

276   *Direct versus net effects of temperature variation*

277   Including indirect effects can qualitatively change the impact of temperature variability on

278   populations (Fig. 3; Fig. S2). The true, 'net', effect on long-run population levels can differ from

279   that suggested by studying the direct effect alone, both in terms of direction of the response (Fig.

280   3) and effects on the stability of predator-prey dynamics (Fig. S2). In other cases, the direct

281   effect of temperature variability may imply an unstable equilibrium, but after accounting for

282   indirect effects, the equilibrium remains stable (Fig. S2).

283

284   *Effects of increased temperature variability versus increased temperature mean*

285   The effects of increasing mean temperature on long-run population sizes without shorter-

286   term variability are qualitatively different than those of variability without warming, even for an

287   identical distribution of temperatures experienced during the simulation (Fig. 4). For example,

288   increasing mean temperature on predator and prey with completely overlapping TPCs can drive

289   the predator extinct (Fig. 4, *red lines*) as higher temperatures eventually lead to extended periods

290   of low attack rates (which asymptote towards 0). In contrast, variability with the same

291   distribution of temperatures can lead to a stable coexistence (Fig. 4, *blue lines*). When mean

292   temperatures increase and variability is present — whether constant (Fig 4, *purple lines*) or

293   increasing (Fig 4, *orange lines*) — the predator population survives for longer than under

294   increasing mean temperature alone.

295   Accounting for stochastic variation in temperature does not change our qualitative

296   conclusions (Figure S6). While moderate stochastic temperature changes knock population

297   trajectories out of asymptotic convergence to equilibrium levels, they do not qualitatively change

298   the means of the long-run population trajectories in response to temperature (Fig. S6)

13

299

Discussion

301   Increases in temperature variability can influence populations of interacting species in

302   ways not predicted by considering increases in mean temperatures or the direct physiological

303   effect of temperature variation alone. First, a focus on mean temperature alone misses the highly

304   non-linear responses of species' demographic rates to changes in temperature [52]. Temperature

305   variability, by directly creating complex nonlinear demographic responses, can alter both the

306   viability and stability of populations in either direction (Fig. 2). Second, the net effect of

307   temperature variability when species interact can 4differ from that predicted by the direct effect

308   of temperature on a single species, and even be of opposite sign (Fig. 3). Thus, ignoring indirect

309   effects and making predictions about population dynamics solely from individual demographic

310   rates (e.g. growth) may create erroneous expectations, somethings in the opposite direction (Fig.

311   3; Fig. S2). This highlights the importance of considering temperature effects in contexts with

312   both intra- and inter-specific interactions. Third, results depend on the differences in predator

313   and prey TPCs (i.e., if the predator TPC is optimized at a higher, identical, or lower temperature

314   than its prey). Finally, results from our model show ignoring temperature variability could over-

315   predict negative impacts of warming on population and community trajectories. Even under

316   warming temperatures, temperature variability results in periods in which temperatures return to

317   a range under which species can grow (Fig. 4), though our results show that the predator

318   populations may still eventually collapse as warming intensifies (Fig. 4d). These findings have

319   important implications for natural communities as temperature variability is predicted to increase

320   further due to global warming.

321   That temperature variability increases species persistence can also be seen in single species

322   models, which provide insights into when this 'rescue effect' occurs. This 'rescue effect'

323   depends on how temperature variability influences temperature-dependent demographic rates for

324   hump-shaped TPCs. In a single-species logistic model with temperature-dependent growth, the

325   prey population at time t depends only on the average growth rate $\bar{r} = \overline{r(T(t))}$ of that time period

326   [53]. Depending on the curvature of the TPC over the range of temperatures that a species

327   experiences, temperature variability can either raise (in convex parts of the TPC) or lower

328   average growth (in concave parts of the TPC), with concomitant change in population levels

329   (Fig. 1; *see also* [54, 55]). If warming drives the mean temperature above the prey's optimal

330   temperature, then temperature variation will span a convex portion of the species TPC, thereby

331   raising average growth and prolonging population persistence (as seen in Fig. 4).

332   Similar insights can be gleaned about the effects of variability on average rates for

333   interacting predator and prey species. Temperature variability is likely to lower average attack

334   rates when the temperature distribution is centered near the peak of the predator's TPC (Fig. 2

335   when TPC offset is around 0), whereas it results in higher average attack rates at lower

336   temperatures (Fig. 2 when TPC offset is large and positive), such that temperature variation

337   occurs in the convex part of the predator's TPC. Temperature variability in these ranges of the

338   TPC thus promotes predator persistence by resulting in sufficiently high attack rates on average.

339   In fact, simulations using the average predator attack and prey growth rates that arise under

340   variable temperatures yield similar overall patterns of stability and coexistence (see Fig. S3 and

341   SI section S1.3 for details).

342   Importantly, our results demonstrate that understanding how a particular temperature regime

343   affects predator populations requires knowledge of temperature dependencies of *both* species and

15

344   how they interact. The true 'net' effect of temperature variability on predator populations may be

345   positive or negative; moreover, because of indirect effects, such responses may differ in sign

346   from predictions made based on changes in attack rate (or other properties in a single species) in

347   isolation (Fig 3). The potential for indirect effects on equilibrium populations is evident from

348   equation (4): prey levels are inversely related to attack rates, while predator levels are

349   proportional to prey growth rates.

