Ecological and demographic drivers of jellyfish blooms

Josephine Goldstein[1,2,3*], Ulrich K. Steiner[1,2]

[1]Max-Planck Odense Center on the Biodemography of Aging, 5230 Odense M, Denmark

[2]Department of Biology, University of Southern Denmark, 5230 Odense M, Denmark

[3]Marine Biological Research Centre, University of Southern Denmark, 5300 Kerteminde, Denmark

[*]Corresponding author; email: jgoldstein@biology.sdu.dk

ABSTRACT: Jellyfish blooms are conspicuous demographic events with significant ecological and socio-economic impact, as they alter aquatic food webs. Despite worldwide concern about an increased frequency and intensity of jellyfish outbreaks, we are challenged to predict their booms and busts. To overcome this issue, we need to identify the ecological drivers of jellyfish blooms by taking into account the complex life cycle of scyphozoans (Cnidaria). Here we present demographic rates of all life stages of the cosmopolitan jellyfish *Aurelia aurita* s. l. within a stage-structured matrix model to investigate the life stage-dynamics of such complex populations under different environments. We illustrate how booms and busts of the medusa stage are highly influenced by non-medusa stage dynamics. We further point out increased food availability as an important ecological driver of jellyfish blooms, as it can shift the population structure of *A. aurita* away from the benthic polyp stage towards more medusae. Comparatively, our projected climate change scenario caused low fluctuations in population density. Overall, our

study reveals ecological and demographic key variables that regulate the intensity and frequency of jellyfish blooms, and thereby contributes to a better understanding of anthropogenic drivers of jellyfish mass occurrence, including habitat eutrophication and climate change.

KEY WORDS: Jellyfish blooms · Biodemography · Global change · Matrix model · Population structure

RUNNING HEAD: Drivers of jellyfish blooms

INTRODUCTION

Jellyfish blooms are demographic events in which the population density of one life stage, the medusa, shows distinct peaks over broad temporal and regional scales (Lucas et al. 2012). Such mass occurrence can have lasting ecological, economic and social consequences by changing the structure of pelagic ecosystems from fish-dominated to jellyfish-dominated food webs (Richardson et al. 2009). Jellyfish directly interfere with human activities; including tourism by stinging swimmers, fisheries by clogging nets, aquaculture by killing fish in net-pens, and power production by clogging cooling-water intake screens (Purcell et al. 2007, Purcell 2012). Concern about a global rise in jellyfish populations is widespread (Sanz-Martín et al. 2016), as jellyfish outbreaks are thought to be favored by several anthropogenic influences such as overfishing, eutrophication, habitat modification, species translocation and climate change (Richardson et al. 2009, Purcell 2012).

Species involved in jellyfish blooms are primarily found within the cnidarian taxon Scyphozoa and feature complex life histories (Hamner & Dawson 2008). Their life cycles typically include a pelagic, sexually reproducing medusa and a benthic, asexually reproducing polyp stage (Lucas et al. 2012). Such life histories facilitate mass occurrence of the medusa stage and previous studies revealed high phenotypic plasticity of specific life stages under changing environmental conditions (e.g. Hamner & Jenssen 1974, Gröndahl 1989, Liu et al. 2009, Fu et al. 2014). Despite mortality of the planula, polyp and ephyra stage could be of major importance for the development of medusa populations (Lucas 2001), information on the demographic rates involved in the complex life cycles of bloom-forming jellyfish has remained extremely scarce (e.g. Xie et al. 2015).

Quantification of demographic rates can identify the life stages that control jellyfish blooms in changing environments. Here, we used *Aurelia aurita* as model organism to reveal the basic demographic phenomena underlying jellyfish blooms and to point out how such drivers are influenced by environmental conditions. We first parameterized a stage structured matrix model based on data of all life stages (larvae, polyps, ephyrae and medusa) from laboratory experiments and the field. We compared the life history of *A. aurita* under different food levels with reference to two contrasting Danish water systems − the food limited Kerteminde Fjord/Kertinge Nor and the eutrophic Limfjorden − where zooplankton biomasses are <1-100 µg C l^{-1} and >10-1000 µg C l^{-1}, respectively (Nielsen et al. 1997, Møller & Riisgård 2007). In Kerteminde Fjord/Kertinge Nor, high density of the local *A. aurita* medusa population exhausts the available food resources and thereby restricts individual growth to maximum umbrella diameters of only 3-7 cm (Olesen et al. 1994, Nielsen et al. 1997). In Limfjorden, umbrella diameters of *A. aurita* medusae are in the range of 10-25 cm (Riisgård et al. 2012a, b), as is commonly observed in open coastal areas

(Möller 1980, Schneider 1989). We used our matrix model to evaluate jellyfish population growth rates with respect to changes in survival, stage-transitions or fecundity, i.e., reproductive rates. We further assessed the impact of high and low food conditions on population dynamics in a life-table response experiment (LTRE). Finally, we investigated the effects of climate change by exploring responses in population structure for a projected winter warming trend. Our results highlight the demographic drivers underlying jellyfish blooms and reveal the role of changing food web structures in combination with increased winter temperatures on their intensity and frequency. Such information is essential to predict the impact of anthropogenic influences on the life histories of the cosmopolitan jellyfish *A. aurita* and other jellyfish species with typical boom and bust population dynamics.

MATERIALS AND METHODS

Model organism

The common jellyfish *Aurelia aurita* s.l. (Scyphozoa, Cnidaria) belongs to an ubiquitous, cosmopolitan genus with several species and subspecies (Dawson 2003). *A. aurita* occurs in a variety of coastal and shelf sea environments, particularly in northwestern Europe, the Black Sea, Japan and parts of North America (Lucas 2001). Its complex life history (Fig. 1a) involves pelagic medusae that reproduce sexually and asexually reproducing benthic polyps. After sexual maturation, medusae produce large numbers of planula larvae (Ishii & Takagi 2003), which spend 12 h to 1 week in the water column (Lucas 2001) prior to settlement and metamorphosis into polyps on suitable hard substrate (Keen 1987, Holst & Jarms 2007). Polyps grow and reproduce asexually by several modes, including the production of well protected chitin-covered resting stages called podocysts (Arai 2009), budding of new polyps (Ishii & Watanabe 2003),

and the release of ephyrae by polyps through polydisc strobilation (Lucas et al. 2012). After asexual propagation, polyps return to the polyp stage and the development of ephyrae into sexually mature medusae closes the life cycle (Lucas et al. 2012).

