Trophic phenological mismatch: Disconnects between underlying ecological theory and climate change responses

1 **Title:** Trophic phenological mismatch: Disconnects between underlying ecological theory and climate

2 change responses

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36

Abstract

Many researchers hypothesize that climate change will lead to phenological mismatches—where the timing of critical life history events between interacting species becomes de-synchronized with potential negative consequences for those interacting species and their ecological communities. Yet, evidence documenting negative impacts on fitness is mixed. The most common ecological theory that underlies these studies is the Cushing match-mismatch hypothesis. It offers a testable hypothesis that—when combined with a system's pre-climate change baseline condition—can predict the consequences of desynchronized phenology due to climate change. However, a review of the current literature shows that none of the studies collected the data required to provide strong tests of this major hypothesis, making it difficult to assess support for it. Further, 74% of studies fail to define pre-climate change baselines in their study system, making predictions about climate change impacts on consumer fitness difficult. To accurately predict the magnitude and prevalence of mismatches due to climate change, relating empirical observations to underlying mechanisms through hypothesis testing will be required. By adjusting their study designs, researchers can more rigorously test the Cushing hypothesis. We highlight how improved approaches could rapidly advance our mechanistic understanding and thus allow robust predictions of shifts with continuing climate change.

Introduction

Climate change is causing phenological shifts—changes in the timing of life history events—that vary across species as well as between functional groups and trophic levels (Ovaskainen et al. 2013; CaraDonna et al. 2014; Thackeray et al. 2016). Such species-specific variation in response to climate change has led to changes in the relative timing of key activities (phenological synchrony) among interacting species (Kharouba et al. 2018). These changes have caused fitness consequences—often termed 'phenological mismatch' (Box 1)—and have influenced ecosystem-level properties in some contexts (Post and Forchhammer 2008; Burkle et al. 2013; Plard et al. 2014; Doiron et al. 2015), but not others (Vatka et al. 2011; Burthe et al. 2012). Recent theoretical (Johansson et al. 2015; Bewick et al.

63 2016) and empirical studies (e.g. Samplonius et al. 2016) based in single systems have worked to improve

64 predictions and address diverse findings. Yet—while there is general agreement that predicting

65 phenological mismatches is critical for determining the extent to which pair-wise species interactions,

66 communities, and ecosystem function (e.g. pollination) will be affected by climate change—we still have

67 no general ability to predict the outcomes of shifts in phenological synchrony due to climate change.

68 Here, we argue that much of the difficulty in predicting the consequences of climate change-driven

69 shifts in synchrony is due to a disconnect between ecological theory and current empirical approaches

70 used in studies of phenological mismatch. Current methodological inconsistencies across studies and

71 intrinsic differences across systems make it difficult to test the relevant underlying ecological theory in

72 the context of climate change. Without better evidence, we cannot attribute variation in findings of

73 phenological match vs. mismatch across studies to species, site, or more specific mechanisms. Without an

74 understanding of the mechanisms underlying the well-documented patterns in phenological shifts, our

75 ability to make accurate predictions about species' responses, and species' interactions, to climate change

76 remains limited (O'Connor et al. 2012; Chmura et al. 2018).

77 Here we focus on the widely-cited Cushing match-mismatch, or trophic mismatch, hypothesis

78 (1974), the most commonly applied hypothesis concerning consumer-resource interactions in this

79 literature. We show how advances could come from direct tests of the hypothesis and clear definitions of

80 baselines, when possible. Our aim is not to put forward additional hypotheses about the context in which

81 phenological mismatch will occur, which has been reviewed extensively elsewhere (e.g., Miller-Rushing

82 2010; Renner and Zohner 2018), but rather to help guide the study of phenological mismatch by outlining

83 a path forward to develop robust climate change predictions that can scale up to inference across sites and

84 systems.

85 Although the Cushing hypothesis has been applied to other types of interactions (e.g. mutualism),

86 we limit our discussion to antagonistic interactions between consumers and their food resources. Below,

87 we provide an overview of the Cushing hypothesis and then outline the divide between the hypothesis and

88 the empirical studies using a systematic literature review of phenological mismatch. We then discuss how

89 current approaches are impeding greater progress in the field, and how changes to research methodologies

90 could rapidly advance our understanding and help forecast of the impacts of climate change on ecological

91 communities—the ultimate goal of most of the phenological mismatch literature.

92

Overview of the main ecological theory

94 The Cushing match-mismatch hypothesis is the most common ecological theory underlying

95 phenological mismatch studies (Appendix). This hypothesis predicts the often-shown concave-down

96 curve between consumer fitness and relative timing between the consumer and its resource (1974; Figure

97 1). While this curve has been applied across many ecosystems (e.g. Winder and Schindler 2004; Vatka et

98 al. 2011; Arula et al. 2014), the theory originally emerged from the marine fisheries literature as a way to

99 explain the variation in population recruitment of fish stocks.

100 Based on life-history theory, the Cushing match-mismatch hypothesis postulates that selective

101 pressure should cause the consumer to temporally 'match' the peak of its energetic phase with the peak of

102 resource availability (Figure 1). Given this strong selective pressure, if there is any change to the relative

103 timing of the interaction, there will be a decrease in fitness for the consumer (i.e., a mismatch), thus

104 producing a concave-down curve (Figure 1). For example, if a consumer emerges too early in the spring

105 (Figure 1b) and the resource has not yet emerged, the consumer will risk starvation. At the curve's limits,

106 consumer fitness should fall to zero when the change in relative timing is sufficiently large (Figure 1). For

107 example, the early-emerging consumer (Figure 1b) can only survive so many days without food.

108 This hypothesis is based on two important assumptions. First, the resource is the major controller

109 on consumer fitness (i.e., strong interaction strength, bottom-up control; Cury et al, 2003). Second, the

110 consumer and resource must present a certain degree of seasonality (e.g., resource is only available for

111 part of the year; Durant et al. 2005; Durant et al. 2007), limiting the optimal period for growth and

112 reproduction for the consumer. If neither of these assumptions is met, then fitness consequences due to

113 changes in the relative timing of the interaction will be either weak or non-existent.

114

Disconnect between theory and empirical studies

In its original state, the hypothesis has been debated, contested and criticized, particularly in the marine literature (Leggett and DeBlois 1994; Durant et al. 2007). In part because, although a relatively simple hypothesis, it is inherently difficult to test in the field, an assertion even Cushing himself made. Indeed, the shape and strength of the relationship of the curve varies greatly across observational studies (e.g., Philippart et al. 2013; Reed et al. 2013; Plard et al. 2014; Atkinson et al. 2015). While some have suggested that this is because of data limitations and the model's implication of complex multitrophic dynamics (Durant et al. 2007; Kerby et al. 2012), we argue that there are two key theoretical areas that make it difficult to determine whether this hypothesis is widely supported in the context of climate change: studies often fail to rigorously test the Cushing hypothesis and/or test pre-climate change conditions (Figure 2). Below, we introduce the current objectives of the phenological mismatch literature and then discuss these two areas.

To put our argument in context, we systematically reviewed the phenological mismatch literature. From this search, we examined 43 observational studies that met our criteria (see Appendix for details) for evaluating the effects of a change in relative timing on the fitness or performance (hereafter referred to as performance) of the consumer. The majority of the studies (27/43) focused on: i) documenting how climate change is affecting the timing of a trophic interaction and how those changes have affected the consumer's performance; and ii) evaluating the roles of abiotic and biotic factors in influencing synchrony. The ultimate goal of these studies was to predict the impacts of climate change on ecological communities (hereafter called 'climate change' studies). Our database also included studies (16/43) whose aim was to understand the underlying processes related to timing (e.g., coevolution, life history trade offs, food web dynamics) that drive consumer or resource dynamics (hereafter called 'fundamental studies'), independently of climate change.

i) Testing the Cushing hypothesis

The Cushing hypothesis offers testable predictions of the magnitude and direction of demographic

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141   changes in response to climate-change driven shifts in synchrony. To date, much research in the

142   biological impacts of climate change literature has focused on the direct relationships between organisms

143   and the abiotic environment (e.g., Menzel et al. 2006, Chen et al. 2011) rather than testing predictions

144   about the outcomes of species' responses to changes in abiotic factors (Lavergne et al. 2010; O'Connor et

145   al. 2012; Mouquet et al. 2015; Barner et al. 2018). However, progress on the Cushing hypothesis requires

146   rigorously testing the assumptions and ultimate mechanisms from a diversity of ecological and

147   evolutionary theory (Figure 2). This represents the major challenge of the hypothesis and—we argue—

148   may be why support for it has been so mixed.

149   Many mechanisms can produce the Cushing curve, and they vary across systems, space and time.

150   Here we focus on the ultimate mechanisms related to life history theory and food web theory.

151   Mechanisms predicted by life-history theory (Box 1), for example, trade-offs between fecundity and

152   mortality, and bet-hedging strategies (Figure 2), can produce the Cushing curve—as consumers maximize

153   their fitness through ideal timing with their primary resource—this forms the theoretical basis for the

154   original hypothesis. The Cushing hypothesis, however, is also connected to food web theory which

155   focuses on predator prey dynamics (Box 1) and is related to the timing of a consumer to its food resource.

156   Identifying the ultimate mechanisms (e.g., a specific life history trade-off) relates to the likelihood

157   that the key assumptions of the Cushing hypothesis are met (Figure 2). For example, if mechanisms such

158   as density dependence or top-down population regulation are thought to be at play, then the first

159   assumption of the hypothesis is unlikely to be met. Even when both of the assumptions of the Cushing

160   hypothesis have been met, identifying the ultimate mechanism is critical to predicting how interactions

161   will respond to climate change (discussed in more detail in the next section; Figure 2). Given the diversity

162   of theory related to the Cushing hypothesis and therefore potential diversity in the outcomes in consumer

163   performance (e.g., magnitude, direction) due to phenological shifts in synchrony, the better our

164   mechanistic understanding is of these patterns, the more robust our predictions will be (e.g., steepness of

165   the Cushing curve).

166   Studies deviate in what forces they hypothesize control the peak in the food resource (a critical

167   component of the Cushing curve and a key assumption, see Figure 1 and 2). For example, in aquatic

168   systems—where top-down forces are generally more influential compared to terrestrial systems (Shurin et

169   al. 2005)—many studies suggest that the resource peak is controlled by release from, or predation by, a

170   consumer (Carpenter and Kitchell 1996; Shurin and Seabloom 2005; Borer et al. 2006). If the resource

171   peak is controlled by release from a predator rather than abiotic factors, then the first assumption of the

172   hypothesis is unlikely to be met and the subsequent predictions from the Cushing hypothesis are unlikely

173   to hold. This is a very different hypothesis from others that suggest seasonality in the environment

174   produces the resource peak (Hampton et al. 2006). In terrestrial systems, the relative contribution of direct

175   vs. indirect effects on consumer dynamics remains poorly understood (e.g. Boggs and Inouye 2012) and

176   these two hypotheses can result in different types of effects on population dynamics.

