



DIGITAL ACCESS TO SCHOLARSHIP AT HARVARD

Analysis of Abrupt Transitions in Ecological Systems

The Harvard community has made this article openly available.
[Please share](#) how this access benefits you. Your story matters.

Citation	Bestelmeyer, Brandon T., Aaron M. Ellison, William R. Fraser, Kristen B. Gorman, Sally J. Holbrook, Christine M. Laney, Mark D. Ohman, et alia. 2011. Analysis of Abrupt Transitions in Ecological Systems. <i>Ecosphere</i> 2(12): Article 129.
Published Version	doi:10.1890/ES11-00216.1
Accessed	February 19, 2015 9:25:48 AM EST
Citable Link	http://nrs.harvard.edu/urn-3:HUL.InstRepos:8298846
Terms of Use	This article was downloaded from Harvard University's DASH repository, and is made available under the terms and conditions applicable to Other Posted Material, as set forth at http://nrs.harvard.edu/urn-3:HUL.InstRepos:dash.current.terms-of-use#LAA

(Article begins on next page)

1 **Manuscript type:** Synthesis and Integration

2

3 **Analysis of abrupt transitions in ecological systems**

4 Brandon T. Bestelmeyer^{1†}, Aaron M. Ellison², William R. Fraser³, Kristen B. Gorman^{3,4}, Sally J.
5 Holbrook^{5,8}, Christine M. Laney⁶, Mark D. Ohman⁷, Debra P.C. Peters¹, Finn C. Pillsbury¹,
6 Andrew Rassweiler⁸, Russell J. Schmitt^{5,8}, Sapna Sharma⁹

7

8 ¹USDA-ARS Jornada Experimental Range, New Mexico State University, MSC 3JER Box
9 30003, Las Cruces, NM, 88003, USA

10 ²Harvard Forest, Harvard University, Petersham, Massachusetts, 01366, USA

11 ³Polar Oceans Research Group, Sheridan, MT, 59749, USA

12 ⁴Simon Fraser University, Department of Biological Sciences, 8888 University Drive, Burnaby,
13 BC V5A 1S6, Canada

14 ⁵Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara,
15 California, 93106, USA

16 ⁶Environmental Science and Engineering Program, University of Texas at El Paso, El Paso,
17 Texas, 79968, USA

18 ⁷Scripps Institution of Oceanography, University of California at San Diego, La Jolla, CA,
19 92093, USA

20 ⁸Marine Science Institute, University of California, Santa Barbara, California, 93106, USA

21 ⁹Center for Limnology, University of Wisconsin-Madison, Madison, Wisconsin, 53706, USA

22

23 [†]E-mail: bbestelm@nmsu.edu

24

25 **ABSTRACT**

26 The occurrence and causes of abrupt transitions, thresholds, or regime shifts between
27 ecosystem states are of great concern and the likelihood of such transitions is increasing for
28 many ecological systems. General understanding of abrupt transitions has been advanced by
29 theory, but hindered by the lack of a common, accessible, and data-driven approach to
30 characterizing them. We apply such an approach to 30 – 60 years of data on environmental
31 drivers, biological responses, and associated evidence from pelagic ocean, coastal benthic, polar
32 marine, and semi-arid grassland ecosystems. Our analyses revealed one case in which the
33 response (krill abundance) linearly tracked abrupt changes in the driver (Pacific Decadal
34 Oscillation), but abrupt transitions detected in the three other cases (sea cucumber abundance,
35 penguin abundance, and black grama grass production) exhibited hysteretic relationships with
36 drivers (wave intensity, sea-ice duration, and amounts of monsoonal rainfall, respectively)
37 through a variety of response mechanisms. The use of a common approach across these case
38 studies illustrates that: the utility of leading indicators is often limited and can depend on the
39 abruptness of a transition relative to the lifespan of responsive organisms and observation
40 intervals; information on spatiotemporal context is useful for comparing transitions; and
41 ancillary information from associated experiments and observations informs interpretations of
42 response-driver relationships. The understanding of abrupt transitions offered by this approach
43 provides information that can be used to manage state changes and underscores the utility of
44 long-term observations in multiple sentinel sites across a variety of ecosystems.

45

46 **Key words:** alternative states; *Bouteloua eriopoda*; desert grassland; krill; leading indicators;
47 *Nyctiphanes simplex*; regime shifts; *Pachythyone rubra*; penguins; *Pygoscelis*; sea cucumbers;
48 thresholds.
49

50 **INTRODUCTION**

51

52 Many ecological systems can exist in two or more states that differ in abundance or
53 composition of species, rates of ecological processes, and ecosystem services provided by them
54 (Beisner et al. 2003, Suding et al. 2004). Smooth, gradual transitions between ecosystem states
55 are unremarkable, occurring during succession or as ecosystems track gradually changing
56 environmental conditions. In contrast, abrupt transitions between ecosystem states are typically
57 unexpected and can have wide-ranging, negative impacts. Abrupt transitions happen either when
58 the gradually changing environment passes a critical point or when discrete perturbations cause
59 sudden changes in underlying environmental drivers. Abrupt and irreversible transitions are
60 forecast to increase as climatic changes and depletion of natural resources both accelerate
61 (Millennium Ecosystem Assessment 2005, Fagre et al. 2009). Such forecasting, however, is
62 difficult because there are many different causes of state changes (Hastings and Wysham 2010)
63 and because existing approaches demand far more data than are normally available (Carpenter et
64 al. 2011).

65 Managing state changes is as difficult as forecasting them. When environmental changes
66 are not severe, or when organisms with short lifespans and generation times rapidly track
67 environmental drivers, some state changes can be reversed in relatively short periods of time
68 (≤ 50 years) if drivers are returned to pre-change conditions or perturbations are eliminated
69 (Jones and Schmitz 2009). In other cases, environmental change can result in state changes that
70 persist long after environmental drivers have returned to earlier conditions. The persistence of
71 these so-called “ecological thresholds”, “regime shifts”, “phase shifts”, or “catastrophes”
72 (Hughes 1994, Scheffer et al. 2001, Groffman et al. 2006) is caused by time-lags in the responses

73 of biological systems to environmental change (hysteresis), differences in the relationships
74 between state variables and environmental drivers before and after the state change, or the
75 appearance of novel feedbacks among state variables and drivers that reinforce the new state
76 (Scheffer et al. 2001, Lindig-Cisneros et al. 2003, Briske et al. 2006, Suding and Hobbs 2009).

77 The development of management strategies to mitigate abrupt transitions requires strong
78 linkages among theory, data, and case studies, but there is little guidance available for using
79 historical or ongoing studies to detect or respond to abrupt transitions. There is confusion and
80 disagreement about what changes constitute transitions (Rudnick and Davis 2003, Schroder et al.
81 2005) and a limited understanding of ecological mechanisms causing them (Brown and Archer
82 1999, Collie et al. 2004). Empiricists disagree about how to best gather and interpret relevant
83 data (Petraitis and Latham 1999, Bertness et al. 2002, Schroder et al. 2005), while theoreticians
84 develop leading indicators of abrupt transitions that demand large amounts of data (Carpenter
85 and Brock 2006, Biggs et al. 2009, Contamin and Ellison 2009). There is little clarity regarding
86 the use of existing data and the design of future studies to detect and mitigate undesired state
87 changes (Bestelmeyer 2006, Groffman et al. 2006).

88 A common, systematic approach to analyzing state changes could allow ecologists to
89 marshal a large body of useful data and detailed knowledge to help society better understand and,
90 ultimately, manage abrupt transitions. Here, we illustrate a general, data-based, and mechanism-
91 centered analysis of abrupt transitions using four datasets from the US Long-Term Ecological
92 Research (LTER) program on pelagic ocean, coastal benthic, polar marine, and semi-arid
93 terrestrial ecosystems. These LTER data include some of the longest time-series available for
94 both causal environmental drivers and biological response variables, and interpretations of

95 associations between the drivers and the response variables are enhanced by experimental and
96 mechanistic studies conducted at the same sites.

97 We first lay out a synthetic framework for describing abrupt transitions and state changes
98 that can be used to compare and contrast among case studies. We then propose a standard
99 analytical approach that provides strong tests for detecting abrupt transitions between states. This
100 approach revealed unexpected results for the pelagic ocean system for which a “regime shift”
101 had been described previously, provided stronger evidence for hypothesized state changes in the
102 coastal benthic ecosystem, and yielded new evidence for state changes in the polar marine and
103 semi-arid terrestrial ecosystems. Our analyses illustrate how to identify and interpret causes of
104 abrupt transitions, and also illustrate limitations common to many datasets used to study abrupt
105 transitions and state changes. We conclude with recommendations for improving ongoing and
106 nascent long-term research programs aimed at detecting and forecasting state changes.

107

108 **A COMMON FRAMEWORK FOR DESCRIBING STATE CHANGE**

109 Studies across a wide range of ecosystems reveal five common data elements used in the
110 recognition and analyses of state change: *environmental drivers*; *triggers*; *biological responses*;
111 *response mechanisms*; and *contextual information* (Fig. 1). We introduce these element
112 categories based on earlier syntheses (Scheffer et al. 2001, Andersen et al. 2009, Suding and
113 Hobbs 2009) and consideration of the datasets presented herein.

114 State changes in biological responses are caused directly or indirectly by changes in
115 *environmental drivers*. Drivers are usually abiotic and include changes in climate (e.g.,
116 temperature, precipitation), or land-use (e.g., resource extraction, nutrient input rates).
117 Environmental drivers usually are considered “slow variables” (e.g., Folke et al. 2004, Carpenter

118 and Brock 2006) because they typically change much more slowly than biological response
119 variables (Fig. 2A). The textbook example of a slow environmental driver leading to a state
120 change is long-term phosphorus input leading to an abrupt shift from oligotrophic (clear blue) to
121 eutrophic (muddy green) lakes (Carpenter and Brock 2006). Drivers can also change abruptly,
122 however, with dramatic effects. *Triggers* (a.k.a. pulse disturbances) are either abrupt shifts in
123 drivers or singular events, such as droughts, hurricanes, disease outbreaks, invasive species
124 introductions, or fire, that directly affect biological responses (Suding and Hobbs 2009). State
125 changes often are caused by interactions among multiple drivers and triggers (Nystrom et al.
126 2000, Breshears et al. 2005). Whereas drivers are typically presented as time series concurrent
127 with biological responses (Fig. 2A), triggers are discrete events in time or relatively short,
128 discrete sections of a time series (e.g., an El Niño period, Holmgren et al. 2006).

129 *Biological responses* (a.k.a. response variables or state variables) are used to recognize
130 alternative states (Mantua 2004, Schroder et al. 2005, Andersen et al. 2009). Response variables
131 are especially important because they usually can be measured or monitored easily, and
132 persistent changes in their mean or increases in their variance are used as indicators of state
133 changes. Like environmental drivers, biological response variables typically are represented as
134 time series of the abundance or biomass of individual species or suites of trophically-similar
135 species (Daskalov et al. 2007, Fig. 2A).

136 *Response mechanisms* describe how drivers and triggers interact and affect responses
137 (Fig. 1). Of particular importance are changes in relationships between drivers and responses
138 caused by positive feedbacks between them that amplify changes in both drivers and responses
139 and reinforce alternative states (Rietkerk et al. 2004). Positive feedbacks often involve complex
140 chains of interactions involving biological and physical processes, including Allee effects

141 (Bourbeau-Lemieux et al. 2011), trophic cascades (Carpenter et al. 1999, Carpenter et al. 2011),
142 habitat fragmentation and extinction cascades (Swift and Hannon 2010, He and Hubbell 2011),
143 land surface-climate feedbacks (Foley et al. 2003, Cook et al. 2009), or spreading desertification
144 (Peters et al. 2004). Data on response mechanisms are derived most frequently from
145 manipulative experiments, natural history observations, and expert knowledge (Choy et al.
146 2009).

147 Finally, *contextual information* documents characteristics of the environmental setting
148 that can influence driver-response relationships and that can vary among case studies. For
149 example, lake morphometry (Genkai-Kato and Carpenter 2005), stream channel geometry
150 (Heffernan et al. 2008), soil texture (Bestelmeyer et al. 2006), and distance to source populations
151 (Hughes et al. 1999) result in spatial variation in biological responses to drivers and triggers.
152 Similarly, the timing of disturbance events with respect to seasonal period can determine their
153 effects on biological responses (Nystrom et al. 2000). Understanding spatiotemporal context can
154 help to reconcile differences among case studies illustrating general types of transitions and state
155 changes (e.g., Petraitis et al. 2009). Contextual information also can help translate scientific
156 analyses into meaningful policy recommendations and management interventions (Carpenter et
157 al. 2011).

158

159 **AN APPROACH FOR IDENTIFYING ABRUPT TRANSITIONS AND STATE CHANGES IN ECOLOGICAL** 160 **SYSTEMS**

161 Three general classes of mechanisms are postulated to produce abrupt transitions: *linear*
162 *tracking*, *threshold response*, and *hysteresis* (following Scheffer et al. 2001, Andersen et al.
163 2009, Suding and Hobbs 2009) (Fig. 2). Note that all three mechanisms can yield patterns that

164 have been referred to as “thresholds” in biological response data. An integration of exploratory
165 data analysis, time-series analysis, and linear or non-linear modeling (see Methods) provide
166 evidence for assigning each case to a class.

167 The distinction between linear tracking and threshold responses is whether: the
168 distribution of the biological response variable is unimodal vs. weakly bimodal (Fig. 2B); the
169 variance in the biological response is constant vs. increasing slightly as the environment changes
170 or a trigger occurs (Fig. 2C); and the relationship between the environmental driver and the
171 biological response is linear vs. nonlinear (Fig. 2D). Following the terminology of preceding
172 authors, both linear tracking and threshold responses can be reversed; as the driver returns to its
173 initial (pre-change) value, environmental conditions and biological response variables often track
174 them with at most short time-lags. Note that the threshold in “threshold response” refers to the
175 nonlinear biological response to a change in driver magnitude, rather than irreversibility.

176 In contrast to threshold responses, hysteretic responses result from persistent
177 environmental changes, changes in feedbacks between drivers and response variables, or long
178 time lags in biological responses to drivers. In such systems, even if the environmental driver
179 returns to earlier values, the biological response may not return to its earlier state, or does so only
180 slowly, at a markedly different magnitude of the driver, or along a different path from the one it
181 took to reach its new state (Fig. 2D). The functional form of the relationship between
182 environmental driver(s) and biological response(s) typically differs before and after a state
183 change.

184

185

186

187 **METHODS**

188

189 *Case studies*

190 We examined long-term datasets from four US-LTER programs to characterize abrupt
191 transitions and state changes following our framework, including the California Current System
192 (California Current Ecosystem LTER; <http://cce.lternet.edu>), Southern California Rocky Reef
193 (Santa Barbara Coastal LTER; <http://sbc.lternet.edu>), Western Antarctic Peninsula (Palmer
194 Station LTER; <http://pal.lternet.edu>), and Chihuahuan Desert (Jornada Basin LTER;
195 <http://jornada-www.nmsu.edu>) case studies. The California Current System study focused on the
196 abundance of a euphausiid (krill) *Nyctiphanes simplex* as a biological response and its
197 relationship to the Pacific Decadal Oscillation Index (PDO) as a primary environmental driver;
198 PDO represents changes in the ocean physical environment that affect krill populations,
199 including advection patterns and water column conditions. The Southern California Rocky Reef
200 study focused on the abundance of the red sea cucumber (*Pachythyone rubra*) and its
201 relationship to the number of days with large waves (>3.25 m) per year. These large waves
202 disrupt the dominance of *P. rubra* and allow dominance of macroalgae and associated fauna. The
203 Western Antarctic Peninsula study considered shifts in the abundances of three *Pygoscelis*
204 penguin species: the Adélie (*P. adeliae*), chinstrap (*P. antarctica*), and gentoo (*P. papua*). These
205 biological responses were considered with respect to changes in the seasonal duration of sea-ice
206 that influences the foraging and breeding biology of these species. Finally, the Chihuahuan
207 Desert study examined changes in the production of the dominant grass species black grama
208 (*Bouteloua eriopoda*) and its relationship to summer rainfall that governs its production. Details
209 on each case study can be found in the Appendix.

210

211 *General analytical approach*

212 For each of the four case studies described individually below, we used a sequence of
213 five steps to identify abrupt transitions and characterize state changes with respect to the classes
214 of mechanisms: i) visualization of temporal patterns in drivers and response variables; ii)
215 locating and statistically testing one or more breakpoints in time-series of response variables; iii)
216 statistical testing of unimodality of frequency distributions of response variables; iv) calculation
217 of temporal variance (leading indicators used to forecast state transitions) of response variables,
218 and v) assessment of relationships between response variables and drivers before and after
219 breakpoints identified in (ii). Contextual information used to interpret the results was derived
220 from ancillary experimental data, expert knowledge on triggers and response mechanisms, and
221 other natural history information (Appendix). Datasets and associated metadata are archived on,
222 and publicly available from, the Harvard Forest Data Archive
223 (<http://harvardforest.fas.harvard.edu/data/archive.html>), dataset HF170 and Ecological Archives
224 XXXXX. All data manipulation and statistical analyses were performed using base and user-
225 contributed functions in the R-language environment (R Development Core Team 2011), as
226 detailed below. The R code used is presented in the Appendix and also available with dataset
227 HF170 described above.

228 Prior to any analyses, observations of response variables were standardized:
229 $z_i = (x_i - \bar{x}) / \text{sd}(x)$. By working in standard-deviation units, data and analyses were comparable
230 across the studies. The response and driver variables were unique to each of the four case studies
231 (Figs. 3-6) and time series ranged from 28 to 59 years long. The time series of the responses in
232 each case study included missing data, so modeled values were used in place of missing values.

233 Modeled values were generated from a normal distribution with the mean and variance equal to
234 the running mean and variance, respectively, of the standardized measured values bracketing the
235 missing value(s). For example, in a time series running from 1970 – 2010, if observations were
236 missing for 1975 – 1978 and 1980, the modeled values would be sampled from $N(\text{mean}[z_{1974},$
237 $z_{1979}, z_{1981}], \text{SD}[z_{1974}, z_{1979}, z_{1981}])$. Below, we use $\{z_i\}$ to refer to the time series that includes both
238 observed and modeled response variables in standard deviation units.

239 Temporal patterns in responses were visualized by fitting a locally-weighted scatterplot
240 smoother (LOESS) (Cleveland and Devlin 1988) to $\{z_i\}$. The smoothed curve was fit using the
241 *loess* function in the R *stats* library. Default settings were used: a weighted least-squares fit to a
242 fraction of the points in a moving window that spanned $\frac{3}{4}$ of the points. The weighting function
243 for each point was proportional to the cube of the distance to each point in the moving window.
244 The curve is fit using a low-degree polynomial to a subset of the data using a weighted least
245 squares method (Cleveland and Devlin 1988).

246 Breakpoints in $\{z_i\}$ were identified using the *strucchange* package (Zeileis et al. 2002).
247 First, the time series was detrended by differencing using the *diff* function in the R *base* library.
248 A detrended time series of standardized observations has slope equal to zero, and if there is no
249 breakpoint in the time series, the intercept also would be equal to zero. Breakpoints are years
250 after which the intercept of the detrended time series changes significantly, and detection of one
251 or more breakpoints would suggest that an abrupt transition may have occurred. A combination
252 of three approaches was used to detect breakpoints and to determine the number of breakpoints
253 in the $\{z_i\}$ for each case study. First, a cumulative sum (CUSUM) plot summarized the
254 cumulative sums of differences between each value and the overall mean. A breakpoint was
255 indicated by a sudden change in direction of the CUSUM plot. Because CUSUM plots are

256 “jagged” and can indicate many directional changes, residual sums of squares (RSS) and the
257 Bayesian Information Criterion (BIC) were used to identify the number of breakpoints that
258 significantly improved the fit of the CUSUM model (Zeileis et al. 2002). Finally, we examined
259 the statistical significance of each breakpoint identified from RSS and BIC using an F statistic
260 (based on the Chow test statistic, Zeileis et al. 2002). CUSUM, RSS, and BIC plots all indicated
261 either one or two breakpoints in each of the case studies. Because changes in response variables
262 exceeded two standard-deviation units only in the case of the gentoo penguins, however, F-
263 statistics were significant only at the $\alpha = 0.1$ level.

264 Histograms and density smoothers of $\{z_i\}$ were plotted to determine if the frequency
265 distribution was unimodal or bimodal. Departures from unimodality were tested using Hartigan’s
266 dip test (Hartigan and Hartigan 1985) as implemented in the *dip* function in the R *diptest* library.
267 This test is very conservative – the distribution of the test statistic is based on asymptotic and
268 empirical samples relative to a uniform distribution. A table of quantiles (*P*-values) is provided
269 in the file qDiptab in the R *diptest* library. The power of the test (for $\alpha = 0.05$) is 80% when
270 sample size = 50; since our sample sizes (excluding missing values) ranged from 27-55, we
271 accepted *P*-values ≤ 0.10 as statistically significant evidence for departure from unimodality. The
272 linear tracking model should yield a unimodal distribution of $\{z_i\}$, whereas a threshold or
273 hysteresis model should yield a bimodal distribution of $\{z_i\}$ (see Fig. 2).

274 Changes in temporal variance of $\{z_i\}$ were assessed because abrupt increases in variance
275 have been demonstrated to be a leading indicator of abrupt transitions in the hysteresis model
276 (Carpenter and Brock 2006). We calculated changes in temporal variance of the differenced time
277 series using the *rollapply* function in the R *zoo* library. The window size used for each case study
278 was the shortest time-interval between breakpoints in the time series; window sizes ranged from

279 seven to 30 years. The temporal variance for years prior to the onset of our moving window
280 could not be calculated (as the number of points available was less than the window size); we
281 indicate those years with dotted lines in Figs 3D, 4D, 5D, and 6D. We note that using temporal
282 variance as a leading indicator works best for very long time series (\gg 50 observations) of
283 temporally autocorrelated data sampled at high frequency. Real ecological data, such as those
284 analyzed here, are of relatively short duration ($<$ 50 observations), and ecologists generally
285 attempt to minimize temporal autocorrelation by sampling less frequently. If the threshold
286 response occurs *within* the lifespan of the organism, but sampling frequency is on the same time-
287 scale as organism lifespan or generation time (*cf.* Fig. 7), a state change or threshold response
288 may not be detected. Finally, if observation errors are relatively large or if multiple linear and
289 non-linear processes interact and mute the response variables, changes in variance may not be
290 detected even though state changes have occurred (Scheffer et al. 2009, Brock and Carpenter
291 2010, Carpenter et al. 2011).

292 Finally, relationships between response and driver variables were examined for the data
293 overall and for data partitioned into before and after breakpoints. For the California Current
294 System data, the data were partitioned into sets when the PDO was either negative (before the
295 first breakpoint and after the second breakpoint) or positive (in between the two breakpoints).
296 For the Southern California Rocky Reef data, we only examined the data before the first
297 breakpoint and after the first, but before the second, breakpoint (only three values for the driver
298 variable were available after the second breakpoint). For the Western Antarctic Peninsula data,
299 we only examined the data for Adélie penguins, because there were too few data for chinstrap or
300 gentoo penguins after their 2004 breakpoints. We used linear (*lm*) and non-linear (*nls*) regression
301 in the R *stats* library to model the relationships between responses and drivers. The expectation

302 for the linear tracking model was that there would be similar response-driver relationships before
303 and after the breakpoint(s), and the expectation for the hysteresis model was that there would be
304 different response-driver relationships before and after the breakpoint(s). For example, a
305 different slope and intercept for a linear regression fitting response-driver relationships or a non-
306 linear *versus* linear fit for data and after the identified breakpoint would support the hysteresis
307 model (Scheffer and Carpenter 2003, Bai et al. 2010).

308

309 **RESULTS**

310

311 *A pelagic ocean ecosystem: The California Current System*

312 Data collected within the California Current System (CCS) provide an example of abrupt
313 transitions with a linear tracking mechanism (Fig. 3). The CCS includes a major coastal
314 upwelling biome that extends from British Columbia to Baja California. A variety of directional
315 changes in the ocean environment (including rising sea level, oceanic warming, increased density
316 stratification, decreased transparency, acidification, and changes in hypoxia) may be affecting
317 planktonic populations and the pelagic food web. There are also important sources of interannual
318 (*e.g.*, El Niño-Southern Oscillation [ENSO]) and decadal (*e.g.*, Pacific Decadal Oscillation
319 [PDO]) (Mantua et al. 1997) variability in this ecosystem. Long-term variations in krill
320 abundance are correlated with the PDO (Brinton and Townsend 2003) and time series of *N.*
321 *simplex* abundance display abrupt shifts from one persistent state to another, which may imply
322 hysteresis (Fig. 2) and/or a positive feedback mechanism (deYoung et al. 2008). We assessed the
323 evidence for alternative states in the krill population in the southern sector where temperate-
324 subarctic, cool-water zooplankton fauna enter from the north, and subtropical, warm-water

325 fauna, including *N. simplex* (Brinton et al. 1999), enter from the south. This geographic location
326 is therefore likely to be sensitive to changes in large-scale ocean circulation patterns incorporated
327 into the PDO.

328 The six-decade California Cooperative Oceanic Fisheries Investigations (CalCOFI)
329 record revealed that *N. simplex* generally was rare when the PDO was in the negative phase
330 (anomalously cool waters in the NE Pacific). Abrupt changes of the PDO from negative to
331 positive were tracked by increases in *N. simplex* abundance and *vice-versa* (Figs. 3A, 3B). Strong
332 El Niño (1958-60, 1997-98) and La Niña (1998-99) events had positive and negative influences,
333 respectively, on *N. simplex* abundance that interacted with changes in the PDO to accentuate
334 abrupt changes or interrupt relationships with PDO (Appendix A).

335 Although the warm phase between 1977-1998 was a period of consistently high
336 abundance of *N. simplex* relative to the time period before and after, our data indicate that
337 contrary to previous work (e.g., deYoung et al. 2008) this should not be considered a different
338 ecological “regime” and hysteresis is not indicated. The frequency distribution of abundances
339 were unimodal and, most definitively, the relationship between *N. simplex* abundance (response
340 variable) and the PDO (driver) varied linearly with the variations in the PDO and was identical in
341 both the warm and the cool phases of the PDO. Thus, the California Current System illustrates a
342 case of linear tracking (Hsieh and Ohman 2006), without discrete, definable (or “preferred”)
343 system states. Such linear tracking may be common in short-lived organisms that can quickly
344 and closely track abrupt changes in drivers.

345

346

347

348 *A coastal benthic ecosystem: The Southern California Rocky Reef*

349 Data from shallow rocky reefs off the coast of Southern California provide evidence of
350 hysteresis due to predation-mediated feedbacks (Fig. 4). The reefs can support either a
351 macroalgae-dominated community or one characterized by high densities ($>10,000/m^2$) of the
352 filter-feeding sea cucumber, *P. rubra*. Spatially extensive sea cucumber-dominated states can
353 persist for decades and dramatically alter reef food webs (Rassweiler et al. 2008, Rassweiler et
354 al. 2010). The loss of macroalgae leads to a reduction in micro-crustaceans and their associated
355 fish predators (Holbrook and Schmitt 1989, Schmitt and Holbrook 1990a, b).

356 Time-series data from nine sites spread along a 5-km stretch of coastline on the north
357 shore of Santa Cruz Island illustrate the mechanisms of abrupt sea cucumber-to-macroalgae
358 transitions (Fig. 4A, see also Rassweiler et al. 2010). The frequency distribution of annual sea
359 cucumber abundance data revealed evidence of bimodality (Fig. 4C). The first transition from
360 macroalgae to sea cucumber dominance occurred in the late 1980s and was associated with a
361 series of years in which there were few high wave events during winter storms (Fig. 4B). High
362 waves dislodge sea cucumbers from algal beds (Rassweiler et al. 2008), but when winter storms
363 are weak, sea cucumbers competitively displace algae by smothering and killing them.

