Ecological drivers of jellyfish blooms – the complex life history of a cosmopolitan medusa (*Aurelia aurita*)

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Running head Drivers of jellyfish blooms

Summary

1. Jellyfish blooms are conspicuous demographic events with significant ecological and socio-economic impact. Despite worldwide concern about an increased frequency and intensity of jellyfish mass occurrences, predicting their booms and busts remains challenging.

2. Forecasting how jellyfish populations may respond to environmental change requires taking into account their complex life histories. Metagenic life cycles, which include a benthic polyp stage, can boost jellyfish outbreaks via asexual recruitment of pelagic medusae.

3. Here we present stage-structured matrix population models with demographic rates of all life stages of the cosmopolitan jellyfish *Aurelia aurita* s. l. for different environments. We investigate the life stage-dynamics of such complex populations to illustrate how changes in medusa density depend on non-medusa stage dynamics.

4. We show that increased food availability is an important ecological driver of jellyfish mass occurrence, as it can shift the population structure from polyp- to medusa-dominated. Projecting populations for a winter warming scenario additionally enhanced the booms and busts of jellyfish blooms.

5. We identify demographic key variables that control the intensity and frequency of jellyfish blooms in response to anthropogenic drivers such as habitat eutrophication and climate change. By contributing to an improved understanding of mass occurrence phenomena, our findings provide perspective for future management of ecosystem health.

Key-words biodemography, environmental change, jellyfish blooms, matrix model, population structure

Introduction

The diversity, productivity and resilience of marine ecosystems worldwide are threatened by an imbalance in the ecological parameters regulating population outbreaks. Mass occurrences of micro- and macroalgae, cnidarians, ctenophores, gastropods, echinoderms, tunicates and fish appear with increased frequency, intensity and geographical distribution (Breithaupt, 2003; Enevoldsen, 2003; Fabricius, Okaji, & De'Ath, 2010; Haddad Junior, Virga, Bechara, Silveira, & Morandini, 2013; Maji, Bhattacharyya, & Pal, 2016; Shiganova et al., 2001; Turner, 1994; Vargas-Ángel, Godwin, Asher, & Brainard, 2009). Despite being a widespread phenomenon which may serve as an indicator for marine ecosystem degradation, mass occurrence is poorly understood and challenging to predict (Van Dolah 2000). Jellyfish blooms are a prominent example for outbreaks in which the population density of one life stage, the medusa, shows distinct peaks over

broad temporal and regional scales (Lucas, Graham, & Widmer, 2012). Jellyfish populations, i.e. aggregations of the medusa stage, have increased in numerous coastal regions around the world over recent decades (Brotz, Cheung, Kleisner, Pakhomov, & Pauly, 2012). Such increase has lasting ecological, economic and social implications. Jellyfish blooms can trigger trophic cascades in pelagic food webs due to their severe predatory impact on a broad spectrum of zooplankton species and fish larvae (Richardson, Bakun, Hays, & Gibbons, 2009; Riisgård, Andersen, & Hoffmann, 2012; Schneider & Behrends 1994, 1998). Further, jellyfish mass occurrences can interfere with human activities such as tourism, fisheries, aquaculture and power production (Purcell, 2012; Purcell, Uye, & Lo, 2007). Concern about a global rise in jellyfish populations is widespread (Sanz-Martín, Pitt, Condon, Lucas, Novaes de Santana, & Duarte, 2016), as jellyfish outbreaks are thought to be favored by anthropogenic influences; in particular overfishing, eutrophication, habitat modification, species translocation and climate change (Purcell, 2012; Richardson, Bakun, Hays, & Gibbons, 2009).

Species that form jellyfish blooms are primarily found within the cnidarian taxon Scyphozoa and feature complex life histories (Hamner & Dawson, 2009). Their metagenic life cycles typically include a pelagic, sexually reproducing medusa and a benthic, asexually reproducing polyp stage (Lucas, Graham, & Widmer, 2012). Such life cycles facilitate mass occurrence and are characterized by high stage-specific plasticity to changing environmental conditions (e.g. Fu, Shibata, Makabe, Ikeda, & Uye, 2014; Gröndahl, 1989; Hamner & Jenssen, 1974; Liu, Lo, Purcell, & Chang, 2009). Although the development of medusa populations is directly linked to survival rates of the planula, polyp and ephyra stage (Lucas, 2001), information on the demographic rates of bloom-

forming jellyfish has remained scarce (Xie, Fan, Wang, & Chen, 2015). Quantifying demographic rates of all stages in the life cycle of species showing mass occurrence is thus fundamental to identify the environmental variables causing changes in population dynamics and structure.