Data collection

We cultivated planula larvae, polyps, ephyrae and medusae of *A. aurita* in the laboratories of the Marine Biological Research Centre, Kerteminde (Denmark), between August 2013 and March 2015. We set up separate experimental series for each life stage using filtered seawater (38 µm) with a constant salinity of 20 PSU and water temperature between 5 and 22 °C. Temperature conditions followed seasonal variability of the local temperate climate zone. We obtained planula larvae from female medusae which we collected in the fjord system Kerteminde Fjord/Kertinge Nor and the major water system Limfjorden (Denmark) in summer 2014. Directly after the release of planulae, we individually transferred larvae to small multi-well containers (n = 960). During daily counts, we determined survival rate and transition rate to the polyp stage by counting the number of living larvae and the number of larvae that had completed metamorphosis into polyps. We continued the counts until all larvae had metamorphosed into polyps or had died. We fed all life stages, except the planula larvae, with low or high amounts (corresponding to a ratio 1:10) of two-day old *Artemia salina* nauplii and regularly exchanged the seawater in our cultivation containers. We determined a mean organic weight (= *AFDW*; Vanhaecke & Sorgeloos 1980) of 2.8 ± 1.3 µg C ind.$^{-1}$ for each prey organism using the dry weight (*DW*; 24 h at 60 °C) to ash weight (*AW*; 4 h at 550 °C) ratio of replicate series with 100 individuals each (n = 10). We adjusted the amount of carbon added through feeding to the body size and resulting energy demands of each life stage. Between summer 2013 and summer 2014,

we cultivated polyps of *A. aurita* in the laboratory. For this purpose, we initially added planulae, released by female medusae collected in Kertinge Nor, to small (50 mL) containers with floating polystyrene substrate plates to facilitate settlement. After 24 h, we removed all but one newly settled polyp per substrate plate and replaced the seawater in the 50 mL containers. We subsequently raised and cultivated the individual polyps (n = 100) under high and low concentrations of *A. salina* nauplii. Polyps of *A. aurita* have maximum feeding rates of 10 µg C ind.$^{-1}$ d^{-1} (Kamiyama 2011); our high and low food levels hence resembled 1 or 10 µg C ind.$^{-1}$ d^{-1}, respectively. Each week we counted the number of live polyps as well as the number of buds, podocysts and ephyrae produced by each polyp. To maintain the initial polyp cohorts, we removed all buds detached from "mother" polyps instantly from substrate plates. During the whole experimental period, no excystment of polyps from podocysts was observed. During spring 2014, we individually transferred ephyrae, which were released by polyps under both high (n = 33) and low food level (n = 33), to 250 mL flasks with constant water movement and air supply, and reared them continuously under either high or low concentrations of *A. salina* nauplii. Food levels for ephyrae corresponded to either minimum energy requirements for maintenance (low food treatment) or a 10-fold carbon load (high food treatment). Based on weekly measurements of inter-rhopalia ephyra diameters, we determined size-specific energy demands to cover minimum energy requirements for maintenance (Frandsen & Riisgård 1997, Båmstedt et al. 1999). We further calculated the number of food organisms offered to each ephyra by converting respiratory maintenance costs into energy demands (1 J = 50 µl O_2; Eckert et al. 1988), assuming an average energy content of 0.055 J per *A. salina* nauplius (Bengston et al. 1991). Each week we counted the number of surviving ephyrae and determined the transition from ephyra to medusa; the latter we defined by the presence of fully developed intermediate

lappets and the final closure of adradial clefts. We performed these counts over 5 months until all ephyrae had either died or completed development into medusae. We tracked the newly transitioned medusae for an additional 9 months in weekly time intervals. During autumn 2014, we collected and individually transferred adult, female, larvae-carrying medusae from Kertinge Nor to 1-L aquaria with constant air supply. We kept these adult medusae either under complete starvation (n = 16) or under food concentrations of ~1000 µg C ind.$^{-1}$ d^{-1} (n = 33) by adding 5 daily rations of 2000 *A. salina* nauplii over a 12-h period followed by 12-h without feeding. We stopped daily recording of medusa survival after 4 months, when all individuals in the low food treatment had died; at that time all medusae in the high food treatment were still alive.

Estimating stage-specific rates

We used the experimental data collected in the lab to parameterize age-stage-structured matrix population models. For these models, we used discrete time steps of one month to estimate survival, fecundity, and stage transitions of *A. aurita* between age x and age x+1. Stages included larvae (L), polyps (P), ephyrae (E) and medusae (M). Since the empirical data was either based on daily (L, M) or weekly records (P, E), we first estimated monthly demographic rates for each life-stage i under low and high food conditions, respectively. We determined the fecundity of polyps under low and high food conditions from monthly budding rates and ephyra release rates. We estimated the number of planula larvae carried per adult female medusa (N_L, ind. ind.$^{-1}$) during the reproductive period (July to November; cf. Goldstein & Riisgård 2016) from average umbrella diameters (d, mm) of 40 mm and 200 mm for low and high food conditions, respectively. In this context, we further used the field observation-based exponential relationship $N_L = 160.8 \times e^{0.029 \times d}$ (Goldstein & Riisgård 2016). From these numbers of planula larvae carried

per medusa, we calculated the daily release of planula larvae (ρ, ind. ind.$^{-1}$ d^{-1}) as $\rho = 0.087 \times N_L$ (Goldstein & Riisgård 2016). We converted the daily release rates into monthly fecundity of medusae, assuming a sex ratio of 1:1.

To convert any of the daily or weekly transition probabilities and fertilities to monthly rates, we assumed that individuals that died during a given month, had died halfway during this month, i.e., they have lived half the month on average. This assumption is needed since both transition and fecundity rates between subsequent time steps depend on survivorship within each monthly time step, as for instance, a medusa might still release larvae before its death during a given month. Some ephyrae completed transition to the medusa stage within less than a month after they were released by a polyp. We therefore corrected the monthly release of ephyrae by polyps (F_{PE}) not only for daily survivorship of ephyrae, but also for the transition probability to the medusa stage within a given month. Further details on estimating monthly stage-specific demographic rates of *A. aurita* are given in the Supplement.