350   The difference in TPCs of interacting species dramatically alters the response of ecological

351   communities to variation in temperature (Fig. 2 & 3). Large differences in temperature optima

352   from $\bar{T}$ lead to predator extinction, regardless of which species has the higher optimum

353   temperature. If prey have lower temperature optima, predator extinction occurs at even lower

354   levels of temperature variability for the same magnitude of TPC offset, compared to if the

355   predator has the lower temperature optimum. The rapid decline of the TPCs above a species'

356   optimum explains this result. Average growth for the prey (or attack rate for predator) is

357   substantially lower when temperature vary above that species' optimum temperature compared

358   to below (i.e. if the temperature optima is shifted downward rather than upward by the same

359   amount). If the prey has a lower temperature optimum than the predator, high temperature

360   variability results in prey population depletion by increasing predator attack rates much more

361   than prey growth rates, eventually leading to predator extinction. These results are consistent

362   with findings from other contexts showing that imbalances in temperature sensitivities of species

363   metabolism and ingestion have important consequences for community dynamics. For example,

364   for invertebrates, metabolism increases faster than ingestion [56,57], which can lead to

365   starvation, and theoretical analyses indicate that this increases population stability but also the

366   risk of starvation and extinction of predators [13,40].

16

367   Comparing the effects of temperature variability with those of warming mean temperatures

368   reveals their different impacts on species coexistence and stability, even when the distribution of

369   temperatures under the two regimes is identical. When temperatures warm, long-run predator

370   populations suffer much more than if the same magnitude of temperature change is experienced

371   in a cyclical fashion (Fig. 4). Warming eventually drives predator attack rates to low levels,

372   leading to population declines from natural mortality and a predator population that is not viable.

373   Prey growth also slows, but with reduced predation, the prey population persists. In contrast,

374   under a variability-only scenario, periods of low attack rates are intermixed with stretches of

375   higher attack rates, such that the predator population can survive. Consistent with that intuition,

376   adding variability to a temperature regime with warming can prolong the existence of the

377   predator population, though in other parameterizations variability can accelerate collapse.

378   We designed our models to quantify the effects that temperature variability can impose

379   on interacting species. However, these models include several simplifying assumptions. Our

380   models assume only the net population growth rate of prey and the attack rate for predators are

381   affected by temperature, but carrying capacities [58], conversion efficiencies [59], mortalities

382   [60,61], and handling times [44,60,62] may also depend on temperature. We also include thermal

383   sensitivity in phenomenological rather than explicitly mechanistic forms. More realistic models

384   (e.g., size-structured, age-structured, or individual-based models) could parse out how

385   maturation, fecundity, mortality, individual growth, and consumption simultaneously respond to

386   thermal regimes in different individuals or size-classes when species interact. For example,

387   accounting for both the temperature-dependent processes underlying body growth and for

388   within-population size structure have proven important for understanding how both consumer

389   populations [35] and food chains [63] vary with temperature. However, while this has been

17

390   addressed in studies of warming of mean temperatures [35,63,64], it remains to be done for

391   increasing temperature variability. Both the complex responses to increasing temperature

392   variability and the importance of accounting also for indirect temperature effects via interacting

393   species that we demonstrate suggest that predicting how temperature variability would impact

394   size-structured food webs cannot be done *a priori*. Our study thus calls for addressing

395   temperature variability effects in food webs with approaches accounting for bioenergetics

396   processes and the size-dependence of species interactions.

397   We demonstrate that the presence as well as the form of temperature variability influence

398   species persistence and coexistence and interact with the effects of warming mean temperatures.

399   Future work could consider the following additional complexities in predicting the effects of

400   temperature dynamics on interacting species in particular systems. First, thermal variability with

401   autocorrelation (e.g., persistent heatwaves) can induce not only prolonged shifts in growth but

402   also mortality, even leading to mass mortality, for instance from oxidative stress shaped by

403   temperature maxima rather than mean temperature [21]. Mass mortality events may be induced

404   by short-term exposure to high temperature, and the threshold temperature for mortality can

405   decrease with greater exposure duration [65], whereas high-frequency variability can also reduce

406   negative effects, such as coral bleaching [66]. Second, the impacts of these short-term events are

407   likely to depend on the species' generation time, relative to time scale of the perturbation. For

408   instance, short-lived species may suffer high mortalities if exposed to unfavorable climate

409   conditions occurring during its short lifespan, compared to longer-lived organism that may better

410   buffer against short-term events. Third, acclimatization [67,68], or short-term evolutionary

411   responses [48,69] to temperature changes could result in inaccurate predictions from models

412   based on historical observations or experiments that are conditional on the environmental history

18

413   or genotypes. Nevertheless, our results show temperature variability can alter predictions

414   compared to accounting for increases in temperature means alone, indicating the need for

415   considering temperature variability shapes population stability, collapse, and coexistence when

416   species interact (Fig. 2; Fig. 4).

417   Finally, climate change in the sea is more than warming, variability, and frequency of

418   extreme temperatures. It also encapsulates changes in dissolved oxygen, pH, surface irradiance,

419   salinity, and circulation dynamics -- biophysical changes that are often correlated with

420   temperature fluctuations (IPCC 2019). We chose to focus on temperature dynamics for several

421   reasons. First, there has been a long history of documenting short and long-term variation in

422   ocean temperature either *in situ* or using satellite reconstruction. In contrast, for other

423   biophysical changes, such widespread and high-resolution data collection and reconstructions are

424   more isolated, sporadic or only recently developed. Second, temperature impacts on physiology

425   and population dynamics have long been a focus in fisheries ecology. Thus, we focus

426   on variation in temperature to quantify how variability in abiotic stressors can alter dynamics

427   with the acknowledgment that other stressors and variability therein are also central in shaping

428   populations and communities and may exhibit independent and multiplicative stresses on

429   communities in unpredictable ways. Here we show that the inherent complex direct and indirect

430   responses of populations and communities to gradual linear temperature changes that

431   characterizes climate warming versus the non-linear and extreme changes that characterize

432   climate variability is challenging. This challenge requires that, before including additional and

433   important complexities, we deeply understand the interplay of climate warming and variability.