364 Frequent, strong storms returned after 1995, but the relationship between days of high
365 waves (driver) and sea cucumber abundance (response) disappeared and sea cucumbers
366 continued to dominate the system (Fig. 4E). Consumption of algal spores by abundant sea
367 cucumbers allowed this species to persist in the face of increased wave disturbance (Rassweiler
368 et al. 2008). This relationship switched to yet another low cucumber state when predatory sea
369 stars colonized the system in late 2002 (Appendix B). Thus, this case conforms to a hysteresis

370 model in which stabilizing feedbacks conferred resilience with respect to the environmental
371 driver.

372

373

374 *A polar marine ecosystem: The Western Antarctic Peninsula*

375 The Western Antarctic Peninsula (WAP) provides another example of hysteresis due to
376 the effects of multiple, interacting drivers (Fig. 5). Since 1950, annual mean air temperature in
377 some regions has increased by 2°C, and winter air temperature has increased by nearly 6°C
378 (Smith et al. 1996, Vaughan et al. 2003, Turner et al. 2006) These climatic changes have caused
379 long-term reductions in the regional extent and duration of winter sea-ice (Smith and
380 Stammerjohn 2001, Stammerjohn et al. 2008a, Stammerjohn et al. 2008b), a proximate driver of
381 directional environmental change in the WAP marine ecosystem (Smith et al. 2003, Ducklow et
382 al. 2007, Moline et al. 2008). One important change is poleward shifts in breeding ranges of
383 three closely related penguin species; the Adélie, chinstrap, and gentoo (Forcada et al. 2006,
384 Ducklow et al. 2007, Forcada and Trathan 2009). There is considerable debate regarding the
385 environmental drivers of change in penguin breeding population dynamics (Patterson et al. 2003,
386 Forcada and Trathan 2009, Trivelpiece et al. 2011).

387 Nearly 40 years of data collected from the Palmer Archipelago near Anvers Island,
388 Antarctica (Appendix C: Fig. A2) illustrate abrupt declines in the Adélie penguin breeding
389 population beginning in 1993, and abrupt increases in numbers of breeding chinstrap and gentoo
390 penguins beginning in 2004 (Fig. 5A). Bimodality of annual abundance data was not clearly
391 evident (Fig. 5C), nor did temporal variance (Fig. 5D) illustrate dramatic changes before or
392 during the observed population changes. However, analysis of the relationship between the

393 proximate driver (sea-ice duration; Fig. 5B) and Adélie penguin breeding population size
394 revealed that prior to the 1993 breakpoint, the abundance of this species was essentially
395 unresponsive to variation in sea-ice duration, however after 1993 these variables were strongly
396 and positively correlated (Fig. 5E), conforming to the hysteresis model. We did not examine
397 driver-response relationships for chinstrap or gentoo penguins because only five data points on
398 yearly numbers of breeding pairs have been obtained since the 2004 breakpoint. Progressive
399 climate warming resulted in an abrupt transition operating through multiple, cascading ecological
400 drivers and feedbacks, including reduced sea-ice duration, changes in terrestrial snowfall
401 accumulation that affect penguin breeding biology, and feedbacks between Adélie population
402 reductions and predator efficiency (Appendix C).

403

404 *A semi-arid grassland ecosystem: The Chihuahuan Desert*

405 Data from northern Chihuahuan Desert grasslands provide an example of hysteresis
406 involving a strong trigger and novel feedbacks (Fig. 6). These grasslands were dominated
407 historically by black grama grass (*Bouteloua eriopoda*), but during the last 150 years, black
408 grama grasslands have shifted to shrublands dominated by xerophytic woody plants. Similar
409 shifts from grasslands to shrublands have occurred in semi-arid systems throughout the world
410 (Archer 1995). Historically, black grama grass persisted through episodic droughts, and shrub
411 cover within black grama grasslands was limited by competition for water, limited shrub seed
412 dispersal, and possibly periodic fire (Peters and Gibbens 2006). Heavy cattle grazing on black
413 grama grass during drought periods is believed to have initiated the grassland-to-shrubland
414 transition (Appendix D). It has not been clear, however, how rapidly the initial grassland loss

415 takes place and therefore how best to employ monitoring strategies to prevent it (Bestelmeyer
416 2006).

417 Time-series data on annual production of black grama grass collected during the mid-
418 1900s from two pastures in the Jornada Experimental Range near Las Cruces, NM, USA,
419 indicate the start of an abrupt transition in 1948. In that year, there was no black grama
420 production (Fig. 6A), and this lack of production coincided with the onset of a prolonged drought
421 (Fig. 6B). Several lines of evidence suggest that this system conforms to the hysteresis model.
422 First, annual production was bimodal (Fig. 6C), indicating two alternative states. Second, black
423 grama production exhibited an increase in temporal variance during the transition (Fig. 6D)
424 associated with a period of low and variable summer rainfall (Fig. 6B). Third, driver-response
425 regressions show that prior to 1948, black grama production had a positive relationship to
426 growing-season (July-September) precipitation (Nelson 1934). After 1948, however, this
427 relationship weakened and overall production was low regardless of growing-season rainfall
428 (Fig. 6E). The shift in black grama production was very abrupt, never attaining previous high
429 values after 1950. A positive feedback between soil erosion and low grass cover appears to have
430 precluded grassland recovery after a return to higher levels of precipitation (Appendix D).

431 To summarize, we used a common approach to determine if and when abrupt transitions
432 occurred, to evaluate leading indicators that could forecast the transitions, and to match each case
433 to the appropriate class of mechanisms (Figs. 3-6). The timing of abrupt transitions was
434 successfully identified in all four cases. An increase in variance that could serve as a leading
435 indicator was observed only in the Chihuahuan Desert case due to the extreme interannual
436 fluctuation preceding grassland collapse. The linear tracking model was indicated for the
437 California Current case due to unimodality in the distribution of biological response values and

438 linearity in the driver-response relationship. The hysteresis model was indicated in the other
439 three cases due to varying combinations of evidence, including the strong nonlinearity in the
440 driver-response relationship for the West Antarctic Peninsula, and both bimodality of biological
441 responses and nonlinear driver-response relationships in the Southern California Rocky Reef and
442 Chihuahuan Desert cases. In all four cases, plausible response mechanisms supported the
443 classification of the case to the general mechanism.

444

445 **DISCUSSION**

446

447 *A common approach*

448 These case studies illustrate that abrupt transitions and state changes not only can be
449 identified, but also can be understood via a suite of general concepts (Fig. 1) and relatively
450 simple methods. Although the availability of long-running time series of both drivers and
451 responses has been limited (Andersen et al. 2009, Carpenter et al. 2011), long-term data now can
452 be accessed from LTER and related sites (<http://ecotrends.info>), and many institutions worldwide
453 are investing considerable resources establishing new ecological observation networks (e.g.,
454 National Ecological Observatory Network, Global Lake Ecological Observatory Network, Ocean
455 Observatory Initiative, Paleoecological Observatory Network). The sequence of methods used
456 here, including an objective evaluation of abrupt transitions and alternative states, examination of
457 frequency distributions of response variables, consideration of variance patterns used in
458 forecasting, and analysis of patterns and mechanisms of driver-response relationships can be
459 applied to many of these datasets.

460 A common, systematic approach applied across different datasets will advance a general
461 understanding of abrupt transitions and state changes. Such a common approach is especially
462 important now, as abrupt, often irreversible transitions are forecast to increase as climatic change
463 accelerates (Millennium Ecosystem Assessment 2005, Fagre et al. 2009); a coherent, integrated
464 strategy is needed to manage and mitigate the expected state changes. Our comparative
465 exploration of case studies suggests some lessons for future analyses of existing data and
466 guidance for new observation and monitoring networks embarking on long-term studies.

467

468 *Leading indicators may have limited utility*

469 Mathematical modeling (Scheffer et al. 2009) and empirical studies conducted in
470 temperate lake ecosystems (Carpenter et al. 2011) suggest that increased variance in the time
471 series of biological responses can be used to forecast abrupt transitions. Many systems, however,
472 may show no change or even decreases in variance (Hastings and Wysham 2010). Our analysis
473 of four different systems, three of which showed clear hysteretic patterns between drivers and
474 responses, suggest that this leading indicator must be carefully scaled to the time-scale of
475 dynamics in the biological response variable (*e.g.*, organism lifespan; Fig. 7). Short-lived
476 organisms can track abrupt changes in drivers closely. Thus, some transitions, such as those in
477 the California Current krill (Fig. 3), may appear abrupt until rescaled to the short lifespan of this
478 organism (Fig. 7). In contrast, especially when lifespan matches the dominant time scale of
479 environmental variability (Hsieh and Ohman 2006), other transitions may appear gradual, but
480 actually occur quite abruptly relative to the organism's lifespan (*e.g.*, penguins: Fig. 5A; black
481 grama grass: Fig. 6A).

482 To be informative, leading indicators of rising variance require many highly
483 autocorrelated samples collected *within* the lifespan of the sentinel organism of interest. The
484 traditional ecological emphasis on temporal trend as opposed to variance has led researchers to
485 undervalue the importance of regularly sampled time series and fine temporal intervals.
486 Detection of abrupt transitions and state changes require time series without missing values (or
487 ones that can be reasonably modeled). If sampling designs capture weakly- or un-correlated
488 measures of abundance, or if studied organisms are long-lived and transitions occur rapidly (i.e.,
489 between samples), measures of temporal variance may not be informative. In such cases, it
490 would be worthwhile to identify faster-changing variables (Carpenter et al. 2011) that reflect
491 organismal performance in populations, such as physiological status. However, if transitions are
492 not caused by “slow” variables but instead are caused by abrupt, unpredictable triggers acting
493 within vulnerable systems, variance-based leading indicators may provide only limited
494 information (Hastings and Wysham 2010). In such cases, mean values of a slow variable might
495 be used to signal heightened susceptibility to abrupt transition given a trigger, but the transition
496 itself may not be predictable.

497

498 *Driver-response relationships are powerful tools.*

499 Researchers should hesitate to infer response mechanisms based solely on the presence of
500 threshold patterns in biological response variables; analysis of driver-response relationships
501 provide stronger tests of such inferences. For example, the linear tracking model (Fig. 2) may
502 appear to have abrupt transitions when biological responses track abrupt changes in drivers, as in
503 the California Current System (Fig. 3A). Such observations have been used to suggest the
504 existence of alternative stable states (deYoung et al. 2008) that is not supported by our analysis

505 (Fig. 3E). Driver-response relationships can then be explained with regard to specific response
506 mechanisms (e.g., grass cover loss leading to soil erosion feedbacks in the Chihuahuan Desert
507 case, Appendix D).

508

509 *Context is critical.*

510 In the four cases that we examined, the historical context and the location in which the
511 study was conducted relative to physical processes occurring at larger spatial scales both had
512 important consequences for the observed dynamics. The location of the California Current
513 System and Western Antarctic Peninsula studies relative to biogeographic transition zones, the
514 Chihuahuan Desert study on sandy soils during a period of comparatively high grazing pressure,
515 and the Southern California Rocky Reef study area relative to the shifting southern range limit of
516 sea-stars each influenced the patterns observed in their respective time-series of biological
517 responses (Appendix). Data on the same response variables collected at other locations or times
518 might yield different results or reveal how large-scale forces such as ocean circulation, regional
519 climate, physiography, or soils mediate abrupt transitions (Rietkerk et al. 2004, Williams et al.
520 2011). As case studies of abrupt transitions accumulate, researchers should ensure that spatial
521 and temporal measurement scales of drivers and response variables are recorded and are
522 appropriately congruent. Researchers should also be alert for changes in context when comparing
523 studies.

524

525 *Multiple lines of evidence aid interpretation.*

526 Different kinds of state changes were identified by different analyses. Interpretations of
527 state changes were greatly facilitated by consideration of data and observations apart from the

528 driver and response time series. The choice of the “right” driver and the “right” response variable
529 was based on detailed short- and long-term experiments along with ancillary information and
530 anecdotal observations that provided important clues to the interpretation of time-series data. In
531 spite of the case-specific nature of response mechanisms, we predict that a systematic review of
532 additional cases will reveal a limited set of classes of interactions between drivers, triggers, and
533 responses (*cf.* Fig. 2). This framework can guide future investigations and promote a data-
534 supported understanding of abrupt transitions (Walker and Meyers 2004).

535

536 *Can we manage state changes?*

537 Long-term, multi-faceted case studies and datasets can provide retrospective explanations
538 of transitions and state changes for specific cases, but can they provide useful information for
539 proactive management? We suggest that a body of transition datasets representing different kinds
540 of ecosystems would provide several useful insights for managing state change. First, they would
541 suggest the appropriate drivers, triggers, and biological response variables to be emphasized in
542 monitoring, as well as the spatial and temporal design elements needed for detection. Second,
543 depending upon the drivers, such analyses would indicate useful strategies for managing the
544 effects of drivers. In some cases, such as when response variables are affected by broad-scale
545 physical drivers (e.g., California Current System) direct control is not feasible but forecasting
546 and adaptation approaches could be developed. Third, case studies can be used to evaluate the
547 abruptness of transitions, particularly with respect to organisms’ lifespans (Fig. 7). Cases of high
548 abruptness, such as in the semi-arid grasslands and Antarctic peninsula, suggest that management
549 reactions to indicators of transition must be especially rapid (*e.g.*, adjust stocking rates in drought
550 periods and establish institutions that can respond rapidly) (Meze-Hausken et al. 2009). Finally,

551 case studies can be used to indicate the potential utility of early warning indicators to forecast
552 transitions given their abruptness and the feasibility of measuring the appropriate attributes with
553 sufficient temporal and/or spatial resolution. Many abrupt transitions may ultimately need to be
554 managed according to a precautionary principle that acknowledges our limited ability to develop
555 indicators of imminent transition or to respond rapidly enough to such indicators (Contamin and
556 Ellison 2009). In those situations, case studies might indicate simple values in driver or
557 biological response levels that are related to the likelihood of abrupt transition. To make
558 informed choices among the wide range of possible strategies for detecting and managing abrupt
559 transitions, ecologists and policymakers must commit to sustaining, renewing, and initiating
560 observational platforms in multiple sentinel sites. The resulting data can, as we have shown,
561 produce useful maps for navigating our changing world.

562

563 **ACKNOWLEDGMENTS**

564

565 Support for this work was provided by NSF LTER awards to the Ecosystems Center of
566 the Marine Biological Laboratory at Woods Hole (08-23101), Harvard University (06-20443),
567 New Mexico State University (06-18210), UC San Diego (04-17616), UC Santa Barbara (06-
568 20276), the University of Wisconsin (08-22700), an NSF contract to the LTER Network Office
569 at the University of New Mexico (08-32652), and the Natural Sciences and Engineering
570 Research Council of Canada (NSERC). The LTER EcoTrends project, the LTER Network
571 Office, and Laurie Chiasson at Harvard Forest supported the data synthesis efforts. The
572 California Current System data were collected in part with the assistance of A. Townsend
573 (Scripps Institution of Oceanography Pelagic Invertebrates Collection) and the late E. Brinton.

574 Collection of the Southern California Rocky Reef data prior to 2000 was supported by NSF
575 awards to RJS and SJH. The Jornada Experimental Range data collection and synthesis was
576 supported by staff of the USDA Agricultural Research Service. The authors thank Ben Baiser,
577 Audrey Barker-Plotkin, Elizabeth Crone, Elizabeth Farnsworth, David Foster, Brian Hall, Dave
578 Orwig, Sydne Record, Kristina Stinson, and Jack Williams for helpful discussions and comments
579 on early versions of the manuscript.
580

581 **LITERATURE CITED**

582

583 Ainley, D. G. 2002. *The Adélie Penguin: Bellwether of Climate Change*. Columbia University
584 Press, New York.

585 Andersen, T., J. Carstensen, E. Hernandez-Garcia, and C. M. Duarte. 2009. Ecological
586 thresholds and regime shifts: approaches to identification. *Trends in Ecology & Evolution*
587 24:49-57.

588 Archer, S. 1995. Tree-grass dynamics in a prosopis-thornscrub savanna parkland - reconstructing
589 the past and predicting the future. *Ecoscience* 2:83-99.

590 Bai, Y. F., J. G. Wu, C. M. Clark, S. Naeem, Q. M. Pan, J. H. Huang, L. X. Zhang, and X. G.
591 Han. 2010. Tradeoffs and thresholds in the effects of nitrogen addition on biodiversity
592 and ecosystem functioning: evidence from inner Mongolia Grasslands. *Global Change*
593 *Biology* 16:358-372.

594 Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology.
595 *Frontiers in Ecology and the Environment* 1:376-382.

596 Bertness, M. D., G. C. Trussell, P. J. Ewanchuk, and B. R. Silliman. 2002. Do alternate stable
597 community states exist in the Gulf of Maine rocky intertidal zone? *Ecology* 83:3434-
598 3448.

599 Bestelmeyer, B. T. 2006. Threshold concepts and their use in rangeland management and
600 restoration: the good, the bad, and the insidious. *Restoration Ecology* 14:325-329.

601 Bestelmeyer, B. T., D. P. Goolsby, and S. R. Archer. 2011. Spatial patterns in state-and-
602 transition models: a missing link to land management? *Journal of Applied Ecology*
603 48:746-757.

604 Bestelmeyer, B. T., J. P. Ward, and K. M. Havstad. 2006. Soil-geomorphic heterogeneity
605 governs patchy vegetation dynamics at an arid ecotone. *Ecology* 87:963-973.

606 Biggs, R., S. R. Carpenter, and W. A. Brock. 2009. Spurious certainty: how ignoring
607 measurement error and environmental heterogeneity may contribute to environmental
608 controversies. *Bioscience* 59:65-76.

609 Bourbeau-Lemieux, A., M. Festa-Bianchet, J. M. Gaillard, and F. Pelletier. 2011. Predator-
610 driven component Allee effects in a wild ungulate. *Ecology Letters* 14:358-363.

611 Breshears, D. D., N. S. Cobb, P. M. Rich, K. P. Price, C. D. Allen, R. G. Balice, W. H. Romme,
612 J. H. Kastens, M. L. Floyd, J. Belnap, J. J. Anderson, O. B. Myers, and C. W. Meyer.
613 2005. Regional vegetation die-off in response to global-change-type drought.
614 *Proceedings of the National Academy of Sciences of the United States of America*
615 102:15144-15148.

616 Brinton, E., M. D. Ohman, A. W. Townsend, M. D. Knight, and A. L. Bridgeman. 1999.
617 *Euphausiids of the World Ocean*.

618 Brinton, E. and A. Townsend. 2003. Decadal variability in abundances of the dominant
619 euphausiid species in southern sectors of the California Current. *Deep-Sea Research Part*
620 *II-Topical Studies in Oceanography* 50:2449-2472.

621 Briske, D. D., S. D. Fuhlendorf, and F. E. Smeins. 2006. A unified framework for assessment
622 and application of ecological thresholds. *Rangeland Ecology & Management* 59:225-236.

623 Brock, W. A. and S. R. Carpenter. 2010. Interacting regime shifts in ecosystems: implication for
624 early warnings. *Ecological Monographs* 80:353-367.

625 Brown, J. R. and S. Archer. 1999. Shrub invasion of grassland: recruitment is continuous and not
626 regulated by herbaceous biomass or density. *Ecology* 80:2385-2396.

627 Carpenter, S. R. and W. A. Brock. 2006. Rising variance: a leading indicator of ecological
628 transition. *Ecology Letters* 9:308-315.

629 Carpenter, S. R., J. J. Cole, M. L. Pace, R. Batt, W. A. Brock, T. Cline, J. Coloso, J. R. Hodgson,
630 J. F. Kitchell, D. A. Seekell, L. Smith, and B. Weidel. 2011. Early warnings of regime
631 shifts: a whole-ecosystem experiment. *Science* 332:1079-1082.

632 Carpenter, S. R., D. Ludwig, and W. A. Brock. 1999. Management of eutrophication for lakes
633 subject to potentially irreversible change. *Ecological Applications* 9:751-771.

634 Choy, S. L., R. O'Leary, and K. Mengersen. 2009. Elicitation by design in ecology: using expert
635 opinion to inform priors for Bayesian statistical models. *Ecology* 90:265-277.

636 Cleveland, W. S. and S. J. Devlin. 1988. Locally weighted regression - an approach to
637 regression-analysis by local fitting. *Journal of the American Statistical Association*
638 83:596-610.

639 Collie, J. S., K. Richardson, and J. H. Steele. 2004. Regime shifts: can ecological theory
640 illuminate the mechanisms? *Progress in Oceanography* 60:281-302.

641 Contamin, R. and A. M. Ellison. 2009. Indicators of regime shifts in ecological systems: what do
642 we need to know and when do we need to know it? *Ecological Applications* 19:799-816.

643 Cook, B. I., R. L. Miller, and R. Seager. 2009. Amplification of the North American "Dust
644 Bowl" drought through human-induced land degradation. *Proceedings of the National
645 Academy of Sciences of the United States of America* 106:4997-5001.

646 Daskalov, G. M., A. N. Grishin, S. Rodionov, and V. Mihneva. 2007. Trophic cascades triggered
647 by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proceedings of
648 the National Academy of Sciences of the United States of America* 104:10518-10523.

649 deYoung, B., M. Barange, G. Beaugrand, R. Harris, R. I. Perry, M. Scheffer, and F. Werner.
650 2008. Regime shifts in marine ecosystems: detection, prediction and management. Trends
651 in Ecology & Evolution 23:402-409.

652 Ducklow, H. W., K. Baker, D. G. Martinson, L. B. Quetin, R. M. Ross, R. C. Smith, S. E.
653 Stammerjohn, M. Vernet, and W. Fraser. 2007. Marine pelagic ecosystems: the west
654 Antarctic peninsula. Philosophical Transactions of the Royal Society of London Series B-
655 Biological Sciences 362:67-94.

656 Eckert, G. L. 2007. Spatial patchiness in the sea cucumber *Pachythyone rubra* in the California
657 Channel Islands. Journal of Experimental Marine Biology and Ecology 348:121-132.

658 Fagre, D. B., C. W. Charles, C. D. Allen, C. Birkeland, F. S. C. III, P. M. Groffman, G. R.
659 Guntenspergen, A. K. Knapp, A. D. McGuire, P. J. Mulholland, D. P. C. Peters, D. D.
660 Roby, and G. Sugihara. 2009. CCSP: Thresholds of Climate Change in Ecosystems. A
661 report by the U.S. Climate Change Science Program and the Subcommittee and Global
662 Change Research:156.

663 Foley, J. A., M. T. Coe, M. Scheffer, and G. L. Wang. 2003. Regime shifts in the Sahara and
664 Sahel: interactions between ecological and climatic systems in northern Africa.
665 Ecosystems 6:524-539.

666 Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling.
667 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual
668 Review of Ecology, Evolution and Systematics 35:557-581.

669 Forcada, J. and P. N. Trathan. 2009. Penguin responses to climate change in the Southern Ocean.
670 Global Change Biology 15:1618–1630.

671 Forcada, J., P. N. Trathan, K. Reid, E. J. Murphy, and J. P. Croxall. 2006. Contrasting population
672 changes in sympatric penguin species in association with climate warming. *Global*
673 *Change Biology* 12:411-423.

674 Fraser, W. R. and E. E. Hofmann. 2003. A predator's perspective on causal links between climate
675 change, physical forcing and ecosystem response. *Marine Ecology-Progress Series* 265:1-
676 15.

677 Fraser, W. R. and D. L. Patterson. 1997. Human disturbance and long-term changes in Adelie
678 penguin populations: a natural experiment at Palmer Station, Antarctic Peninsula. Pages
679 445–452 *in* B. Battaglia, J. Valencia, and D. W. H. Walton, editors. *Antarctic*
680 *communities: species, structure and survival*, scientific committee for Antarctic research
681 (SCAR), sixth biological symposium. Cambridge University Press, New York, NY.

682 Fraser, W. R. and W. Z. Trivelpiece. 1996. Factors controlling the distribution of seabirds:
683 winter-summer heterogeneity in the distribution of Adelie penguin populations. Pages
684 257-272 *in* R. M. Ross, E. E. Hoffman, and L. B. Quetin, editors. *Foundations for*
685 *ecological research west of the Antarctic Peninsula*. American Geophysical Union,
686 Washington, D.C.

687 Fraser, W. R., W. Z. Trivelpiece, D. G. Ainley, and S. G. Trivelpiece. 1992. Increases in
688 Antarctic penguin populations - reduced competition with whales or a loss of sea ice due
689 to environmental warming. *Polar Biology* 11:525-531.

690 Genkai-Kato, M. and S. R. Carpenter. 2005. Eutrophication due to phosphorus recycling in
691 relation to lake morphometry, temperature, and macrophytes. *Ecology* 86:210-219.

692 Gibbens, R. P. and R. F. Beck. 1987. Increase in number of dominant plants and dominance
693 classes on a grassland in the northern Chihuahuan Desert. *Journal of Range Management*
694 40:136-139.

695 Gorman, K. B., E. S. Erdmann, B. C. Pickering, P. J. Horne, J. R. Blum, H. M. Lucas, D. L.
696 Patterson-Fraser, and W. R. Fraser. 2010. A new high-latitude record for the macaroni
697 penguin (*Eudyptes chrysolophus*) at Avian Island, Antarctica. *Polar Biology* 33:1155-
698 1158.

699 Groffman, P., J. Baron, T. Blett, A. Gold, I. Goodman, L. Gunderson, B. Levinson, M. Palmer,
700 H. Paerl, G. Peterson, N. Poff, D. Rejeski, J. Reynolds, M. Turner, K. Weathers, and J.
701 Wiens. 2006. Ecological thresholds: the key to successful environmental management or
702 an important concept with no practical application? *Ecosystems* 9:1-13.

703 Hartigan, J. A. and P. M. Hartigan. 1985. The dip test of unimodality. *Annals of Statistics* 13:70-
704 84.

705 Hastings, A. and D. B. Wysham. 2010. Regime shifts in ecological systems can occur with no
706 warning. *Ecology Letters* 13:464-472.

707 He, F. and S. P. Hubbell. 2011. Species-area relationships always overestimate extinction rates
708 from habitat loss. *Nature* 473:368-371.

709 Heffernan, J. B., R. A. Sponseller, and S. G. Fisher. 2008. Consequences of a biogeomorphic
710 regime shift for the hyporheic zone of a Sonoran Desert stream. *Freshwater Biology*
711 53:1954-1968.

712 Herbel, C. H., F. N. Ares, and R. A. Wright. 1972. Drought effects on a semidesert grassland
713 range. *Ecology* 53:1084-1093.

- 714 Herbel, C. H. and R. P. Gibbens. 1996. Post-drought vegetation dynamics on arid rangelands in
715 southern New Mexico. *New Mexico Agricultural Experiment Station Bulletin* 776.
- 716 Herrick, J. E., J. R. Brown, A. J. Tugel, P. L. Shaver, and K. M. Havstad. 2002. Application of
717 soil quality to monitoring and management: Paradigms from rangeland ecology.
718 *Agronomy Journal* 94:3-11.
- 719 Holbrook, S. J. and R. J. Schmitt. 1989. Resource overlap, prey dynamics and the strength of
720 competition. *Ecology* 70:1943-1953.
- 721 Holmgren, C. A., J. L. Betancourt, and K. A. Rylander. 2006. A 36,000-yr vegetation history
722 from the Peloncillo Mountains, southeastern Arizona, USA. *Palaeogeography*
723 *Palaeoclimatology Palaeoecology* 240:405-422.
- 724 Hsieh, C. H. and M. D. Ohman. 2006. Biological responses to environmental forcing: the linear
725 tracking window hypothesis. *Ecology* 87:1932-1938.
- 726 Hughes, T. P. 1994. Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral-
727 reef. *Science* 265:1547-1551.
- 728 Hughes, T. P., A. H. Baird, E. A. Dinsdale, N. A. Moltschaniwskyj, M. S. Pratchett, J. E. Tanner,
729 and B. L. Willis. 1999. Patterns of recruitment and abundance of corals along the Great
730 Barrier Reef. *Nature* 397:59-63.
- 731 Jones, H. P. and O. J. Schmitz. 2009. Rapid recovery of damaged ecosystems. *PLoS One*
732 4:e5653.
- 733 Lavaniegos, B. E. and M. D. Ohman. 2007. Coherence of long-term variations of zooplankton in
734 two sectors of the California Current System. *Progress in Oceanography* 75:42-69.