Monthly stage-structured matrix model

Our matrix model included monthly stage-specific vital rates for each of the 12 month of a year. Age is determined by month, and the final stages are polyp, ephyra, and medusa. Individuals in each life stage have a certain monthly probability to survive in their current stage i (t_{ii}), or to transition to another stage j (t_{ij}). Stage transitions are possible from larva to polyp (t_{LP}, month^{-1}) or from ephyra to medusa (t_{EM}, month^{-1}). Fecundity includes asexual reproduction of polyps by budding (F_{PP}, ind. ind.$^{-1}$ month^{-1}) or release of ephyrae (F_{PE}, ind. ind.$^{-1}$ month^{-1}), and sexual reproduction of medusae by the release of planula larvae (F_{ML}, ind. ind.$^{-1}$ month^{-1}; Fig. 1b). Since larval transition to the polyp stage was very fast (within days or even hours), we linked the

185 monthly transition from larva to polyp stage to fecundity of medusae ($F_{ML} \times t_{LP}$) to build the
186 basic structure of an irreducible monthly stage-structured population matrix model (Fig. 1c).
187 Using empirical datasets on all demographic rates of *A. aurita* under low and high food
188 conditions, respectively, we constructed monthly stage-structured submatrices A_x (3 × 3) of the
189 following structure:

$$A_x = \begin{pmatrix} t_{PP} + F_{PP} & 0 & F_{ML} \times t_{LP} \\ F_{PE} & t_{EE} & 0 \\ F_{PE} \times t_{EM} & t_{EM} & t_{MM} \end{pmatrix},$$

190

191 where x denotes the age in months, t_{ij} the transition probability from stage i to j, with the
192 survivorship of stage i expressed as $s_i = \sum_{j=1}^{i} t_{ij}$ and F_{ij} describes the fecundity of stage i to
193 produce offspring of stage j (cf. Fig. 1c). Note that parameters $F_{PE} \times t_{EM}$ and $F_{ML} \times t_{LP}$ are part
194 of the fecundity and not to be considered for estimating survival s_i. With the 12 monthly
195 submatrices (cf. Figs. S1 & S2 in the Supplement), we constructed yearly population projection
196 matrices A (36 × 36; time step = 1 month), one for each food level:

$$A = \begin{pmatrix} \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & A_{12} \\ A_1 & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & A_2 & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & A_3 & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & A_4 & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & A_5 & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & A_6 & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & A_7 & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & A_8 & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & A_9 & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & A_{10} & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & A_{11} & \cdot \end{pmatrix}.$$

197

198 In some months we observed no survivorship for ephyrae or medusae, which would lead to
199 reducible matrices (Caswell 2001); we therefore included a small transition probability of 10^{-10}
200 as placeholder (Figs. S1 & S2 in the Supplement). Our results were robust to this assumption.
201
202 **Demographic parameters and population projection**
203 We analyzed our two (low and high food) population projection matrices using R version 3.1.3
204 (R Core Team 2015) and compared the demographic dynamics of *A. aurita* under both food
205 levels. We used R packages 'popbio' (Stubben & Milligan 2007) and 'popdemo' (Stott et al.
206 2012) to compute population growth rate λ (dominant eigenvalue), stable stage distribution *SSD*
207 (right eigenvector **w** corresponding to dominant eigenvalue), reproductive value *R* (left
208 eigenvector **v** corresponding to dominant eigenvalue), the net reproductive rate R_0, the generation
209 time, the life expectancy e_0, and the sensitivity of λ to perturbations of the matrix elements (only
210 elements >0 are considered). We further used the two matrices to perform life-table response
211 experiment (LTRE) analysis (Caswell 1996, Tuljapurkar & Caswell 1997) with focus on the
212 sensitivity of λ to perturbations in stage-specific transitions when comparing high to low food
213 levels.
214
215 **Adjusting matrix parameters with respect to population growth rates**
216 Our matrix model for low food conditions resulted in a population growth rate λ of 1.32 $month^{-1}$.
217 Such growth rates are not realistic, at least not over extended periods in the field. The
218 unrealistically high λ reflects our sheltered laboratory environment under which we collected the
219 data to parameterize the models. As an important microzooplankton component, planula larvae
220 are highly subject to predation under natural conditions. We therefore reduced the transition rates

221 from larva to polyp of the two annual population matrices to a level that resulted in a stationary
222 population ($\lambda = 1$ month^{-1}) under low food conditions. We applied the same calibration to the
223 high food condition, leaving us with a still rapidly growing population under high food
224 conditions.
225
226 **Population projection in a climate change scenario**
227 We altered the population matrices to investigate potential effects of climate warming on the
228 population growth, stable stage distribution, net reproductive rate and life expectancy of *A.*
229 *aurita*. Increased water temperatures from 5 to 10 °C during winter are predicted to benefit the
230 production of *A. aurita* ephyrae by extended strobilation periods and enhanced ephyra release per
231 polyp (Holst 2012). We established such a warming scenario by increasing ephyra production
232 1.8-fold during the entire strobilation periods (cf. Tables S1 & S2 in the Supplement). We
233 additionally extended strobilation periods by one month (i.e., January or February for high and
234 low food conditions, respectively). With these modified matrices we investigated the
235 demographic effects of a predicted winter warming trend on *A. aurita* populations under low and
236 high food conditions.
237
238 **RESULTS**
239 **Demographic dynamics of Aurelia aurita under low and high food levels**
240 The metagenic life cycle of *Aurelia aurita* (Fig. 1a) was resembled by cyclic (imprimitive)
241 structure of our matrix model, expressing annual peak and pit dynamics in projected population
242 density (Fig. 2). The calibrated population growth rate under 10-fold increased food levels was λ
243 = 1.63 month^{-1}, indicating a 345-fold yearly increase in population size compared to the

calibrated stationary stable population under low food conditions ($\lambda = 1$ month^{-1}). Similar to low food levels, the projection matrix showed cyclic annual structure with typical peak and pit dynamics in projected population density, but amplitudes of cycles were much increased under high food availability (Fig. 2a).

Under low food conditions, population density increased to a peak during spring and summer and thereafter decreased to low densities during fall and winter. Under high food levels, peak density and dynamics differed significantly compared to low food conditions, by showing two distinct maxima in population density, one during spring and one during autumn, each followed by a subsequent minimum in summer and winter (Figs. 2a−b). The convergence time to stable stage, i.e. the damping ratio, of our modelled *A. aurita* population was 59 months (~5 years) under low food conditions and only 3 months for the high food population.

The stable stage distribution under low food availability was vastly dominated by polyps (~0.94) that survived throughout the year. Ephyrae and medusae accounted for comparatively small fractions of the population (0.04 and 0.02, respectively) and showed typical seasonal patterns (Fig. 2b). These included the release of ephyrae during April/May and their survival into September. Only few ephyrae transitioned to the medusa stage under low food conditions, so that medusae were present from June to December and contributed only marginally to restocking polyp densities by the release of planula larvae during autumn and winter. Under high food supply, the stable stage distribution of the *A. aurita* population was characterized by less polyps (0.76) compared to low food conditions. Medusae played a more pronounced role (0.2) under high food levels and ephyrae accounted for a small fraction of the overall population (0.04) due to faster transition to the medusa stage. Compared to a year-round standing stock of polyps under low food conditions, the stable stage distribution under high food levels was characterized by

lower proportions of polyps, which were predominant from September to March. Ephyrae were released in March/April, and medusae dominated the *A. aurita* population from April to June under high food levels. In autumn, the release of planula larvae restocked the polyp fraction (Fig. 2b).