177   The diversity of ecological theory that can produce the basic shape of the Cushing curve means that

178   different researchers may collect very different data depending on what mechanism they suspect underlies

179   the curve in their particular system or what their main objective is. Researchers studying the hypothesis

180   from the lens of life history theory require per capita estimates of fitness, including measurements of

181   fecundity and mortality, and how they vary across ontogeny; such measurements allow researchers to

182   assess fitness consequences at the level of selection (i.e., the individual) and to directly link any fitness

183   changes to timing. Studies addressing the Cushing hypothesis from the perspective of food web theory

184   require equivalent data on the consumer and resource but do not require per capita fitness consequences

185   for the consumer.

186   Strong tests of the Cushing hypothesis include clear tests of the assumptions alongside tests of

187   multiple potential mechanisms underlying relationships between phenological match and consumer

188   performance. To accomplish this, equivalent data would ideally be assessed for both the consumer and

189   resource—at the level of the individual when possible. Equivalent data for the consumer and resource

190   facilitate testing assumptions and multiple mechanisms related to the Cushing hypothesis at once.

191   Without at least population-level data on the resource, it is difficult to test the second assumption of the

192   hypothesis; for example, resource abundance can be used to determine the likelihood that consumers will

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193 encounter enough resource at the tails of their temporal distributions, thus defining the degree of

194 seasonality in the resource. Per-capita data on the resource, when available, also extend our mechanistic

195 understanding beyond the consumer, thus improving our ability to make predictions of climate change-

196 driven phenological mismatches for the interaction in its entirety. For example, fine-scale data on the

197 resource are needed to fully incorporate feedbacks between the consumer and resource (e.g., Thackeray

198 2012), measure interaction strength (which informs a key assumption of the hypothesis, Miller-Rushing et

199 al. 2010), and accurately predict changes in resource abundance due to climate change. Together, these

200 data help to determine the wider implications of phenological mismatches for the community (e.g.,

201 Nakazawa and Doi 2012; Revilla et al. 2014).

202 Currently such data are non-existent in this literature (i.e. none of the pair-wise interactions had

203 individual-level data for both the consumer and resource). Of the interactions we examined with per-

204 capita performance data on the consumer (i.e. life history; n=28 interactions), none had equivalent

205 measures of performance on the resource (Table 1). For the majority of these interactions (18/28), the

206 researchers measured performance at the community level for the resource (e.g. biomass; Table 1) and

207 many had no measure at all for the resource (6/28 interactions; Table 1). As expected, researchers that

208 measured population- or community-level data on the consumer (i.e. food-web; n=18 interactions)

209 collected equivalent data on the resource and consumer (e.g. abundance). For the majority of these

210 interactions, researchers also collected population-level (7/18) or community level data for the resource

211 (7/18) (Table 1). Across all life history and food-web interactions, researchers measured per-capita

212 performance on the resource for only one interaction (Philippart et al. 2003).

213 Part of these discrepancies may stem from differing generation times—studies that can easily

214 observe a resource curve shaped by predation often focus on organisms with generation times on the scale

215 of days to week. For example, aquatic studies that focus on phytoplankton as the resource may observe

216 many generations in one summer while a terrestrial study focused on caterpillars in temperate areas would

217 generally observe a comparably smaller number generations (e.g. 1-2, depending on latitude and species

218 for caterpillars). When populations turn over too quickly to track individuals, researchers struggle to

219   collect robust data on per capita fitness. The fundamental difference in the scale of generation times

220   pervades aquatic/terrestrial comparisons, particularly at lower trophic levels (Borer et al. 2005; Shurin et

221   al. 2005; Gruner et al. 2008), and may drive the difference in the objectives of aquatic vs. terrestrial

222   studies in the phenological mismatch literature. Indeed, the majority of researchers studying aquatic-based

223   interactions in our review approached the Cushing hypothesis from the perspective of food-web theory

224   (15/20 interactions), whereas researchers approached terrestrial-based interactions from life-history theory

225   (23/26; Table 2).

226   A further divide across studies may come from the size, and population size, of the consumer,

227   properties correlated with generation time: it can be difficult to collect per capita fitness data when

228   consumers are too small and numerous, ultimately making it difficult to track the fate of individuals. In

229   cases where individuals can be distinguished, marked and monitored, it is possible to gather per-capita

230   data; otherwise data are more likely to be aggregated at the population or community-level. Of the life

231   history interactions, the majority of consumers were birds (19/28) and mammals (6/25; Table 2).

232   Comparatively, invertebrates were measured at the population or community level and the vast majority

233   were aquatic (11/12) (Table 2). Therefore, only certain classes of organisms are tested for each category

234   of mechanisms and in one type of biome, further limiting generalizations across systems.

235   This places the phenological mismatch studies on a continuum: at one end, aquatic studies focus

236   generally on food web mechanisms, collect equivalent data on the consumer and resource but no per-

237   capita fitness data and at the other end, terrestrial studies focus on life history theory from the lens of the

238   consumer, collect individual-level data on the timing and fitness of the consumer, with much less

239   information on the resource. The fundamental problem with these approaches is that researchers test only

240   one piece of the much larger field of mechanisms that could underlie the Cushing curve. Though it is

241   highly possible that both food web and life history theory together explain many of the consumer-

242   resource systems studied, data limitations make it hard to assess mechanisms related to both theories at

243   once. Consequently, most studies do not actually provide strong tests of the Cushing hypothesis, making

244   it difficult to refute the hypothesis if no evidence is found, a prevalent issue in ecology and evolution

245   (Betini et al. 2017). If researchers find their proposed mechanisms explain little of the variation they

246   observe, they rarely have the data to test alternative hypotheses.

247   Without strong support for the Cushing hypothesis (i.e., high explained variation and clear

248   patterns that align with predictions), the mechanisms underlying it will be uncertain. This uncertainty can

249   be caused by two reasons: (1) hypotheses that are not mutually exclusive (i.e. different mechanisms have

250   the same predictions). For example, the relative timing of an interaction will change in the same direction

251   regardless of whether temperature (or some other abiotic factor) directly or indirectly affects a resource's

252   peak; or (2) considering multiple mechanisms yields different predictions than considering only a single

253   mechanism. For example, researchers have pointed out how a broader perspective on life history, such as

254   including other sources of mortality beyond those related to resource access or alternative resource types

255   (Samplonius et al. 2016), can lead to alternative predictions than the synchrony predicted by the Cushing

256   curve (Singer and Parmesan 2010; Johannsson & Jonzen 2012).

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258

259   *ii) Testing pre-climate change conditions*

260   Applying the Cushing hypothesis to understanding—and ideally predicting—the consequences of

261   climate change for interacting species requires more than testing the assumptions and underlying

262   mechanisms of the hypothesis (Figure 2). If the assumptions of the Cushing hypothesis are met and the

263   mechanisms understood, researchers still need an understanding of the system dynamics before climate

264   change, and the phenological cues that affect the timing of consumer and resource levels, to predict what

265   shifts in the climate have—and will—do to the timing and fitness of the players (Figure 2). Below we

266   discuss these steps in more detail.

267

268   *(a) Identifying pre-climate change baselines*

269   The concept of pre-climate change baseline (i.e., defining the range of natural variation) is rarely, if

270   ever, considered by phenological mismatch studies; yet, establishing a baseline in a system has important

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271 implications for the Cushing hypothesis in both climate change and fundamental studies. Of the studies

272 we considered, only 26% (11/43) of the studies began before the early 1980s, the same time that

273 pronounced recent climate change began (Solomon et al. 2007). Even in this subset of studies, not all

274 studies had more than three years of data (2/11 had only one or two years of data for inference). This is

275 also an issue with the phenological synchrony literature (Box 1), which does not necessarily consider the

276 ecological consequences of shifts in synchrony (Kharouba et al. 2018). Even those studies with time-

277 series that extend into decades before the 1980s do not explicitly define a pre-climate change baseline in

278 synchrony (but see Philippart et al. 2003; Adrian et al. 2006; Arula et al. 2014).

279   There are several major implications of not establishing a pre-climate change baseline (Figure 3).

280 First, studies without a baseline are implicitly assuming conditions of stationarity (i.e., a constant

281 underlying probability distribution) before climate change occurred (Figure 3a; Wolkovich et al. 2014).

282 This is problematic when climate change has led to non-stationarity to different extents in different

283 systems (Figure 3a). Without a defined pre-climate change baseline in the system, we do not know

284 whether, and to what magnitude, we should predict a divergence in synchrony due to climate change

285 (Figure 3a). It is then further difficult to determine how much of the observed change in the interaction

286 can be attributed to climate change, some other driver, for example nitrogen deposition (Edmondson

287 1994), land use change (Sala et al. 2000), species introductions (e.g., Ricciardi et al. 1998; Fritts and

288 Rodda 1998; Verschuren et al. 2002;), or natural variation. Thus, knowledge of the pre-climate change

289 baseline may rule out climate change and identify other drivers, which is key for the prioritization of

290 conservation management decisions for threatened species.

291   Second, these studies confound a pre-climate change baseline with the peak of the Cushing curve:

292 that is, they assume that fitness was highest before climate change because the consumer's timing was

293 well matched to the resource's (i.e. the synchrony hypothesis; Box 1; Figure 3b; Singer and Parmesan

294 2010). The resulting prediction is that climate change will necessarily change the relative timing of the

295 interaction (i.e. non-stationarity) leading to a decline in the consumer's fitness (Figure 2, Figure 3b).

296 However, without knowledge of the pre-climate change baseline, it is difficult to predict the direction and

297 magnitude of fitness consequences due to climate change-driven shifts in synchrony, especially when

298 alternative conditions could be the baseline (Figure 3b,c).

299   An alternative hypothesis put forward by Singer and Parmesan (2010) suggests that in some

300 contexts, 'adaptive asynchrony' (i.e. when the most energetically demanding phase of the consumer is not

301 lined up with the peak resource availability for many individuals in the population; Box 1; Figure 3b).