735 Lindig-Cisneros, R., J. Desmond, K. E. Boyer, and J. B. Zedler. 2003. Wetland restoration
736 thresholds: can a degradation transition be reversed with increased effort? *Ecological*
737 *Applications* 13:193-205.

738 Lommasson, T. and C. Jensen. 1943. Determining utilization of range grasses by height-weight
739 tables. *Journal of Forestry* 41:589-593.

740 Mantua, N. 2004. Methods for detecting regime shifts in large marine ecosystems: a review with
741 approaches applied to North Pacific data. *Progress in Oceanography* 60:165-182.

742 Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific
743 interdecadal climate oscillation with impacts on salmon production. *Bulletin of the*
744 *American Meteorological Society* 78:1069-1079.

745 Marshall, G. J., P. A. Stott, J. Turner, W. M. Connolley, J. C. King, and T. A. Lachlan-Cope.
746 2004. Causes of exceptional atmospheric circulation changes in the Southern
747 Hemisphere. *Geophysical Research Letters* 31:L14205.

748 Martinson, D. G., S. E. Stammerjohn, R. A. Iannuzzi, R. C. Smith, and M. Vernet. 2008.
749 Western Antarctic Peninsula physical oceanography and spatio-temporal variability.
750 *Deep-Sea Research Part II-Topical Studies in Oceanography* 55:1964-1987.

751 Massom, R. A., S. E. Stammerjohn, R. C. Smith, M. J. Pook, R. A. Iannuzzi, N. Adams, D. G.
752 Martinson, M. Vernet, W. R. Fraser, L. B. Quetin, R. M. Ross, Y. Massom, and H. R.
753 Krouse. 2006. Extreme anomalous atmospheric circulation in the West Antarctic
754 Peninsula region in Austral Spring and Summer 2001/02, and its profound impact on sea
755 ice and biota. *Journal of Climate* 19:3544-3571.

756 Mauzey, K. P., Birkelan.C, and P. K. Dayton. 1968. Feeding behavior of asteroids and escape
757 responses of their prey in Puget Sound region. *Ecology* 49:603-&.

758 Meredith, M. P., E. J. Murphy, E. J. Hawker, J. C. King, and M. I. Wallace. 2008. On the
759 interannual variability of ocean temperatures around South Georgia, Southern Ocean:
760 Forcing by El Nino/Southern Oscillation and the Southern Annular Mode. *Deep-Sea*
761 *Research Part II-Topical Studies in Oceanography* 55:2007-2022.

762 Meze-Hausken, E., A. Patt, and S. Fritz. 2009. Reducing climate risk for micro-insurance
763 providers in Africa: a case study of Ethiopia. *Global Environmental Change-Human and*
764 *Policy Dimensions* 19:66-73.

765 Millennium Ecosystem Assessment. 2005. *Ecosystems and Human Well-being: Desertification*
766 *Synthesis*

767 Moline, M. A., N. J. Karnovsky, Z. Brown, G. J. Divoky, T. K. Frazer, C. A. Jacoby, J. J. Torres,
768 and W. R. Fraser. 2008. High latitude changes in ice dynamics and their impact on polar
769 marine ecosystems. *Annals of the New York Academy of Sciences* 1134:267-319.

770 Nelson, E. W. 1934. The influence of precipitation and grazing upon black grama grass range.
771 U.S. Department of Agriculture Technical Bulletin No. 409.

772 Nystrom, M., C. Folke, and F. Moberg. 2000. Coral reef disturbance and resilience in a human-
773 dominated environment. *Trends in Ecology & Evolution* 15:413-417.

774 Ohman, M. D. and P. E. Smith. 1995. A comparison of zooplankton sampling methods in the
775 CalCOFI time series. *California Cooperative Oceanic Fisheries Investigations Reports*,
776 36:153-158.

777 Okin, G. S., D. A. Gillette, and J. E. Herrick. 2006. Multi-scale controls on and consequences of
778 aeolian processes in landscape change in arid and semi-arid environments. *Journal of*
779 *Arid Environments* 65:253-275.

780 Patterson, D. L., A. L. Easter-Pilcher, and W. R. Fraser. 2003. The effects of human activity and
781 environmental variability on long-term changes in Adelie penguin populations at Palmer
782 Station, Antarctica. Pages 301–307 *in* A. H. L. Huiskes, W. W. C. Gieskes, J. Rozema, R.
783 M. L. Schorno, S. M. van der Vies, and W. J. Wolf, editors. *Antarctic Biology in a*
784 *Global Context*. Backhuys Publishers, Leiden.

785 Pearse, J. S. and A. H. Hines. 1987. Long-term population-dynamics of sea-urchins in a central
786 California kelp forest - rare recruitment and rapid decline. *Marine Ecology-Progress*
787 *Series* 39:275-283.

788 Peters, D. P. C., B. T. Bestelmeyer, J. E. Herrick, E. L. Fredrickson, H. C. Monger, and K. M.
789 Havstad. 2006. Disentangling complex landscapes: new insights into arid and semiarid
790 system dynamics. *Bioscience* 56:491-501.

791 Peters, D. P. C. and R. P. Gibbens. 2006. Plant communities in the Jornada Basin: the dynamic
792 landscape. Pages 211-231 *in* K. M. Havstad, L. F. Huenneke, and W. H. Schlesinger,
793 editors. *Structure and Function of a Chihuahuan Desert Ecosystem: The Jornada Basin*
794 *Long-Term Ecological Research Site*. Oxford University Press, New York, NY.

795 Peters, D. P. C., R. A. Pielke, B. T. Bestelmeyer, C. D. Allen, S. Munson-McGee, and K. M.
796 Havstad. 2004. Cross-scale interactions, nonlinearities, and forecasting catastrophic
797 events. *Proceedings of the National Academy of Sciences of the United States of*
798 *America* 101:15130-15135.

799 Petraitis, P. S. and R. E. Latham. 1999. The importance of scale in testing the origins of
800 alternative community states. *Ecology* 80:429-442.

801 Petraitis, P. S., E. T. Methratta, E. C. Rhile, N. A. Vidargas, and S. R. Dudgeon. 2009.
802 Experimental confirmation of multiple community states in a marine ecosystem.
803 *Oecologia* 161:139-148.

804 R Development Core Team. 2011.

805 Rassweiler, A., K. K. Arkema, D. C. Reed, R. C. Zimmerman, and M. A. Brzezinski. 2008. Net
806 primary production, growth, and standing crop of *Macrocystis pyrifera* in Southern
807 California. *Ecology* 89:2068.

808 Rassweiler, A., R. J. Schmitt, and S. J. Holbrook. 2010. Triggers and maintenance of multiple
809 shifts in the state of a natural community. *Oecologia* 164:489-498.

810 Rietkerk, M., S. C. Dekker, P. C. de Ruiter, and J. van de Koppel. 2004. Self-organized
811 patchiness and catastrophic shifts in ecosystems. *Science* 305:1926-1929.

812 Rudnick, D. L. and R. E. Davis. 2003. Red noise and regime shifts. *Deep-Sea Research Part I-*
813 *Oceanographic Research Papers* 50:691-699.

814 Scheffer, M., J. Bascompte, W. A. Brock, V. Brovkin, S. R. Carpenter, V. Dakos, H. Held, E. H.
815 van Nes, M. Rietkerk, and G. Sugihara. 2009. Early-warning signals for critical
816 transitions. *Nature* 461:53-59.

817 Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in
818 ecosystems. *Nature* 413:591-596.

819 Scheffer, M. and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory
820 to observation. *Trends in Ecology & Evolution* 18:648-656.

821 Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A.
822 Virginia, and W. G. Whitford. 1990. Biological feedbacks in global desertification.
823 *Science* 247:1043-1048.

824 Schmitt, R. J. and S. J. Holbrook. 1986. Seasonally fluctuating resources and temporal variability
825 of interspecific competition. *Oecologia* 69:1-11.

826 Schmitt, R. J. and S. J. Holbrook. 1990a. Contrasting effects of giant-kelp on dynamics of
827 surfperch populations. *Oecologia* 84:419-429.

828 Schmitt, R. J. and S. J. Holbrook. 1990b. Populations responses of surfperch released from
829 competition. *Ecology* 71:1653-1665.

830 Schroder, A., L. Persson, and A. M. De Roos. 2005. Direct experimental evidence for alternative
831 stable states: a review. *Oikos* 110:3-19.

832 Schwinning, S. and O. E. Sala. 2004. Hierarchy of responses to resource pulses in semi-arid
833 ecosystems. *Oecologia* 141:211-220.

834 Siniff, D. B., R. A. Garrott, J. J. Rotella, W. R. Fraser, and D. G. Ainley. 2008. Projecting the
835 effects of environmental change on Antarctic seals. *Antarctic Science* 20:425-435.

836 Smith, R. C., W. R. Fraser, and S. E. Stammerjohn. 2003. Climate variability and ecological
837 response of the marine ecosystem in the western Antarctic Peninsula (WAP) region.
838 Pages 158–173 in D. Greenland, D. G. Goodin, and R. C. Smith, editors. *Climate*
839 *variability and ecosystem response at longterm ecological research sites*. Oxford
840 University Press., New York, NY.

841 Smith, R. C. and S. E. Stammerjohn. 2001. Variations of surface air temperature and sea-ice
842 extent in the western Antarctic Peninsula region. *Annals of Glaciology* 33:493-500.

843 Smith, R. C., S. E. Stammerjohn, and K. S. Baker. 1996. Surface air temperature variations in the
844 Western Antarctic Peninsula. Pages 105-122 in R. M. Ross, E. E. Hofmann, and L. B.
845 Quetin, editors. *Foundations for Ecological Research West of the Antarctic Peninsula*.
846 American Geophysical Union, Washington, DC.

847 Stammerjohn, S. E., D. G. Martinson, R. C. Smith, and R. A. Iannuzzi. 2008a. Sea ice in the
848 western Antarctic Peninsula region: Spatio-temporal variability from ecological and
849 climate change perspectives. *Deep-Sea Research Part II-Topical Studies in Oceanography*
850 55:2041-2058.

851 Stammerjohn, S. E., D. G. Martinson, R. C. Smith, X. Yuan, and D. Rind. 2008b. Trends in
852 Antarctic annual sea ice retreat and advance and their relation to El Nino-Southern
853 Oscillation and Southern Annular Mode variability. *Journal of Geophysical Research-*
854 *Oceans* 113:Article Number C03S90.

855 Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. Alternative states and positive feedbacks
856 in restoration ecology. *Trends in Ecology & Evolution* 19:46-53.

857 Suding, K. N. and R. J. Hobbs. 2009. Threshold models in restoration and conservation: a
858 developing framework. *Trends in Ecology & Evolution* 24:271-279.

859 Swift, T. L. and S. J. Hannon. 2010. Critical thresholds associated with habitat loss: a review of
860 the concepts, evidence, and applications. *Biological Reviews* 85:35-53.

861 Thompson, D. W. J. and S. Solomon. 2002. Interpretation of recent Southern Hemisphere
862 climate change. *Science* 296:895-899.

863 Thompson, L. G., D. A. Peel, E. Mosleythompson, R. Mulvaney, J. Dai, P. N. Lin, M. E. Davis,
864 and C. F. Raymond. 1994. Climate since AD1510 on Dyer Plateau, Antarctic Peninsula
865 - evidence for recent climate change. Pages 420-426 *in* E. M. Morris, editor. *Annals of*
866 *Glaciology*, Vol 20, 1994 - Proceedings of the Fifth International Symposium on
867 Antarctic Glaciology. Int Glaciological Soc, Cambridge.

868 Todd, R. E., D. L. Rudnick, R. E. Davis, and M. D. Ohman. 2011. Underwater gliders reveal
869 rapid arrival of El Nino effects off California's coast. *Geophysical Research Letters* 38.

870 Trathan, P. N., P. T. Fretwell, and B. Stonehouse. 2011. First recorded loss of an emperor
871 penguin colony in the recent period of Antarctic regional warming: implications for other
872 colonies. *PLoS One* 6:e14738.

873 Trivelpiece, W. Z., J. T. Hinke, A. K. Miller, C. S. Reiss, S. G. Trivelpiece, and G. M. Watters.
874 2011. Variability in krill biomass links harvesting and climate warming to penguin
875 population changes in Antarctica. *Proceedings of the National Academy of Sciences of*
876 *the United States of America* 108:7625-7628.

877 Turner, J., T. A. Lachlan-Cope, S. Colwell, G. J. Marshall, and W. M. Connolley. 2006.
878 Significant warming of the Antarctic winter troposphere. *Science* 311:1914-1917.

879 Vaughan, D. G., G. J. Marshall, W. M. Connolley, C. Parkinson, R. Mulvaney, D. A. Hodgson,
880 J. C. King, C. J. Pudsey, and J. Turner. 2003. Recent rapid regional climate warming on
881 the Antarctic peninsula. *Climatic Change* 60:243-274.

882 Walker, B. and J. A. Meyers. 2004. Thresholds in ecological and social-ecological systems: a
883 developing database. *Ecology and Society* 9:3.

884 Williams, J. W., J. L. Blois, and B. N. Shuman. 2011. Extrinsic and intrinsic forcing of abrupt
885 ecological change: case studies from the late Quaternary. *Journal of Ecology* 99:664-677.

886 Williams, T. D. 1995. *The penguins: Spheniscidae*.

887 Woehler, E. J., J. Cooper, J. P. Croxall, W. R. Fraser, G. L. Kooyman, G. D. Miller, D. C. Nel,
888 D. L. Patterson, H.-U. Peter, C. A. Ribic, K. Salwicka, W. Z. Trivelpiece, and H.
889 Weimerskirch. 2001. *A Statistical Assessment of the Status and Trends of Antarctic and*
890 *subAntarctic Seabirds*.45.

891 Yahdjian, L. and O. E. Sala. 2006. Vegetation structure constrains primary production response
892 to water availability in the Patagonian steppe. *Ecology* 87:952-962.

893 Zeileis, A., F. Leisch, K. Hornik, and C. Kleiber. 2002. strucchange: An R package for testing
894 for structural change in linear regression models. *Journal of Statistical Software* 7:1-38.
895
896
897

898 **Figure Legends**
899

900 **Figure 1.** A conceptual model of the relationships between the elements of abrupt transitions and
901 analytical approaches used to investigate them.

902

903 **Figure 2.** Three classes of driver-response relationships and analytical indicators of transitions
904 and state changes. The top row (**A**) illustrates time series of driver and response variables in
905 linear tracking, threshold, and hysteretic systems. The second row (**B**) illustrates that the
906 frequency distribution of the observations should shift from unimodal to bimodal when a
907 threshold or hysteretic change occurs. The third row (**C**) illustrates how one leading indicator,
908 the variance of the time series, should differ among the three classes of driver-response
909 relationships. As the transition becomes more abrupt and the post-transition state becomes more
910 distinctive from the pre-transition state, the variance should become more peaked at the
911 transition point. The bottom row (**D**) illustrates changes in the driver-response relationships from
912 linear (in the linear tracking class) to nonlinear (in the threshold class) to hysteretic.

913

914 **Figure 3.** Results of analyses for the California Current System. In the time series of the
915 biological response (**A**), the observed data are shown as points scaled in standard deviation units,
916 the time series (which include modeled values) as grey lines connecting the points, and the
917 locally weighted regression (loess) illustrating the temporal pattern as a solid black line.

918 Breakpoints identified using CUSUM, RSS, and BIC are identified with arrows on the x -axis.

919 The potential alternate state begins the year *after* the breakpoint. In the time series of the driver

920 (**B**), the observed data are shown as points and the time series as grey lines connecting the points.

921 There are no missing values in the time series of drivers in Figs. 3-6. The frequency distributions

922 (C) are equivalently scaled across Figs. 3-6, and all bins are the same width (0.5 SD units). The
923 probability density function of the observations is overlain on the histogram. Similarly, the time
924 series of variance (D) are all equivalently scaled across Figs. 3-6, and breakpoints again are
925 identified. Finally, the relationship between the driver and response (E) are illustrated for the
926 initial state (solid symbols, black lines) and post-transition state (open symbols, grey lines). In
927 this figure only, the data from the third state are combined with those from the first state
928 (negative phase of the PDO).

929

930 **Figure 4.** Results of analyses for the Southern California Rocky Reef (A-E), following the same
931 order and rules as for Fig. 3. For the relationship between the driver and response (E), only data
932 from the first and second states are shown.

933

934 **Figure 5.** Results of analyses for the Western Antarctic Peninsula (A-E), following the same
935 order and rules as for Fig. 3. The three species of penguins are illustrated in three colors (Adélie
936 penguins in black, chinstrap penguins in orange, gentoo penguins in blue). The relationship
937 between the driver and response is shown only for Adélies because there are too few data for the
938 other species.

939

940 **Figure 6.** Results of analyses for the northern Chihuahuan Desert (A-E), following the same
941 order and rules as for Fig. 3. The two pastures are illustrated in black (Pasture 2) and orange
942 (Pasture 9).

943

944 **Figure 7.** The time series of the biological responses from each case study rescaled to the
945 maximum life span of each organism. Maximum lifespan was used to ensure complete
946 population turnover. Each tick on the *x*-axis indicates one lifespan (value in parentheses).
947

948 **APPENDIX**

949

950 *A. Detail on the California Current System case study*

951 To assess the likely mechanism underlying the relationship between variations in the
952 California Current euphausiid (krill) *Nyctiphanes simplex* and the Pacific Decadal Oscillation
953 (PDO) first shown by (Brinton and Townsend 2003) and re-examined in this paper (Figs. 3A-E),
954 we analyzed the life-history structure of *N. simplex* from 1951 to 2009. Zooplankton were
955 sampled in the upper 210 m or 140 m of the water column using 0.5-mm mesh plankton nets
956 (Ohman and Smith 1995) and analyzed by E. Brinton. The stations used in the analysis were
957 from Southern California reported in (Lavaniegos and Ohman 2007): the California Cooperative
958 Oceanic Fisheries Investigations (CalCOFI) lines 80 through 93, from shore to station 70,
959 springtime cruises, and night-time samples only. This station pattern differs slightly from that
960 used by (Brinton and Townsend 2003). Annual averages of the Pacific Decadal Oscillation
961 (Mantua et al. 1997) were obtained from the monthly values posted at:

962 <http://jisao.washington.edu/pdo/PDO.latest>.

963 Counts of krill during these 48 years were available for four life-history stages:
964 calytopis, furcilia, juveniles, and adults. The proportional composition of each stage (Fig. A1)
965 was used to differentiate between two primary means by which changes in the physical
966 environment, as represented by the PDO, might have influenced euphausiid abundance: altered
967 advection of organisms into or out of the study region, and altered in situ changes in water
968 column conditions (*e.g.*, temperature, food, predators) that can affect population growth of *N.*
969 *simplex*.

970 The primary breeding center of *N. simplex* is located off Baja California (Brinton et al.
971 1999), to the south of our study site. Abrupt increases in advection of organisms into our region
972 from the south, reflecting individuals introduced from a population showing regular recruitment
973 in a favorable habitat, would have rapidly increased the proportion of younger individuals
974 (calyptopis larvae) in the population. Conversely, if conditions changed favorably in situ,
975 without corresponding changes in advection, the contribution of calyptopis larvae would have
976 increased more gradually over time. Finally, if in situ conditions for *N. simplex* deteriorated
977 without a corresponding change in advection, there should have been a decline in relative
978 abundance of larval stages due to reduced egg production by adults.

979 Inspection of Fig. A1 relative to the two abrupt transitions identified in the population
980 time series (Fig. 3A) suggested that altered advection was the more plausible hypothesis. The
981 1976-77 abrupt increase in total abundance of *N. simplex* was accompanied by a simultaneous
982 increase in the proportion of larvae, without a temporally lagged response. The explanatory
983 power of the PDO for the temporal variability in *N. simplex* is corroborated by modeling
984 variations in *N. simplex* as an autoregressive (AR-1) process related only to present and one
985 previous state of the PDO, which shows excellent agreement with observations.

986 Furthermore, the rapid decline in total abundance in 1999-2000 was not accompanied by
987 a gradual diminution in contribution by larvae. Rather, the proportion of larvae remained roughly
988 constant, although production was intermittent. Hence, we conclude that the predominant
989 mechanism underlying rapid changes in the euphausiid-PDO time series was the introduction or
990 flushing out of individuals through altered transport. Once introduced into the study site, *N.*
991 *simplex* were able to reproduce and survive for extended periods of time because of more
992 favorable conditions in situ, but the rapid increases/decreases in abundance were initiated by

993 altered advection. Further support for this interpretation comes from observations of responses
994 by *N. simplex* to major El Niño events. These events typically have resulted only in transient
995 increases in abundance of *N. simplex* (Figs. 3A, 3B, see also Brinton and Townsend 2003)
996 initiated by transport from the south. The unusual El Niño of 2009-2010 was not accompanied by
997 changes in *N. simplex* abundance because this particular event propagated through atmospheric
998 teleconnections rather than through altered ocean advection (Todd et al. 2011).

999

1000 *B. Detail on the Southern California Rocky Reef case study*

1001 We used data on abundance of red sea cucumbers (*Pachythyone rubra*) from nine sites on
1002 the north shore of Santa Cruz Island, CA. Sites were situated along a 5 km stretch of coastline
1003 (centered on 34.05°N, 119.737°W), with six sites established in 1982 and three more added in
1004 1989 (for a complete description of the sites see Schmitt and Holbrook 1986, Holbrook and
1005 Schmitt 1989). Sampling was usually annual between September and November; in some
1006 instances not all sites were sampled every year. Sites were similar in depth, slope, exposure and
1007 initial benthic community structure. At each site there were two fixed 40 m transects, one each
1008 along the 6-m and 9-m isobath. The percent cover of *P. rubra*, understory macroalgae (mainly
1009 species in the genera *Eisenia*, *Laurencia*, *Gelidium*, *Rhodymenia*, *Codium* and *Corallina*), sea
1010 urchins, and *Macrocystis pyrifera* were estimated using point-contact methods (eight randomly
1011 located points per meter per transect). The sea-star *Pycnopodia helianthoides* was counted in a 2-
1012 m wide swath centered on each transect. Abundance of *P. rubra* was estimated as the average
1013 percent cover across all transects sampled in each year. Similarly, abundance of *P. helianthoides*
1014 was estimated as the mean density across all transects sampled in each year.

1015 Data on wave heights were taken from buoys operated by the National Oceanic and
1016 Atmospheric Administration (www.ndbc.noaa.gov). Because no single buoy operated without
1017 interruption between 1982 and 2008, data from three buoys were combined. The East Santa
1018 Barbara buoy (No. 46053) is located nearest to the sites where organismal cover and abundance
1019 data were collected (23 km NNW of the study sites) and, therefore, wave heights recorded at this
1020 buoy were used when available. On days when data were not available from the East Santa
1021 Barbara buoy, data from the Point Arguello and Santa Maria buoys (Nos. 46023 and 46011,
1022 ~135 km NW of the monitoring sites) were used to estimate wave height and water temperature
1023 in the east channel. Estimates were made based on linear regressions developed from days when
1024 all three buoys were operational (Rassweiler et al. 2008).

1025 To quantify wave intensity, we calculated the number of days each year when maximum
1026 significant wave height exceeded 3.25 m. October 1 was the cut-off between years, because
1027 biological sampling typically occurred near this date. We chose 3.25 m as our definition of a
1028 large storm because previous experiments revealed that the competitive effects of algae on *P.*
1029 *rubra* abundance only occurred when waves exceeded this height (Rassweiler et al. 2008,
1030 Rassweiler et al. 2010). We did not include wave data from the summer period of each year
1031 (May through September), because summer swells typically come from a southerly direction and
1032 the northern shores of the Channel Islands, where our sites are located, are sheltered from these
1033 waves.

1034 One challenge in analyzing state changes is that there can be more than two states. In this
1035 case study, an exclusive focus on *P. rubra* initially suggested only two states: prior to 1987 the
1036 sea cucumbers were nearly absent, from 1987 to 2002 they were very abundant although
1037 variable, and after 2002 they returned to their low density state, approaching the densities

1038 initially observed in the early 1980s (Figs. 4A, 4E). However, when other invertebrates were
1039 considered, it became apparent that the post-2002 low abundance state was not equivalent to the
1040 pre-1987 state. Rather, the post-2002 system consists of different species and is maintained by a
1041 new mechanism – predation. The third state was initiated by the sudden arrival of the predatory
1042 sea star, *P. helianthoides*, a mobile and voracious predator, with well-established potential to
1043 decimate echinoderm populations (Mauzey et al. 1968, Pearse and Hines 1987). In 2003 when
1044 sea stars first became abundant they were typically large – 35 cm or more across – suggesting
1045 that they immigrated into these sites, either from deeper water or from the western end of the
1046 island where they have been previously observed (Eckert 2007).

1047 The role of sea stars in the initiation and maintenance of the third state illustrates that an
1048 interaction between multiple environmental factors triggered the post-1987 shift into the high *P.*
1049 *rubra* state. The absence of predators alone was not sufficient to have caused this shift; before
1050 1987, *P. rubra* was rare even though predators were absent. Similarly, it is unlikely that low
1051 waves could have triggered a shift into the high density state if *P. helianthoides* had been
1052 present, because the sea stars exert strong top-down control on *P. rubra* abundance. Our results
1053 underscore the complex nature of state changes. Different mechanisms can initiate, maintain, or
1054 end a state, and interactions between multiple drivers may be necessary to trigger shifts in states.

1055

1056 *C. Detail on the Western Antarctic Peninsula case study*

1057 Species comprising polar marine systems have evolved life histories associated with the
1058 presence or absence of sea-ice, often broadly termed sea-ice obligate or sea-ice intolerant
1059 species, respectively (Ducklow et al. 2007, Moline et al. 2008, Siniff et al. 2008). *Pygoscelis*
1060 penguins of the Western Antarctic Peninsula (WAP, Fig. A2) integrate environmental variability

1061 over large spatio-temporal scales due to their longevity and spatially extensive foraging (Fraser
1062 and Trivelpiece 1996). Relationships between environmental drivers and penguin population
1063 dynamics (Figs. 5A, 5B, 5E) reflect life history integration of this variability, and the abundance
1064 and distribution of these species provided some of the earliest evidence of rapid climate-induced
1065 change in the WAP (Fraser et al. 1992, Woehler et al. 2001, Forcada et al. 2006, Siniff et al.
1066 2008, Forcada and Trathan 2009, Gorman et al. 2010, Trathan et al. 2011, Trivelpiece et al.
1067 2011). Physical oceanographic processes occurring along the WAP are important proximate
1068 drivers of changes in regional climatology (Thompson and Solomon 2002, Marshall et al. 2004,
1069 Ducklow et al. 2007, Martinson et al. 2008, Meredith et al. 2008). Interactions between climate
1070 phases and physical oceanography has resulted in displacement of the cold, dry polar climate that
1071 historically dominated the region by a warm, moist sub-Antarctic system characteristic of the
1072 northern WAP and Scotia Arc (Ducklow et al. 2007).