434

435   **Conclusions**

19

436   Climate change is increasing not only mean temperatures but also temperature variability

437   (IPCC 2019). Understanding the consequences of temperature variability for population

438   trajectories and dynamics is critical for anticipating how climate change will affect the

439   productivity and stability of animal communities that support important functions and services.

440   Here we find that shifts in temperature variability can destabilize, stabilize or lead to predator

441   collapses, depending on interaction strengths and differences in thermal performance between

442   predators and prey. Our results also show that impacts on species' growth from concurrent

443   changes in variability with warming can change predictions from considering warming alone.

444   Counterintuitively, temperature variability can help a population that would otherwise go extinct

445   due to warming, when warming negatively impacts population growth, and some forms of

446   variability can offset these effects. In other cases, however, ignoring increases in temperature

447   variability associated with climate change leads to underestimation of predator extinction risks.

448   Our results contribute to a growing understanding of how temperature variation will alter

449   life in the oceans, though the theoretical results extend more generally to other predator-prey

450   systems facing variability. Our findings call for future studies advancing the theory on increasing

451   temperature variation in foodwebs. In particular, we encourage accounting for within-species

452   structure and variation in TPCs, as well as testing this in experimental studies in interacting

453   species (over temperature ranges large enough for the non-linear responses to matter). Moving

454   beyond a focus on mean temperatures alone, to advance our understanding of the consequences

455   of temperature variation in complex ecosystems, can improve our ability to inform management

456   responses that are robust to future climates with increasing variability and extremes.

457

458   **Acknowledgements**:

464

465

21

466   **Figures**
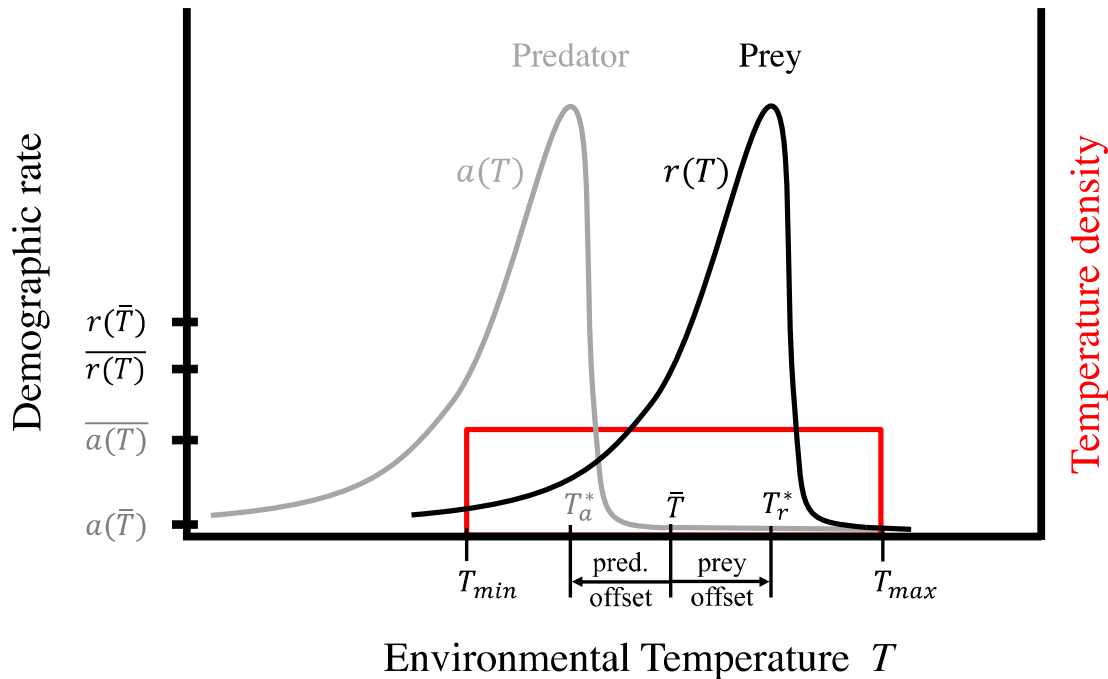
467

468   **Figure 1. Nonlinear responses to temperature.** A conceptual figure of how variable

469   temperatures affect demographic rates, e.g., intrinsic per-capita growth rate $r(T)$ or attack rate

470    $a(T)$, following thermal performance curves (TPCs). Each individual of a species has a

471   temperature optimum T^* at which its performance is maximized, which may be offset from the

472   mean environmental temperature $\bar{T}$. When temperature varies, average demographic rates $\overline{r(T)}$

473   and $\overline{a(T)}$ may be higher or lower than demographic rates at the mean temperature ($r(\bar{T})$ and

474   a($\bar{T}$)) due to Jensen's inequality. For example, average rates are likely to be smaller for species

475   adapted to their average ecosystem temperature, i.e. $T^* \approx \bar{T}$. If the range of temperatures

476   encompasses both convex and concave regions of the TPC, the net effect is indeterminate but

477   generally nonzero. In experiments, we vary (1) the amplitude of temperature variability ($T_{max} -$

478   T_{min}), and (2) how far the TPCs are offset from the environmental mean temperature ($T_r^* - \bar{T}$

479   and $T_a^* - \bar{T}$). We restrict offsets to be equal in magnitude but have opposite sign, reporting

480   results in terms of the predator's TPC offset ($T_r^* - \bar{T}$).