302 They postulate that in some systems, asynchrony in many individuals in a population might be adaptive

303 due to life-history tradeoffs. This could happen when a consumer cannot measure the timing of its

304 resource well (Singer and Parmesan 2010), for example; in this scenario, some individuals would appear

305 mismatched, while others would appear matched. This scenario may persist most often when fitness

306 consequences of mismatch are not extremely high; otherwise it could lead to population extirpation

307 (Figure 3b).

308   In either hypothesis (i.e. synchrony vs. adaptive asynchrony; Figure 3b), a pre-climate change

309 baseline of asynchrony (Box 1; Figure 3c) could occur through several mechanisms. Shifts in the drivers

310 of phenology for the consumer or resource (e.g., nutrient enrichment) could have pushed the system away

311 from synchrony before climate change. An asynchronous baseline would also be predicted—at times—by

312 a co-evolutionary arms race: when the resource is ahead in the arms-race, asynchrony would the predicted

313 baseline (Figure 3c), this would then shift back towards synchrony when the consumer is winning the

314 arms race. In systems where asynchrony or other transient conditions might be the baseline state, our

315 ability to anticipate the effects of climate change will be even more challenging as these transient

316 conditions could lead to vastly different predictions under climate change (Figure 3c). For example,

317 interactions might become less (i.e. fitness increases) or even more mismatched (i.e. fitness decreases)

318 with climate change (Figure 3b-c).

319   The pre-climate change baseline is also dependent on the ultimate mechanism(s) generating the

320 Cushing curve (Figure 2). For example, a species that provisions its offspring with resources acquired

321 during the breeding period (i.e., an income breeder; e.g., West Greenland caribou: *Rangifer tarandus*) is

322 predicted to have a pre-climate change baseline of synchrony, whereas a species that provisions its

323   offspring with resources gained prior to reproduction (i.e., a capital breeder; e.g., muskoxen*: Ovibos*

324   *moschatus*) is more likely to have a baseline of asynchrony (Kerby and Post 2013). Therefore, researchers

325   need an understanding of the system dynamics before climate change began.

326   Establishing a pre-climate change baseline also has implications for fundamental studies that aim

327   to understand the underlying processes of consumer-resource dynamics. A pre-climate change baseline

328   would determine whether the system is most probably in equilibrium or in transient dynamics. For

329   example, life-history trade-offs, including those that can cause patterns predicted by the Cushing

330   hypothesis, predict some form of equilibrium conditions, but if climate change has pushed the system

331   away from a previous baseline, then the system might likely be in a transient phase rather than at

332   equilibrium (Figure 3). To this end, an understanding of the system's pre-climate change baseline state is

333   important for providing context and even designing fundamental studies.

334

335   *(b) Identifying proximate cues*

336   For climate change to lead to phenological mismatch, the underlying assumption is that changes in

337   climate will drive changes in the relative timing of species interactions. Therefore, predicting how climate

338   change will affect the relative timing of a consumer and resource, and potentially the fitness of the

339   consumer, will also depend on the identification of the proximate phenological cues of the consumer and

340   resource (Figure 2). For example, climate change is likely to lead to fitness declines for a consumer that

341   has a pre-climate change baseline of synchrony and that shares different environmental cues with its

342   resource (Figure 2). Currently, relatively little is known about the similarity of cues for interacting species

343   across trophic levels (Chmura et al. 2018). Finally, predictions will also depend on how phenological cues

344   will change under climate change scenarios (Chmura et al. 2018).

345

346

347   **Towards robust forecasting of phenological mismatch**

348   While the Cushing hypothesis provides testable predictions regarding the consequences of

349 phenological mismatch in response to climate change, it is uncertain how much support there is for it.

350 Here we have suggested two major reasons for this, both of which provide a clear path forward for

351 progress in the field (Figure 2). First, most studies do not actually provide strong tests of the Cushing

352 hypothesis because (a) studies do not collect equivalent fitness and population data on the consumer and

353 resource, and (b) multiple mechanisms are not evaluated. This makes it difficult to refute the Cushing

354 hypothesis if no evidence is found. Unless researchers are extremely clear about the mechanistic

355 hypotheses they are testing, progress will continue to be slow. Second, pre-climate change baselines are

356 not defined in the majority of studies in this literature. Lack of a relevant baseline makes it difficult to

357 determine whether recent phenological mismatch can be attributed to climate change and limits our ability

358 to understand and predict the direction and magnitude of phenological mismatch due to climate change.

359   Moving the field of phenological mismatch forward (i.e., from documentation towards forecasting)

360 requires higher quality data that enables the testing of fundamental hypotheses and defining of key

361 baselines. Below, we highlight how new approaches can improve testing of the Cushing hypothesis.

362 These approaches will also provide the framework for building the required depth in evidence across

363 studies to determine general quantitative patterns in phenological mismatch and their underlying

364 mechanisms, an approach not currently possible given the state of the field.

365

366 *(i) Testing fundamental theory*

367   By having the potential to test multiple mechanisms and define key baselines, the integration of

368 long-term data (i.e. that start before the1980s) and an experimental approach in a single system represents

369 the 'gold standard' to move the field of phenological mismatch forward. However, in the absence of long-

370 term data, the integration of observational data across a spatial gradient in climatic conditions, and thus

371 variation in the relative timing of the interaction, with an experimental study can provide a powerful

372 approach to test multiple hypotheses. For example, Samplonius et al. (2016) combine descriptive and

373 experimental data to test many confounding factors and key assumptions of the Cushing hypothesis in

374 their system (e.g., ontogenetic dietary shifts, habitat quality). Consequently, they advanced the field by

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375 providing a strong test of the Cushing hypothesis, demonstrating that this hypothesis is pertinent in their

376 system, and ruling out competing hypotheses related to habitat quality.

377   Independent of whether observational data is available, experiments can be used to test and

378 disentangle multiple mechanisms, for example direct from indirect effects or abiotic mismatches from

379 phenological ones (e.g., Bauerfeind and Fischer 2013; Rudolf and Singh 2013). Experiments provide a

380 high degree of inference about mechanism that descriptive data alone cannot provide. For example,

381 Berger et al. (2014) manipulated water temperature, stratification depth and the presence/absence of

382 zooplankton in lake mesocosms to separate the direct effects of light and temperature on spring plankton

383 dynamics from effects mediated through the consumer. They showed that temperature had little effect on

384 zooplankton phenology and performance suggesting that climate change is unlikely to result in

385 phenological mismatch in this system. The extrapolation of their results to the lake ecosystem are

386 uncertain, however, given the lack of long-term data in the system and the uncertainty about phenological

387 cues for *Daphnia* in the field (Berger et al. 2014).

388   Baselines themselves can also be used to test multiple mechanisms. Researchers with long-term

389 data can define specific hypotheses about the expected vs. observed patterns of environmental change in

390 their systems and then attribute variation in phenological mismatch to the main driver. For example, many

391 lakes experienced large changes in nutrient inputs in the 1960s and 1970s (e.g., George 2012; Lake

392 Washington (Edmondson 1994)), before the onset of recent climate change in the early 1980s.

393 Researchers can test different breakpoints with their long-term data to determine where the non-linearity

394 most likely began, thus providing evidence for which factor is likely to be the major driver of changes in

395 phenological synchrony. For example, studies have shown that changes in nutrient inputs have had larger

396 impacts on plankton dynamics in Lake Washington than warming over the past three decades (Law et al.

397 2009; Francis et al. 2014).

398   Higher temporal resolution data in some systems may help with teasing apart different mechanisms

399 and testing the assumptions of the Cushing hypothesis. Regardless of aim, ideally, sampling frequency

400 should be relative to the life history of the species of interest. For example, testing any mechanism related

401 to life history theory requires data about ontogeny. In the great tit-winter moth system, caterpillar biomass

402 sampling is usually conducted a few times a week (e.g., Vatka et al. 2014). Given that the larval stage of

403 the winter moth life cycle is typically 4-6 weeks (Holliday 1977; Tikkanen et al. 2000), this sampling

404 frequency allows researchers to obtain an accurate estimate of growth and development for this life cycle

405 stage. In the lower trophic levels of aquatic systems, where there is often quick turnaround between

406 producers and consumers, it can be difficult to determine how strong of an influence producers have on

407 consumers and vice versa (Carpenter and Kitchell 1996). Without higher temporal resolution data, it is

408 difficult to assess whether this key assumption of the Cushing hypothesis (i.e., the dependence of the

409 consumer on the producer) is supported. In cases where there are multiple short, potentially overlapping,

410 generations, determining the seasonal order of the consumer vs. producer is necessary to assess the degree

411 of dependence of the consumer on the producer.

412   Higher temporal resolution data will also help determine the seasonal availability of the consumer

413 and resource, the other key assumption of the Cushing hypothesis (Figure 1b-d). For example, temperate

414 aquatic and terrestrial systems differ in how many organisms survive the winter. While many terrestrial

415 plants and herbivores have dormancy phases during the winter, in aquatic systems some zooplankton are

416 never in complete dormancy (i.e., they remain at low densities), and thus do not fully meet the assumption

417 of the hypothesis. Without more frequent data, accurately estimating the seasonal distribution of the lower

418 trophic levels of some aquatic systems will be difficult. Nevertheless, some aquatic studies have been

419 successful in achieving daily sampling frequency of lower trophic levels (e.g., Wiltshire et al. 2008),

420 suggesting that—though more challenging—critical assumptions of the Cushing hypothesis can be tested

421 in aquatic systems.

422

423 *ii) Defining baselines*

424   Researchers with long-term data have the potential to test whether synchrony vs. asynchrony was

425 the pre-climate change baseline (Figure 2; Figure 3). By testing for a clear peak in fitness across years in

426 relation to the relative timing of the interaction (i.e. evidence for the synchrony hypothesis) in the pre-

16

427 climate change data, researchers can place their system on the Cushing curve (Figure 3). Whenever

428 possible, incorporating the most energetically expensive part of the consumer's phenology or estimating

429 when the measured phenological phase occurs relative to the most expensive part (e.g., food demands of

430 the great tit (*Parus major*)) chicks are highest 9 days after hatching, the phenological phase most

431 commonly monitored; Gebhardt-Henrich 1990; Keller and van Noordwijk 1994; Visser et al. 2006) will

432 help define a peak in consumer fitness. If there is no clear peak in fitness, then well-designed experiments

433 (in systems where possible) that have the ability to reveal the limits of the curve (i.e. where consumer

434 fitness reaches zero) can be used to reject the hypothesis of an asynchrony baseline. Knowledge of

435 when/if different resources are available (e.g. Samplonius et al. 2016) and whether the interaction type

436 changes throughout the season (add example from meta-analysis) can also help describe the limits of the

437 curve.