Here, we use the common jellyfish *Aurelia aurita* s. l. (Linnaeus, 1758) to explore the demographic structure and environmental drivers underlying mass occurrence of a cosmopolitan jellyfish species. We quantify demographic rates of all life stages of *A. aurita* (larvae, polyps, ephyrae and medusae), i.e. survival, stage-transitions and fecundity, based on experimental and field data. Using these demographic rates, we parameterize stage-structured population models to project the life cycle of jellyfish populations for low and high food levels relating to prey availability in two contrasting temperate water systems. We further predict the impact of a winter warming scenario on the demographic dynamics of *A. aurita*. Our results provide novel insights into the development of metagenic jellyfish populations under increased food levels and increased winter temperatures. Such information is essential to assess the boosting potential of environmental drivers on species showing mass occurrence and provides a milestone for identifying and managing demographic irregularities in marine ecosystems.

Materials and Methods

Study organism

The common jellyfish *A. aurita* s.l. (Scyphozoa, Cnidaria) belongs to an ubiquitous, cosmopolitan genus with several species and subspecies (Dawson, 2003). *Aurelia aurita* is well-studied and 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 life history, i.e. individual stage-trajectory, is subject to a complex life cycle (Fig. 1a) which involves pelagic medusae that reproduce sexually and benthic polyps that reproduce asexually. 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) before they settle and metamorphose into polyps on suitable hard substrate (Holst & Jarms, 2007; Keen, 1987). Polyps reproduce asexually by several modes, including i) the production of well protected chitin-covered resting stages called podocysts (Arai, 2009), ii) budding of new polyps (Ishii & Watanabe, 2003), and iii) the release of ephyrae through polydisc strobilation. After asexual propagation, polyps remain in the polyp stage and the development of ephyrae into sexually mature medusae closes the life cycle (Lucas, Graham, & Widmer, 2012).

Data collection

We cultivated planula larvae (L), polyps (P), ephyrae (E) and medusae (M) of *A. aurita* in the laboratories of the Marine Biological Research Centre, Kerteminde (Denmark) between August 2013 and November 2014. We set up separate experimental series for each life stage using filtered (38 µm) seawater at constant salinity (20 PSU) and with water temperature following seasonal variability of the local temperate climate zone (5-22 °C). 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 adjusted the fed biomass of *A.*

salina (2.55 µg C ind.$^{-1}$; Vanhaecke & Sorgeloos, 1980) to the size-specific energy demands of each life stage.

We obtained planula larvae from female medusae that were collected in two contrasting Danish water systems from June to September 2013 – the fjord system Kerteminde Fjord/Kertinge Nor and the major water system Limfjorden − where zooplankton prey biomasses are <1−100 µg C L^{-1} (Nielsen, Pedersen, & Riisgård, 1997) and >10−1000 µg C L^{-1}, respectively (Møller & Riisgård, 2007). Directly after the release of planulae, we transferred the larvae individually to multi-well (200 µL) containers (initial number of individuals, l_{L0} = 960 ind.). During daily counts, we determined the number of living larvae (l_{LL}, ind. day^{-1}) and the number of larvae that had completed metamorphosis into polyps (l_{LP}, ind. day^{-1}) until all planulae had metamorphosed into polyps or had died after ~50 days. From August 2013, we cultivated polyps of *A. aurita* in the laboratory. To do so, we initially added planulae, released by female medusae from Kertinge Nor, to small (50 mL) seawater 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 containers. We subsequently raised and cultivated the individual polyps under low or high food conditions (l_{P0} = 100 ind.) of 1 or 10 µg C ind.$^{-1}$ day^{-1} (cf. Kamiyama, 2011). To maintain the initial polyp cohorts, we instantly removed any buds of the "mother" polyps from substrate plates. During the whole experimental period of 12 months, no excystment of polyps from podocysts was observed. Each week we counted the number of live polyps (l_{PP}, ind. week^{-1}) as well as the number of buds (N_{PP}, ind. week^{-1}) and ephyrae per polyp (N_{PE}, ind. week^{-1}). From January 2014, we individually transferred ephyrae, which were released by polyps under