481
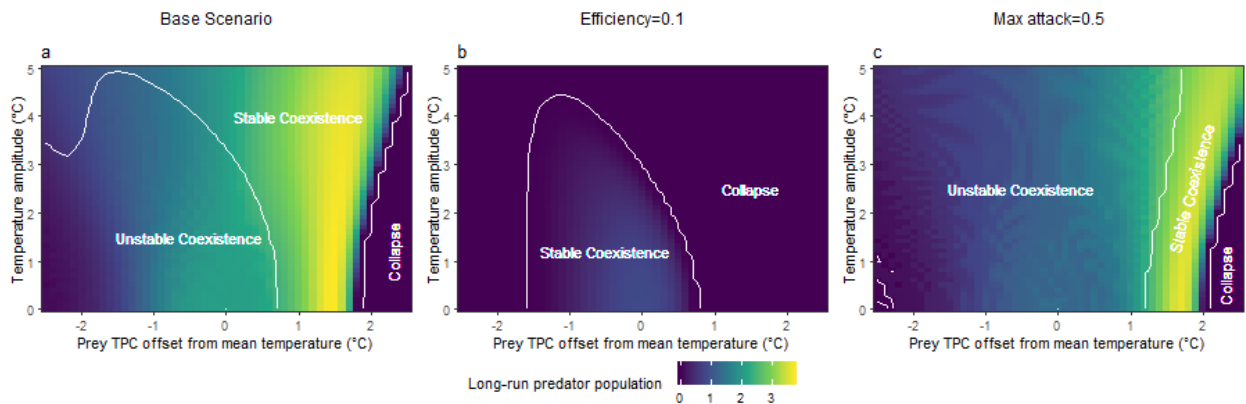
482

483   **Figure 2: Stable predator collapse or predator-prey coexistence depends on both the offset**

484   **in the predator and prey thermal performance curves (TPCs) and amplitude of**

485   **temperature variability.** Effects of offset in the predator and prey TPCs (x-axis) and amplitude

486   of temperature variability (y-axis) on predator population abundance (colors) and the type of

487   equilibrium that arises: predator collapse or predator-prey coexistence, and whether the latter is

488   stable or unstable (e.g., cycles or oscillatory behavior). Base scenario parameters (a) are

489   mortality $m = 0.2$, carrying capacity $K = 20$, conversion efficiency $c = 0.3$, maximum attack rate

490     $a = 0.3$, and handling time $h = 0.3$, whereas species interactions are modified in (b-c) by

491   lowering conversion efficiency $c = 0.1$ (B) or increasing attack rate $a = 0.5$ (C). TPC parameters

492   are in Table S1.

493

494
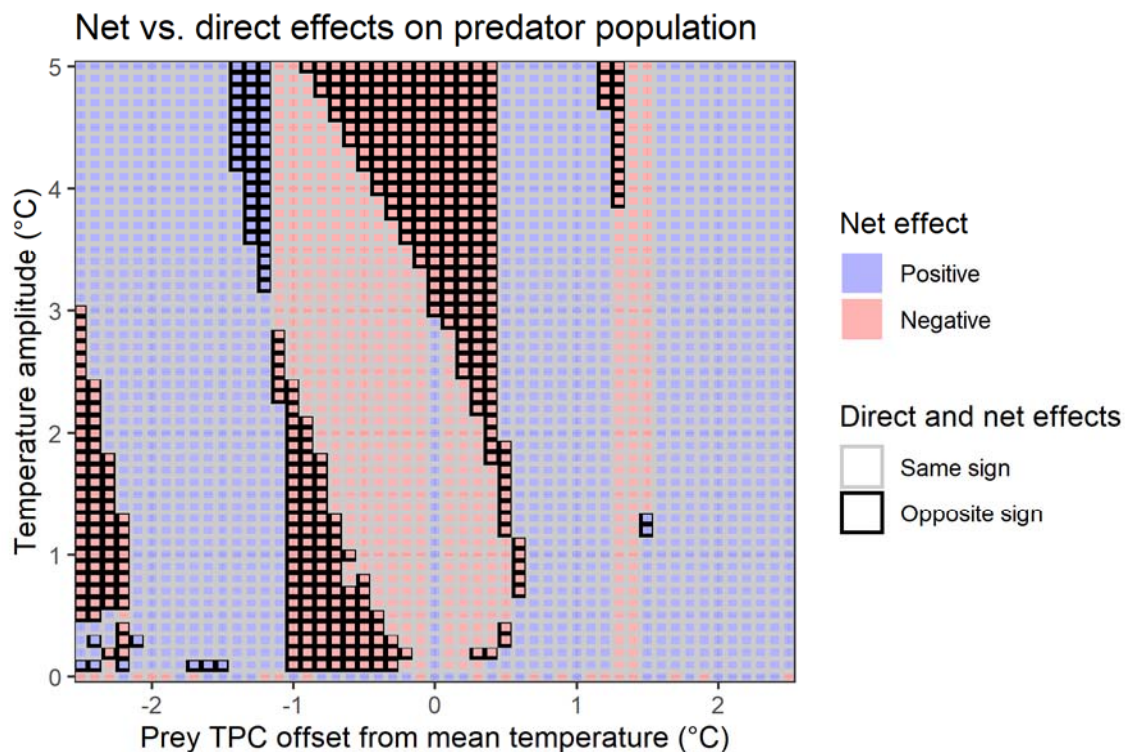
Figure 3: The net and direct effects of temperature variability on predator population.