Our findings illustrate a shift from polyp-dominated *A. aurita* populations towards more medusae under increased food conditions (see Table S3 in the Supplement). The reproductive value describes the contribution of an individual in a given stage to future generations. It was low for ephyrae (0.03) under low food conditions, and sexual reproduction of medusae contributed about half as much (0.42) compared to the asexually reproducing polyp stage (1; the reproductive values are scaled for January). The importance of the medusa stage under high food conditions was reflected in a reproductive value that increased to 0.27 for ephyrae and to 9.13 for medusae (note scaling to 1 for polyps in January). A net reproductive rate of 1 indicated that each polyp is replaced by 1 new polyp at the end of its life under low food conditions which resulted in long generation times of (200 months) ~16.7 years. Under high food levels, the net reproductive rate increased to 57 polyps replacing each polyp at the end of its life, highlighting the production of increased numbers of offspring compared to low food conditions. Due to this high net reproductive rate, high food conditions also boosted the average time between two consecutive generations to 8 months.

Life expectancy of polyps, estimated from the fundamental matrix as the mean time to death, was 33 years under low food conditions, while ephyrae and medusae revealed much shorter life expectancies of 2 and 3 months, respectively. In consensus with a more pronounced impact of the medusa stage on population structure under high food levels, life expectancy of polyps

289 decreased to 7 years, while the length of ephyra and especially medusa lives extended to 3 and 8
290 months, respectively (cf. Table S3 in the Supplement).

291 Population growth λ under low food conditions was most sensitive to changes in polyp
292 survival ($s_P = t_{PP}$), with constantly high sensitivity of 0.08 throughout the months of the year
293 (Fig. 2c). Sensitivity analysis further highlighted a lower influence of fecundity on growth rates
294 compared to survival rates. We detected sensitivities of λ between 0.01 and 0.02 for
295 perturbations in ephyra production (F_{PE}) from March to May and of 0.01 to 0.05 for perturbed
296 transition probability from ephyra to medusa (t_{EM}) from March to June. Under high food
297 conditions, the estimated sensitivity of λ was generally higher than under low food levels. The
298 population growth rate was most sensitive to changes in medusa survival, with sensitivity
299 remaining high, in a range of 0.07 to 0.16 from April to October, and reaching a maximum of
300 0.32 from June to July when medusa survival decreased. Changes in polyp survival affected λ
301 particularly from October to April, with sensitivities ranging from 0.04 to 0.13. To investigate
302 differences in the sensitivity of λ between food treatments, we performed a life table response
303 experiment (LTRE) analysis. Our results showed a maximum sensitivity of 0.14 for the transition
304 from ephyra to medusa stage in April/May, followed by high sensitivities of 0.08 for medusa
305 survival in the same time period. We further observed high sensitivities of 0.05 to 0.07 for
306 combined larva production and subsequent transition to the polyp stage from August to
307 December (Table S4 in the Supplement).

308

309 **Effects of climate change**

310 For our winter warming scenario with extended strobilation periods and increased ephyra
311 release, population growth rates of *A. aurita* increased to 1.03 month^{-1} and 1.65 month^{-1} under

low and high food conditions, corresponding to relative monthly increases of 2.5 and 1.3 %, respectively. The projected winter warming trend enhanced the variability in inter-annual population structure in both food treatments. We also observed slightly more distinct peak and pit dynamics in population density (Fig. 2a). The stable population structure of *A. aurita* we predicted for winter warming shifted slightly towards ephyrae (0.08) and medusae (0.03), with polyps still dominating (0.9) under low food levels (Fig. 2b). In relative terms, we observed 1.2 % more medusae, 3.8 % more ephyrae and 5.0 % less polyps per year. Under high food levels, our increased winter temperature scenario shifted the stable stage distribution to 9.9 % more medusae, 2.3 % less ephyrae and 7.6 % less polyps (see Table S5 in the Supplement). As a consequence of an earlier onset of strobilation periods in the scenario, fast transition of ephyrae resulted in significant proportions of medusae already present in February and March under high food levels (Fig. 2b).

Our winter warming scenario further increased reproductive values in both ephyrae and medusae by enhancing their relative contributions to the number of offspring of future generations by 4.3 % and 0.2 % per year under low and by 5.1 % and 2.8 % per year under high food levels, respectively. We found that winter warming increased the net reproductive rate by 1.35 polyps replacing every polyp at the end of its life under low food conditions, which corresponds to a relative difference of 35 %. Under high food conditions, we found a net reproductive rate of 62, indicating a relative increase by 8 % as a result of higher winter temperatures. The generation time under low food conditions was shortened to 12.3 years, corresponding to a difference of 4.4 years made up by the projected winter warming trend, while generation times were only marginally shortened by 2 days under high food conditions. Winter warming increased life expectancy of ephyrae by 12 day and 19 days, respectively (Table S5 in

335 the Supplement), whereas life expectancy of polyps and medusae remained unchanged under
336 both low and high food levels.
337
338 **DISCUSSION**
339 We reveal the demographic dynamics and life history shifts underlying jellyfish blooms and
340 show that the intensity and frequency of jellyfish booms and busts is subject to specific
341 ecological triggers. We illustrate that the typical peak and pit dynamics of jellyfish populations
342 are significantly enhanced by natural variations in the food regime, while other ecological
343 changes, such as a predicted winter warming, has a comparatively low impact on the
344 development of jellyfish blooms. Despite our winter warming scenario causing substantial
345 changes in population stage structure and dynamics, it is not sufficient to shift the predominant
346 mode of reproduction from asexual to sexual. We suggest this latter shift from polyp- to medusa-
347 dominated populations as a key mechanism causing jellyfish outbreaks. Our findings support
348 several previous studies which have identified metagenic life cycles as the base for boom and
349 bust population dynamics (Hamner & Dawson 2008, Pitt et al. 2008, Brotz et al. 2012). Since
350 jellyfish blooms have been suggested as indicators for ocean degradation (Schrope 2012), the
351 present insights may provide important basic knowledge regarding the health of ecosystems
352 worldwide.
353
354 **The demographic dynamics behind jellyfish blooms**
355 Our findings suggest food availability as a major constraint for the intensity and frequency of
356 jellyfish blooms, confirming recent observations that have pointed out food supply as limiting
357 factor for the development of ephyrae (Fu et al. 2014) as well as the survivorship and fecundity