low and high food level, to seawater flasks (250 mL) with constant water movement and air supply, and reared them continuously under either low or high food conditions (l_{E0} = 33 ind.). Food levels for ephyrae were 10 or 100 µg C ind.$^{-1}$ day^{-1}, and corresponded to the minimum energy demands for maintenance of a 'standard' ephyra with 8 mm inter-rhopalia diameter (Båmstedt, Lane, & Martinussen, 1999; Bengtson, Leger, & Sorgeloos, 1991; Eckert, Randall, & Augustine, 1988; Frandsen & Riisgård, 1997), or the 10-fold carbon load, respectively. Each week we counted the number of surviving ephyrae (l_{EE}, ind. week^{-1}) and the number of ephyrae that had completed transition to medusa (l_{EM}, ind. week^{-1}); the latter we defined by the presence of fully developed intermediate lappets and the final closure of adradial clefts. We performed these counts for 8 months until all ephyrae had either developed into medusae or had died. We continuously tracked all newly transitioned medusae from February/March 2014, and additional sexually mature females collected in Kertinge Nor from September 2014, in individual aquaria (1 L) with constant air supply. We kept the medusae under low (l_{M0} = 16 ind.) or high food levels (l_{M0} = 33 ind.) which resembled complete starvation, i.e. 0 µg C ind.$^{-1}$ day^{-1}, or >1000 µg C ind.$^{-1}$ day^{-1}, with the latter covering the 10-fold energy demands of a 'standard' 50 mm umbrella diameter medusa (Olesen, Frandsen, & Riisgård, 1994; Goldstein & Riisgård, 2016). We recorded the survival of medusae (l_{MM}, ind. day^{-1}) daily until all individuals in the low food treatment had died after 9 months; at that time all medusae in the high food treatment were still alive. We estimated the daily release of planula larvae by female medusae during the reproductive period (N_{ML}, ind. day^{-1}) using the field observation-based relationship $N_{ML} = 0.087 \times 160.8 \times e^{0.029d}$ (Goldstein & Riisgård, 2016), where

average umbrella diameters (d, mm) of 40 mm and 200 mm reflected low and high food conditions.

Estimating stage-specific demographic rates

We used the experimental data to parameterize age-stage-structured matrix population models. For these models, we used discrete time steps of one month to estimate survival, stage transitions and fecundity of the stages L, P, E and M between age x and age x+1. Individuals in each life stage i have a certain monthly probability to survive in their current stage (t_{ii}), or to transition to another stage j (t_{ij}) or to produce offspring of stage j (F_{ij}). Each stage has its unique survival rate (t_{LL}, t_{PP}, t_{EE}, t_{MM}, month^{-1}) and 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 our 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. To convert any of the daily or weekly transition probabilities and fecundities to monthly rates, we assumed that individuals that died during a given month, had died halfway during this month, i.e. they survived throughout 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 within 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 not only for daily survivorship of ephyrae, but also for the transition probability to the medusa stage within a given month. For converting the daily release of planula larvae into monthly fecundity of medusae, we assumed a sex ratio of 1:1. Further details on estimating monthly stage-specific demographic rates of *A. aurita* are available from the Supporting Information (Appendix S1 & S2).

Monthly stage-structured matrix population model

Our matrix population model describes the transitions of each life stage taking place during each projection interval, as defined by monthly stage-specific demographic rates for each of the 12 month of a year. Age is determined by month, and the final stages are polyp, ephyra and medusa. Since larval transition to the polyp stage was very fast (within days or hours), we linked the monthly transition from larva to polyp stage to fecundity of medusae ($F_{\mathrm{ML}} \times t_{\mathrm{LP}}$) to build the basic structure of an irreducible monthly stage-structured matrix model (Fig. 1c). Using our empirical datasets on all demographic rates of *A. aurita* under low and high food conditions, respectively, we constructed monthly stage-structured submatrices A_x (3 × 3) of the following structure:

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

where x denotes the age in months. With the 12 monthly submatrices (cf. Appendix S3: Figs. S1 & S2), we constructed yearly population projection matrices A (36 × 36; time step = 1 month):

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

In some months, we observed no survivorship of ephyrae or medusae, which would lead to reducible matrices (Caswell, 2001); we therefore included a small transition probability $c = 1 \times 10^{-10}$ as placeholder (Appendix S3: Figs. S1 & S2). Our results were robust to this assumption.

Adjusting matrix parameters to environmental change

We constructed yearly projection matrix models for the jellyfish population under low and high food conditions. Since our transition probabilities from larva to polyp were unrealistically high due to the sheltered laboratory environment (as an important microzooplankton component, planula larvae are highly subject to predation under natural conditions), we calibrated the larva to polyp transition (t_{LP}) to a level that resulted in a stationary population (i.e. characterized by constant population size over time) under low food conditions. We applied the same level of calibration as for the low food condition to the projection matrix model for high food conditions, leaving us with a rapidly growing population.