Net effects (blue: positive; red: negative) of temperature variability on long-run population levels

for the predator, as a function of how far the prey TPC is offset relative to the mean temperature

(x-axis) and the amplitude of temperature variability (y-axis). Outlines indicate whether net

effects have the same sign (black outline) or not (light gray outline) as when only considering the

effects of temperature variability on the predator, ignoring the temperature-dependence of its

prey ('direct effects'). For example, red-filled and black-outlined regions indicate

parameterizations where considering only temperature effects on the predator would suggest a

positive effect of temperature variability for the predator population when the true net effect is

negative, due to species interactions. Parameters as in Fig. 2a with TPC parameters in Table S1;

see Fig S4 for results from additional parameterizations.

506
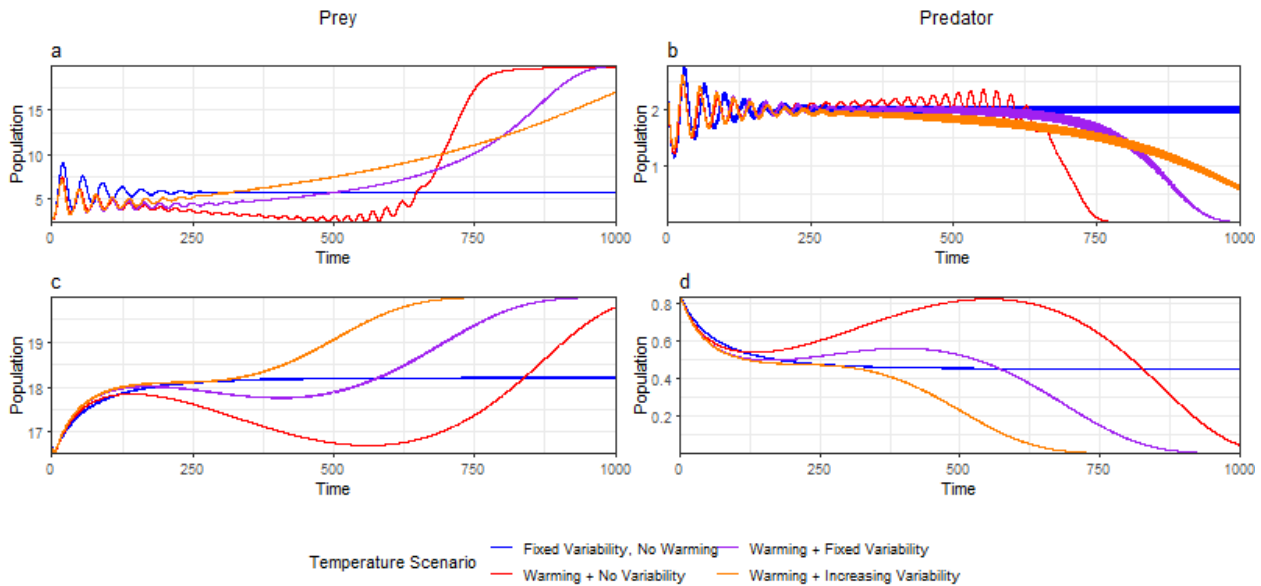
507
508 **Figure 4. Interacting effects of warming and temperature variability.**

509 Population trajectories for the prey (a,c) and predator (b,d) under scenarios of warming

510 (increasing mean temperatures) with no variability (red), constant temperature variability with

511 constant mean temperatures (blue), increases in mean temperatures with constant variability

512 (purple), and increases in both mean temperatures and temperatures variability (orange).

513 Variability on top of warming can either delay (panel b) or accelerate (panel d) predator collapse.

514 Panels a and b reflect model parameters as in Fig 2a with $T_{max} - T_{min} = 8°C$; panels c and d

515 reflect model parameters as in Fig 2b with $T_{max} - T_{min} = 2°C$ TPC parameters are in Table S1

516 with zero offset.

References

1.   Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R. & Mearns, L. O. 2000 Climate Extremes: Observations, Modeling, and Impacts. *Science (80-.).* **289**, 2068–2075.

2.   Pecl, G. T. et al. 2017 Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. **9214**. (doi:10.1126/science.aai9214)

3.   Poloczanska, E. S. et al. 2013 Global imprint of climate change on marine life. *Nat. Clim. Chang.* , 1–7. (doi:10.1038/nclimate1958)

4.   Cai, W. et al. 2014 Increasing frequency of extreme El Niño events due to greenhouse warming. *Nat. Clim. Chang.* **4**, 111–116. (doi:10.1038/nclimate2100)

5.   Holbrook, N. J. et al. 2019 A global assessment of marine heatwaves and their drivers. *Nat. Commun.* **10**, 1–13. (doi:10.1038/s41467-019-10206-z)

6.   Frölicher, T. L., Fischer, E. M. & Gruber, N. 2018 Marine heatwaves under global warming. *Nature* **560**, 360–364. (doi:10.1038/s41586-018-0383-9)

7.   Pansch, C. et al. 2018 Heat waves and their significance for a temperate benthic community: A near-natural experimental approach. *Glob. Chang. Biol.* **24**, 4357–4367. (doi:10.1111/gcb.14282)

8.   Vasseur, D. A., DeLong, J. P., Gilbert, B., Greig, H. S., Harley, C. D. G., McCann, K. S., Savage, V., Tunney, T. D. & O'Connor, M. I. 2014 Increased temperature variation poses a greater risk to species than climate warming. *Proc. Biol. Sci.* **281**, 20132612. (doi:10.1098/rspb.2013.2612)

9.   Svensson, F., Karlsson, E., Gårdmark, A., Olsson, J., Adill, A., Zie, J., Snoeijs, P. & Eklöf, J. S. 2017 In situ warming strengthens trophic cascades in a coastal food web.