of medusae (Goldstein & Riisgård 2016). Further, prey removal has been suggested as highly efficient management strategy in reducing the population size of cubomedusae (Bordehore et al. 2015). Yet, to our knowledge, we present the first comprehensive quantitative study of how increased food availability can trigger demographic changes in *Aurelia aurita* populations. Such changes include sharpened seasonal dynamics and shorter generation times of the pelagic medusa stage. We show that jellyfish blooms are a natural consequence of complex life cycles and confirm the key role of benthic polyps in ensuring long-term survival of *A. aurita* populations (Boero et al. 2008, Lucas et al. 2012), particularly when food is scarce. Increased food levels are associated with boosted population growth and dramatic life history shifts in *A. aurita*, as expressed by longer-lived medusae with enhanced release of planula larvae, increased ephyra production, as well as faster and more successful development of ephyrae into medusae. Our study provides important basic knowledge on the consequences of habitat eutrophication in context with jellyfish blooms, as investigated food levels are motivated by eutrophic to hypereutrophic conditions (cf. Riisgård et al. 2008) which are observed in our study areas Kerteminde Fjord/Kertinge Nor (Olesen et al. 1994, Nielsen et al. 1997) and Limfjorden (Møller & Riisgård 2007, Riisgård et al. 2012b).

Indicated by our life table response experiment analysis, which showed high sensitivities for the fecundity of medusae combined with the transition from larvae to polyps, an increased natural mortality risk is especially likely for the planktonic planula stage of *A. aurita* (cf. Lucas 2001). A transition probability of 0.001 $month^{-1}$ from larva to polyp matches well previous estimates (Xie et al. 2015) and was used to calibrate our presented matrix models for the *A. aurita* population under low and high food conditions. Our resulting stable population under low food levels is comparable to the local *A. aurita* jellyfish population in the semi-enclosed fjord

system Kerteminde Fjord/Kertinge Nor, which has remained unchanged over the last 24 years (Olesen et al. 1994, Nielsen et al. 1997, Riisgård et al. 2010, Goldstein & Riisgård 2016). The rapid growth potential we show for our calibrated jellyfish population under constantly high food (optimum) conditions however is in contrast to rather low abundances of *A. aurita* medusae observed in open coastal waters (Möller 1980, Goldstein & Riisgård 2016) or in Limfjorden (Hansson et al. 2005, Møller & Riisgård 2007), where *A. aurit*a may currently experience the process of being outcompeted by the invasive ctenophore *Mnemiopsis leidyi* (Riisgård et al. 2015). This implies additional factors regulating polyp, ephyra and medusa density in less protected ecosystems. According to our model for high food levels, an increased polyp mortality of 0.3 d^{-1} (Xie et al. 2015; i.e., a survivorship of 2.3×10^{-5} $month^{-1}$) would decrease population growth rates to 1.44 $month^{-1}$. Reduced medusa survival to 0.1 $month^{-1}$ (corresponding to a mortality of 0.07 d^{-1}; cf. Xie et al. 2015, Table 1 therein) or alternatively, a lowered transition probability from ephyra to medusa stage to 0.0001 $month^{-1}$, would result in remarkably decelerated population growth rates of $\lambda = 1.10$ $month^{-1}$ and 1.09 $month^{-1}$, respectively. Since population growth of *A. aurita* is less dependent on the survival of benthic polyps under increased food levels, our estimates suggest that transition from ephyra to medusa stage and survival of medusae are the most critical parameters for the development of jellyfish blooms in exposed coastal regions. This finding is additionally supported by the results of our life table response experiment analysis.

Besides food availability, intra- and inter-specific competition, predation (Kakinuma 1975, Hernroth & Gröndahl 1985, Hansson 1997, Arai 2005), substrate availability, hydrodynamic currents (Johnson et al. 2001, Xie et al. 2015) and extreme environmental conditions (Lucas et al. 2012) should be considered as important constraints for the development of jellyfish blooms.

In particular, population density-dependent mechanisms controlling individual size (Schneider & Behrends 1994, Lucas 2001, Riisgård et al. 2010, Goldstein & Riisgård 2016) could further play a major role for the demography of *A. aurita*. Especially size-structure should hence be taken into account in future population models (cf. Bordehore et al. 2015) to evaluate the importance of individual density for the development of jellyfish blooms.

Climate change and jellyfish blooms

Warm temperature can lead to enhanced asexual reproduction and has therefore been associated with greater numbers of medusae for most temperate scyphozoan species (Purcell 2005). Our findings do not support rather qualitative arguments about increased water temperature boosting the boom and bust dynamics of jellyfish blooms (Richardson et al. 2009, Xie et al. 2016). At least winter warming has comparatively weak effects on the growth of *A. aurita* populations due to resulting seasonal changes in population composition and structure. Our winter warming scenario led to only slightly enhanced seasonal variability in population structure which involved changes towards less polyps and more medusae but did not cause a shift from asexual polyp- to sexual medusa-dominated *A. aurita* populations as observed under increased food conditions. Winter warming however can increase the population growth of temperate jellyfish populations, which may be especially pronounced for populations in regions with limited food availability. As a consequence of enhanced strobilation periods and increased numbers of ephyrae released per polyp (Holst 2012), warmer winter temperatures shorten generation times due to more medusae with increased reproductive value. Climate warming has previously been suggested to benefit the population size of temperate scyphozoan species, but not tropical or boreal species (Holst 2012, Purcell et al. 2012). Based on recent climate analyses, rises in sea surface temperature by 5 °C

427 are expected within the next 100 years (Belkin 2009). Our results indicate a maximum increase
428 in jellyfish density by 1.1 during this warming period, while long-term observations in Kertinge
429 Nor have shown that fluctuations by a factor of up to 1.6 are common among years (Olesen et al.
430 1994, Riisgård et al. 2010, Goldstein & Riisgård 2016). Further taking into account the
431 requirement of a cold trigger to stimulate strobilation in *A. aurita* (Holst 2012), we suggest that
432 winter warming has marginal effects compared to regionally observed increases in food level.
433