1073 Penguin population data in this case study span nearly four decades, a period during
1074 which sea-ice extent decreased by 50% and sea-ice duration decreased by 85 days (Smith et al.
1075 2003, Stammerjohn et al. 2008b). Number of breeding pairs of *Pygoscelis* penguins has been
1076 estimated annually since the mid-1970's from surveys of nesting individuals on seven islands
1077 within 15 km of Palmer Station, a US scientific research station located on Anvers Island (Fig.
1078 A2). Most of the data used in these analyses were based on numbers obtained immediately
1079 following peak clutch completion (November-December). In the few years where this peak was
1080 missed due to weather and sea-ice conditions hindering island access, the next survey conducted
1081 closest to this period was used. During 1980, 1984, 1985 and 1988, regional totals were
1082 estimated from partial surveys (*i.e.*, data from islands not surveyed were estimated based on
1083 percent increases or decreases on adjacent islands that were surveyed). Analyses to examine

1084 relationships between sea-ice duration and Adélie penguin population response were lagged by
1085 four years to account for delayed reproductive maturity of these species (Ainley 2002), however,
1086 results were qualitatively similar for lags equal to zero and five. Following (Stammerjohn et al.
1087 2008b), annual sea-ice duration was based on the number of days that elapsed between the first
1088 day of advance and the first day of retreat for the Palmer LTER study region near Anvers Island
1089 (Figure A2); an “ice year” begins in mid-February of year y and ended in mid-February of year
1090 $y+1$.

1091 Since 1975, the breeding population of the true Antarctic, sea-ice obligate, Adélie
1092 penguin (Ainley 2002) along the Palmer Archipelago has declined by 85% (Fig. 5A). The
1093 breakpoint in Adélie population dynamics occurred in 1993 (Fig. 5A); this response is
1094 temporally consistent, given the species lag in reproductive maturity, with the poorest sea-ice
1095 conditions evident in the remote sensing record (Fraser and Hofmann 2003, Stammerjohn et al.
1096 2008b) and the lowest abundance of Antarctic krill (*Euphausia superba*) in the contemporary
1097 WAP record (Fraser and Hofmann 2003) that occurred in 1990. Krill is the current dominant
1098 prey not only of Adélie penguins along the Palmer Archipelago, but also of sub-Antarctic, sea-
1099 ice-intolerant chinstrap and gentoo penguins (cf. Fraser et al. 1992, Williams 1995, Fraser and
1100 Hofmann 2003, Trivelpiece et al. 2011) species whose breeding populations increased
1101 dramatically beginning in 2004. Although it has been hypothesized that krill abundance is a
1102 primary driver of the population dynamics of all three *Pygoscelis* species (Forcada and Trathan
1103 2009, Trivelpiece et al. 2011), their contrasting population dynamics along the Palmer
1104 Archipelago do not support this general hypothesis. For example, chinstrap and gentoo penguin
1105 established local founder colonies in 1975 and 1993, respectively (Fig. 5A). Although several
1106 lines of evidence suggest that krill has important nutritional impacts on reproduction and survival

1107 of these penguins, these impacts, both positive and negative, are ultimately mediated by species-
1108 specific life history affinities to sea-ice (Fraser et al. 1992, Ducklow et al. 2007, Forcada and
1109 Trathan 2009).

1110 An additional key environmental driver in this system appears to be increased snowfall
1111 due to escalating oceanic venting of moisture resulting from reduced winter sea-ice conditions
1112 (Thompson et al. 1994, Fraser and Patterson 1997, Patterson et al. 2003, Massom et al. 2006).
1113 This increased snowfall affects penguin demography via two response mechanisms. First, heavy
1114 spring snow eventually floods nests and drowns chicks (Fraser and Patterson 1997, Patterson et
1115 al. 2003). Adélie penguins are particularly vulnerable to flooding because their breeding
1116 phenology is highly synchronized, and they initiate egg production earlier than the other
1117 *Pygoscelis* species, when snow accumulations peak (Williams 1995, Massom et al. 2006). In
1118 contrast, gentoo penguins have a much more plastic breeding phenology, and along with
1119 chinstraps, typically breed 3-4 weeks later than Adélie penguins (Williams 1995, Ducklow et al.
1120 2007). Second, brown skuas (*Catharacta lonnbergi*), territorial avian predators, prey on penguin
1121 eggs and chicks. As the size of Adélie colonies declines within skua territories due to snowfall,
1122 penguins become progressively more vulnerable to skua depredation. Once colonies have
1123 decreased to ~50 breeding pairs, skuas appear to locally extirpate these colonies by annually
1124 consuming all penguin eggs and chicks (Fraser and Patterson 1997, Patterson et al. 2003). As
1125 with the sea cucumbers and sea stars, different mechanisms can initiate, maintain, or end penguin
1126 population states.

1127

1128

1129

1130 *D. Detail on the Chihuahuan Desert case study*

1131 This case pertains to the sandy soils (typic aridic, thermic, coarse-loamy Calcids,
1132 Cambids, and Argids) of southern New Mexico, west Texas (USA) and northern Chihuahua
1133 states (Mexico), where mean annual precipitation is ~250-350 mm. In these areas, state changes
1134 from grasslands to shrublands are among the best recognized of terrestrial transitions (Scheffer
1135 and Carpenter 2003), but there is considerable debate about their underlying causes and timing.
1136 A combination of overgrazing and drought is thought to have caused the transition by shifting
1137 the interaction of competition and physical processes in favor of shrubland (i.e., the so-called
1138 teeter-totter model of Schlesinger et al. 1990). This simple model belies a more complex, multi-
1139 staged process that we have recently revealed by analyzing historical and long-term data. This
1140 evolving “multi-stage model” breaks up the grassland-shrubland transition into a series of stages,
1141 including: loss of dominant grass cover in discrete areas (stage I); invasion or expansion of
1142 shrubs within low-grass cover conditions (stage II); and lateral expansion of soil erosion,
1143 grassland loss, and expansion of shrub populations (stage III) (Peters et al. 2006, Bestelmeyer et
1144 al. 2011).

1145 Black grama grass (*Bouteloua eriopoda*) initially is the dominant plant and ground cover
1146 (> 60%), with very few or no shrubs. It persists in the face of periodic droughts, grows and sets
1147 seed reliably, and stabilizes surface soil horizons, and may competitively exclude shrubs (Herbel
1148 and Gibbens 1996). In contrast, other perennial grass species have lower canopy cover, die out
1149 during droughts, and coexist with shrubs (Nelson 1934, Herbel et al. 1972, Gibbens and Beck
1150 1987, Herrick et al. 2002).

1151 Data for this case study were obtained from annual reports archived between 1938 and
1152 1972 at the Jornada Experimental Range. Production of black grama grass (lbs/acre) was

1153 extracted from tables in these reports for pastures 2 and 9, which were dominated by this species.
1154 Estimates were based on an annually varying number of 15-m long × 10-cm wide transects.
1155 Transects were added until the standard error of the estimate was within 10% of mean production
1156 value. On each transect, 100 plants were measured and the height of grazed and ungrazed tillers
1157 was recorded. Standing crop of different perennial grass species was estimated by clipping all
1158 aboveground grass parts, air-drying them, and weighing them (Jornada Forage Crop Report,
1159 1942, Jornada archives). Areas of each pasture that were not dominated by black grama grass
1160 (due to variation in soils) were excluded from sampling. A utilization scale (Lommasson and
1161 Jensen 1943) was used to estimate the percent of grazing use for each species, which was
1162 averaged over hundreds of plants (Fig. A3). Utilization values equaled the percentage of the
1163 recommended biomass removed (35% at that time), and were determined from a “large number
1164 of transects” randomly placed throughout each pasture in each year; values over 100% (*i.e.*, more
1165 than 100% of the 35% recommended use) indicated overgrazing. Precipitation data were from
1166 the West Well rain gauge of the USDA Rain Gauge Network ([http://usda-](http://usda-ars.nmsu.edu/data_long-term-datasets.html)
1167 [ars.nmsu.edu/data_long-term-datasets.html](http://usda-ars.nmsu.edu/data_long-term-datasets.html)), which lay at the southwest and northwest corners of
1168 pastures 2 and 9, respectively. We paired growth year black grama grass production (measured in
1169 fall) with the monsoonal rainfall totals (July-September) of that same year. Known limitations of
1170 the data include: 1) a lack of precise spatial relationships between production, patchy rainfall,
1171 and pasture utilization; and 2) complex relationships between intra- and interannual rainfall and
1172 plant production that are not reflected in the data (Schwinning and Sala 2004, Yahdjian and Sala
1173 2006).

1174 The state change data reflect the loss of black grama grass cover in discrete areas (*i.e.*,
1175 stage I of the “multi-stage model”). The observed state change was initiated by severe drought

1176 years occurring during a period with intermittently high levels of utilization (cattle grazing; Fig.
1177 A3). Years of very low summer (July-September) rainfall led to years of relatively low black
1178 grama production (Figs. 6A, 6B, 6E). The failure to reduce livestock numbers during those years
1179 led to overgrazing, and successive years of overgrazing (measured as high utilization values)
1180 were followed by years of reduced black grama grass production (Fig. A3). That dry, extremely
1181 windy conditions occurring in low grass cover conditions could initiate extensive, severe soil
1182 erosion and subsequent collapse of black grama grassland became widely appreciated in the
1183 early 1950's (see also Okin et al. 2006)). These data, however, reveal how rapidly (over 2 years)
1184 these effects can lead to persistent reductions in black grama.

1185

1186

1187 **Figure Legends (Appendix)**

1188

1189 **Figure A1.** Time series of life-history stages (calyptopis, furcilia, juveniles, and adults) of the
1190 euphausiid *Nyctiphanes simplex* from the Southern California sector of the California Current
1191 System. Illustrated are the proportions each life-history stage of total *N. simplex* springtime
1192 abundance, night-time samples only, averaged over the region sampled.

1193

1194 **Figure A2.** The Western Antarctica Peninsula (WAP). Lower left box shows the WAP relative
1195 to other regions of the Antarctic. Upper right box shows the Palmer LTER study area near
1196 Anvers Island. Data from penguin colonies used in these analyses are located on islands within
1197 the Palmer Archipelago that are shaded in yellow. The location of Palmer Station is shaded in
1198 gray. Image generated from base maps provided by the National Snow and Ice Data Center's
1199 map server A-CAP (<http://nsidc.org/agdc/acap/>).

1200

1201 **Figure A3.** The time series of black grama grass (*Bouteloua eriopoda*) production plotted along
1202 with utilization for one pasture (Pasture 2). Pasture 9 exhibited a similar pattern. Note the high
1203 utilization in 1951, coinciding with the onset of extensive soil erosion noted in the Jornada
1204 monthly report in December 1951.

1205

1206

1207

1208

1209

Context

Biological response

- ***Breakpoint analysis***
- ***Bimodality***
- ***Leading indicators***

Response mechanisms



Drivers, Triggers

- ***Response-driver regressions***

Linear Tracking

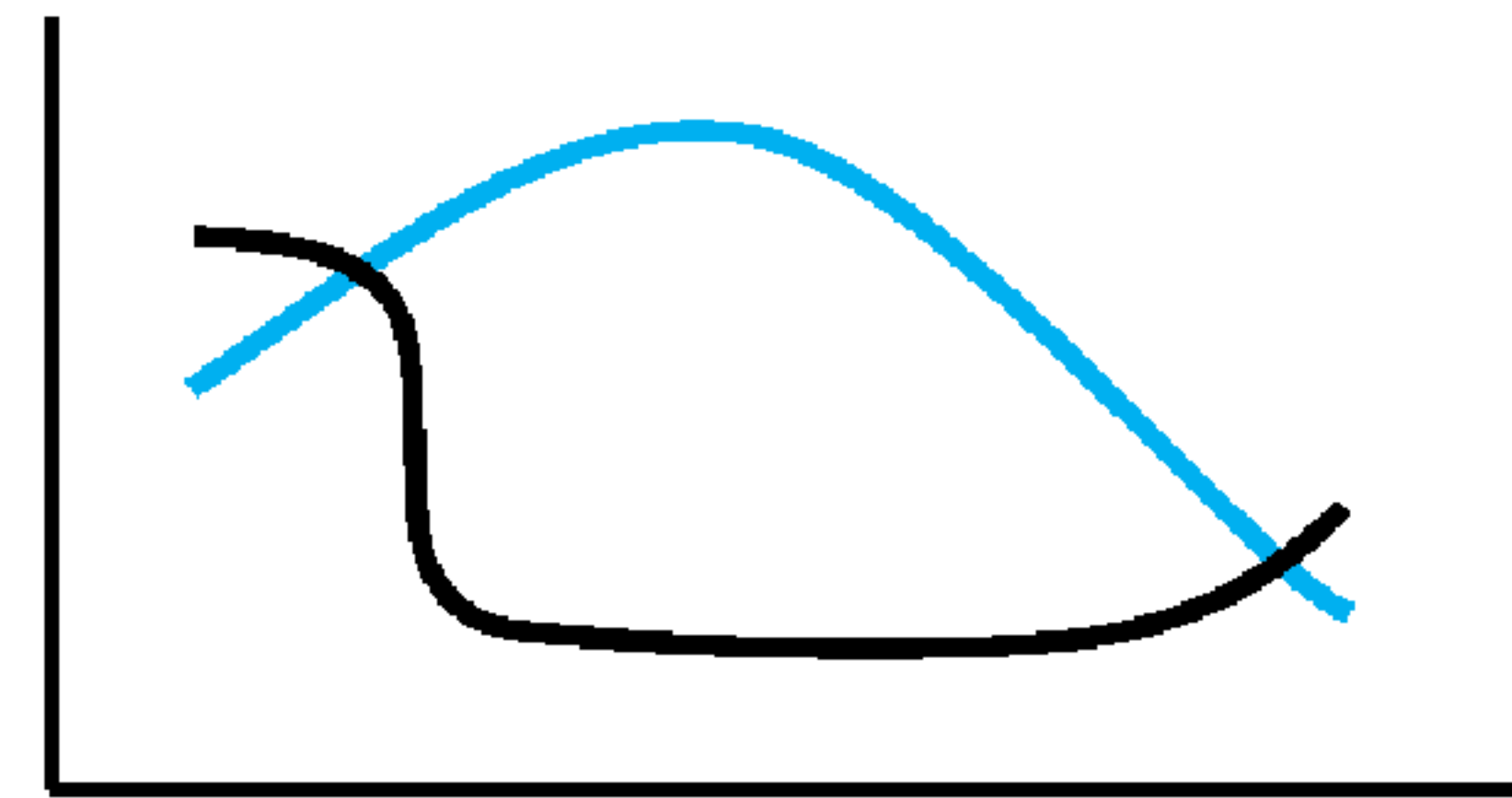
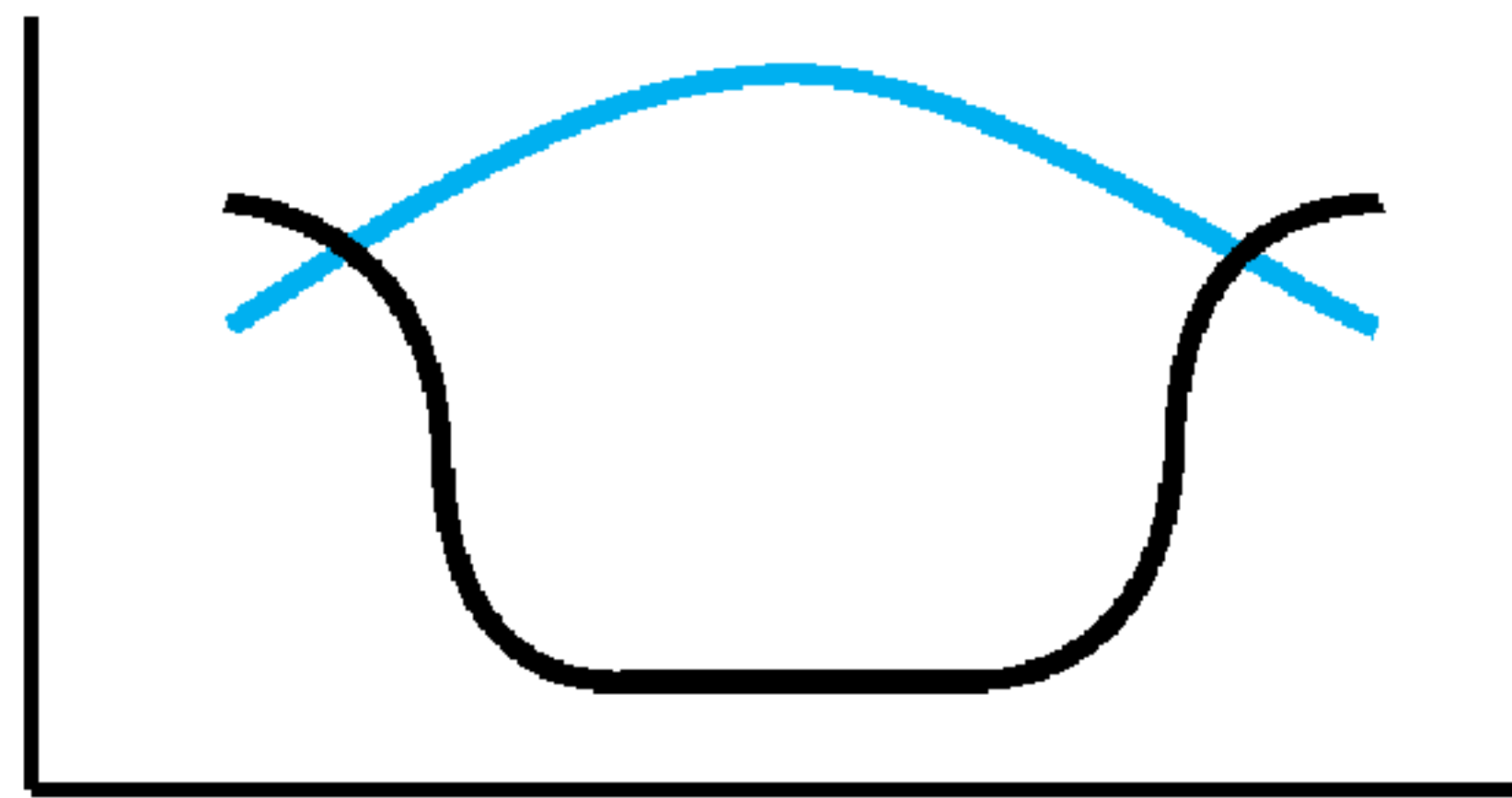
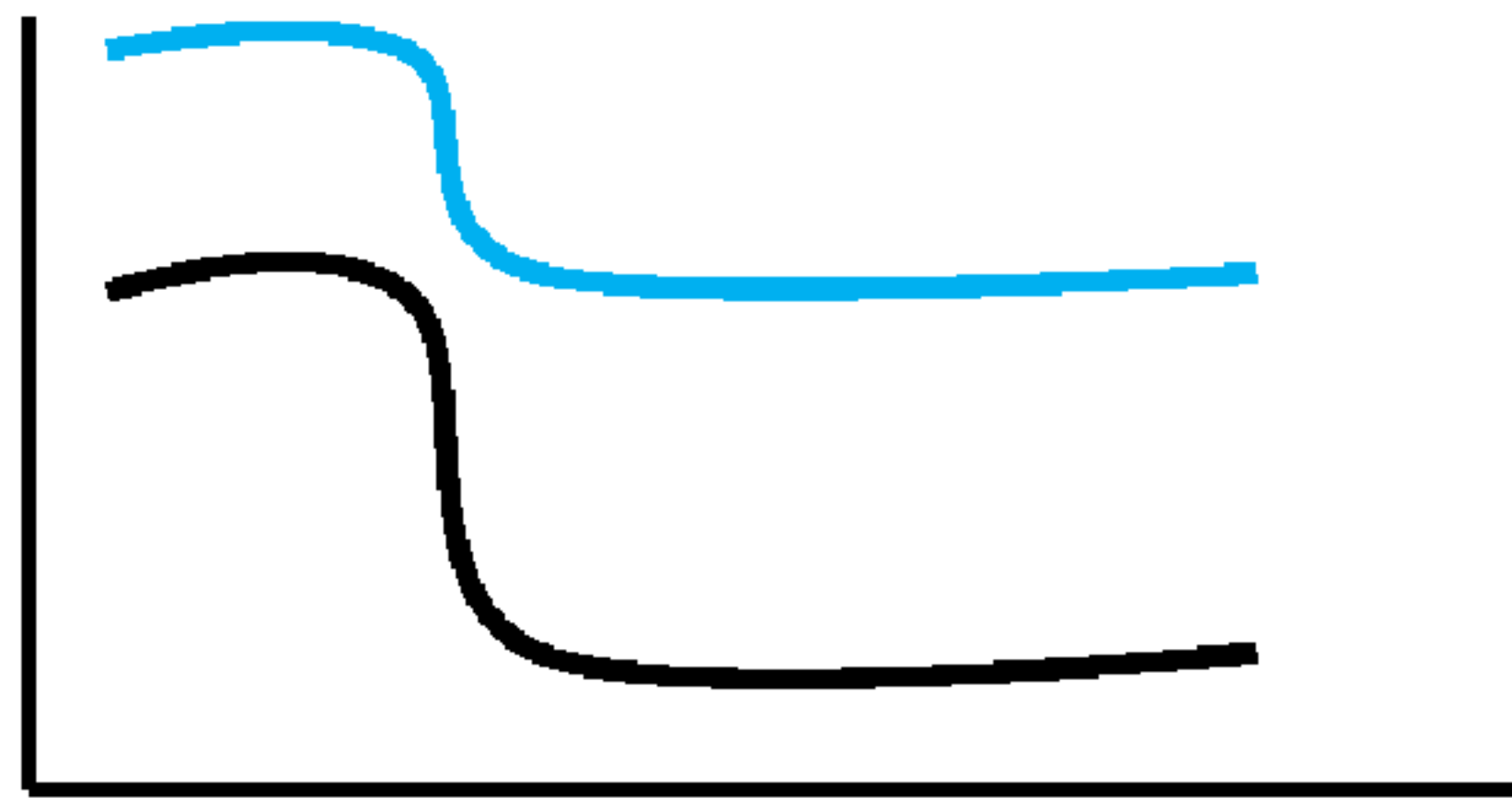
Threshold

Hysteresis



Driver

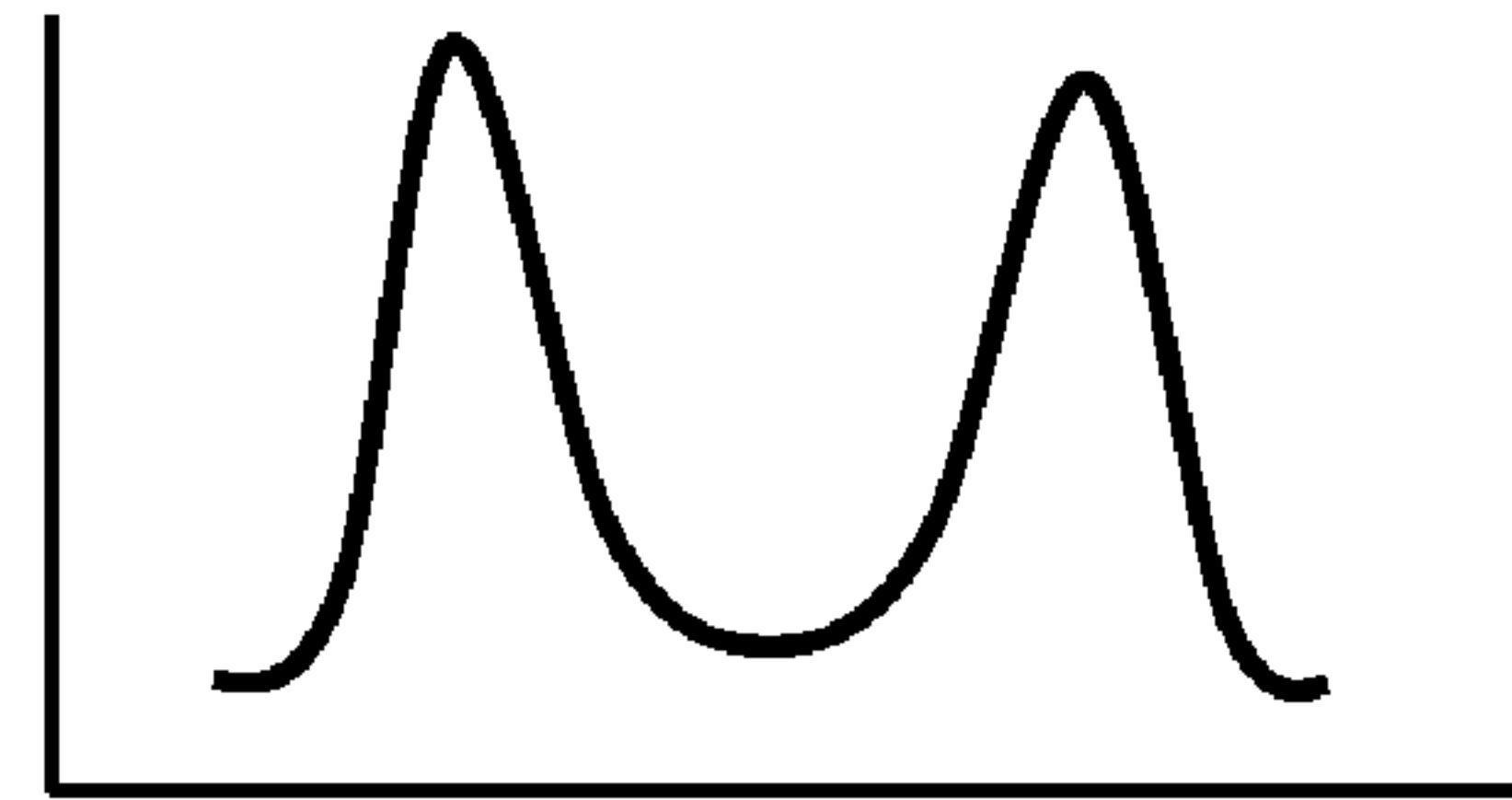
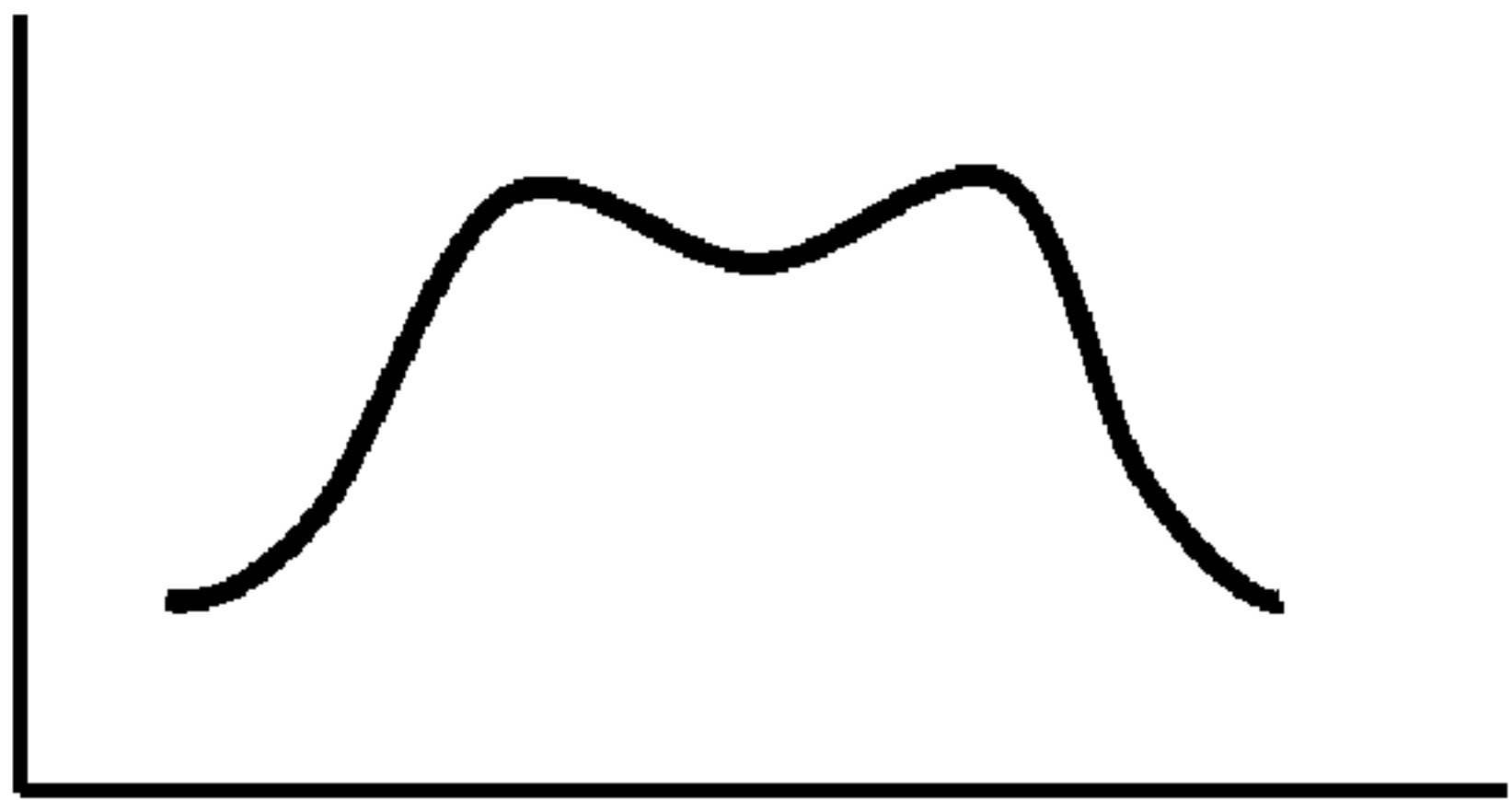
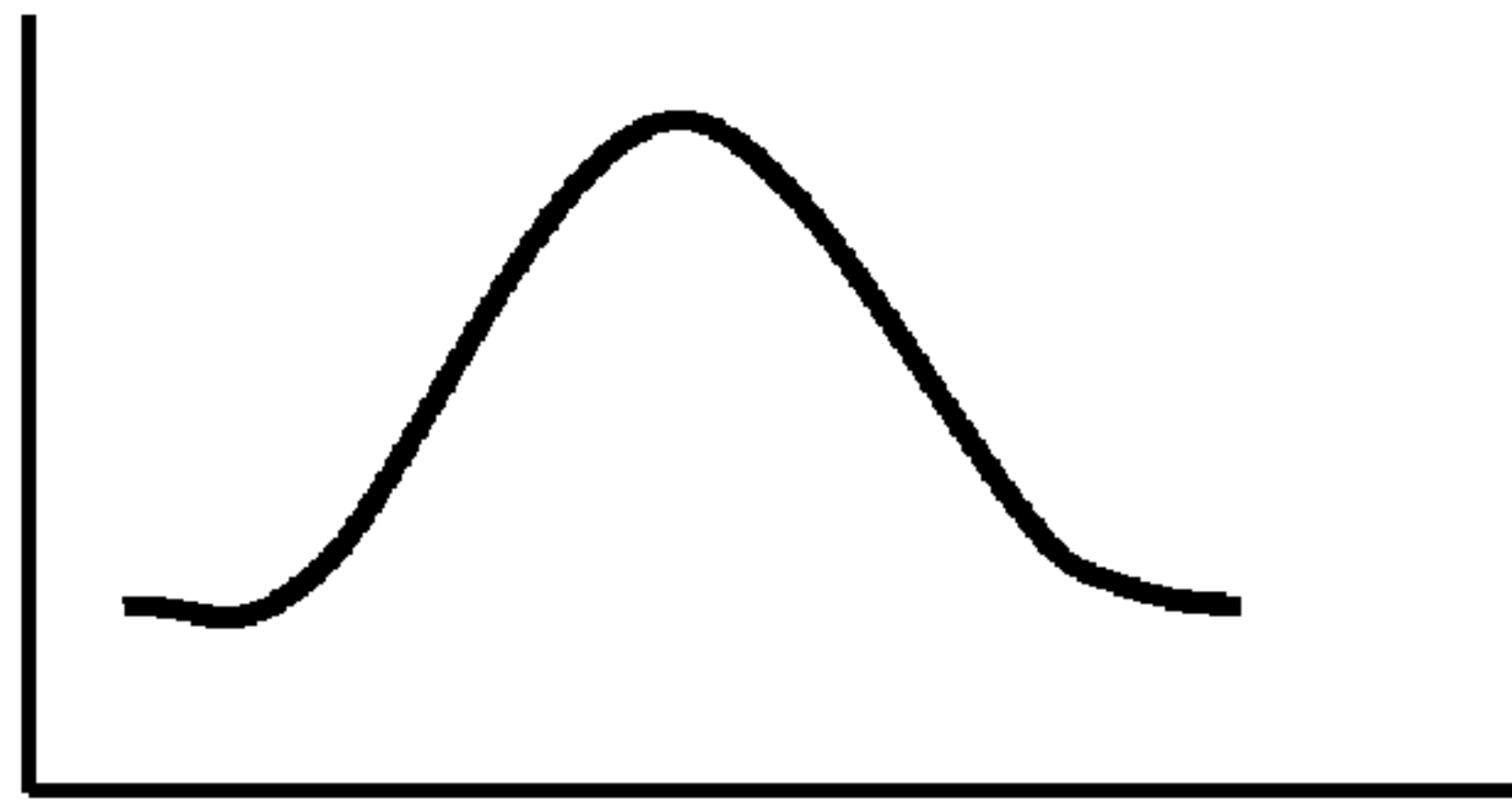
Response