26

540   *Oikos* **126**, 1150–1161. (doi:10.1111/oik.03773)

541   10.   Dee, L. E. et al. 2016 Functional diversity of catch mitigates negative effects of

542   temperature variability on fisheries yields. *Proc. R. Soc. B* **283**, 20161435.

543   (doi:http://dx.doi.org/10.1098/rspb.2016.1435)

544   11.   Helmuth, B., Russell, B. D., Connell, S. D., Dong, Y., Harley, C., Lima, F. P., Sará, G.,

545   Williams, G. a & Mieszkowska, N. 2014 Beyond long-term averages: making biological

546   sense of a rapidly changing world. *Clim. Chang. Responses* **1**, 6. (doi:10.1186/s40665-

547   014-0006-0)

548   12.   Rijnsdorp, A. D., Peck, M. A., Engelhard, G. H., Möllmann, C. & Pinnegar, J. K. 2009

549   Resolving the effect of climate change on fish populations. *ICES J. Mar. Sci.* **66**, 1570–

550   1583. (doi:10.1093/icesjms/fsp056)

551   13.   Gilbert, B. et al. 2014 A bioenergetic framework for the temperature dependence of

552   trophic interactions. *Ecol. Lett.* **17**, 902–14. (doi:10.1111/ele.12307)

553   14.   O'Connor, M. I., Gilbert, B. & Brown, C. J. 2011 Theoretical predictions for how

554   temperature affects the dynamics of interacting herbivores and plants. *Am. Nat.* **178**, 626–

555   38. (doi:10.1086/662171)

556   15.   Frances, D. N. & McCauley, S. J. 2018 Warming drives higher rates of prey consumption

557   and increases rates of intraguild predation. *Oecologia* **187**, 585–596. (doi:10.1007/s00442-

558   018-4146-y)

559   16.   Lurgi, M., López, B. C. & Montoya, J. M. 2012 Novel communities from climate change.

560   *Philos. Trans. R. Soc. B Biol. Sci.* **367**, 2913–2922. (doi:10.1098/rstb.2012.0238)

561   17.   Shurin, J. B., Clasen, J. L., Greig, H. S., Kratina, P. & Thompson, P. L. 2012 Warming

562   shifts top-down and bottom-up control of pond food web structure and function. *Philos.*

563   *Trans. R. Soc. B Biol. Sci.* **367**, 3008–3017. (doi:10.1098/rstb.2012.0243)

564   18.   Yvon-Durocher, G. et al. 2015 Five Years of Experimental Warming Increases the

565   Biodiversity and Productivity of Phytoplankton. *PLoS Biol.* **13**, 1–22.

566   (doi:10.1371/journal.pbio.1002324)

567   19.   Ruel, J. J. & Ayres, M. P. 1999 Jensen's inequality predicts effects of environmental

568   variation. *Trends Ecol. Evol.* **14**, 361–366. (doi:10.1016/S0169-5347(99)01664-X)

569   20.   Roitberg, B. D. & Mangel, M. 2016 Cold snaps, heatwaves, and arthropod growth. *Ecol.*

570   *Entomol.* **41**, 653–659. (doi:10.1111/een.12324)

571   21.   Pörtner, H. O. & Knust, R. 2007 Climate Change Affects Marine Fishes Through the

572   Oxygen Limitation of Thermal Tolerance. *Science (80-.).* **315**, 95–97.

573   (doi:10.1126/science.1135471)

574   22.   Rideout, R. M., Rose, G. A. & Burton, M. P. M. 2005 Skipped spawning in female

575   iteroparous fishes. *Fish Fish.* **6**, 50–72.

576   23.   Pauly, D. & Pullin, R. S. V 1988 Hatching time in spherical, pelagic, marine fish eggs in

577   response to temperature and egg size. *Environ. Biol. fishes* **22**, 261–271.

578   24.   O'Connor, M. I., Bruno, J. F., Gaines, S. D., Halpern, B. S., Lester, S. E., Kinlan, B. P. &

579   Weiss, J. M. 2007 Temperature control of larval dispersal and the implications for marine

580   ecology, evolution, and conservation. *Proc. Natl. Acad. Sci. U. S. A.* **104**, 1266–1271.

581   (doi:10.1073/pnas.0603422104)

582   25.   Neuheimer, A. B., Thresher, R. E., Lyle, J. M. & Semmens, J. M. 2011 Tolerance limit for

583   fish growth exceeded by warming waters. *Nat. Clim. Chang.* **1**, 110–113.

584   (doi:doi:10.1038/nclimate1084)

585   26.   Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D.

586   C. & Martin, P. R. 2008 Impacts of climate warming on terrestrial ectotherms across

587   latitude. *Proc. Natl. Acad. Sci. U. S. A.* **105**, 6668–6672. (doi:10.1073/pnas.0709472105)

588   27.   Paaijmans, K. P., Heinig, R. L., Seliga, R. a., Blanford, J. I., Blanford, S., Murdock, C. C.