434 **CONCLUSIONS**

435 Our study highlights that food availability drives and specifically shapes the booms and busts of
436 jellyfish blooms. We show that predicted changes in water temperature likely cause much less
437 dramatic increases in the density of *Aurelia aurita* medusae than already established food
438 concentrations in several eutrophic regions around the world. The importance of natural
439 competitors and predators for keeping jellyfish blooms in check needs further exploration, but
440 our findings might serve as a promising starting point. We conclude that a combination of
441 environmental triggers, such as habitat eutrophication, overfishing, artificial settlement substrates
442 and climate change, can promote jellyfish outbreaks severely. Our findings emphasize the
443 fundamental importance of an integral, quantitative view on jellyfish life histories. We believe
444 such inclusive knowledge, comprising species-specific, life stage-specific and age-specific traits,
445 is an inevitable prerequisite in providing perspective for future management of jellyfish blooms.
446

447 *Acknowledgements.* We thank Kim Lundgreen for technical assistance and are grateful to Hans
448 Ulrik Riisgård, Hal Caswell, Iain Stott, Cesar Bordehore, Per Andersen, Owen Jones and Cathy

449 H. Lucas for comments and/or discussions. This study was financially supported by the Max-
450 Planck Society (Max-Planck Odense Center on the Biodemography of Aging, Denmark).

451

452 **REFERENCES**

453 Arai MN (2005) Predation on pelagic coelenterates: a review. J Mar Biol Assoc UK 85:523–536

454 Arai MN (2009) The potential importance of podocysts to the formation of scyphozoan blooms:
455 a review. In: Purcell JE, Pitt KA (eds) Jellyfish Blooms: Causes, Consequences, and Recent
456 Advances. Springer, Netherlands, p 241–246

457 Båmstedt U, Lane J, Martinussen MB (1999) Bioenergetics of ephyra larvae of the scyphozoan
458 jellyfish *Aurelia aurita* in relation to temperature and salinity. Mar Biol 135:89–98

459 Belkin IM (2009) Rapid warming of large marine ecosystems. Prog Oceanogr 81:207–213

460 Bengtson DA, Leger P, Sorgeloos P (1991) Use of *Artemia* as a food source for aquaculture. In:
461 Browne RA, Sorgeloos P, Trotman CAN (eds) Artemia Biology. CRC Press, Boca Raton,
462 Florida, USA, p 255–285

463 Boero F, Bouillon J, Gravili C, Miglietta MP, Parsons T, Piraino S (2008) Gelatinous plankton:
464 irregularities rule the world (sometimes). Mar Ecol Prog Ser 356:299–310

465 Bordehore C, Fuentes VL, Segarra JG, Acevedo M, Canepa A, Raventós J (2015) Use of an
466 inverse method for time series to estimate the dynamics of and management strategies for the
467 box jellyfish *Carybdea marsupialis*. PLOS ONE 10:e0137272, doi:
468 10.1371/journal.pone.0137272

469 Brotz L, Cheung WW, Kleisner K, Pakhomov E, Pauly D (2012) Increasing jellyfish
470 populations: trends in large marine ecosystems. Hydrobiologia 690:3–20

471 Caswell H (1996) Analysis of life table response experiments II. Alternative parameterizations
472 for size-and stage-structured models. Ecol Modell 88:73–82
473 Caswell H (2001) Matrix population models: construction, analysis, and interpretation. Sinauer
474 Associates, Sunderland, Massachusetts, USA
475 Dawson MN (2003) Macro-morphological variation among cryptic species of the moon jellyfish,
476 *Aurelia* (Cnidaria: Scyphozoa). Mar Biol 143:369–379
477 Eckert R, Randall D, Augustine G (1988) Animal energetics and temperature relations. In:
478 Eckert R, Augustine G (eds) Animal Physiology, Mechanisms and Adaptions. WH Freeman
479 and Company, USA, p 555–605
480 Frandsen KT, Riisgård HU (1997) Size dependent respiration and growth of jellyfish, *Aurelia*
481 *aurita*. Sarsia 82:307–312
482 Fu Z, Shibata M, Makabe R, Ikeda H, Uye SI (2014) Body size reduction under starvation, and
483 the point of no return, in ephyrae of the moon jellyfish *Aurelia aurita*. Mar Ecol Prog Ser
484 510:255–263
485 Goldstein J, Riisgård HU (2016) Population dynamics and factors controlling somatic degrowth
486 of the common jellyfish, *Aurelia aurita*, in a temperate semi-enclosed cove (Kertinge Nor,
487 Denmark). Mar Biol 163:33–44
488 Gröndahl F (1989) Evidence of gregarious settlement of planula larvae of the scyphozoan
489 *Aurelia aurita*: An experimental study. Mar Ecol Prog Ser 56:119–125
490 Hamner WM, Dawson MN (2008) A review and synthesis on the systematics and evolution of
491 jellyfish blooms: advantageous aggregations and adaptive assemblages. In: Purcell JE, Pitt
492 KA (eds) Jellyfish Blooms: Causes, Consequences, and Recent Advances. Springer,
493 Netherlands, p 161–191

494 Hamner WM, Jenssen RM (1974) Growth, degrowth, and irreversible cell differentiation in
495 *Aurelia aurita*. Am Zool 14:833–849
496 Hansson LJ (1997) Capture and digestion of the scyphozoan jellyfish *Aurelia aurita* by *Cyanea*
497 *capillata* and prey response to predator contact. J Plankton Res 19:195–208
498 Hansson LJ, Moeslund O, Kiørboe T, Riisgård HU (2005) Clearance rates of jellyfish and their
499 potential predation impact on zooplankton and fish larvae in a neritic ecosystem (Limfjorden,
500 Denmark). Mar Ecol Prog Ser 304:117–131
501 Hernroth L, Gröndahl F (1985) On the biology of *Aurelia aurita* (L.) 3. Predation by *Coryphella*
502 *verrucosa* (Gastropoda, Opisthobranchia), a major factor regulating the development of
503 *Aurelia* populations in the Gullmar Fjord, western Sweden. Ophelia 24:37–45
504 Holst S (2012) Effects of climate warming on strobilation and ephyra production of North Sea
505 scyphozoan jellyfish. Hydrobiologia 690:127–140
506 Holst S, Jarms G (2007) Substrate choice and settlement preferences of planula larvae of five
507 Scyphozoa (Cnidaria) from German Bight, North Sea. Mar Biol 151:863–871
508 Ishii H, Takagi A (2003) Development time of planula larvae on the oral arms of the
509 scyphomedusa *Aurelia aurita*. J Plankton Res 25:1447–1450
510 Ishii H, Watanabe T (2003) Experimental study of growth and asexual reproduction in *Aurelia*
511 *aurita* polyps. Sessile Organisms 20:69–73
512 Johnson DR, Perry HM, and Burke WD (2001) Developing jellyfish strategy hypotheses using
513 circulation models. Hydrobiologia 451:213–221
514 Kakinuma Y (1975) An experimental study of the life cycle and organ differentiation of *Aurelia*
515 *aurita* Lamarck. Bulletin of the Marine Biological Station of Asamushi 15:101–113