A

Time

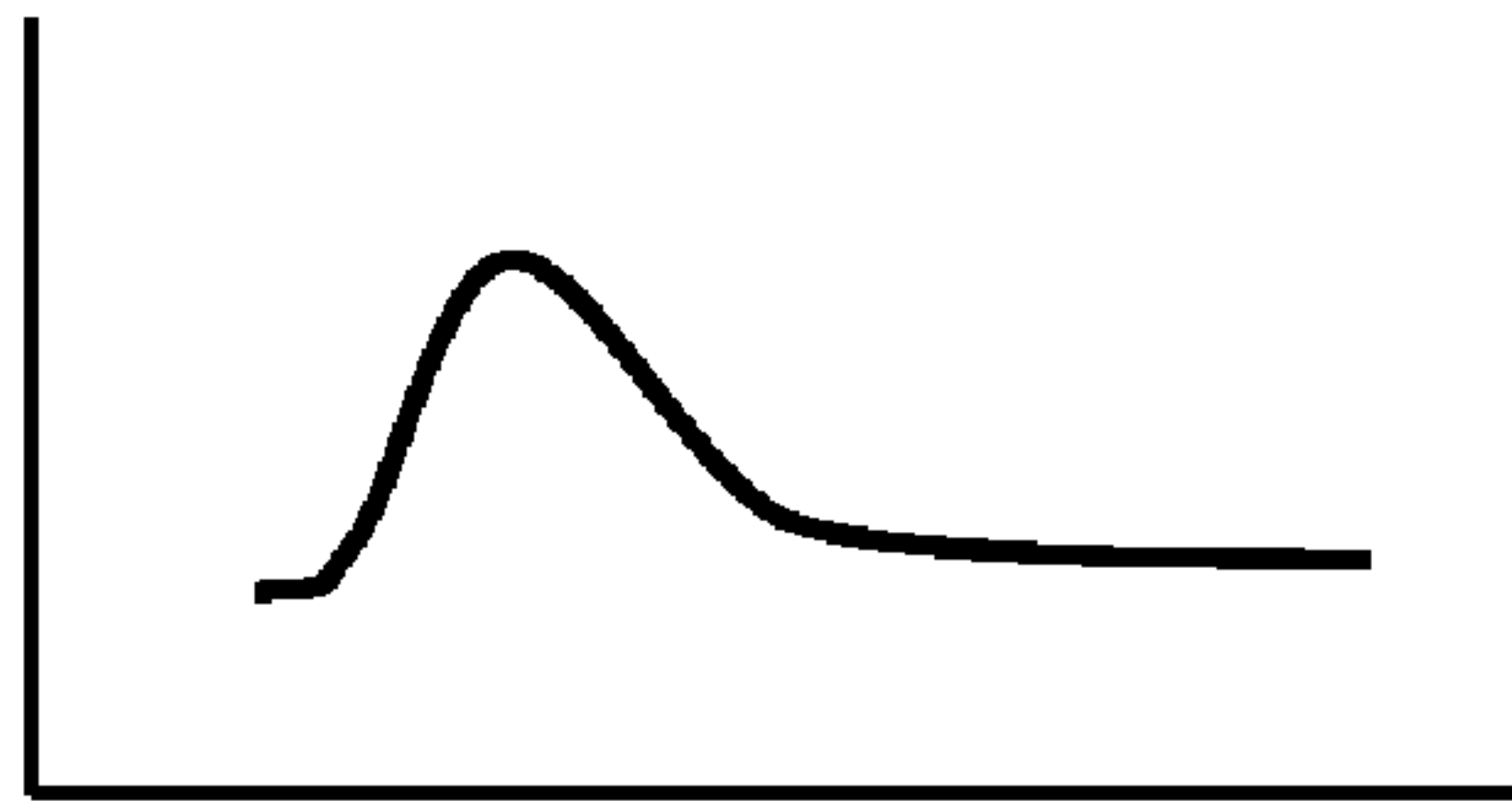
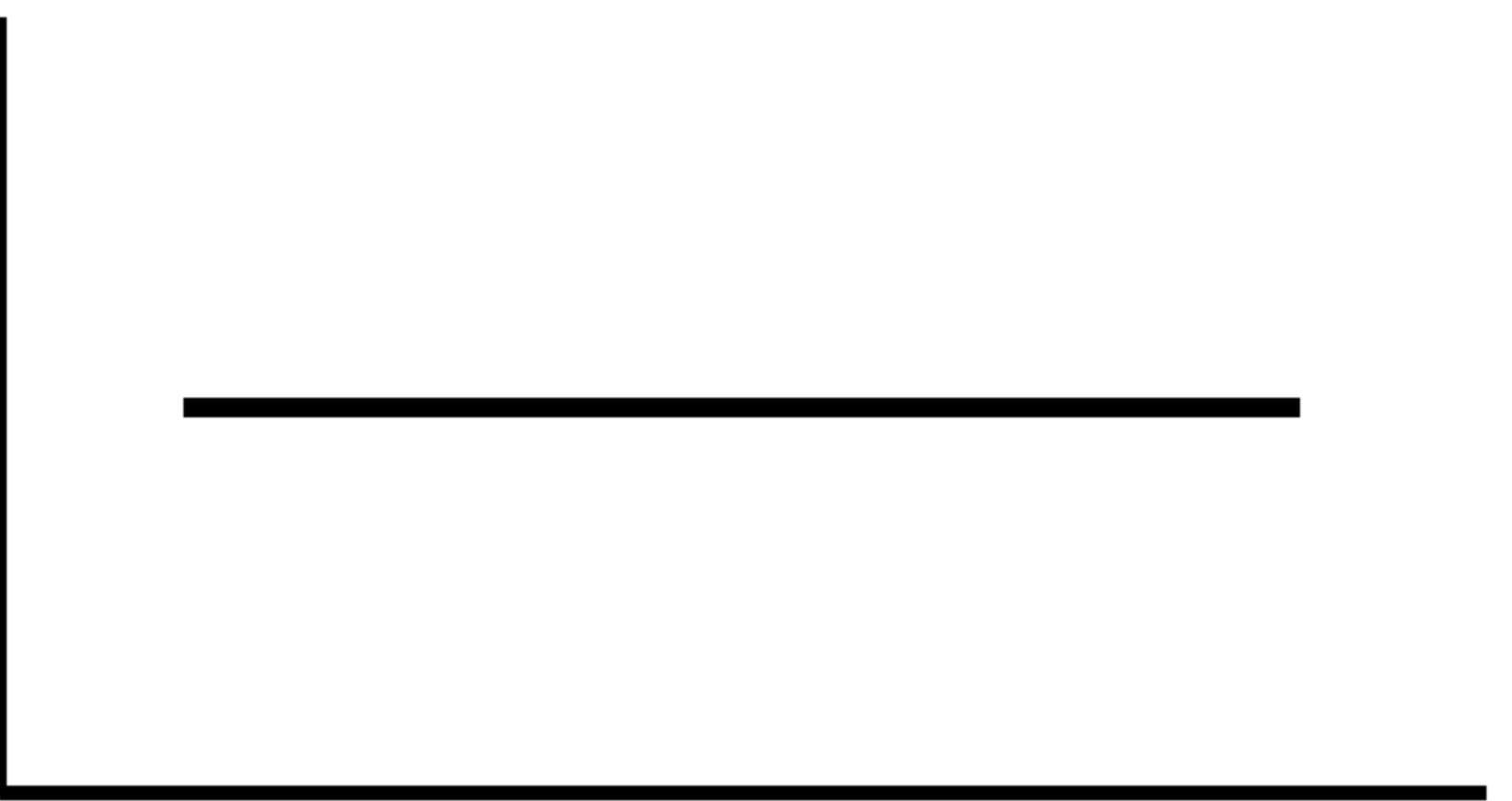
Frequency



B

Biological response

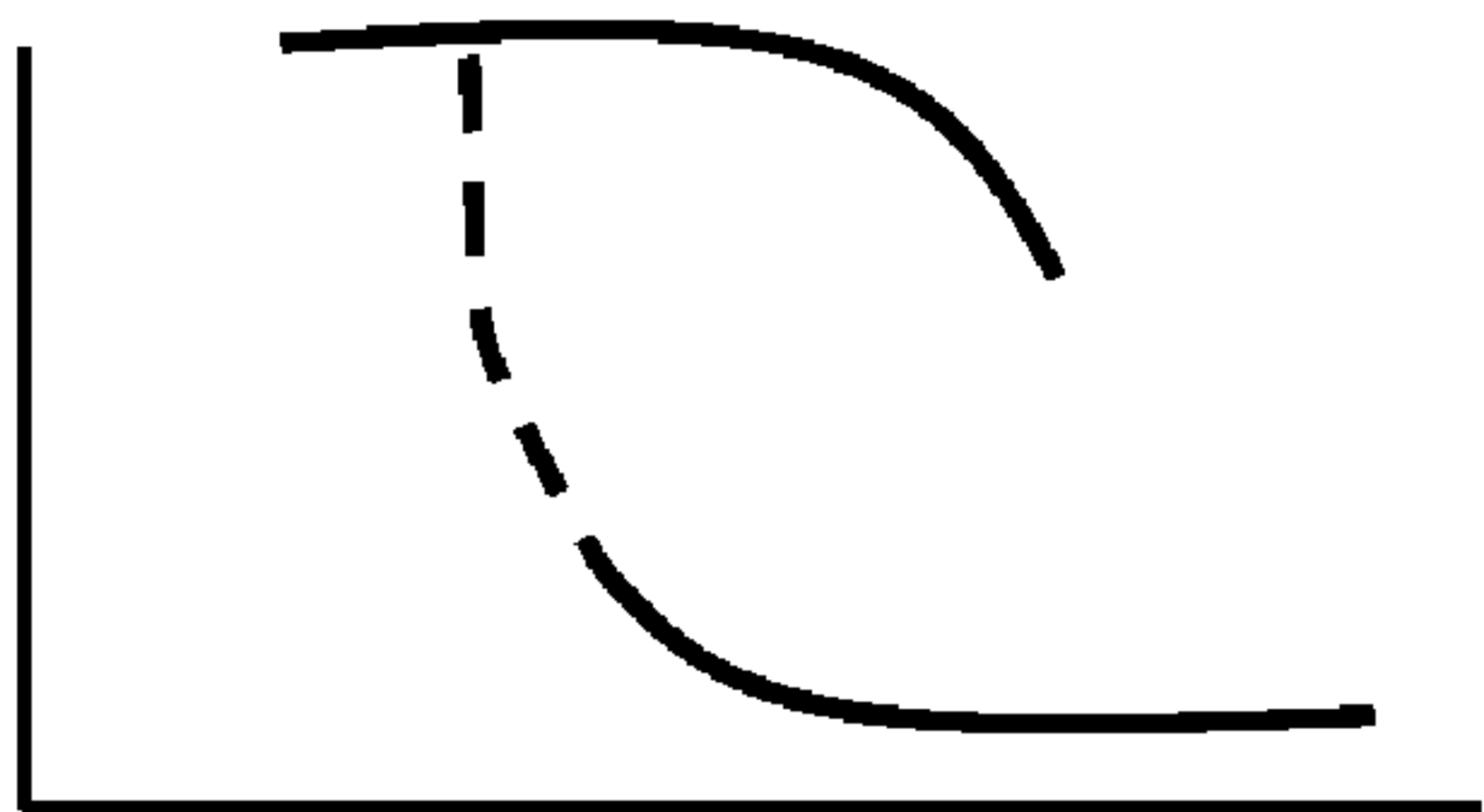
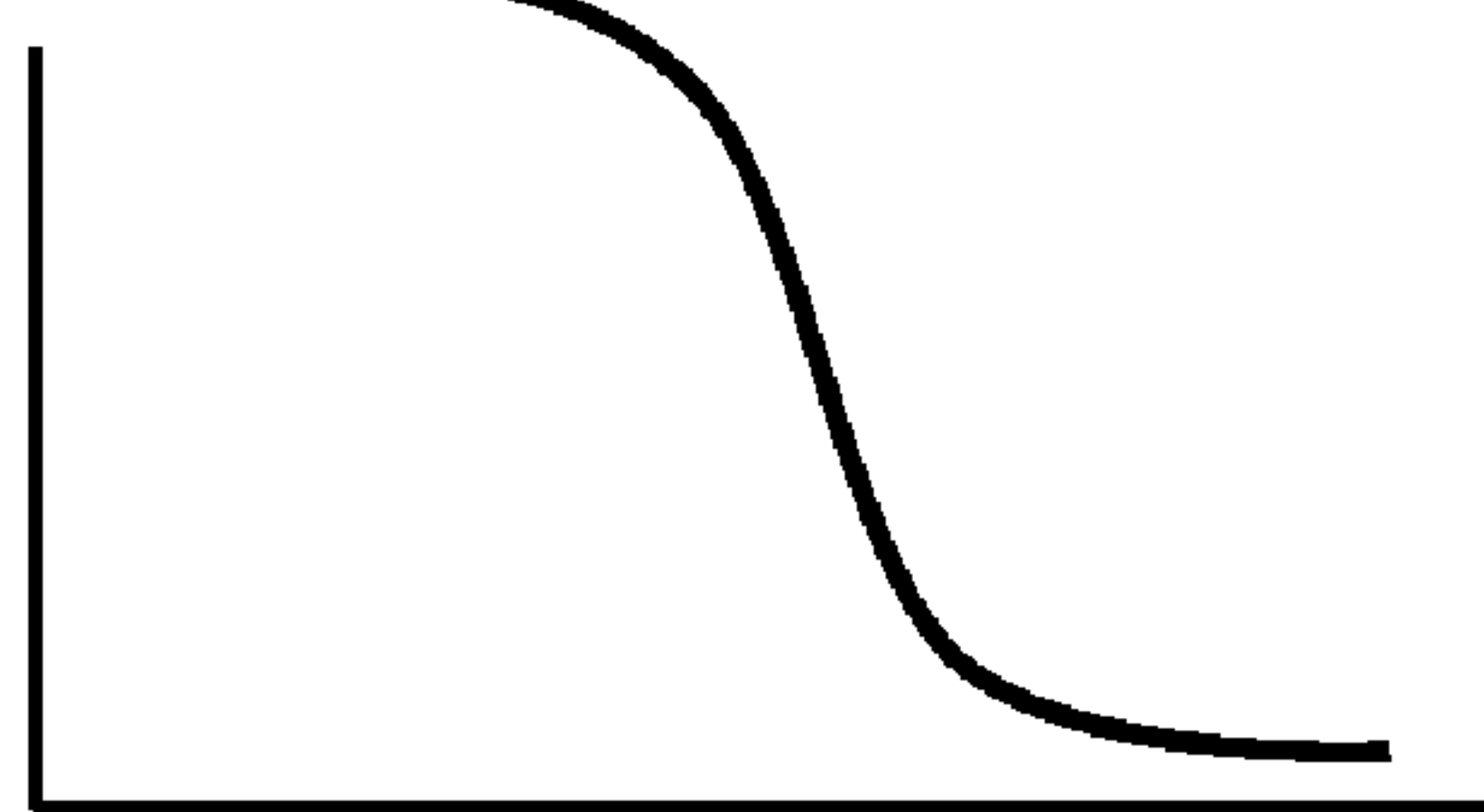
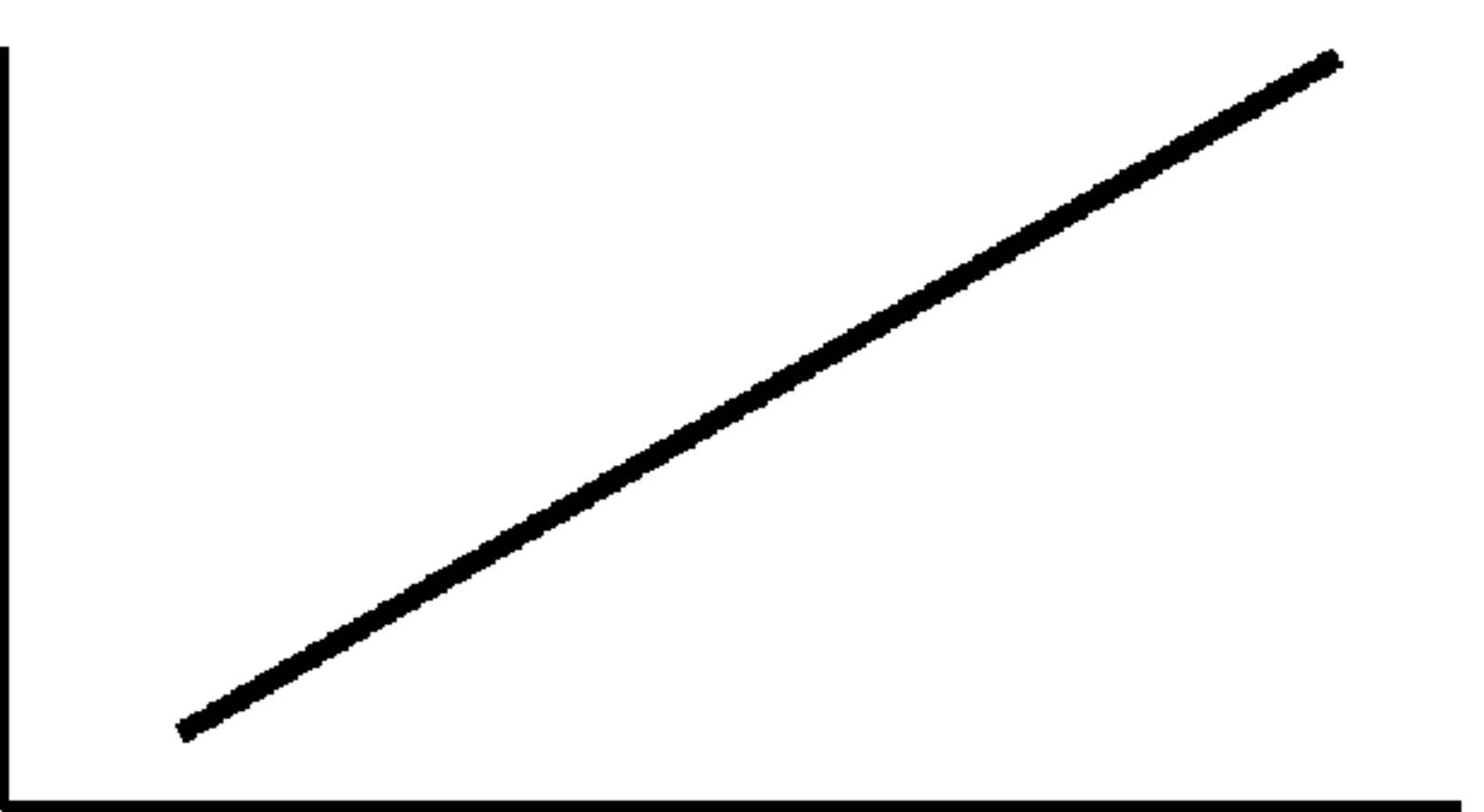
Variance