438   Where long-term data are not available, there is no perfect solution to the challenge of defining a

439 baseline. Researchers with multiple years of data may be able to use inter-annual variation in abiotic

440 conditions (e.g., temperature) to define a baseline, where closer-to mean conditions represent a proxy for

441 a historical baseline and, for example, cooler vs. warmer years act as alternatives to pre- and post- climate

442 change, respectively (e.g., Gullett et al. 2013; Francis et al. 2014). However, extrapolation from short-

443 term datasets can only work if the species responses' to varying climate themselves are not in flux, a

444 criterion difficult to meet in many systems already (Visser et al. 2006; Singer and Parmesan 2010). Null

445 modeling to simulate historical data may be another alternative (e.g., Dornelas et al. 2014; Sgardeli et al.

446 2016; Kharouba et al. 2018). This null model could be used to put the magnitude of observed changes in

447 phenology and performance since significant climate change began into context and to quantify how

448 much variation may be due to noise (i.e., factors other than climate change; Kharouba et al. 2018).

449   When not all required data are available across a long time period, the integration of experimental

450 and observational data for a single system could again be a useful approach (Figure 4). For example, in

451 one study the performance data for an insect herbivore (winter moth; *Operophtera brumata*), and its main

452 host plant (common oak; *Quercus robur*) are not available for more than 10 years from a single location

453 (van Asch and Visser 2007); however, different researchers manipulated the timing of larval emergence

454 relative to bud break to test for support for the Cushing hypothesis (Tikkanen and Julkunen-Tiitto 2003;

455 Figure 4). Although the strength of the relationship may vary across populations (e.g., Visser et al. 1998;

456 Charmantier et al. 2008), a synthesis of the findings from the two approaches (i.e. observational and

457 experimental) can shed light on the state of our knowledge of the system and can guide future research.

458 Here, for this system, we learned where the interaction is currently placed along the curve, how little of

459 the curve is sampled with a 10 year post-climate change time-series, and that—without a clear baseline—

460 it is difficult to predict how the performance of *O. brumata* will be affected by changes in phenological

461 synchrony. Given the knowledge about the Cushing curve for this interaction, modelling pre-climate

462 change baselines based on knowledge of phenological cues using a hindcasting approach (Senner et al.

463 2016; Deacy et al. 2017), process-based phenological models (Chuine and Régnière 2017), and/or

464 phenologically explicit consumer-resource models (Bewick et al. 2016) could help to fill in data about the

465 interaction before climate change began. Experiments could help define the parameters of a process-based

466 model which could then elucidate that mechanisms may—or may not—appear feasible for the interaction

467 (Chuine and Régnière 2017).

468

469 *Final thoughts on forecasting*

470 Given the complexity involved, accurately forecasting phenological mismatch in response to

471 climate change is a major test of ecological theory and methods, and requires a mechanistic understanding

472 of the processes involved to ensure robust predictions of changes in consumer performance (e.g.,

473 steepness of the Cushing curve). Previous work has identified factors that will help predict *when* a

474 mismatch is more likely to lead to a population decline but this work is largely theoretical. While we have

475 outlined here how to work around data limitations, the best tests of mismatch theory will come from data-

476 rich systems where the energetic links between consumer and resource species are well understood. With

477 such information in hand, researchers can then begin to consider forecasting longer-term demographic

478 responses due to mismatch with continued climate change. Forecasting of phenological synchrony can be

479   built off climate projection forecasts whenever phenological cues for both species (Chuine and Régnière

480   2017; Chmura et al. 2018) are well known. Forecasting longer-term demographic responses will require

481   data about lifetime fitness for the consumer and comprehensive data on the resource, a standard that, to

482   our knowledge, has yet to be met by any empirical study to date.

483   As more information is gathered across habitats and diverse consumer-resource interactions,

484   forecasting should eventually move beyond a system-specific approach and towards forecasting diverse

485   systems through a multi-level modeling approach based on our mechanistic understanding of what drives

486   mismatch. Such a model would be built on mechanistic studies of the mismatch hypothesis that carefully

487   measure the fitness, phenologies, interactions and other still-unknown critical attributes of systems. The

488   model would then allow researchers to measure currently unknown but critical attributes of species, sites,

489   and ecosystems that control the shape, strength and uncertainty surrounding the Cushing curve. But

490   progress towards such an approach requires the ability to combine knowledge from across diverse

491   systems into one complex but well-defined mechanistic model. As we have outlined above, most current

492   data in the field make it hard or impossible to compare across systems. Given intrinsic differences

493   between aquatic and terrestrial systems, progress may be accelerated if these systems are considered

494   separately before being combined. Nevertheless, without improved methods – to test multiple

495   mechanisms and define pre-climate change baselines – the goal of general predictions of the ecological

496   consequences of shifts in phenological synchrony will remain well out of reach.

497

503

504

505 **References**

506 Adrian, R., Wilhelm, S. and Gerten, D.*Life-history traits of lake plankton species may govern their phenological*
507 *response to climate warming*. Global change biology, **2006**, Vol. 12(4), pp. 652-661
508

509 Arula, T., Gröger, J., Ojaveer, H. and Simm, M. *Shifts in the spring herring (Clupea harengus membras) larvae and*
510 *related environment in the Eastern Baltic Sea over the past 50 years* PloS one, **2014**, Vol. 9(3), pp. e91304.
511

512 van Asch, M. and Visser, M. E. *Phenology of forest caterpillars and their host trees: the importance of synchrony*
513 Annu. Rev. Entomol., Annual Reviews, **2007**, Vol. 52, pp. 37-55
514

515 Atkinson, A., Harmer, R. A., Widdicombe, C. E., McEvoy, A. J., Smyth, T. J., Cummings, D. G., Somerfield, P. J.,
516 Maud, J. L. and McConville, K. *Questioning the role of phenology shifts and trophic mismatching in a planktonic*
517 *food web*. Progress in Oceanography, **2015**, Vol. 137, pp. 498-512
518

519 Barner, A. K., Chan, F., Hettinger, A., Hacker, S. D., Marshall, K. and Menge, B. A.*Generality in multispecies*
520 *responses to ocean acidification revealed through multiple hypothesis testing*. Global change biology, **2018**, Vol.
521 24(10), pp. 4464-4477.
522

523 Bauerfeind, S. S. and Fischer, K. *Increased temperature reduces herbivore host-plant quality*. Global Change
524 Biology, **2013**, Vol. 19(11), pp. 3272-3282
525

526 Berger, S. A., Diehl, S., Stibor, H., Sebastian, P. and Scherz, A. *Separating effects of climatic drivers and biotic*
527 *feedbacks on seasonal plankton dynamics: no sign of trophic mismatch*. Freshwater Biology, **2014**, Vol. 59(10), pp.
528 2204-2220.
529

530 Betini, G. S., Avgar, T. and Fryxell, J. M. *Why are we not evaluating multiple competing hypotheses in ecology and*
531 *evolution?* Royal Society open science, The Royal Society Publishing, **2017**, Vol. 4(1), pp. 160756
532

533 Bewick, S., Cantrell, R. S., Cosner, C. and Fagan, W. F. *How resource phenology affects consumer population*
534 *dynamics.* The American Naturalist, University of Chicago Press Chicago, IL, **2016**, Vol. 187(2), pp. 151-166
535

536 Boggs, C. L. and Inouye, D. W. *A single climate driver has direct and indirect effects on insect population*
537 *dynamics.* Ecology Letters, **2012**, Vol. 15(5), pp. 502-508
538

539 Borer, E., Seabloom, E., Shurin, J., Anderson, K., Blanchette, C., Broitman, B., Cooper, S. and Halpern, B. *What*
540 *determines the strength of a trophic cascade?* Ecology, **2005**, Vol. 86(2), pp. 528-537
541

542 Borer, E. T., Halpern, B. S. and Seabloom, E. W. *Asymmetry in community regulation: effects of predators and*
543 *productivity*. Ecology, **2006**, Vol. 87(11), pp. 2813-2820
544

545 Burkle, L. A., Marlin, J. C. and Knight, T. M. *Plant-pollinator interactions over 120 years: loss of species, co-*
546 *occurrence, and function*. Science, American Association for the Advancement of Science, **2013**, Vol. 339(6127),
547 pp. 1611-1615.
548

549 Burthe, S., Daunt, F., Butler, A., Elston, D. A., Frederiksen, M., Johns, D., Newell, M., Thackeray, S. J. and
550 Wanless, S. *Phenological trends and trophic mismatch across multiple levels of a North Sea pelagic food web*.
551 Marine Ecology Progress Series, **2012**, Vol. 454, pp. 119-133.
552

553 CaraDonna, P. J., Iler, A. M. and Inouye, D. W. *Shifts in flowering phenology reshape a subalpine plant community*.
554 Proceedings of the National Academy of Sciences, **2014**, Vol. 111(13), pp. 4916-4921.
555

556 Carpenter, S. R. and Kitchell, J. F. *The trophic cascade in lakes*. Cambridge University Press, **1996**
557

558 Charmantier A, et al. *Adaptive Phenotypic Plasticity in Response to Climate Change in a Wild Bird Population*.
559 Science*, **2008**, 320:800-803.