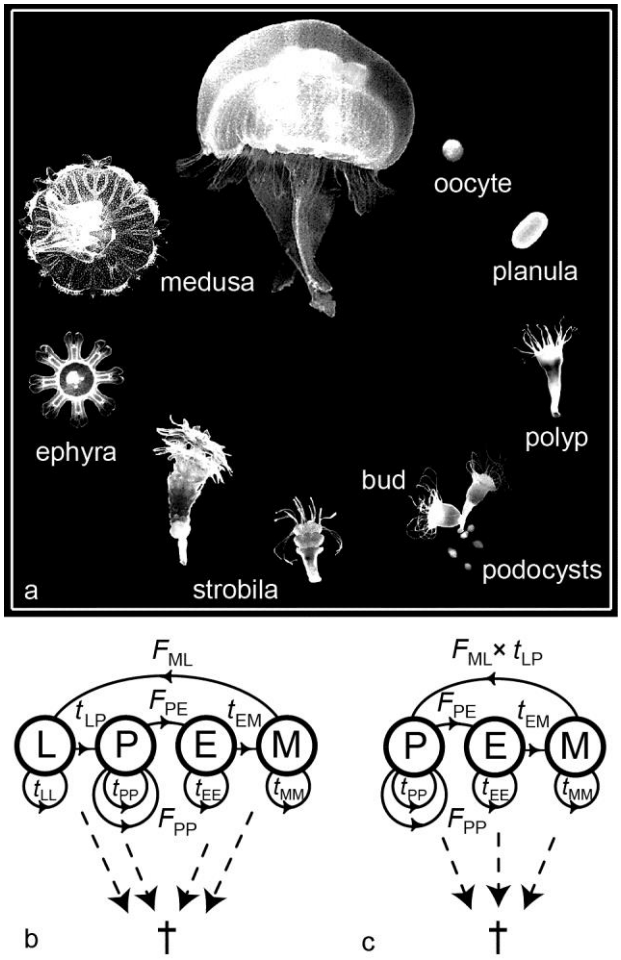
516 Kamiyama T (2011) Planktonic ciliates as a food source for the scyphozoan *Aurelia aurita* (s.l.):
517 Feeding activity and assimilation of the polyp stage. J Exp Mar Biol Ecol 407:207–215
518 Keen SL (1987) Recruitment of *Aurelia aurita* (Cnidaria: Scyphozoa) larvae is position-
519 dependent, and independent of conspecific density, within a settling surface. Mar Ecol Prog
520 Ser 38:151–160
521 Liu WC, Lo WT, Purcell JE, Chang HH (2009) Effects of temperature and light intensity on
522 asexual reproduction of the scyphozoan, *Aurelia aurita* (L.) in Taiwan. Hydrobiologia
523 616:247–258
524 Lucas CH (2001) Reproduction and life history strategies of the common jellyfish, *Aurelia*
525 *aurita*, in relation to its ambient environment. Hydrobiologia 451:229–246
526 Lucas CH, Graham WM, Widmer C (2012) Jellyfish Life Histories: Role of Polyps in Forming
527 and Maintaining Scyphomedusa Populations. Adv Mar Biol 63: 133–196
528 Möller H (1980) Population dynamics of *Aurelia aurita* medusae in Kiel Bight, Germany (FRG).
529 Mar Biol 60:123–128
530 Møller LF, Riisgård HU (2007) Population dynamics, growth and predation impact of the
531 common jellyfish *Aurelia aurita* and two hydromedusae (*Sarsia tubulosa* and *Aequorea*
532 *vitrina*) in Limfjorden (Denmark). Mar Ecol Prog Ser 346: 153–165
533 Nielsen AS, Pedersen AW, Riisgård HU (1997) Implications of density driven currents for
534 interaction between jellyfish (*Aurelia aurita*) and zooplankton in a Danish fjord. Sarsia
535 82:297–305
536 Olesen NJ, Frandsen K, Riisgård HU (1994) Population Dynamic, Growth and Energetics of
537 Jellyfish, *Aurelia aurita*, in a Shallow Fjord. Mar Ecol Prog Ser 105:9–18

538 Pitt KA, Welsh DT, Condon RH (2008) Influence of jellyfish blooms on carbon, nitrogen and
539 phosphorus cycling and plankton production. In: Purcell JE, Pitt KA (eds) Jellyfish Blooms:
540 Causes, Consequences, and Recent Advances. Springer, Netherlands, p 133–149
541 Purcell JE (2005) Climate effects on formation of jellyfish and ctenophore blooms: a review. J
542 Mar Biol Assoc UK 85:461–476
543 Purcell JE (2012) Jellyfish and ctenophore blooms coincide with human proliferations and
544 environmental perturbations. Annu Rev Mar Sci 4:209–235
545 Purcell JE, Uye SI, Lo WT (2007) Anthropogenic causes of jellyfish blooms and their direct
546 consequences for humans: a review. Mar Ecol Prog Ser 350:153–174
547 Purcell JE, Atienza D, Fuentes VL, Olariaga A, Tilves U, Colahan C, Gili JM (2012)
548 Temperature effects on asexual reproduction rates of scyphozoan species from the northwest
549 Mediterranean Sea. Hydrobiologia 690:169–180
550 R Core Team (2015) R: A language and environment for statistical computing. R Foundation for
551 Statistical Computing, Vienna, Austria. http://www.r-project.org
552 Richardson AJ, Bakun A, Hays GC, Gibbons MJ (2009) The jellyfish joyride: causes,
553 consequences and management responses to a more gelatinous future. Trends Ecol Evol
554 24:312–322
555 Riisgård HU, Jensen MH, Rask N (2008) Odense Fjord and Kerteminde Fjord/Kertinge Nor.
556 Ecology of Baltic Coastal Waters. Springer Berlin Heidelberg
557 Riisgård HU, Barth-Jensen C, Madsen CV (2010) High abundance of the jellyfish *Aurelia aurita*
558 excludes the invasive ctenophore *Mnemiopsis leidyi* to establish in a shallow cove (Kertinge
559 Nor, Denmark). Aquat Invasions 5:347–356