589   & Thomas, M. B. 2013 Temperature variation makes ectotherms more sensitive to climate

590   change. *Glob. Chang. Biol.* **19**, 2373–2380. (doi:10.1111/gcb.12240)

591   28.   Estay, S., Clavijo-Baquet, S., Lima, M. & Bozinovic, F. 2011 Beyond average: An

592   experimental test of temperature variability on the population dynamics of Tribolium

593   confusum. *Popul. Ecol.* **53**, 53–58. (doi:10.1007/s10144-010-0216-7)

594   29.   Pickett, E. J., Thomson, D. L., Li, T. A. & Xing, S. 2015 Jensen's Inequality and the

595   Impact of Short-Term Environmental Variability on Long-Term Population Growth Rates.

596   *PLoS One* **10**, e0136072. (doi:10.1371/journal.pone.0136072)

597   30.   Bernhardt, J. R., Sunday, J. M., Thompson, P. L. & O'Connor, M. I. 2018 Nonlinear

598   averaging of thermal experience predicts population growth rates in a thermally variable

599   environment. *Proc. R. Soc. B Biol. Sci.* **285**. (doi:10.1098/rspb.2018.1076)

600   31.   Stillman, J. H. 2019 Heat waves, the new normal: Summertime temperature extremes will

601   impact animals, ecosystems, and human communities. *Physiology* **34**, 86–100.

602   (doi:10.1152/physiol.00040.2018)

603   32.   Schulte, P. M., Healy, T. M. & Fangue, N. a. 2011 Thermal performance curves,

604   phenotypic plasticity, and the time scales of temperature exposure. *Integr. Comp. Biol.* **51**,

605   691–702. (doi:10.1093/icb/icr097)

606   33.   Dell, A. I., Pawar, S. & Savage, V. M. 2011 Systematic variation in the temperature

607   dependence of physiological and ecological traits. *Proc. Natl. Acad. Sci. U. S. A.* **108**,

608   10591–6. (doi:10.1073/pnas.1015178108)

609   34.   Dell, M., Jones, B. F., Olken, B. A. & Gates, M. 2014 What Do We Learn from the

610   Weather☐? The New Climate – Economy Literature. **52**, 740–798.

611   35.   Ohlberger, J., Edeline, E., Vøllestad, L. A., Stenseth, N. C. & Claessen, D. 2011

612   Temperature-driven regime shifts in the dynamics of size-structured populations. *Am. Nat.*

613   **177**, 211–223. (doi:10.1086/657925)

614   36.   Lindmark, M., Huss, M., Ohlberger, J. & Gårdmark, A. 2018 Temperature-dependent

615   body size effects determine population responses to climate warming. *Ecol. Lett.* **21**, 181–

616   189. (doi:10.1111/ele.12880)

617   37.   Rudolf, V. H. W. & Roman, A. 2018 Trophic structure alters consequences of

618   environmental warming. *Oikos* **127**, 1646–1656. (doi:10.1111/oik.05535)

619   38.   Vázquez, D. P., Gianoli, E., Morris, W. F. & Bozinovic, F. 2017 Ecological and

620   evolutionary impacts of changing climatic variability. *Biol. Rev.* **92**, 22–42.

621   (doi:10.1111/brv.12216)

622   39.   Post, E. 2013 *Ecology of climate change: the importance of biotic interactions*. Princeton

623   University Press.

624   40.   Vasseur, D. A. & McCann, K. S. 2005 A mechanistic approach for modeling temperature-

625   dependent consumer-resource dynamics. *Am. Nat.* **166**, 184–198. (doi:10.1086/431285)

626   41.   Binzer, A., Guill, C., Rall, B. C. & Brose, U. 2016 Interactive effects of warming,

627   eutrophication and size structure: Impacts on biodiversity and food-web structure. *Glob.*

628   *Chang. Biol.* **22**, 220–227. (doi:10.1111/gcb.13086)

629   42.   Sentis, A., Binzer, A. & Boukal, D. S. 2017 Temperature-size responses alter food chain

630   persistence across environmental gradients. *Ecol. Lett.* **20**, 852–862.

631   (doi:10.1111/ele.12779)

632   43.   Fussmann, K. E., Schwarzmüller, F., Brose, U., Jousset, A. & Rall, B. C. 2014 Ecological

633   stability in response to warming. *Nat. Clim. Chang.* **4**, 206–210.

634   (doi:10.1038/nclimate2134)

635   44.   Englund, G., Öhlund, G., Hein, C. L. & Diehl, S. 2011 Temperature dependence of the

636   functional response. *Ecol. Lett.* **14**, 914–921. (doi:10.1111/j.1461-0248.2011.01661.x)

637   45.   Angilletta, M. J. 2006 Estimating and comparing thermal performance curves. *J. Therm.*

638   *Biol.* **31**, 541–545. (doi:10.1016/j.jtherbio.2006.06.002)

639   46.   Amarasekare, P. & Savage, V. 2012 A framework for elucidating the temperature

640   dependence of fitness. *Am. Nat.* **179**, 178–91. (doi:10.1086/663677)

641   47.   Schoolfield,R. M., Sharpe,P. J. & Magnuson,C. E. 1981 Non-linear regression of

642   biological temperature-dependent rate models based on absolute reaction-rate theory. *J.*

643   *Theor. Biol.* **88**, 719–719.

644   48.   Padfield, D., Yvon-Durocher, G., Buckling, A., Jennings, S. & Yvon-Durocher, G. 2016

645   Rapid evolution of metabolic traits explains thermal adaptation in phytoplankton. *Ecol.*

646   *Lett.* **19**, 133–142. (doi:10.1111/ele.12545)

647   49.   Bernhardt, J. R., Sunday, J. M. & O'Connor, M. I. 2018 Metabolic Theory and the

648   Temperature-Size Rule Explain the Temperature Dependence of Population Carrying

649   Capacity. *Am. Nat.* **192**, 687–697. (doi:10.1086/700114)

650   50.   Sentis, A., Haegeman, B. & Montoya, J. M. 2019 Stoichiometric constraints modulate the

651   effects of temperature and nutrients on biomass distribution and community stability.