We parameterized additional projection matrix models to investigate the potential effects of winter warming under low and high food conditions. A predicted winter warming trend will likely increase present water temperatures from 5−10 °C and thus benefit the production of *A. aurita* ephyrae by extended strobilation periods and enhanced ephyra release per polyp (Holst, 2012). Our winter warming scenario included 1.8-fold increased ephyra production (i.e. $F_{PE} \times 1.8$) during strobilation periods that we extended by one month (i.e. mean F_{PE} of proceeding and subsequent month). We additionally adjusted the corresponding probabilities for ephyra survival and transition from ephyra to medusa (i.e. t_{EE} and t_{EM} of subsequent month). With these modified matrices (Appendix S3: Figs. S1 & S2), we investigated the demographic effects of a predicted winter warming trend on *A. aurita* populations under low and high food conditions.

Computing demographic parameters and population projection

We analyzed our population projection matrices using R version 3.1.3 (R Core Team, 2015) and compared the demographic dynamics of *A. aurita* under low and high food levels, and in combination with a winter warming trend. We used R packages 'popbio' (Stubben & Milligan, 2007) and 'popdemo' (Stott, Hodgson, & Townley, 2012) to compute population growth rate λ (dominant eigenvalue), stable stage distribution (right eigenvector **w** corresponding to the dominant eigenvalue; i.e. proportions of individuals in each stage remain constant on the long-term), reproductive value R (left eigenvector **v** corresponding to the dominant eigenvalue; i.e. expected lifetime reproduction of an individual in stage i), the net reproductive rate R_0 (i.e. average number of offspring by which an individual will be replaced during its lifetime), the generation time (i.e. average

age at which an individual has produced the average number of offspring, R_0), the life expectancy e_0 (i.e. mean time to death), and the sensitivity of λ to perturbations of the matrix elements (only elements >0 are considered). We further performed life-table response experiment (LTRE) analysis (Caswell, 1996; Tuljapurkar & Caswell, 1997) with focus on the sensitivity of λ to perturbations in stage-specific transitions when comparing low and high food levels.

Results

Demographic dynamics of the common jellyfish under increased food levels

The metagenic life cycle of *A. aurita* (Fig. 1a) was resembled by cyclic (imprimitive) structure of our matrix model, expressing annual peak and pit dynamics in projected population density (Fig. 2a). The calibrated population growth rate $\lambda = 1.63$ month^{-1} for 10-fold increased food availability indicated 346-fold yearly increase in population size relative to the calibrated stationary stable population with $\lambda = 1$ month^{-1} under low food conditions. Such differences in growth rate due to changes in food availability provide high leverage for population booms and busts. Similar to low food levels, the projection matrix under high food availability showed cyclic annual structure with typical peak and pit dynamics in projected population density, but life cycle amplitudes were much increased (Fig. 2b).

Under low food conditions, the overall population density (taking into account all life stages) increased to a peak during spring and summer and thereafter decreased to low densities during autumn 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, i.e. reduced by a factor 20, 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. The latter included 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 (Fig. 2c). 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. 2d).

Our findings illustrate a shift from polyp-dominated towards medusa-dominated *A. aurita* populations under increased food conditions. The reproductive value was low for

ephyrae (0.03) under low food conditions, and sexual reproduction of medusae contributed only about half as much (0.42) to future generations as 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 (F_{PP}: 1.3-fold increase ind.$^{-1}$ year^{-1}, F_{PE}: 36-fold increase ind.$^{-1}$ year^{-1}, F_{ML}: 104-fold increase ind.$^{-1}$ year^{-1}). Due to an increased net reproductive rate, high food conditions boosted the average time between two consecutive generations to 8 months. Life expectancy of polyps, estimated 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 decreased to 7 years, while the length of ephyra and especially medusa lives extended to 3 and 8 months, respectively.