560 Riisgård HU, Madsen CV, Barth-Jensen C, Purcell JE (2012a) Population dynamics and
561 zooplankton-predation impact of the indigenous scyphozoan *Aurelia aurita* and the invasive
562 ctenophore *Mnemiopsis leidyi* in Limfjorden (Denmark). Aquat Invasions 7:147–162
563 Riisgard HU, Jaspers C, Serre S, Lundgreen K (2012b) Occurrence, inter-annual variability and
564 zooplankton-predation impact of the invasive ctenophore *Mnemiopsis leidyi* and the native
565 jellyfish *Aurelia aurita* in Limfjorden (Denmark) in 2010 and 2011. Bioinvasions Rec
566 1:145–159
567 Riisgård HU, Goldstein J, Lundgreen K, Lüskow F (2015) Jellyfish and Ctenophores in the
568 Environmentally Degraded Limfjorden (Denmark) During 2014 − Species Composition,
569 Population Densities and Predation Impact. Fish Aquac J 6:137–146
570 Sanz-Martín M, Pitt KA, Condon RH, Lucas CH, Novaes de Santana C, Duarte CM (2016)
571 Flawed citation practices facilitates the unsubstantiated perception of a global trend toward
572 increased jellyfish blooms. doi: 10.1111/geb.12474
573 Schneider G (1989) The common jellyfish *Aurelia aurita*: standing stock, excretion and nutrient
574 regeneration in the Kiel Bight, Western Baltic. Mar Biol 100:507–514
575 Schneider G, Behrends G (1994) Population dynamics and the trophic role of *Aurelia aurita*
576 medusae in the Kiel Bight and western Baltic. ICES J Mar Sci 51:359–367
577 Schrope M (2012) Marine ecology: attack of the blobs. Nature 482:20–21
578 Stott I, Hodgson DJ, Townley S (2012) popdemo: an R package for population demography
579 using projection matrix analysis. Methods Ecol Evol 3:797–802
580 Stubben CJ, Milligan BG (2007) Estimating and Analyzing Demographic Models Using the
581 popbio Package in R. J Stat Softw 22:1−23.

582 Tuljapurkar S, Caswell H (1997) Structured-population models in marine, terrestrial, and
583 freshwater systems. Springer Science & Business Media
584 Vanhaecke P, Sorgeloos P (1980) International Study on *Artemia*. IV. The biometrics of *Artemia*
585 strains from different geographical origin. The brine shrimp Artemia 3:393–405
586 Xie C, Fan M, Wang X, Chen M (2015) Dynamic Model for Life History of Scyphozoa. PLOS
587 ONE 10, doi: 10.1371/journal.pone.0130669

588 **FIGURES**



589

590 Fig. 1. Life history of the common jellyfish *Aurelia aurita* (Scyphozoa, Cnidaria). (a) Metagenic
591 life cycle with alternation of generations between the sexually reproducing medusa and the
592 asexually reproducing polyp stage. (b) Life cycle graph for *A. aurita*, including transition
593 probability *t*, fecundity *F* (solid arrows) and mortality † (broken arrows) of all life stages, i.e.,
594 planula larva (L), polyp (P), ephyra (E) and medusa (M). (c) Reduced life cycle graph for polyps,
595 ephyrae and medusae considering fast (daily) transition from larva to polyp stage.

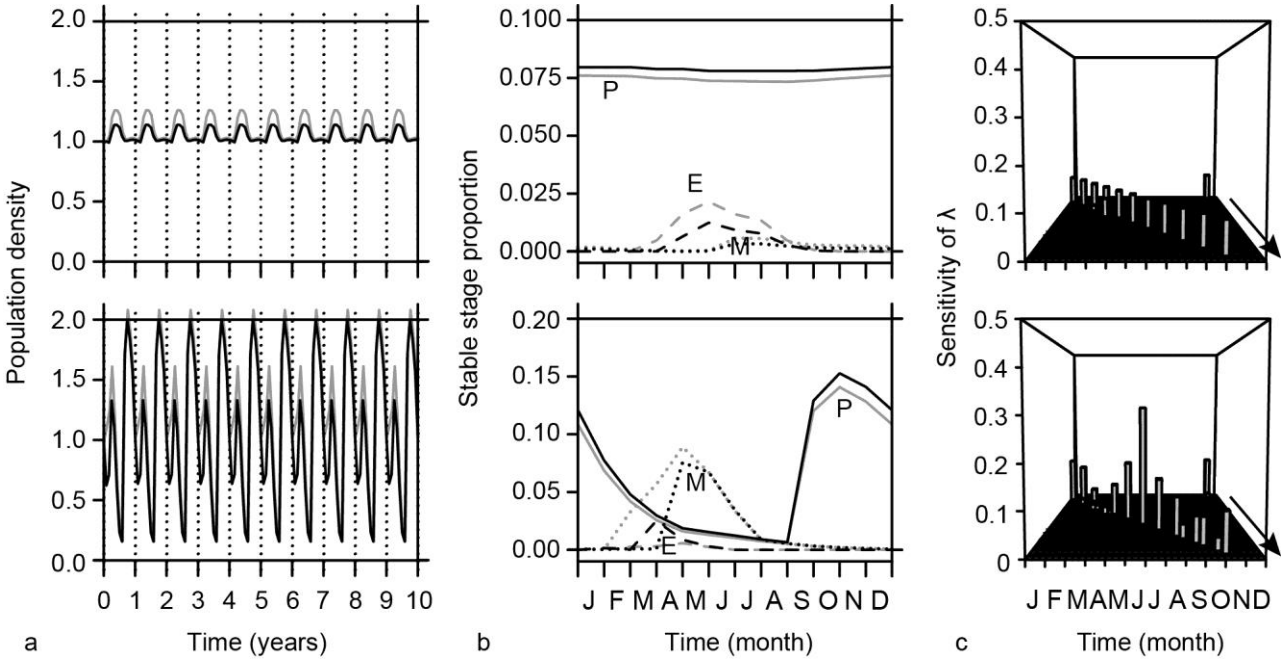


Fig. 2. Population matrix model for *Aurelia aurita* under low (upper panels) and high food (lower panels) conditions (1:10). (a) Matrix projection over a 10-year period (dotted lines), standardized to the long-term effects of population growth rates $\lambda = 1$ month^{-1} and $\lambda = 1.63$ month^{-1}, respectively, for present temperature conditions (solid black lines) and for a predicted winter warming trend (solid grey lines). (b) Stable stage proportion of polyps (P), ephyrae (E) and medusae (M) for present temperature conditions (black lines) and for a winter warming scenario (gray lines). (c) Sensitivity of λ to changes in monthly stage transitions.