652   *bioRxiv* , 1–52. (doi:10.1101/589895)

653   51.   Fussmann, G. F. & Heber, G. 2002 Food web complexity and chaotic population

654   dynamics. *Ecol. Lett.* **5**, 394–401. (doi:10.1046/j.1461-0248.2002.00329.x)

655   52.   Pörtner, H. O. & Farrell, A. P. 2008 ECOLOGY: Physiology and Climate Change.

656   *Science (80-.).* **322**, 690–692. (doi:10.1126/science.1163156)

657   53.   Quinn, T. J. & Deriso, R. B. 1999 *Quantitative fish dynamics*. New York: Oxford

658   University Press.

659   54.   Estay, S., Lima, M. & Bozinovic, F. 2014 The role of temperature variability on insect

660   performance and population dynamics in a warming world. *Oikos* **123**, 131–140.

661   (doi:10.1111/j.1600-0706.2013.00607.x)

662   55.   Bozinovic, F., Bastías, D. a., Boher, F., Clavijo-Baquet, S., Estay, S. A. & Angilletta, M.

663   J. 2011 The Mean and Variance of Environmental Temperature Interact to Determine

664   Physiological Tolerance and Fitness. *Physiol. Biochem. Zool.* **84**, 543–552.

665   (doi:10.1086/662551)

666   56.   Rall, B. Ö. C., Vucic-Pestic, O., Ehnes, R. B., EmmersoN, M. & Brose, U. 2010

667   Temperature, predator-prey interaction strength and population stability. *Glob. Chang.*

668   *Biol.* **16**, 2145–2157. (doi:10.1111/j.1365-2486.2009.02124.x)

669   57.   Iles, A. C. 2014 Toward predicting community-level effects of climate: Relative

670   temperature scaling of metabolic and ingestion rates. *Ecology* **95**, 2657–2668.

671   (doi:10.1890/13-1342.1)

672   58.   Kratina, P., Greig, H. S., Thompson, P. L., Carvalho-Pereira, T. S. A. & Shurin, J. B. 2012

673   Warming modifies trophic cascades and eutrophication in experimental freshwater

674   communities. *Ecology* **93**, 1421–1430. (doi:10.1890/11-1595.1)

675   59.   Imsland, A. K., Foss, A., Folkvord, A., Stefansson, S. O. & Jonassen, T. M. 2005 The

676   interrelation between temperature regimes and fish size in juvenile Atlantic cod (Gadus

677   morhua): Effects on growth and feed conversion efficiency. *Fish Physiol. Biochem.* **31**,

678   347–361. (doi:10.1007/s10695-005-4244-8)

679   60.   Dell, A. I., Pawar, S. & Savage, V. M. 2011 Systematic variation in the temperature

680   dependence of physiological and ecological traits. *Proc. Natl. Acad. Sci. U. S. A.* **108**,

681   10591–10596. (doi:10.1073/pnas.1015178108)

682   61.   Savage, V. M., Gillooly, J. F., Brown, J. H., West, G. B. & Charnov, E. L. 2004 Effects of

683   body size and temperature on population growth. *Am. Nat.* **163**, 429–441.

684   (doi:10.1086/381872)

685   62.   Uszko, W., Diehl, S., Englund, G. & Amarasekare, P. 2017 Effects of warming on

686   predator–prey interactions – a resource-based approach and a theoretical synthesis. *Ecol.*

687   *Lett.* **20**, 513–523. (doi:10.1111/ele.12755)

688   63.   Lindmark, M., Ohlberger, J., Huss, M. & Gårdmark, A. 2019 Size-based ecological

689   interactions drive food web responses to climate warming. *Ecol. Lett.* **22**, 778–786.

690   (doi:10.1111/ele.13235)

691   64.   Van De Wolfshaar, K. E., De Roos, A. M. & Persson, L. 2008 Population feedback after

692   successful invasion leads to ecological suicide in seasonal environments. *Ecology* **89**,

693   259–268. (doi:10.1890/06-2058.1)

694   65.   Crisci, C., Bensoussan, N., Romano, J. C. & Garrabou, J. 2011 Temperature anomalies

695   and mortality events in marine communities: Insights on factors behind differential

696   mortality impacts in the NW Mediterranean. *PLoS One* **6**.

697   (doi:10.1371/journal.pone.0023814)

698   66.   Safaie, A., Silbiger, N. J., McClanahan, T. R., Pawlak, G., Barshis, D. J., Hench, J. L.,

699   Rogers, J. S., Williams, G. J. & Davis, K. A. 2018 High frequency temperature variability

700   reduces the risk of coral bleaching. *Nat. Commun.* **9**, 1–12. (doi:10.1038/s41467-018-

701   04074-2)

702   67.   Temple, G. K. & Johnston, I. A. 1997 The thermal dependence of fast-start performance

703   in fish. *J. Therm. Biol.* **22**, 391–401. (doi:10.1016/S0306-4565(97)00058-2)

704   68.   Grigaltchik, V. S., Ward, A. J. W. & Seebacher, F. 2012 Thermal acclimation of

705   interactions: Differential responses to temperature change alter predator-prey relationship.

706   *Proc. R. Soc. B Biol. Sci.* **279**, 4058–4064. (doi:10.1098/rspb.2012.1277)

707   69.   Geerts, A. N. et al. 2015 Rapid evolution of thermal tolerance in the water flea Daphnia.

708   *Nat. Clim. Chang.* **5**, 665–668. (doi:10.1038/nclimate2628)

709