C

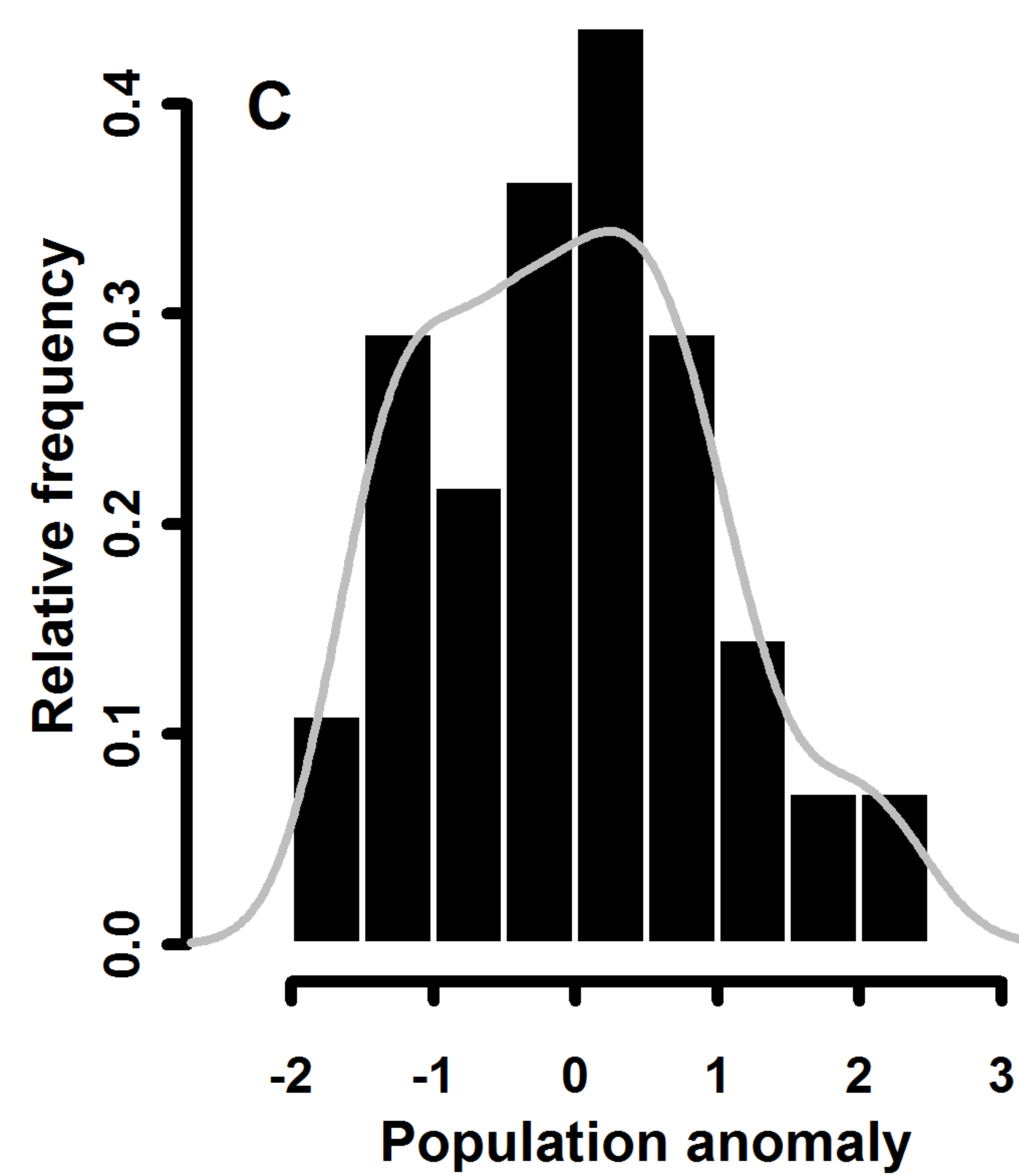
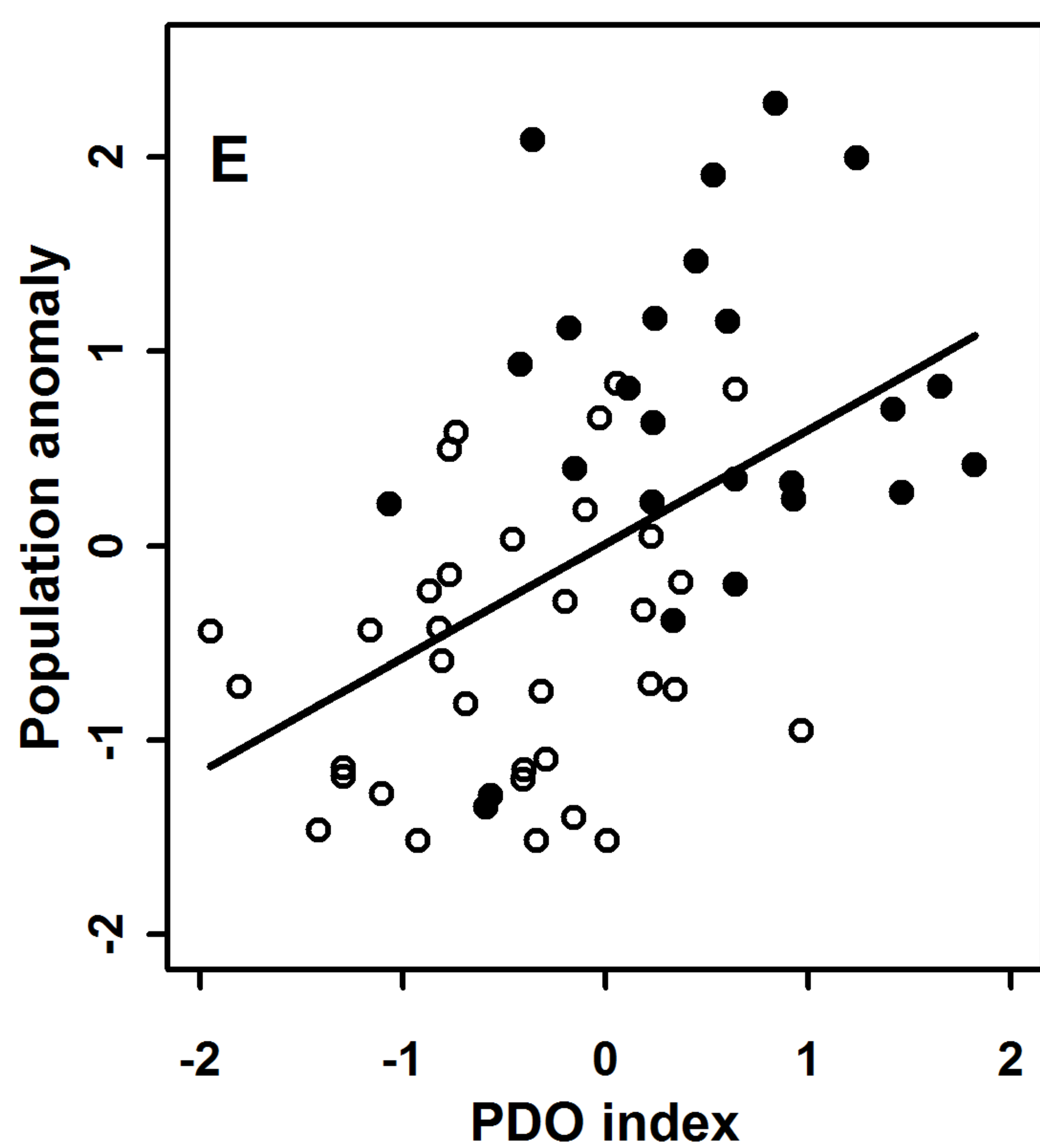
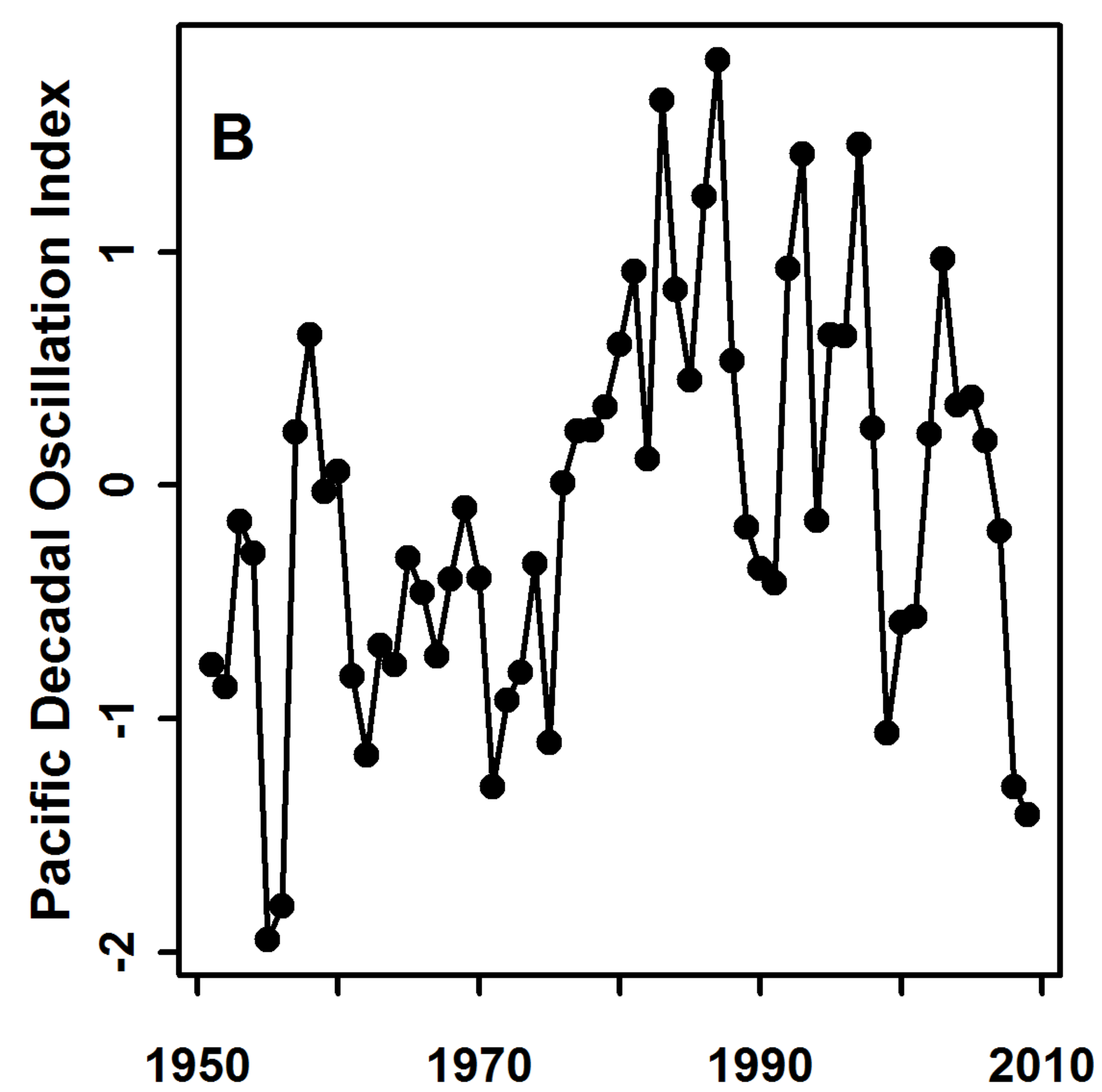
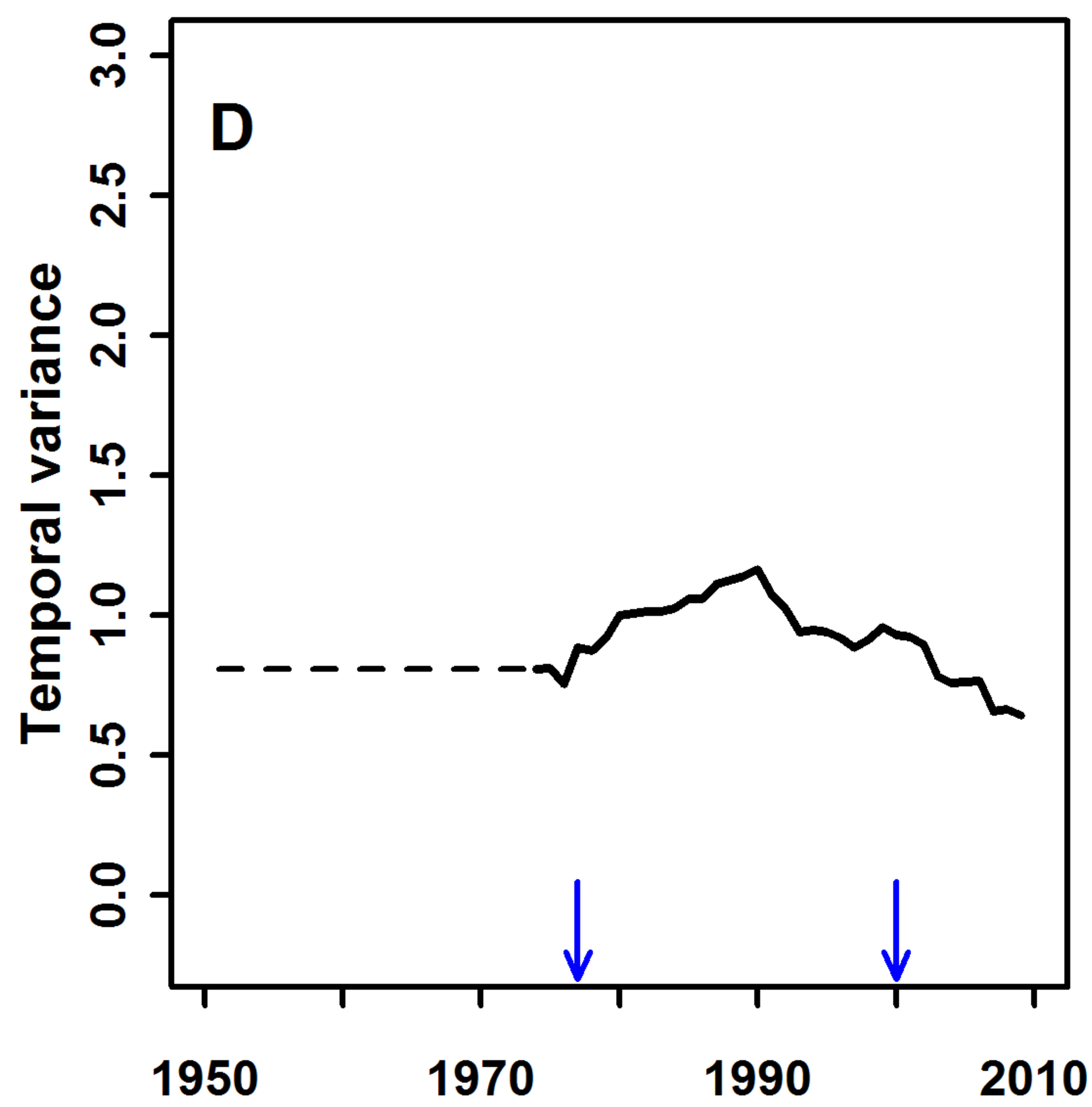
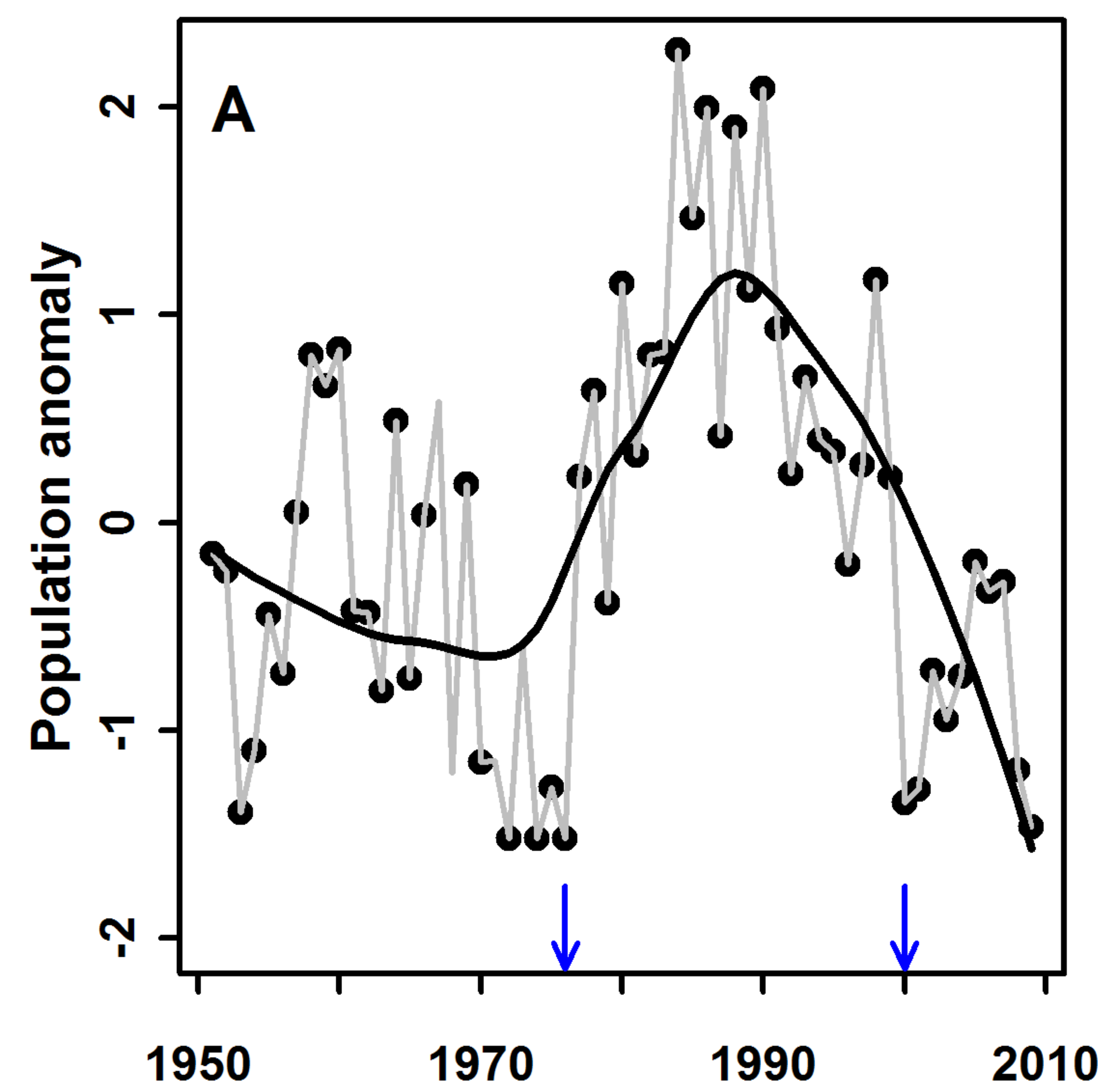
Time

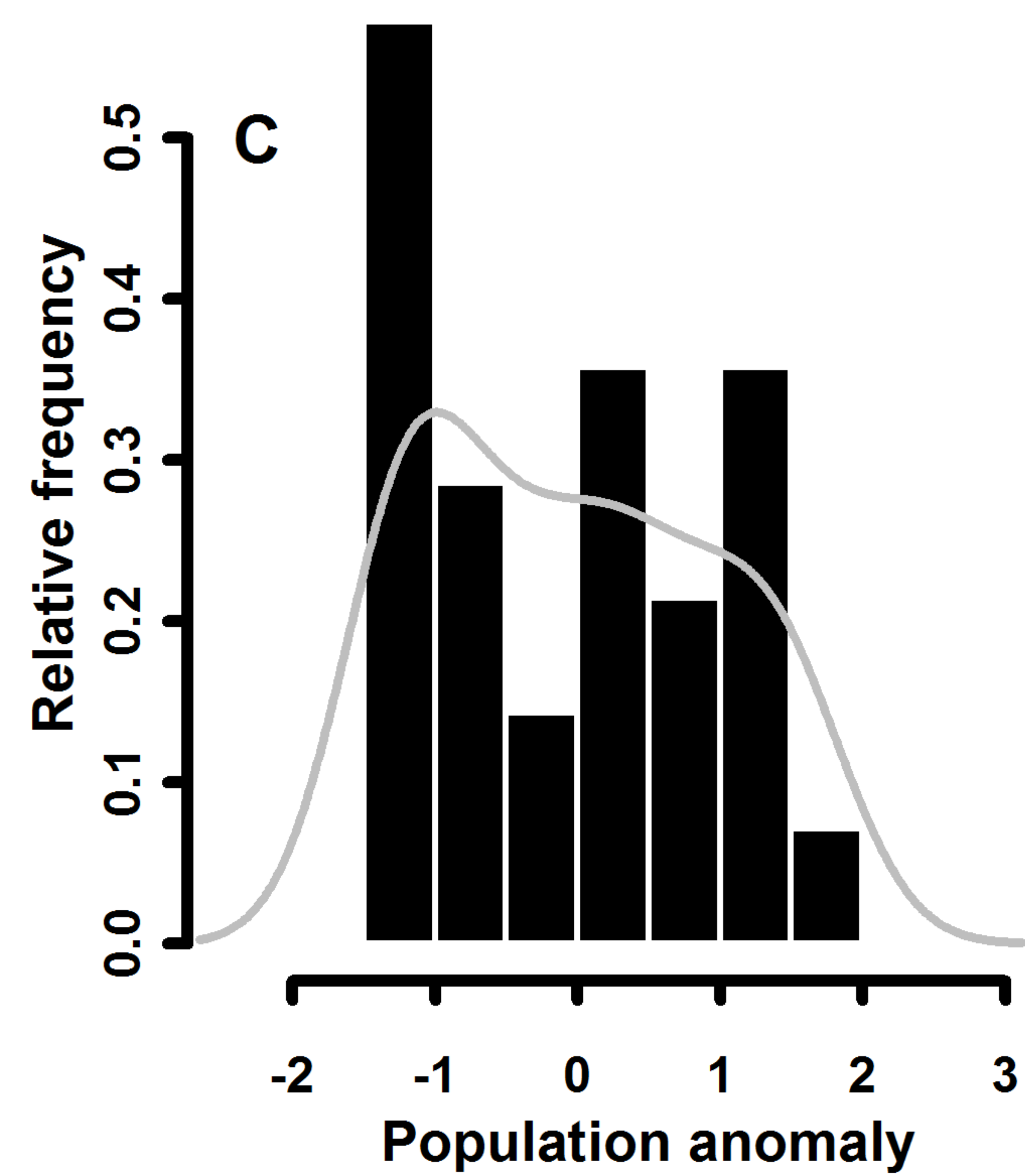
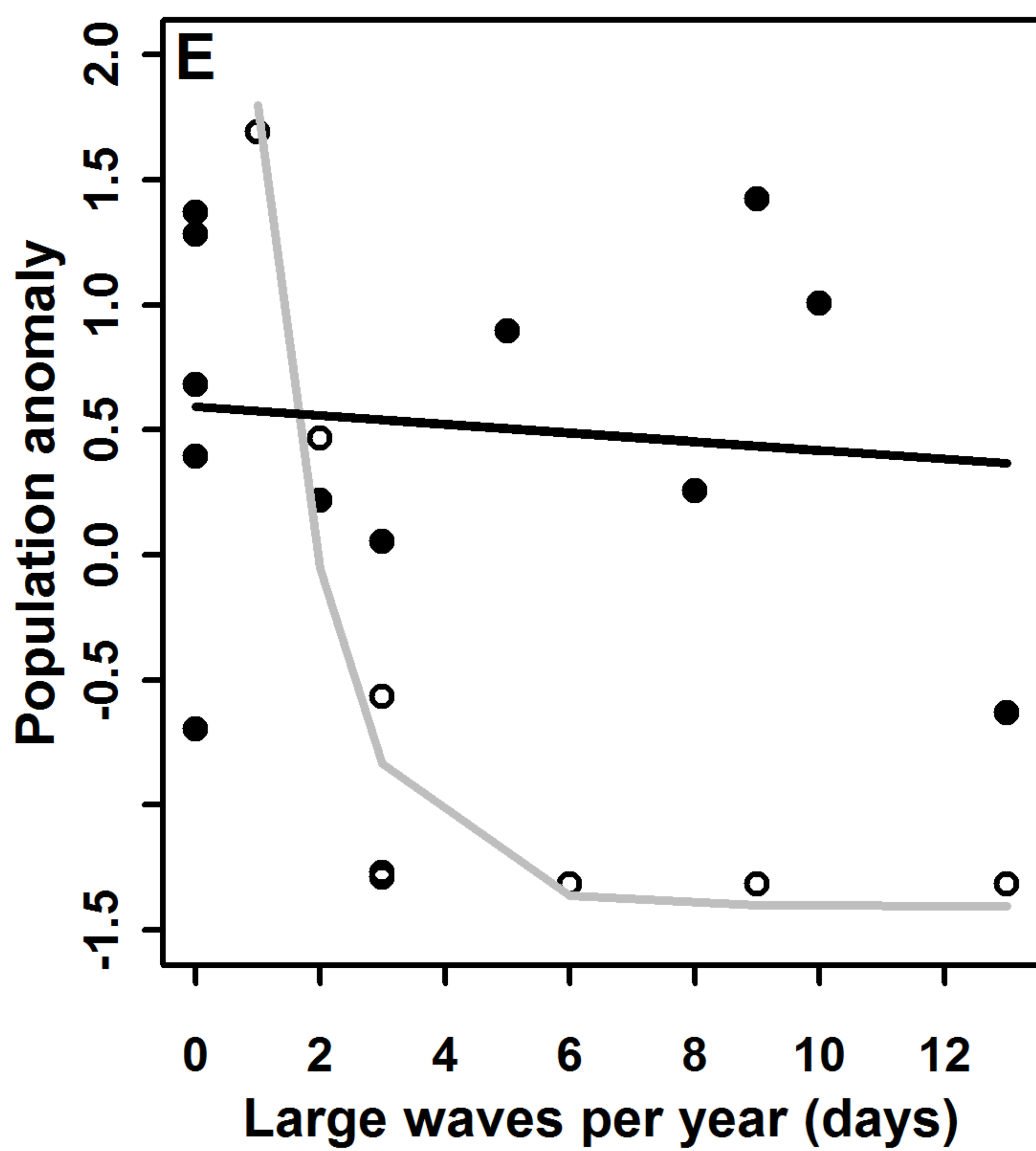
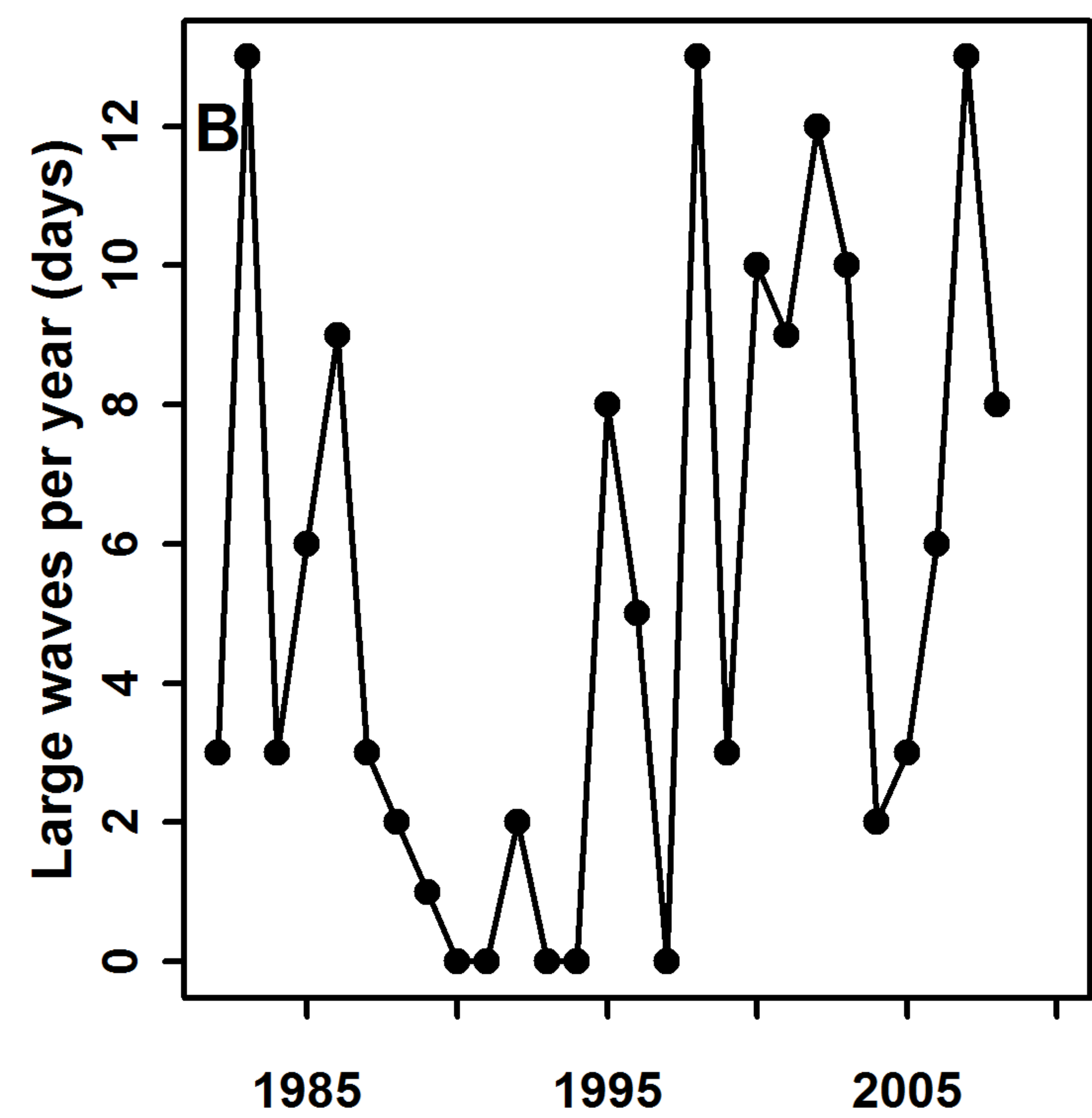
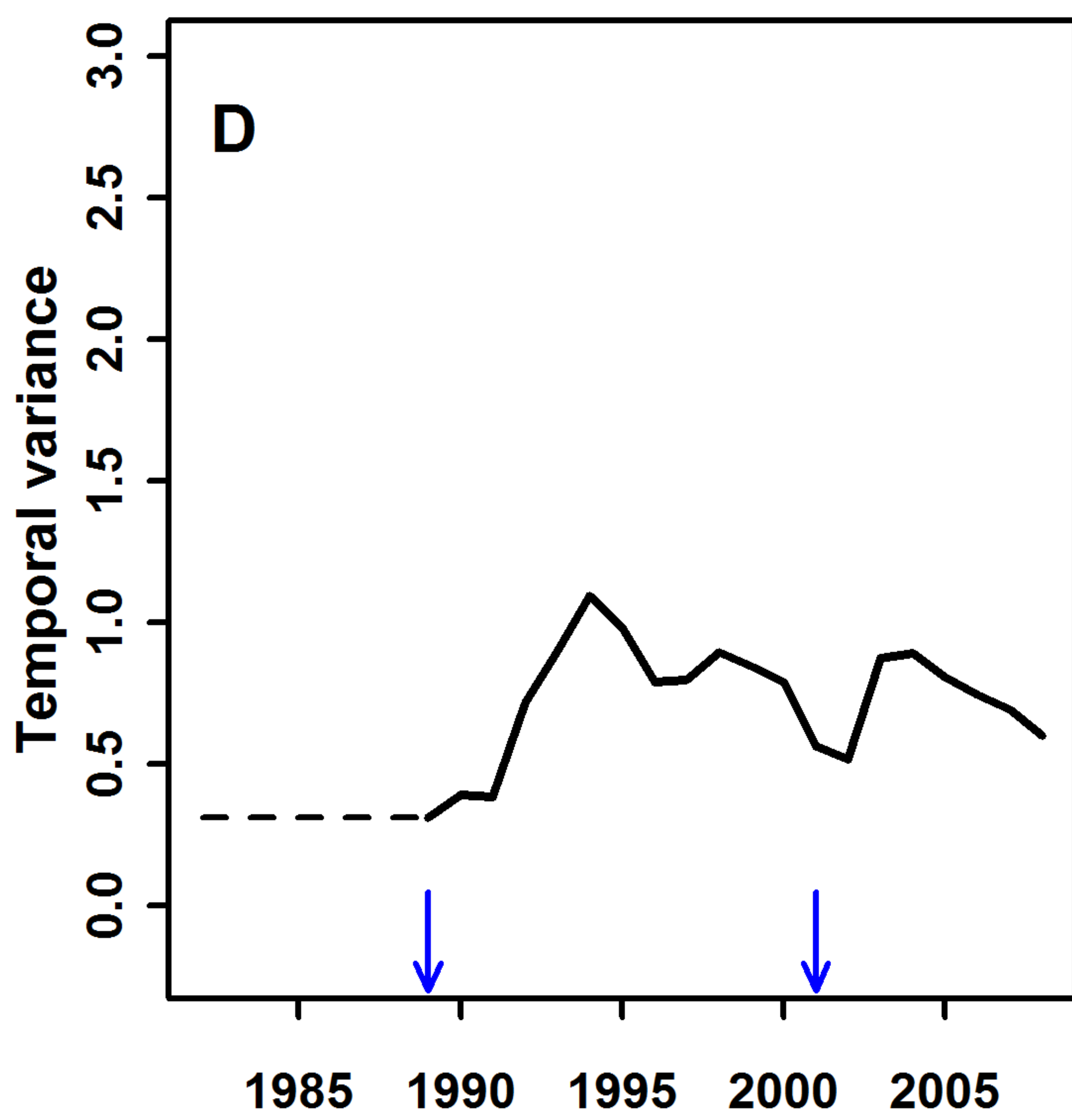
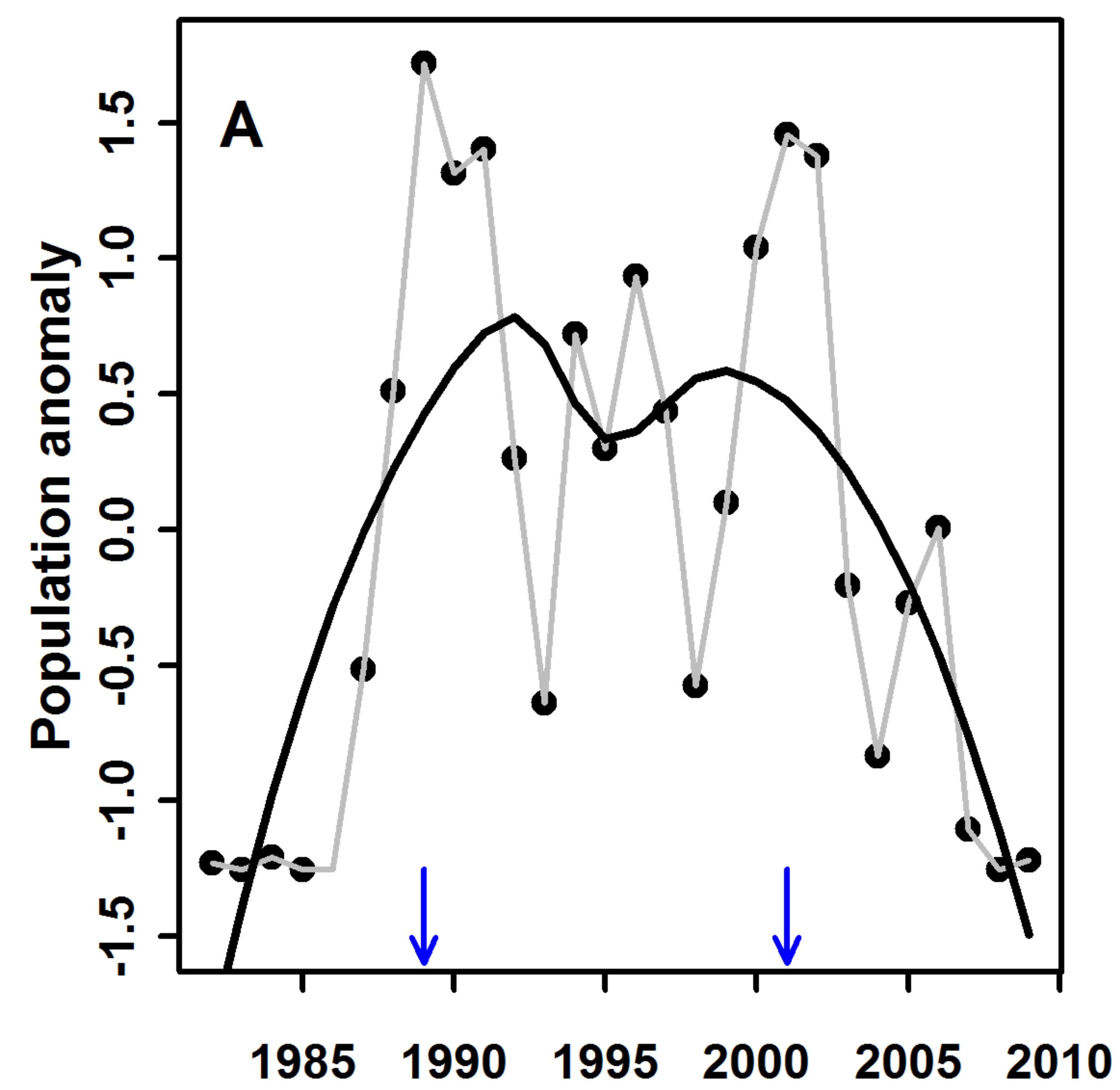
Biological Response