560

561   Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B. and Thomas, C. D. *Rapid range shifts of species associated with*
562   *high levels of climate warming.* Science, American Association for the Advancement of Science, **2011**, Vol.
563   333(6045), pp. 1024-1026.
564
565   Chmura, H. E., Kharouba, H. M., Ashander, J., Ehlman, S. M., Rivest, E. B. and Yang, L. H. *The mechanisms of*
566   *phenology: the patterns and processes of phenological shifts.* Ecological Monographs, **2018**
567
568   Chuine, I. and Régnière, J. *Process-based models of phenology for plants and animals/* Annual Review of Ecology,
569   Evolution, and Systematics, Annual Reviews, **2017**, Vol. 48, pp. 159-182
570
571   Cury, P, Shannon, L and Shin, YJ. *The functioning of marineecosystems: a fisheries perspective.* Responsible
572   fisheries in the marineecosystem. FAO, Rome and CABI Publishing, **2003**, pp. 103–123
573
574   Cushing, D. H. *The natural regulation of fish populations*. HardenJones, F. R. *(ed.)* Sea Fisheries Research. Elek
575   Science, **1974**, pp. 399-412
576
577   Deacy, W. W., Armstrong, J. B., Leacock, W. B., Robbins, C. T., Gustine, D. D., Ward, E. J., Erlenbach, J. A. and
578   Stanford, J. A. *Phenological synchronization disrupts trophic interactions between Kodiak brown bears and salmon.*
579   Proceedings of the National Academy of Sciences, **2017**, Vol. 114(39), pp. 10432-10437
580
581   Doiron, M., Gauthier, G. and Lévesque, E. *Trophic mismatch and its effects on the growth of young in an Arctic*
582   *herbivore.* Global Change Biology, **2015**, Vol. 21(12), pp. 4364-4376
583
584   Dornelas, M., Gotelli, N. J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C. and Magurran, A. E. *Assemblage time*
585   *series reveal biodiversity change but not systematic loss.* Science, **2014**, Vol. 344(6181), pp. 296-299.
586
587   Durant, J. M., Hjermann, D. Ø., Anker-Nilssen, T., Beaugrand, G., Mysterud, A., Pettorelli, N. and Stenseth, N. C.
588   *Timing and abundance as key mechanisms affecting trophic interactions in variable environments.* Ecology
589   Letters, **2005**, Vol. 8(9), pp. 952-958.
590
591   Durant, J. M., Hjermann, D. Ø., Ottersen, G. and Stenseth, N. C. *Climate and the match or mismatch between*
592   *predator requirements and resource availability.* Climate research, **2007**, Vol. 33(3), pp. 271-283
593
594   Edmondson, W. *Sixty years of Lake Washington: a curriculum vitae.* Lake and Reservoir Management, **1994**, Vol.
595   10(2), pp. 75-84.
596
597   Francis, T. B., Wolkovich, E. M., Scheuerell, M. D., Katz, S. L., Holmes, E. E. and Hampton, S. E. *Shifting regimes*
598   *and changing interactions in the Lake Washington, USA, plankton community from 1962—1994.* PloS one, **2014**,
599   Vol. 9(10), pp. e110363
600
601   Fritts, T. H. and Rodda, G. H. *The role of introduced species in the degradation of island ecosystems: a case history*
602   *of Guam.* Annual review of Ecology and Systematics, **1998**, Vol. 29(1), pp. 113-140.
603
604   George, D.*The effect of nutrient enrichment and changes in the weather on the abundance of Daphnia in Esthwaite*
605   *Water, Cumbria.* Freshwater Biology, **2012**, Vol. 57(2), pp. 360-372
606
607   Gruner, D. S., Smith, J. E., Seabloom, E. W., Sandin, S. A., Ngai, J. T., Hillebrand, H., Harpole, W. S., Elser, J. J.,
608   Cleland, E. E., Bracken, M. E. and others. *A cross-system synthesis of consumer and nutrient resource control on*
609   *producer biomass.* Ecology letters, **2008**, Vol. 11(7), pp. 740-755
610
611   Gullett, P., Hatchwell, B. J., Robinson, R. A. and Evans, K. L. *Phenological indices of avian reproduction: cryptic*
612   *shifts and prediction across large spatial and temporal scales.* Ecology and evolution, **2013**, Vol. 3(7), pp. 1864-
613   1877.
614

615 Hampton, S. E., Scheuerell, M. D. and Schindler, D. E. *Coalescence in the Lake Washington story: interaction*
616 *strengths in a planktonic food web.* Limnology and Oceanography, **2006**, Vol. 51(5), pp. 2042-2051.
617

618 Henrich-Gebhardt, S. G. *Temporal and spatial variation in food availability and its effects on fledgling size in the*
619 *great tit*. Population biology of passerine birds **1990**, pp. 175-185.
620

621 Holliday, N. *Population ecology of winter moth (Operophtera brumata) on apple in relation to larval dispersal and*
622 *time of bud burst*. Journal of Applied Ecology, JSTOR, **1977**, pp. 803-813.
623

624 Johansson, J. and Jonzén, N.*Game theory sheds new light on ecological responses to current climate change when*
625 *phenology is historically mismatched*. Ecology letters, **2012**, Vol. 15(8), pp. 881-888.
626

627 Johansson, J., Kristensen, N. P., Nilsson, J.-Å. and Jonzén, N.*The eco-evolutionary consequences of interspecific*
628 *phenological asynchrony--a theoretical perspective*. Oikos, **2015**, Vol. 124(1), pp. 102-112.
629

630 KELLERI, L. F. and VAN NOORDWIJK, A. J. *Effects of local environmental conditions*. Ardea, **1994**, Vol. 82, pp.
631 349-362
632

633 Kerby, J., Wilmers, C. and Post, E. *Climate change, phenology, and the nature of consumer--resource interactions:*
634 *advancing the match/mismatch hypothesis*. Ohgushi, T., Schmitz, O. J. & Holt, R. D. *(ed.)* Trait-mediated indirect
635 interactions: ecological and evolutionary perspectives, Cambridge University Press Cambridge, UK, **2012**, pp. 508-
636 525.
637

638 Kharouba, H. M., Ehrlén, J., Gelman, A., Bolmgren, K., Allen, J. M., Travers, S. E. and Wolkovich, E. M. *Global*
639 *shifts in the phenological synchrony of species interactions over recent decades*. Proceedings of the National
640 Academy of Sciences, **2018**, Vol. 115(20), pp. 5211-5216.
641

642 Lavergne, S., Mouquet, N., Thuiller, W. and Ronce, O. *Biodiversity and climate change: integrating evolutionary*
643 *and ecological responses of species and communities*. Annual review of ecology, evolution, and systematics, Annual
644 Reviews, **2010**, Vol. 41, pp. 321-350.
645

646 Law, T., Zhang, W., Zhao, J. and Arhonditsis, G. B. *Structural changes in lake functioning induced from nutrient*
647 *loading and climate variability*. Ecological Modelling, **2009**, Vol. 220(7), pp. 979-997.
648

649 Leggett, W. and Deblois, E. *Recruitment in marine fishes: is it regulated by starvation and predation in the egg and*
650 *larval stages?* Netherlands Journal of Sea Research, **1994**, Vol. 32(2), pp. 119-134.
651

652 Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O.,
653 Briede, A. and others *European phenological response to climate change matches the warming pattern*. Global
654 change biology, **2006**, Vol. 12(10), pp. 1969-1976.
655

656 Miller-Rushing, A. J., Høye, T. T., Inouye, D. W. and Post, E. *The effects of phenological mismatches on*
657 *demography*. Philosophical Transactions of the Royal Society B: Biological Sciences, **2010**, Vol. 365(1555), pp.
658 3177-3186.
659

660 Mouquet, N., Lagadeuc, Y., Devictor, V., Doyen, L., Duputié, A., Eveillard, D., Faure, D., Garnier, E., Gimenez, O.,
661 Huneman, P. and others. *Predictive ecology in a changing world*. Journal of Applied Ecology, **2015**, Vol. 52(5), pp.
662 1293-1310.
663

664 Nakazawa, T. and Doi, H. *A perspective on match/mismatch of phenology in community contexts*. Oikos, **2012**, Vol.
665 121(4), pp. 489-495.
666

667 O'Connor, M. I., Selig, E. R., Pinsky, M. L. and Altermatt, F.*Toward a conceptual synthesis for climate change*
668 *responses*. Global Ecology and Biogeography, **2012**, Vol. 21(7), pp. 693-703
669

670 Ovaskainen, O., Skorokhodova, S., Yakovleva, M., Sukhov, A., Kutenkov, A., Kutenkova, N., Shcherbakov, A.,
671 Meyke, E. and del Mar Delgado, M. *Community-level phenological response to climate change*. Proceedings of the
672 National Academy of Sciences, **2013**, Vol. 110(33), pp. 13434-13439
673

674 Philippart, C. J., van Aken, H. M., Beukema, J. J., Bos, O. G., Cadée, G. C. and Dekker, R.*Climate-related changes
675 in recruitment of the bivalve Macoma balthica.* Limnology and Oceanography, **2003**, Vol. 48(6), pp. 2171-2185
676

677 Plard, F., Gaillard, J.-M., Coulson, T., Hewison, A. M., Delorme, D., Warnant, C. and Bonenfant, C. *Mismatch
678 between birth date and vegetation phenology slows the demography of roe deer*. PLoS biology, **2014**, Vol. 12(4), pp.
679 e1001828
680

681 Post, E. and Forchhammer, M. C. *Climate change reduces reproductive success of an Arctic herbivore through
682 trophic mismatch*. Philosophical Transactions of the Royal Society B: Biological Sciences, The Royal Society
683 London, **2007**, Vol. 363(1501), pp. 2367-2373
684

685 Reed, T. E., Jenouvrier, S. and Visser, M. E. *Phenological mismatch strongly affects individual fitness but not
686 population demography in a woodland passerine*. Journal of Animal Ecology, **2013**, Vol. 82(1), pp. 131-144
687

688 Renner, S. S. and Zohner, C. M. *Climate change and phenological mismatch in trophic interactions among plants,
689 insects, and vertebrates*. Annual Review of Ecology, Evolution, and Systematics, Annual Reviews, **2018**, Vol. 49,
690 pp. 165-182.
691

692 Revilla, T. A., Encinas-Viso, F. and Loreau, M. *(A bit) Earlier or later is always better: Phenological shifts in
693 consumer--resource interactions*. Theoretical ecology, **2014**, Vol. 7(2), pp. 149-162.
694

695 Ricciardi, A., Neves, R. J. and Rasmussen, J. B. *Impending extinctions of North American freshwater mussels
696 (Unionoida) following the zebra mussel (Dreissena polymorpha) invasion*. Journal of animal ecology, **1998**, Vol.
697 67(4), pp. 613-619.
698

699 Rudolf, V. H. and Singh, M. *Disentangling climate change effects on species interactions: effects of temperature,
700 phenological shifts, and body size*. Oecologia, **2013**, Vol. 173(3), pp. 1043-1052
701 Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F.,
702 Jackson, R. B., Kinzig, A. and others. *Global biodiversity scenarios for the year 2100***.** Science, **2000**, Vol.
703 287(5459), pp. 1770-1774**.**

704 Samplonius, J. M., Kappers, E. F., Brands, S. and Both, C. *Phenological mismatch and ontogenetic diet shifts
705 interactively affect offspring condition in a passerine*. Journal of Animal Ecology, **2016**, Vol. 85(5), pp. 1255-1264.