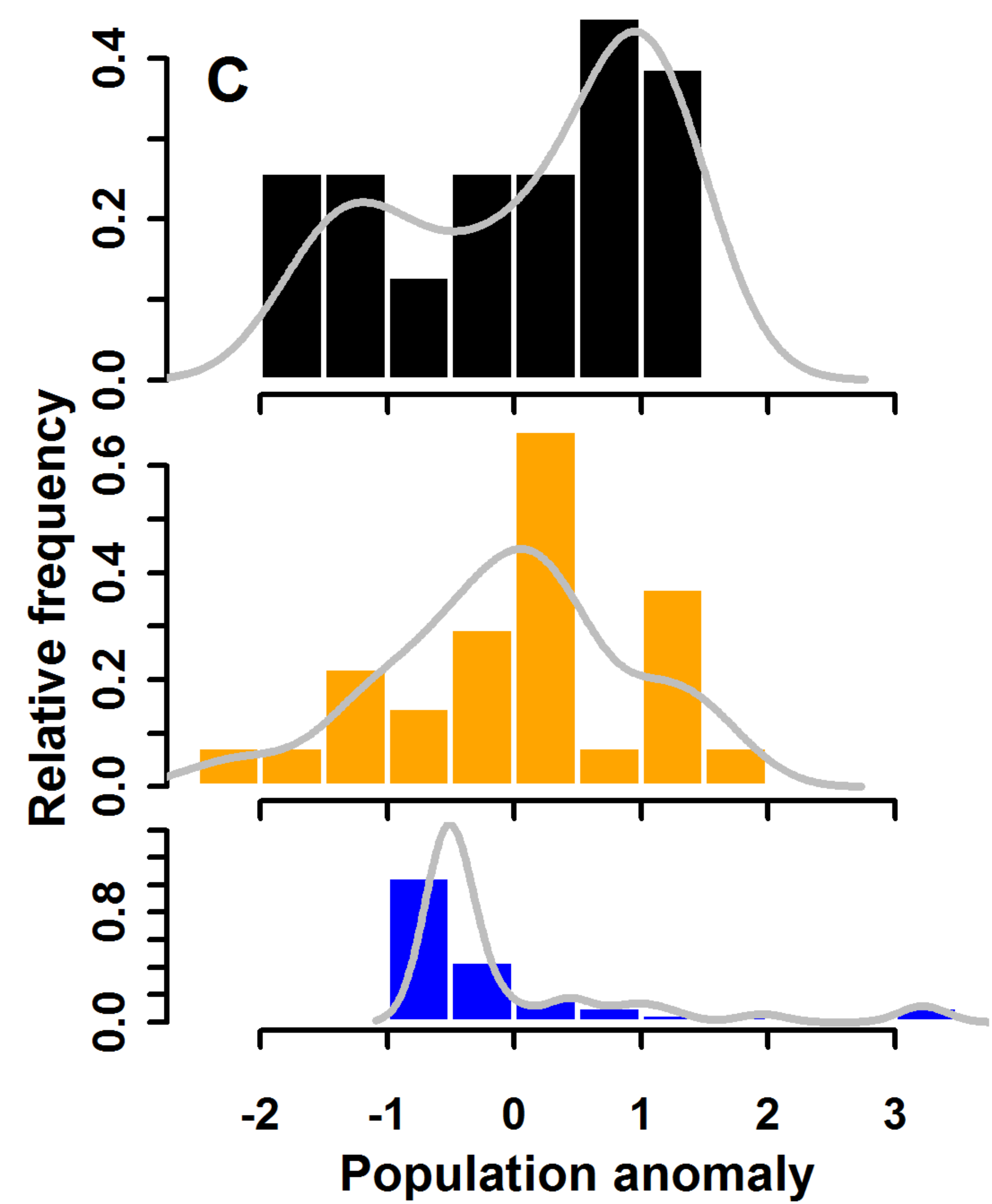
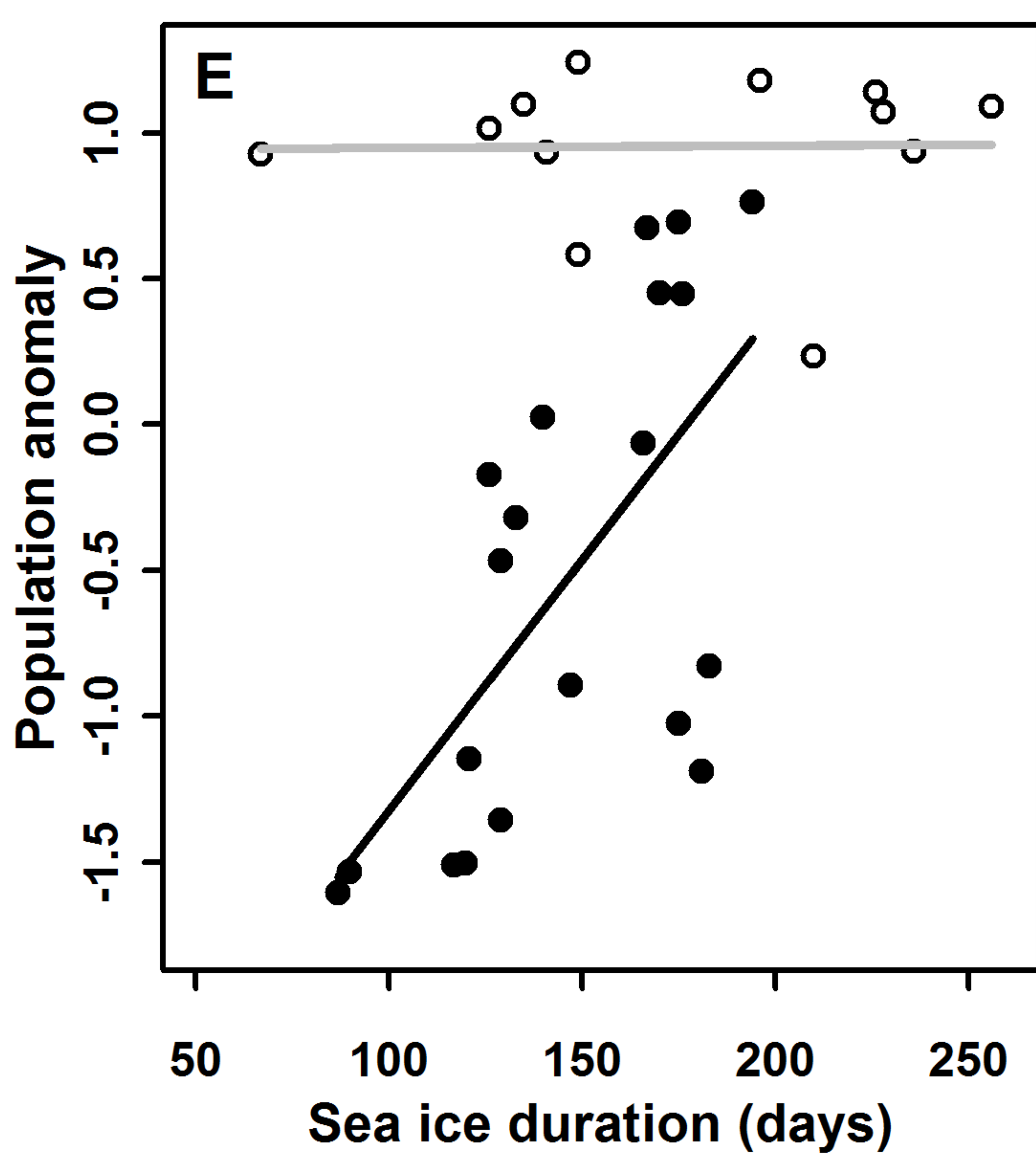
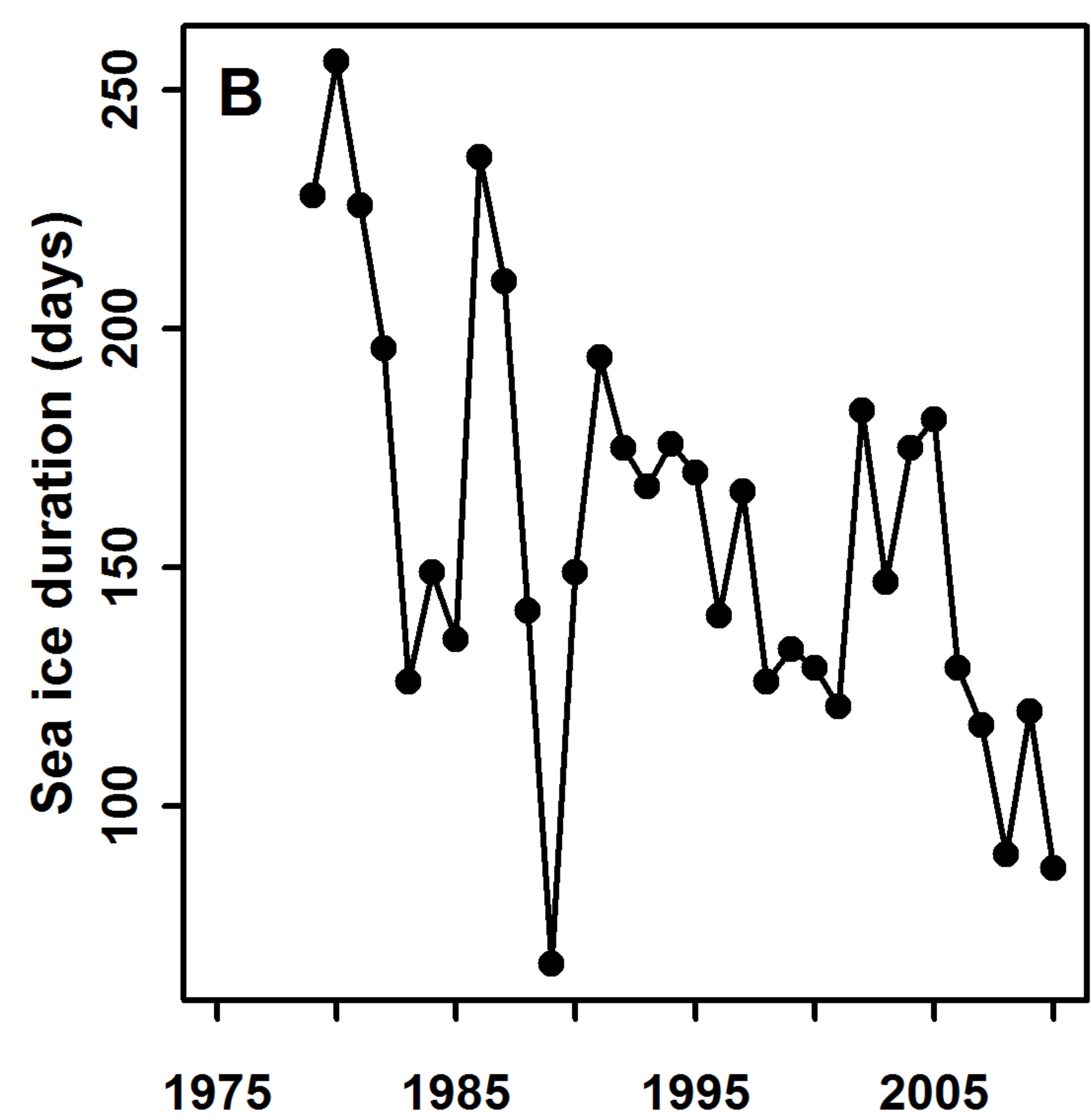
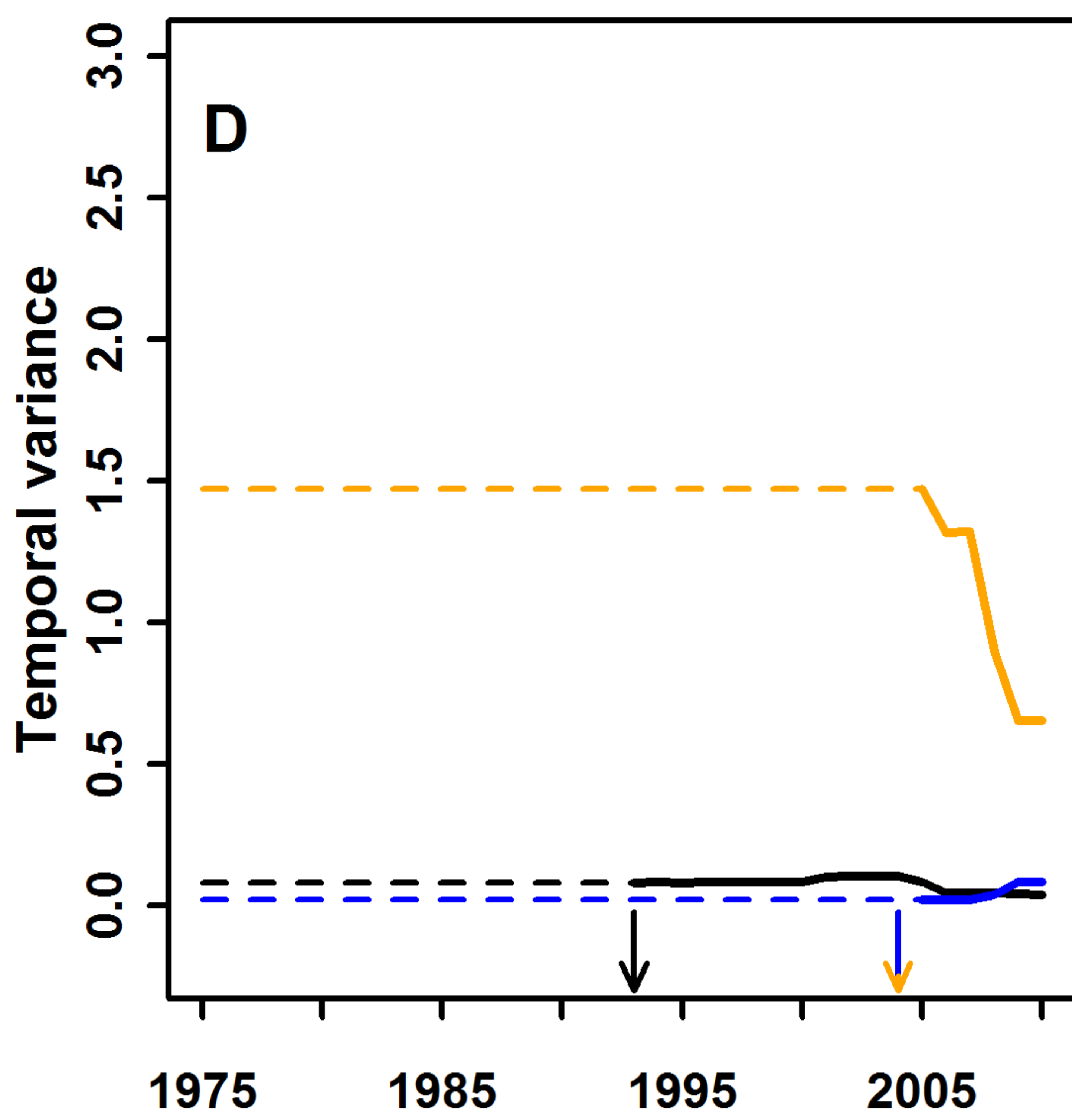
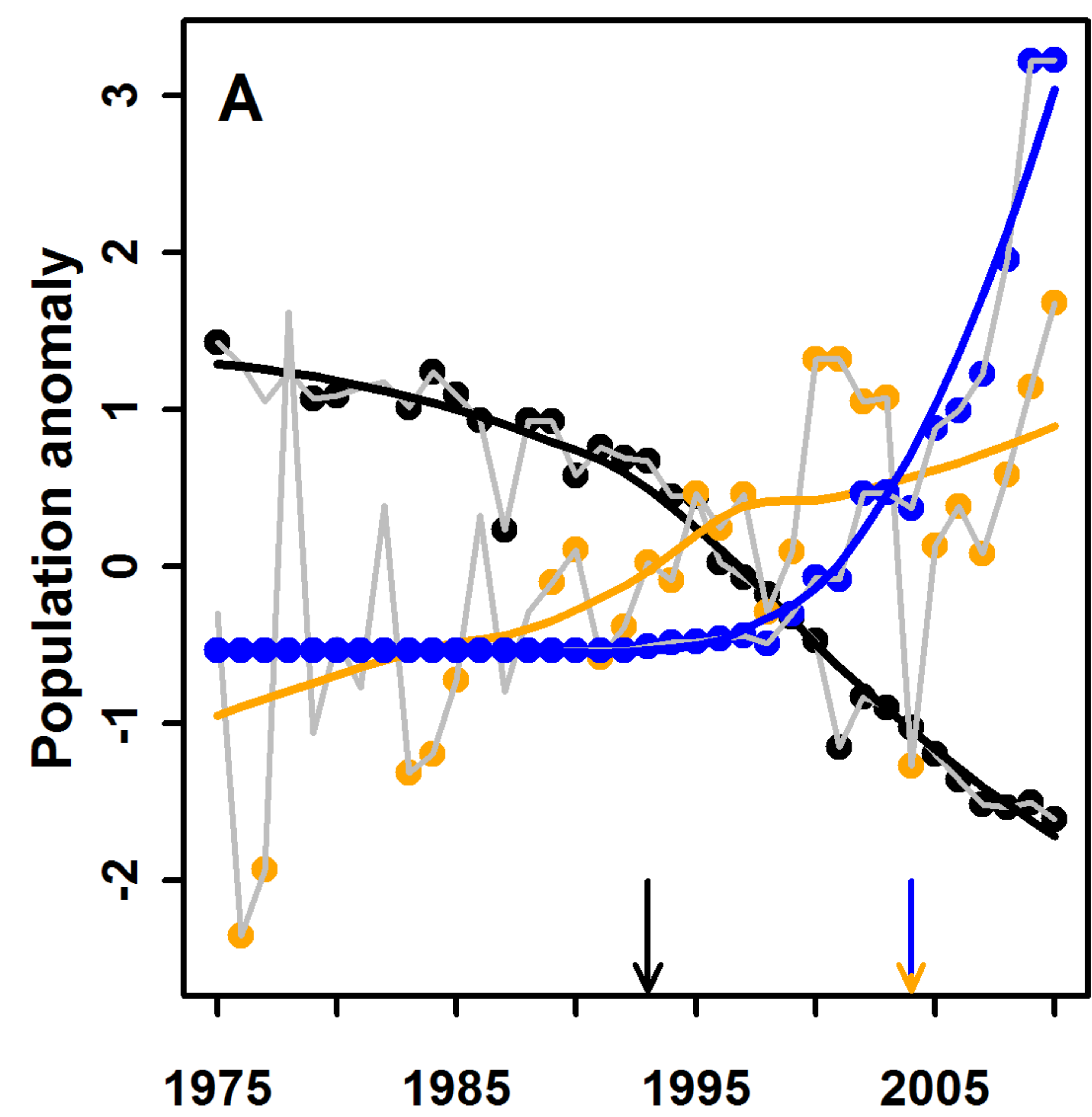