706 Senner, N. R., Stager, M. and Sandercock, B. K. *Ecological mismatches are moderated by local conditions for two
707 populations of a long-distance migratory bird*. Oikos, **2017**, Vol. 126(1), pp. 61-72
708

709 Sgardeli, V., Zografou, K. and Halley, J. M. *Climate change versus ecological drift: assessing 13 years of turnover
710 in a butterfly community*. Basic and applied ecology, **2016**, Vol. 17(4), pp. 283-290
711

712 Shurin, J. B., Borer, E. T., Seabloom, E. W., Anderson, K., Blanchette, C. A., Broitman, B., Cooper, S. D. and
713 Halpern, B. S. *A cross-ecosystem comparison of the strength of trophic cascades*. Ecology letters, **2002**, Vol. 5(6),
714 pp. 785-791
715

716 Shurin, J. B., Gruner, D. S. and Hillebrand, H. *All wet or dried up? Real differences between aquatic and terrestrial
717 food webs*. Proceedings of the Royal Society B: Biological Sciences, The Royal Society London, **2005**, Vol.
718 273(1582), pp. 1-9
719

720 Shurin, J. B. and Seabloom, E. W.*The strength of trophic cascades across ecosystems: predictions from allometry
721 and energetics*. Journal of animal Ecology, **2005**, Vol. 74(6), pp. 1029-1038
722

Singer, M. C. and Parmesan, C. *Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy?* Philosophical Transactions of the Royal Society B: Biological Sciences, **2010**, Vol. 365(1555), pp. 3161-3176

Solomon, S. *IPCC (2007): Climate change the physical science basis* **2007**

Thackeray, S. J. *Mismatch revisited: what is trophic mismatching from the perspective of the plankton?* Journal of Plankton Research, Oxford University Press, **2012**, Vol. 34(12), pp. 1001-1010

Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., Johns, D. G., Jones, I. D., Leech, D. I. and others. *Phenological sensitivity to climate across taxa and trophic levels*. Nature, **2016**, Vol. 535(7611), pp. 241

Tikkanen, O.-P. and Julkunen-Tiitto, R. *Phenological variation as protection against defoliating insects: the case of Quercus robur and Operophtera brumata*. Oecologia, **2003**, Vol. 136(2), pp. 244-251

Tikkanen, O.-P., Niemelä, P. and Keränen, J. *Growth and development of a generalist insect herbivore, Operophtera brumata, on original and alternative host plants*. Oecologia, **2000**, Vol. 122(4), pp. 529-536

Vatka, E., Orell, M. and RytkÖnen, S. *Warming climate advances breeding and improves synchrony of food demand and food availability in a boreal passerine*. Global Change Biology, **2011**, Vol. 17(9), pp. 3002-3009

Vatka, E., Rytkönen, S. and Orell, M. *Does the temporal mismatch hypothesis match in boreal populations?* Oecologia, **2014**, Vol. 176(2), pp. 595-605

Verschuren, D., Johnson, T. C., Kling, H. J., Edgington, D. N., Leavitt, P. R., Brown, E. T., Talbot, M. R. and Hecky, R. E. *History and timing of human impact on Lake Victoria, East Africa*. Proceedings of the Royal Society of London. Series B: Biological Sciences, **2002**, Vol. 269(1488), pp. 289-294

Visser, M. E., Holleman, L. J. M. and Gienapp, P. *Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird*. Oecologia, **2006**, Vol. 147(1), pp. 164-172.

Visser, M.E., Van Noordwijk, A.J., Tinbergen, J.M., and Lessells, C.M. *Warmer springs lead to mistimed reproduction in great tits (Parus major)*. Philos. Trans. R. Soc. London B, **1998**, 265:1867-1870.

Wiltshire, K. H., Malzahn, A. M., Wirtz, K., Greve, W., Janisch, S., Mangelsdorf, P., Manly, B. F. and Boersma, M. *Resilience of North Sea phytoplankton spring bloom dynamics: An analysis of long-term data at Helgoland Roads*. Limnology and Oceanography, **2008**, Vol. 53(4), pp. 1294-1302

Winder, M. and Schindler, D. E. *Climate change uncouples trophic interactions in an aquatic ecosystem*. Ecology, **2004**, Vol. 85(8), pp. 2100-2106

Wolkovich, E., Cook, B., McLauchlan, K. and Davies, T. *Temporal ecology in the Anthropocene*. Ecology letters, **2014**, Vol. 17(11), pp. 1365-1379

765 **Box 1. Glossary**

766 **Phenological synchrony-** changes in the relative timing of key life history events among pair-wise
767 interacting species. Importantly, this term does not incorporate fitness consequences for either species.
768

769 **Phenological mismatch-** decreases in consumer fitness associated with changes in the relative timing of
770 key life history activities among interacting species. This mismatch occurs between interacting species; it
771 does not occur with the abiotic environment or due intraspecific processes.
772

773 **Cushing match-mismatch hypothesis-** this hypothesis postulates that there should be selective pressure
774 for the consumer to temporally 'match' the peak of its energetic phase (i.e. reaching maximum fitness)
775 with the peak of resource availability and if there is any change to the relative timing of the interaction,
776 there will be a decrease in fitness for the consumer (i.e., a mismatch). At the curve's limits, consumer
777 fitness should fall to zero when the change in relative timing is sufficiently large. (Figure 1)
778

779 **Baseline-** a representative or benchmark time series of conditions that describes the species interaction. A
780 baseline incorporates the historical range of variability in the relative timing of the interaction.
781

782 **Synchrony hypothesis-** a hypothesis that before climate change, the most energetically demanding phase
783 of the consumer was at the same time of peak resource availability, and thus consumer fitness was at its
784 maximum (i.e. a match).
785

786 **Asynchrony baseline** - a hypothesis that before climate change, the most energetically demanding phase
787 of the consumer was not timed to the peak resource availability, and thus consumer fitness was not at its
788 maximum. This could occur for various reasons (e.g., co-evolutionary arms race, other transient
789 dynamics).
790

791 **Adaptive asynchrony hypothesis-** a hypothesis put forward by Singer and Parmesan (2010) that
792 postulates that, in some systems, life-history trade-offs will promote asynchrony for many or most
793 individuals in a population.
794

795 **Stationarity-** any stochastic process with a constant underlying probability distribution
796

797 **Life-history theory-** the study of the causes and consequences of the diversity of life history strategies
798 based on evolutionary theory.
799

800 **Food web theory-** the study of the patterns, causes and consequences of food-web structure.
801

802

803

804

805 **Tables**

806 Table 1. A comparison across studies of the type of performance data collected for consumer and
807 resource. We define a life-history study as one that collected data at the individual level and a food-web
808 study as one that collected data at the population or community (i.e., across species) level. Counts in the
809 table are numbers of individual pair-wise interactions (n=46).

810

			Resource performance				
			Life-history		Food-web		
			None	Individual	Population	Community	*Totals*
Consumer performance	Life-history	Individual	6	0	4	18	*28*
	Food-web	Population	1	1	7	7	*16*
		Community	0	0	1	1	*2*
		Total	**7**	**1**	**12**	**26**	**46**

811

812 Table 2. A comparison across studies of the type of performance data collected for the consumer across
813 systems and taxonomic group. Counts in the table are numbers of individual pair-wise interactions
814 (n=46).
815

		System		Taxonomic group			
						Vertebrate	
		Aquatic	Terrestrial	Invertebrate	Fish	Bird	Mammal
Level of consumer performance	Individual	5	23	1	2	19	6
	Population	14	2	9	4	2	1
	Community	1	1	2	0	0	0
	Sub-totals	**20**	**26**	**12**	**6**	**21**	**7**
	Totals		**46**				**46**

816

817

818

819 **Figures**

820 Figure 1. Conceptualization of the Cushing match-mismatch hypothesis represented by the curve in panel

821 (a). The hypothesis postulates that a consumer should temporally 'match' the peak of its energetic phase

822 with the peak of resource availability and thus have the highest fitness (a,c) and if there is any change to

823 the relative timing of the interaction (e.g., because the consumer shifts its phenology earlier (b) or later (d)

824 relative to the resource), there will be a decrease in the consumer's fitness (i.e., a mismatch) (a). At the

825 curve's limits, consumer fitness should fall to zero when the change in relative timing is sufficiently large

826 (a). Curves in panels b-d represent the seasonal changes in the abundance of the consumer (black) and

827 resource (red) where during some part of the year abundance declines to zero.

828

829 Figure 2. A simplified flow diagram for forecasting climate change effects on consumer fitness as

830 predicted by the Cushing hypothesis. First, both major assumptions must be met; if, for example,

831 consumer density is the major controller on its own fitness, then no further work is warranted. If both

832 assumptions are met, forecasting requires both knowledge of the ultimate mechanisms (which often relate

833 to testing the 1st assumption) and the pre-climate change baseline. In some cases, the mechanism predicts

834 the pre-climate change baseline (i.e., in both our examples); we colour mechanisms in whether they

835 predict both pre-climate change synchrony and asynchrony depending on specifics (purple), synchrony

836 (blue) or asynchrony (red). Note that multiple mechanisms may operate in many systems, and that this

837 figure is in no way exhaustive, but rather serves to highlight a pathway that researchers can take.

838

839 Figure 3. Conceptualization of key assumptions, and resulting implications for climate change

840 predictions, often made about the Cushing hypothesis when pre-climate change baselines are not defined.

841 (a) Differences in the phenological time-series of a consumer-resource interaction, where red represents

842 the resource and black represents the consumer, during conditions of stationarity; when the environment

843 becomes non-stationary (shown here just after 1980) the consumer and resource each can shift in varying

844 directions, representing the range of recent documented phenological shifts (e.g. Thackeray et al. 2016),
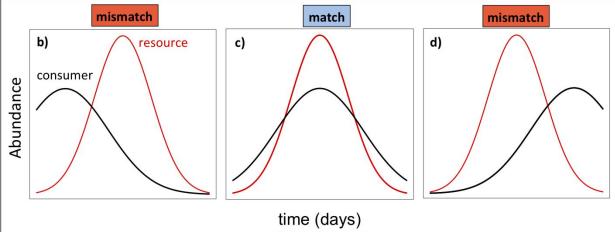
845   leading potentially to shifts in synchrony. (b) Most studies in the current literature assume that consumer

846   fitness was highest before climate change (i.e., a match; synchrony hypothesis) leading to a 'synchrony

847   baseline'. However, an alternative hypothesis put forward by Singer and Parmesan (2010) (i.e., what they

848   term as the 'adaptive asynchrony' hypothesis) postulates that conditions before climate change may not

849   represent a 'match' in the system for many individuals. This hypothesis may lead to asynchrony as a pre-

850   climate change baseline (see c) or a population where few individuals are matched; we show this latter

851   possibility here (i.e. 'adaptive asynchrony hypothesis with synchrony baseline'; our representation of this

852   hypothesis is at the population level). The implications for climate change predictions for the two

853   hypotheses are illustrated: If the synchrony baseline is supported, then climate change will necessarily

854   lead to declines in consumer fitness. If the 'adaptive asynchrony hypothesis' with a synchrony baseline is

855   supported, climate change may not lead to large declines in consumer fitness. (c) Without establishing a

856   pre-climate change baseline and defining where an interaction falls along a curve, it is difficult to predict

857   how climate change-driven changes to the relative timing of the interaction may affect consumer fitness.