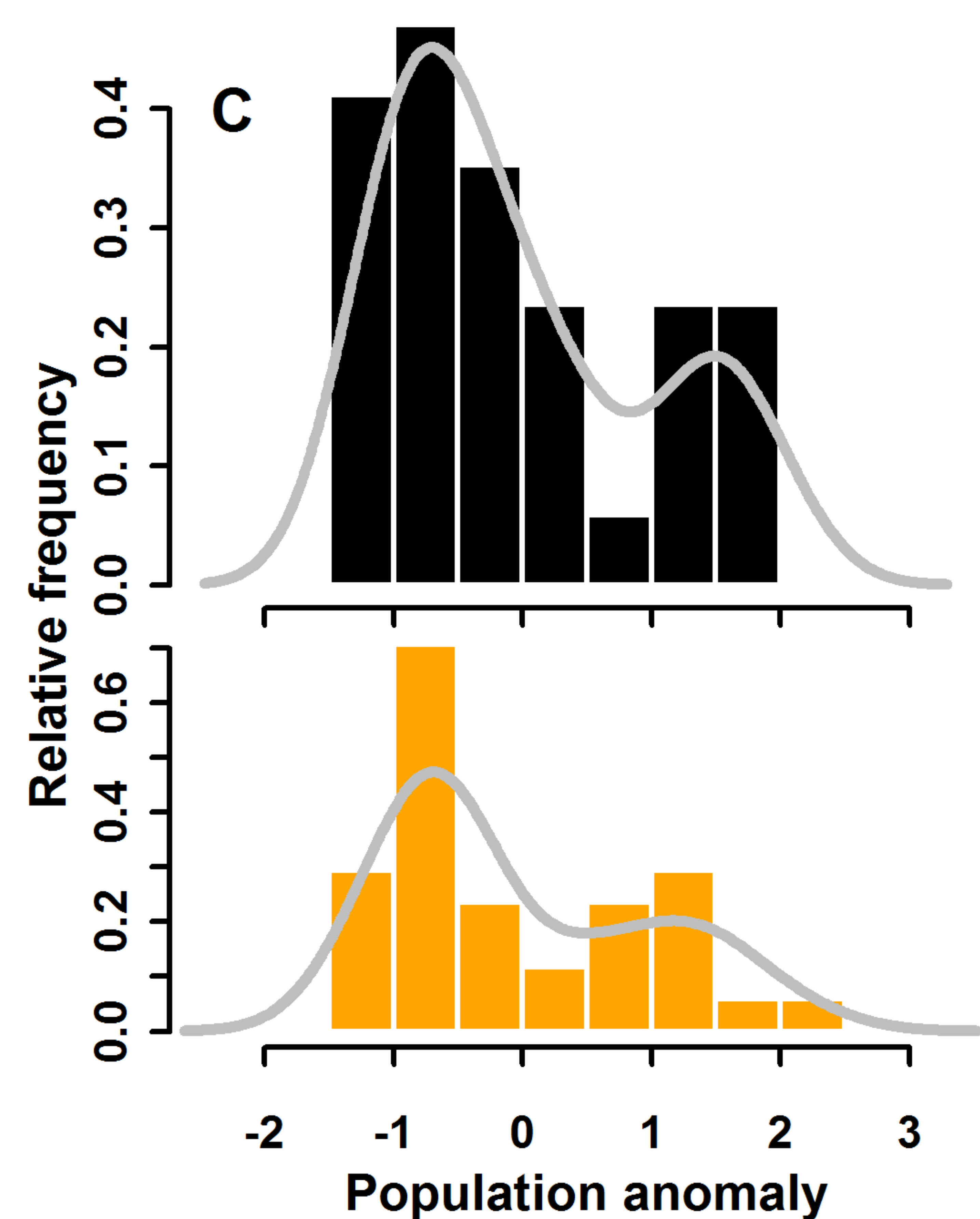
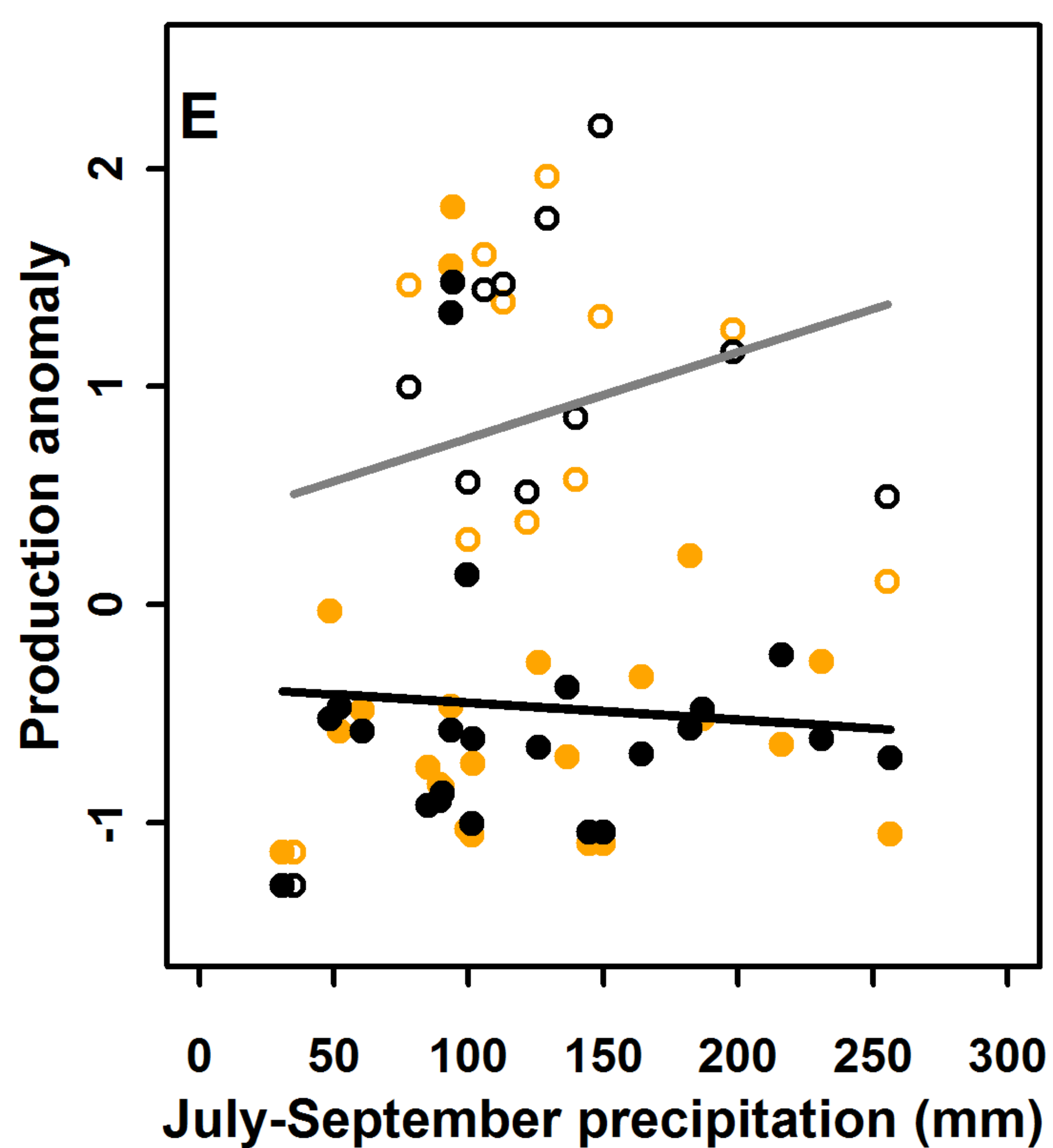
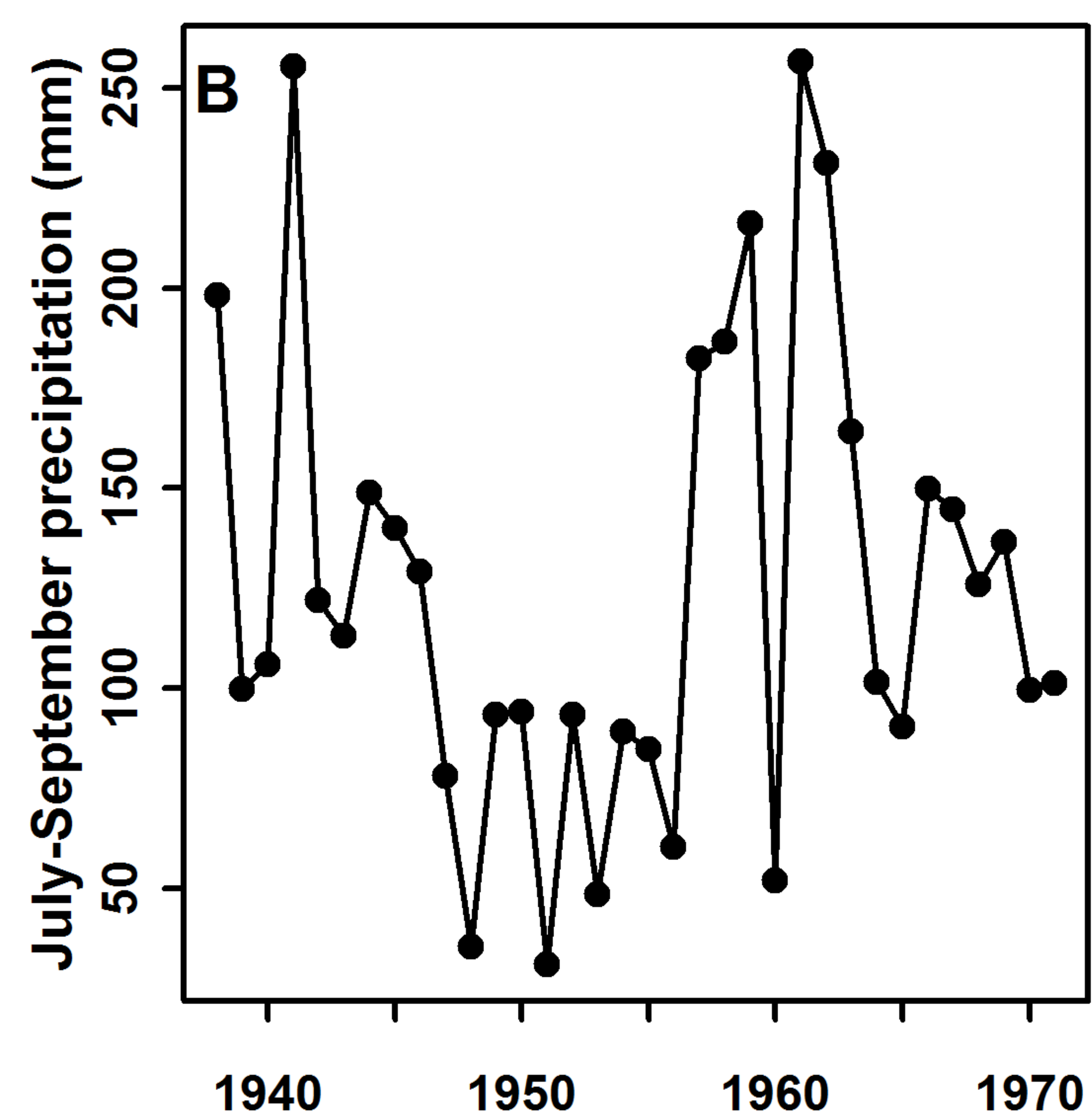
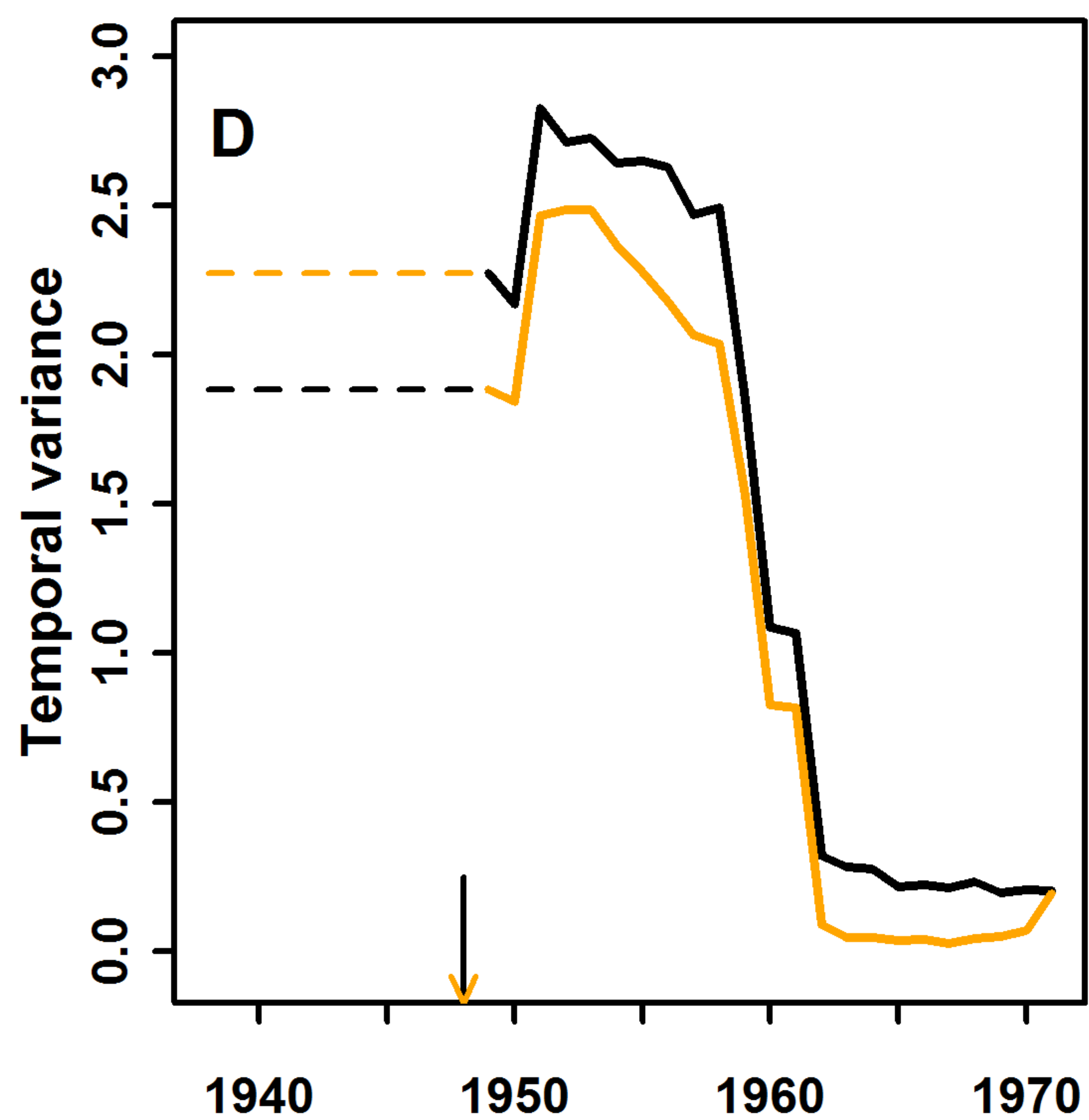
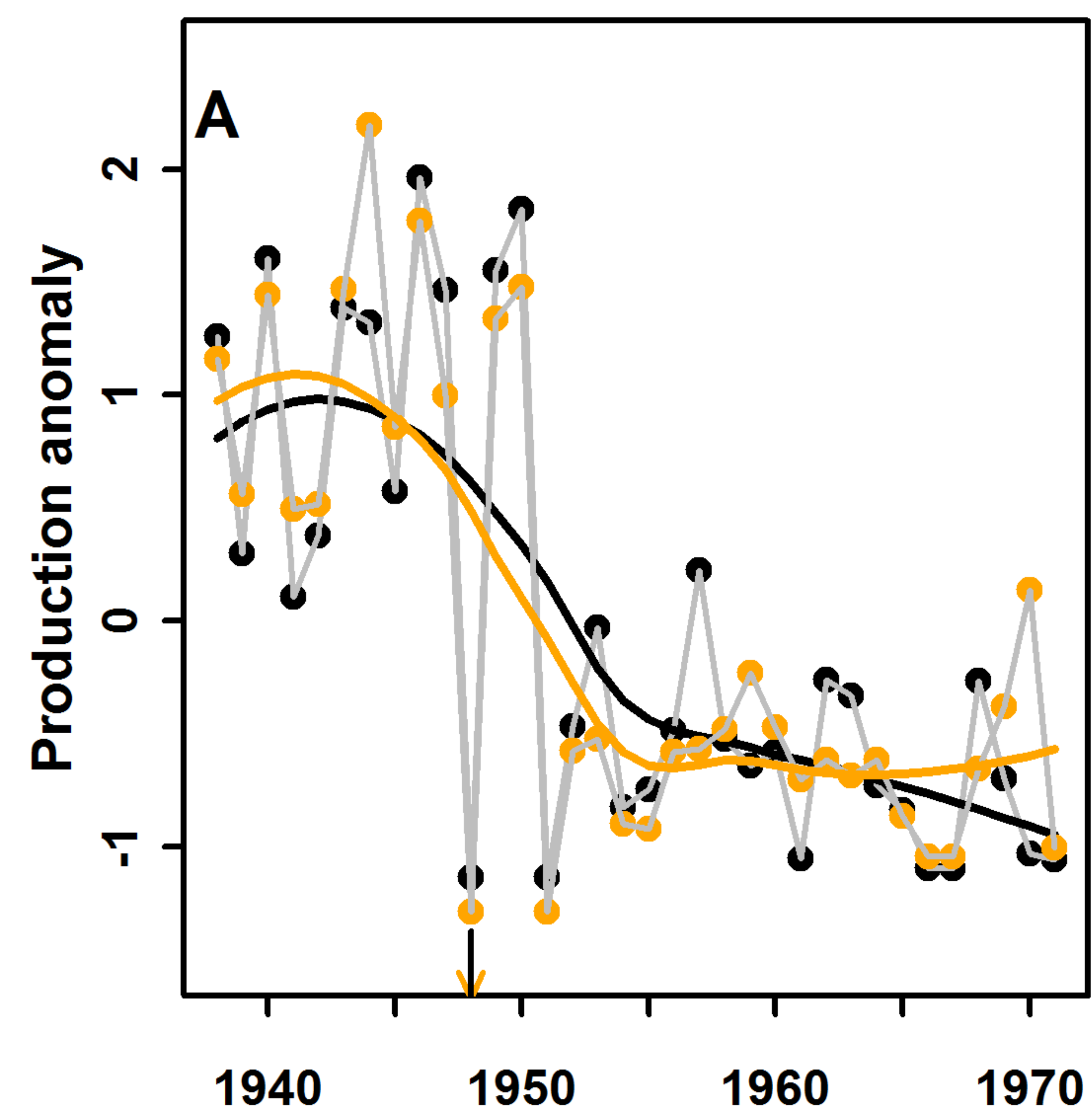
D

Environmental Driver

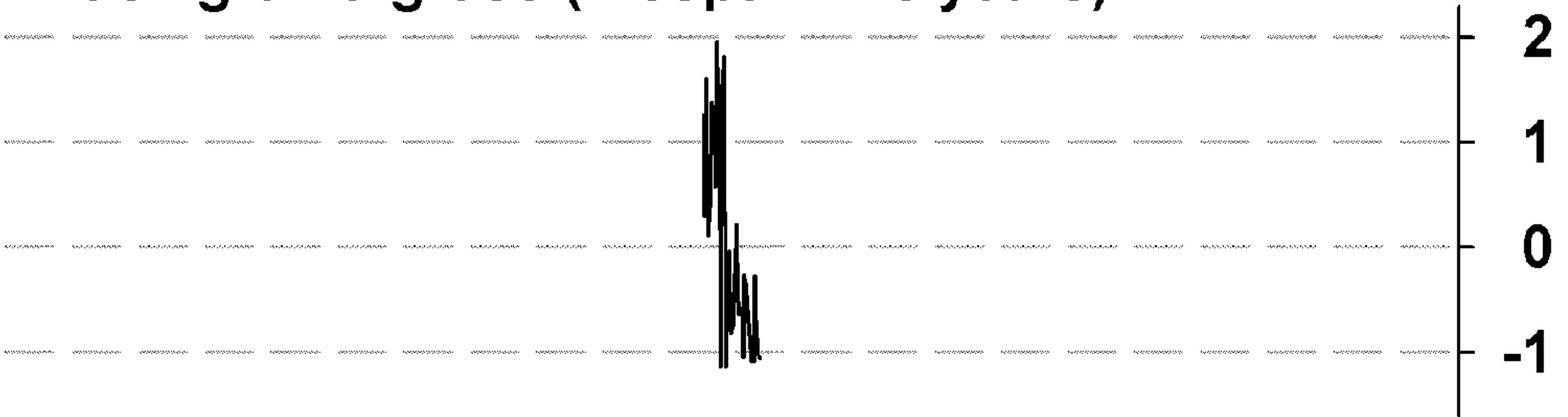




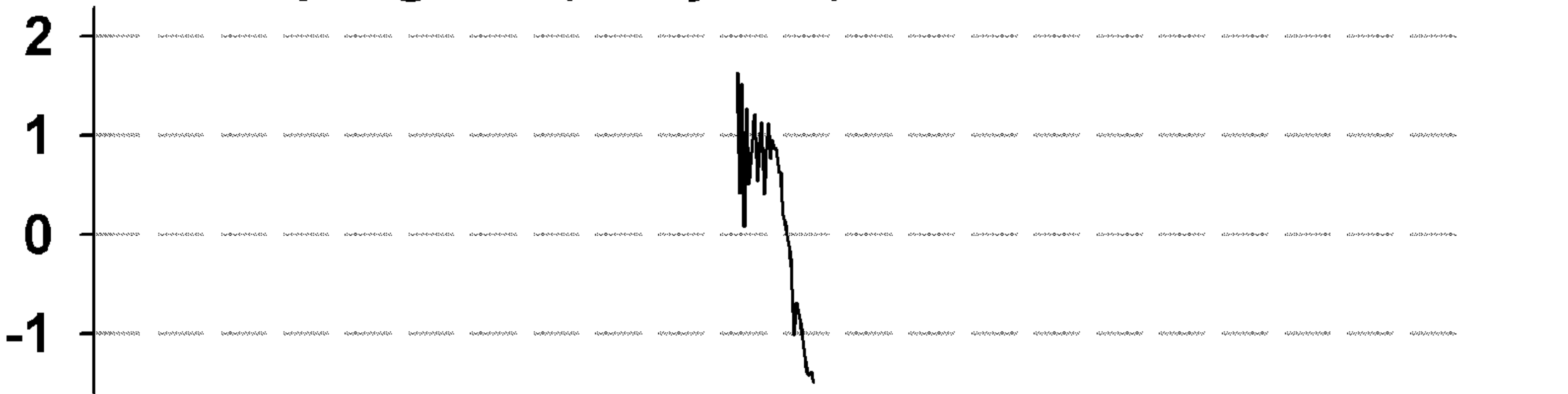




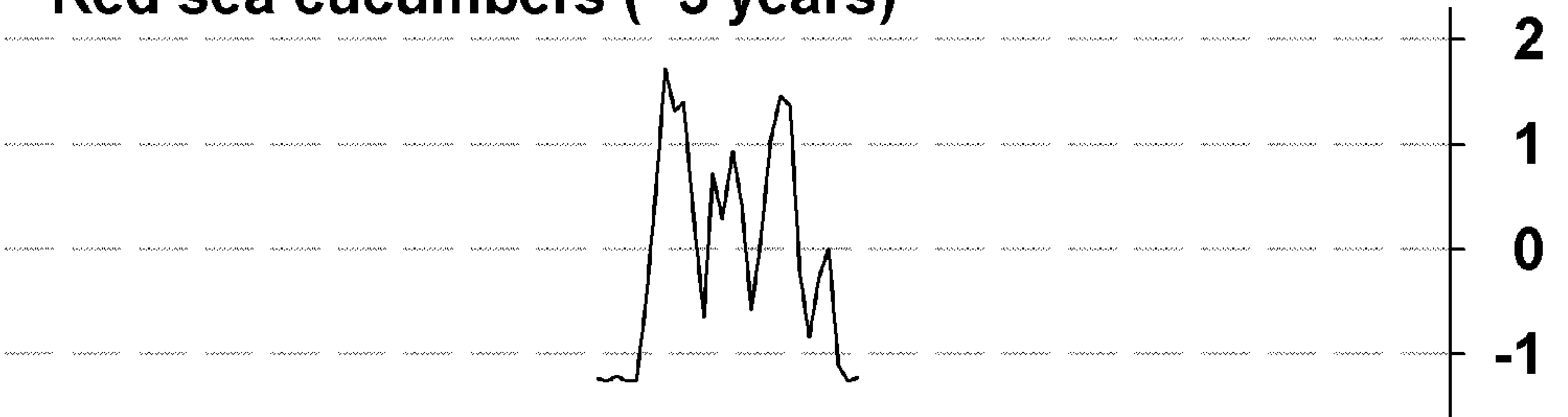
Black grama grass (lifespan ~28 years)



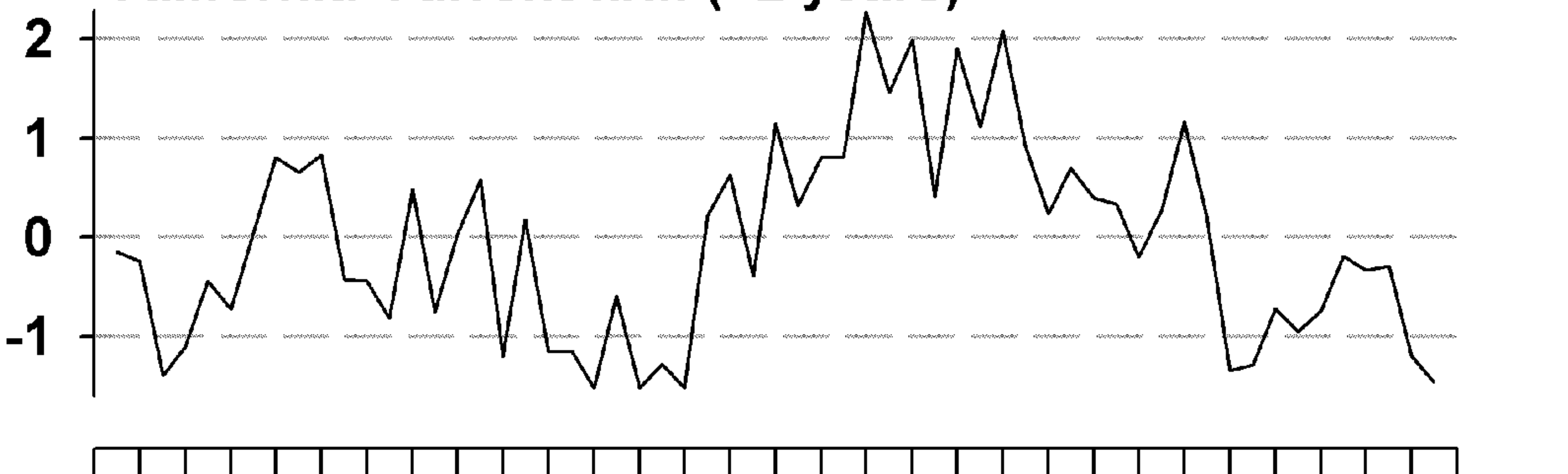
Adélie penguins (~21 years)



Red sea cucumbers (~5 years)



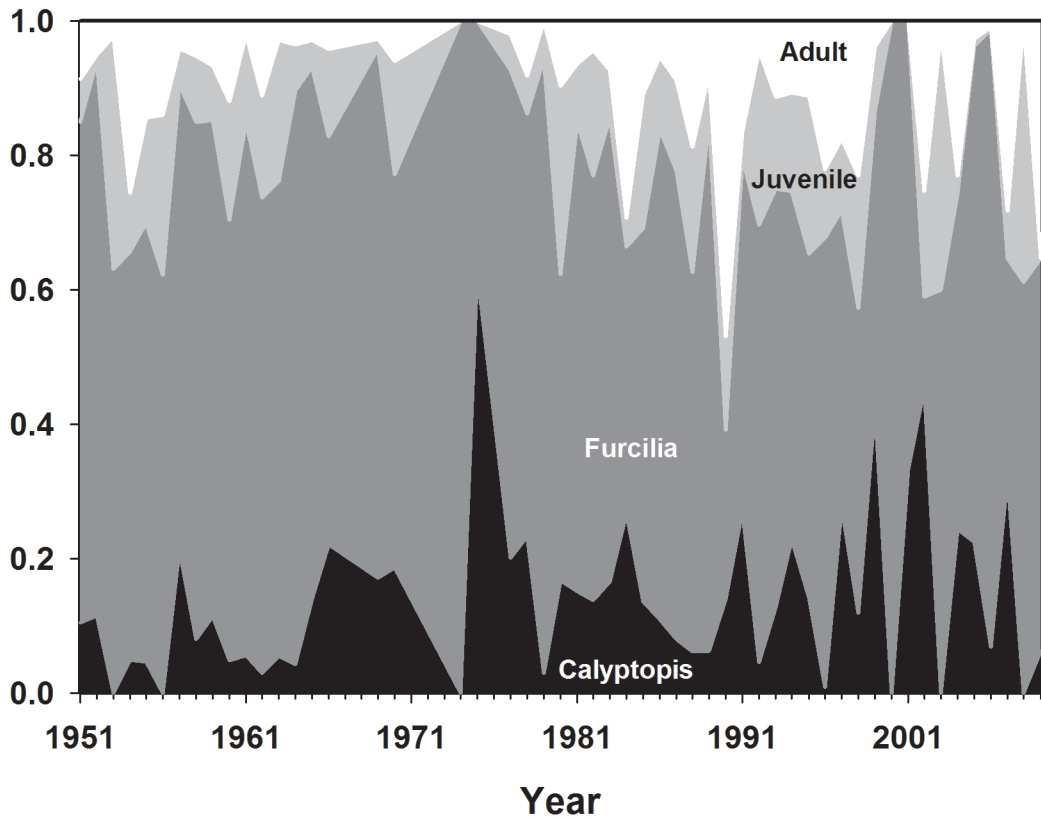
California Current krill (~2 years)



Lifespans

Biological response (standard deviation units)

Nyctiphanes simplex life-history stage (proportion)



50°0'0"W 60°0'0"S

40°0'0"W 65°0'0"S

30°0'0"W

20°0'0"W

0 120 240 480 720 Kilometers

60°0'0"W

70°0'0"W

80°0'0"W

70°0'0"S

75°0'0"S

80°0'0"S

Antarctic Circle
66° 33' 39" S

Anvers Island

Antarctic Peninsula

Anvers Island

Palmer Station

Antarctica

0 1.5 3 6 9 Kilometers