858   For example, with an asynchrony baseline, climate change could lead to an increase or decrease, or to

859   varying magnitudes, in consumer fitness depending on how the relative timing of the interaction changes.

860   For panels b and c, blue boxes represent the range of conditions detected in the system over a long time

861   period.

862

863   Figure 4. Case study demonstrating the integration of experimental (a) and observational data (b) relating

864   to the Cushing hypothesis in a single system- the winter moth (*Operophtera brumata*) and oak (*Quercus*

865   *robur*). (a) The results from two related experiments (green, red points) where the authors manipulated

866   the number of days that neonates (i.e. early instar larvae) spent without food (green points; first

867   experiment) and the emergence times of larvae relative to budburst (red points; second experiment). Raw

868   data was obtained from Tikkanen and Julkunen-Tiitto (2003; Figure 3). See Appendix for more details.

869   (b) Inter-annual variation in relative timing between median egg hatch date of *O. brumata* and the median

870   bud opening date of *Q. robur* from 1996-2005 in the Netherlands. Horizontal error bars represent the

871 lower and upper quartiles of the data. Raw data from the observational study was retrieved from VanAsch

872 and Visser 2007 Figure 2. For both panels, negative values along the x-axis denote where egg hatching

873 occurred before bud opening (i.e. time without food), whereas positive values indicate egg hatching

874 occurred after bud opening (i.e. time with food). While the experimental data from panel (a) shows

875 support for the Cushing hypothesis, and the ultimate mechanism in this system suggests that the pre-

876 climate change baseline was likely synchrony (Figure 2), empirical data from a 10 year post-climate

877 change time-series (panel (b) only covers a small portion of the Cushing curve. This makes it difficult to

878 define the pre-climate change baseline and thus accurately predict how the performance of *O. brumata*

879 will be affected by changes in phenological synchrony due to climate change (Figure 2).

880

881   Figure 1.

882

883   Figure 2.

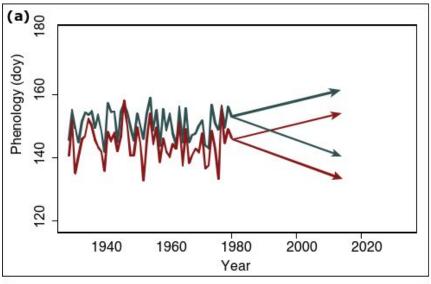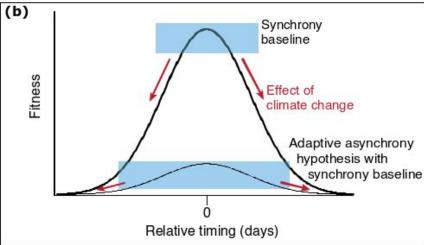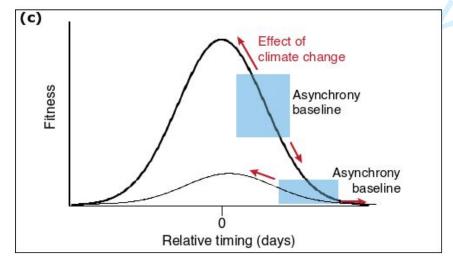884

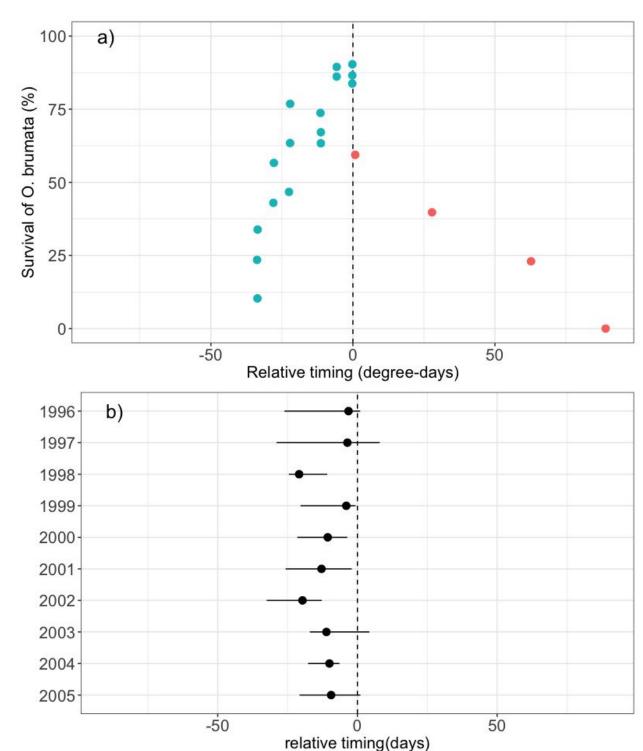**Using the Cushing hypothesis to predict and forecast consumer fitness with climate change**

Test Cushing hypothesis

Step 1:Test assumptions

Assumption 1: Resource is the major controller on consumer fitness

(i.e., not related to density, spatial resources, upper trophic level)

Assumption 2: Consumer and resource show seasonality (activity vs. dormancy periods)

Both assumptions met?

Assumption 1 uncertain?

Step 2:Test ultimate mechanisms

Life history strategies:
1. Fitness trade-offs between fecundity & mortality
2. Breeding strategies
3. Bet-hedging

Food web dynamics:
Bottom up

Depending on mechanism

Test pre-climate conditions and cues to predict climate change effects

Step 3: Identify pre-climate change baseline

Synchrony

Asychrony

Depending on mechanism

Step 4: Identify proximate cues of consumer and resource

Test proximate cues

Consumer and resource share similar environmental cues

Consumer and resource differ in some cues

Ultimate aim

Accurately forecast match/mismatch with climate change

Yes

Example: Bird limited by nest site availability

Step 1: Consumerfitness controlled strongly by density. Thus, assumption 1 violated.

No → Cushing hypothesis does not apply

Example: Insect that ovipositions across space

Step 1: Both assumptions met.

Yes → Step 2: Consumer bet-hedging via spatiotemporal reproduction. → Given bet-hedging mechanism, unlikely to see major climate change impacts

Example: Income breeder

Step 1: Both assumptions met.

Yes → Step 2: Consumer provisions offspring with resources acquired during breeding season → Step 3: Pre-climate change baseline was synchrony. → Step 4: Consumer and resource have slightly different environmental cues (e.g., to temperature). → Potential for asynchrony-related fitness declines

885

886   Figure 3.

887

888

889   Figure 4.

890

891

892 **Appendix**

893 *Literature search*

894   We located papers relating phenological data from trophic interactions to fitness and/or

895 performance of the consumer and/or the resource by conducting keyword searches in ISI Web of Science

896 published up to June 2017. Keywords included phenolog* AND mismatch* OR synchron* AND

897 interact* AND (fitness* OR performance*). Our initial search netted 2906 papers so we further refined

898 our search by excluding categories that included engineering and computer science. This resulted in 393

899 papers. From these, we focused on observational studies and excluded studies if they did not: (1) measure

900 phenology directly (e.g. used derived measures of phenology, such as NDVI or spring temperature); (2)

901 measure phenology of at least one of the species; (3) quantitatively link consumer fitness or performance

902 to the relative timing between consumer and resource; and (4) explicitly state that the two species

903 interacted (e.g. specifying type of interaction). Estimates of consumer fitness or performance (i.e., growth

904 or development) had to be direct estimates (e.g. we did not include studies that used diet proportions to

905 measure consumer performance) and included a range of proxies, for example, growth, survival,

906 abundance. To ensure a reasonable sample size and to include studies across different major biomes, we

907 included interactions that were resolved to the family-level and below. To reduce redundancy within

908 systems, we only kept studies that were unique across pairs-location-year combinations. If more than one

909 measure of phenology was included, we chose the one used by the authors to calculate mismatch and

910 examine its impact on performance.

911   Our final review included 43 studies with 46 pair-wise species interactions (3 studies had 2

912 interactions). These studies encompassed terrestrial, marine and freshwater ecosystems as well as a large

913 latitudinal gradient.

914

915 *Summary of studies and interactions*

916   We classified studies as 'climate change' or 'fundamental' depending on whether they mentioned

917 climate change in the abstract or in the introduction of the paper. Based on the type of data collected for

918 the consumer and resource, we classified these studies as life history (i.e. one that collected data at the

919 individual level) or food web-based (i.e. one that collected data at the population or community (i.e.,

920 across species)). To determine whether studies had the potential to define pre-climate change baselines,

921 we measured the study's time span and years of data based on the years where phenology data was

922 available for both the consumer and resource, and consumer performance data was available.

923

924 *Additional details for Figure 4*

925 Raw data for panel (a) was obtained from Figure 3 in Tikkanen and Julkunen-Tiitto (2003). The

926 data come from two related experiments where the authors manipulated the number of days that neonates

927 (i.e. early instar larvae) spent without food (first experiment) and the emergence times of larvae relative to

928 budburst (second experiment). In the first experiment, there were six groups of 30 larvae that spent 0, 5.5,

929 11, 22, 27,5 and 33 degree-days without food. In the second experiment, there were four cohorts, each

930 separated by intervals of 3-5 days. All *O. brumata* eggs and larvae originated from laboratory stock

931 originally from Turku, Finland whereas the foliage originated from trees near Banchory, NW Scotland.

932

933 *References for systematic literature review*

934 Adrian, R., Wilhelm, S. and Gerten, D. *Life-history traits of lake plankton species may govern their*
935 *phenological response to climate warming*. Global change biology, **2006**, Vol. 12(4), pp. 652-661.
936
937 Arula, T., Gröger, J., Ojaveer, H. and Simm, M.*Shifts in the spring herring (Clupea harengus membras)*
938 *larvae and related environment in the Eastern Baltic Sea over the past 50 years*. PloS one, Public Library
939 of Science, **2014**, Vol. 9(3), pp. e91304
940
941 Atkinson, A., Harmer, R. A., Widdicombe, C. E., McEvoy, A. J., Smyth, T. J., Cummings, D. G.,
942 Somerfield, P. J., Maud, J. L. and McConville, K. *Questioning the role of phenology shifts and trophic*
943 *mismatching in a planktonic food web*. Progress in Oceanography, **2015**, Vol. 137, pp. 498-512.
944
945 Blackett, M., Lucas, C. H., Harmer, R. A. and Licandro, P. *Population ecology of Muggiaea atlantica*
946 *(Cnidaria, Siphonophora) in the Western English Channel*. Marine Ecology Progress Series, **2015**, Vol.
947 535, pp. 129-144
948
949 Borcherding, J., Beeck, P., DeAngelis, D. L. and Scharf, W. R. *Match or mismatch: the influence of*
950 *phenology on size-dependent life history and divergence in population structure*. Journal of animal
951 ecology, **2010**, Vol. 79(5), pp. 1101-1112
952

953 Cresswell, W. and Mccleery, R. *How great tits maintain synchronization of their hatch date with food*
954 *supply in response to long-term variability in temperature*. Journal of Animal Ecology, **2003**, Vol. 72(2),
955 pp. 356-366
956

957 Dekker, R. and Beukema, J. *Phenology of abundance of bivalve spat and of their epibenthic predators:*
958 *limited evidence for mismatches after cold winters*. Marine Ecology Progress Series, **2014**, Vol. 513, pp.
959 17-27
960

961 Dessborn, L., Elmberg, J., Nummi, P., Pöysä, H. and Sjöberg, K. *Hatching in dabbling ducks and*
962 *emergence in chironomids: a case of predator--prey synchrony?* Hydrobiologia, **2009**, Vol. 636(1), pp.
963 319-329
964

965 Dias, P. C. and Blondel, J. *Breeding time, food supply and fitness components of Blue Tits Parus*
966 *caeruleus in Mediterranean habitats*. Ibis, **1996**, Vol. 138(4), pp. 644-649.
967

968 Dunn, P. O., Winkler, D. W., Whittingham, L. A., Hannon, S. J. and Robertson, R. J. *A test of the*
969 *mismatch hypothesis: How is timing of reproduction related to food abundance in an aerial insectivore?*
970 Ecology, **2011**, Vol. 92(2), pp. 450-461
971

972 Fortierl, L. and Gilbert, M.*The match/mismatch hypothesis and the feeding success of fish larvae in ice-*
973 *covered southeastern Hudson Bay* Mar. Ecol. Prog. Ser, **1995**, Vol. 120, pp. 11-27

974 George, D.*The effect of nutrient enrichment and changes in the weather on the abundance of Daphnia in*
975 *Esthwaite Water, Cumbria.* Freshwater Biology, **2012**, Vol. 57(2), pp. 360-372
976

977 Gullett, P., Hatchwell, B. J., Robinson, R. A. and Evans, K. L. *Phenological indices of avian*
978 *reproduction: cryptic shifts and prediction across large spatial and temporal scales*. Ecology and
979 evolution, **2013**, Vol. 3(7), pp. 1864-1877.
980

981 Hipfner, J. M. *Matches and mismatches: ocean climate, prey phenology and breeding success in a*
982 *zooplanktivorous seabird*. Marine Ecology Progress Series, **2008**, Vol. 368, pp. 295-304
983

984 Jolley, J. C., Willis, D. W. and Holland, R. S. *Match--mismatch regulation for bluegill and yellow perch*
985 *larvae and their prey in Sandhill lakes*. Journal of Fish and Wildlife Management, **2010**, Vol. 1(2), pp.
986 73-85
987

988 Kerby, J. and Post, E. *Capital and income breeding traits differentiate trophic match--mismatch dynamics*
989 *in large herbivores*. Philosophical Transactions of the Royal Society B: Biological Sciences, **2013**, Vol.
990 368(1624), pp. 20120484.
991

992 Kerby, J. T. and Post, E. *Advancing plant phenology and reduced herbivore production in a terrestrial*
993 *system associated with sea ice decline*. Nature Communications, **2013**, Vol. 4, pp. 2514

994 Kourkgy, C., Garel, M., Appolinaire, J., Loison, A. and To\igo, C. *Onset of autumn shapes the timing of*
995 *birth in Pyrenean chamois more than onset of spring*. Journal of Animal Ecology, **2016**, Vol. 85(2), pp.
996 581-590

997 Lany, N. K., Ayres, M. P., Stange, E. E., Sillett, T. S., Rodenhouse, N. L. and Holmes, R. T. *Breeding*
998 *timed to maximize reproductive success for a migratory songbird: The importance of phenological*
999 *asynchrony*. Oikos, **2016**, Vol. 125(5), pp. 656-666
1000

McKinnon, L., Picotin, M., Bolduc, E., Juillet, C. and Bêty, J. *Timing of breeding, peak food availability, and effects of mismatch on chick growth in birds nesting in the High Arctic*. Canadian Journal of Zoology, **2012**, Vol. 90(8), pp. 961-971

Mortensen, L. O., Schmidt, N. M., Høye, T. T., Damgaard, C. and Forchhammer, M. C. *Analysis of trophic interactions reveals highly plastic response to climate change in a tri-trophic high-Arctic ecosystem*. Polar Biology, **2016**, Vol. 39(8), pp. 1467-1478

Pakanen, V.-M., Orell, M., Vatka, E., Rytkönen, S. and Broggi, J. *Different ultimate factors define timing of breeding in two related species*. PloS one, Public Library of Science, **2016**, Vol. 11(9), pp. e0162643

Philippart, C. J., van Aken, H. M., Beukema, J. J., Bos, O. G., Cadée, G. C. and Dekker, R. *Climate-related changes in recruitment of the bivalve Macoma balthica*. Limnology and Oceanography, **2003**, Vol. 48(6), pp. 2171-2185.

Plard, F., Gaillard, J.-M., Coulson, T., Hewison, A. M., Delorme, D., Warnant, C. and Bonenfant, C. *Mismatch between birth date and vegetation phenology slows the demography of roe deer*. PLoS biology, Public Library of Science, **2014**, Vol. 12(4), pp. e1001828.

Post, E. and Forchhammer, M. C. *Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch*. Philosophical Transactions of the Royal Society B: Biological Sciences, The Royal Society London, **2007**, Vol. 363(1501), pp. 2367-2373.

Reed, T. E., Grøtan, V., Jenouvrier, S., Sæther, B.-E. and Visser, M. E. *Population growth in a wild bird is buffered against phenological mismatch*. Science, **2013**, Vol. 340(6131), pp. 488-491.

Reed, T. E., Jenouvrier, S. and Visser, M. E. *Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine*. Journal of Animal Ecology, **2013**, Vol. 82(1), pp. 131-144.

Régnier, T., Gibb, F. and Wright, P. *Importance of trophic mismatch in a winter-hatching species: evidence from lesser sandeel*. Marine Ecology Progress Series, **2017**, Vol. 567, pp. 185-197

Reneerkens, J., Schmidt, N. M., Gilg, O., Hansen, J., Hansen, L. H., Moreau, J. and Piersma, T. *Effects of food abundance and early clutch predation on reproductive timing in a high Arctic shorebird exposed to advancements in arthropod abundance*. Ecology and Evolution, **2016**, Vol. 6(20), pp. 7375-7386

Salamolard, M., Butet, A., Leroux, A. and Bretagnolle, V. *Responses of an avian predator to variations in prey density at a temperate latitude*. Ecology, **2000**, Vol. 81(9), pp. 2428-2441

Seebens, H., Einsle, U. and Straile, D. *Copepod life cycle adaptations and success in response to phytoplankton spring bloom phenology*. Global Change Biology, **2009**, Vol. 15(6), pp. 1394-1404

Senner, N. R., Stager, M. and Sandercock, B. K. *Ecological mismatches are moderated by local conditions for two populations of a long-distance migratory bird*. Oikos, **2017**, Vol. 126(1), pp. 61-72

Sergeant, C. J., Armstrong, J. B. and Ward, E. J. *Predator-prey migration phenologies remain synchronised in a warming catchment*. Freshwater Biology, **2015**, Vol. 60(4), pp. 724-732

1050 Shultz, M. T., Piatt, J. F., Harding, A. M., Kettle, A. B. and Van Pelt, T. I. *Timing of breeding and*
1051 *reproductive performance in murres and kittiwakes reflect mismatched seasonal prey dynamics*. Marine
1052 Ecology Progress Series, **2009**, Vol. 393, pp. 247-258
1053

1054 Sullivan, B. K., Costello, J. H. and Van Keuren, D. *Seasonality of the copepods Acartia hudsonica and*
1055 *Acartia tonsa in Narragansett Bay, RI, USA during a period of climate change*. Estuarine, Coastal and
1056 Shelf Science, **2007**, Vol. 73(1-2), pp. 259-267
1057

1058 Thomas, D. W., Blondel, J., Perret, P., Lambrechts, M. M. and Speakman, J. R. *Energetic and fitness*
1059 *costs of mismatching resource supply and demand in seasonally breeding birds.* Science, American
1060 Association for the Advancement of Science, **2001**, Vol. 291(5513), pp. 2598-2600
1061

1062 Vatka, E., Orell, M. and RytkÖnen, S. *Warming climate advances breeding and improves synchrony of*
1063 *food demand and food availability in a boreal passerine.* Global Change Biology, **2011**, Vol. 17(9), pp.
1064 3002-3009.
1065

1066 Vatka, E., Rytkönen, S. and Orell, M. *Does the temporal mismatch hypothesis match in boreal*
1067 *populations?* Oecologia, **2014**, Vol. 176(2), pp. 595-605
1068

1069 Visser, M. E., Gienapp, P., Husby, A., Morrisey, M., de la Hera, I., Pulido, F. and Both, C. *Effects of*
1070 *spring temperatures on the strength of selection on timing of reproduction in a long-distance migratory*
1071 *bird*. PLoS Biology, Public Library of Science, **2015**, Vol. 13(4), pp. e1002120
1072

1073 Watanuki, Y., Ito, M., Deguchi, T. and Minobe, S. *Climate-forced seasonal mismatch between the*
1074 *hatching of rhinoceros auklets and the availability of anchovy*. Marine Ecology Progress Series, **2009**,
1075 Vol. 393, pp. 259-271
1076

1077 Wiltshire, K. H., Malzahn, A. M., Wirtz, K., Greve, W., Janisch, S., Mangelsdorf, P., Manly, B. F. and
1078 Boersma, M. *Resilience of North Sea phytoplankton spring bloom dynamics: An analysis of long-term*
1079 *data at Helgoland Roads*. Limnology and Oceanography, **2008**, Vol. 53(4), pp. 1294-1302
1080

1081 Winder, M. and Schindler, D. E. *Climate change uncouples trophic interactions in an aquatic ecosystem*.
1082 Ecology, **2004**, Vol. 85(8), pp. 2100-2106
1083