Sensitivity analysis generally highlighted a strong influence of survival rates and less pronounced effects of fecundity on the growth of jellyfish populations. Under low food conditions, population growth was most sensitive to changes in polyp survival (t_{PP}), with constantly high sensitivity of 0.08 (relative maximum value in the sensitivity matrix)

throughout the months of the year (Fig. 2e). In addition, λ showed increased sensitivity of 0.02 to changes in ephyra production (F_{PE}) from March to May. The overall sensitivity of λ increased under high compared to low food levels. Under high food conditions, changes in polyp survival affected λ particularly from October to April, with sensitivities of 0.06−0.13. In contrast to low food levels however, λ was most sensitive to changes in medusa survival under high food levels, with sensitivity remaining high, ranging within 0.07−0.16 from April to October, and reaching a maximum of 0.32 from June to July (Fig. 2f). We further detected sensitivities of λ in the range 0.02−0.03 for perturbations in ephyra production from March to May under high food conditions. Differences in the sensitivity of λ between food treatments were expressed by the results of our life table response experiment (LTRE) analysis. High food availability led to 7.7−13.6 % increased sensitivity for the transition probabilities from polyp to medusa stage (i.e. F_{PE} and t_{EM}) from March to May. Further, increased food conditions enhanced sensitivity for medusa survival during April by 7.7 % and for polyp production via sexual reproduction of medusae (i.e. F_{ML} and t_{LP}) from August to December by 5.1−6.8 % (Table 1).

Effects of a predicted winter warming trend

For our winter warming scenario with extended strobilation periods and increased ephyra release, population growth rates of *A. aurita* increased to 1.01 and 1.73 per month under low and high food conditions, corresponding to 1.1- and 730-fold yearly increases in population size, respectively. Winter warming led to stronger variability in inter-annual population structure in both food treatments, expressed by more distinct peaks and pits in population density (Figs. 2a−b) due to a general trend towards more medusae and less

polyps. Under low food levels, the stable population structure of *A. aurita* predicted for winter warming consisted of more ephyrae (0.12) and medusae (0.04), and less polyps (0.84; Fig. 2c). In relative terms, we observed 2.7 % more medusae, 7.9 % more ephyrae and 10.6 % less polyps per year as a consequence of winter warming. Under high food levels, increased winter temperatures resulted in a stable stage distribution with 17.6 % more medusae, while the proportions of ephyrae and polyps decreased by 1.8 % and 15.8 %, respectively. An earlier onset of strobilation periods in the scenario and fast transition of ephyrae caused significant proportions of medusae to be already present from February (Fig. 2d).

Winter warming caused substantial changes in reproductive rates and generation times of the projected jellyfish populations; these changes were particularly pronounced under low food conditions. The reproductive value of ephyrae was magnified to 8.53, while the relative contribution to the number of offspring by medusae decreased to near zero for the low food population. Winter warming in combination with high food levels decreased reproductive values of both ephyrae and medusae to 0.18 and 7.43, respectively. Under low food conditions, increased winter temperatures raised the net reproductive rate to 1.75 polyps replacing each polyp during its life time, corresponding to a relative increase by 75.1 %. Under high food conditions, the net reproductive rate increased to 80.9 as a consequence of the warming trend, indicating a relative increase by 42.1 %. The winter warming scenario shortened the generation time to 9.3 years under low food conditions, corresponding to a difference of 7.4 years due to increased winter temperatures, while generation times were shortened by only 9 days under high food conditions. Winter warming increased life expectancy of ephyrae by 12 and 19 days, respectively, whereas

life expectancy of polyps and medusae remained unchanged under both low and high food levels.

Discussion

We reveal the demographic dynamics and life history shifts underlying jellyfish blooms and show that the intensity and frequency of jellyfish booms and busts is subject to specific ecological triggers. We quantify how the typical boom and bust dynamics characterizing jellyfish blooms are significantly enhanced by natural variations in the food regime. While the combined effects of environmental change, including a predicted winter warming, may further boost the intensity and frequency of jellyfish outbreaks, increased food availability shows great potential to shift the predominant mode of reproduction from asexual to sexual. We suggest this latter shift from polyp- to medusa-dominated populations as a key mechanism causing jellyfish outbreaks. Our findings support previous studies which have pointed out metagenic life cycles as an ultimate driver of boom and bust population dynamics (Brotz, Cheung, Kleisner, Pakhomov, & Pauly, 2012; Hamner & Dawson, 2009; Pitt, Welsh, & Condon, 2009). Our results also confirm the predicted seasonal pattern in jellyfish abundance by a recent food web model for semi-enclosed temperate ecosystems (Schnedler-Meyer, Kiørbøe, & Mariani, 2018). Considering jellyfish blooms as highly sensitive indicators for ocean degradation (Schrope, 2012), the present insights may provide fundamental knowledge regarding the health of marine ecosystems worldwide.

The demographic dynamics behind jellyfish blooms

Our findings suggest food availability as a major constraint for the intensity and frequency of jellyfish blooms, confirming that food availability limits the development of ephyrae (Fu, Shibata, Makabe, Ikeda, & Uye, 2014) and the survivorship and fecundity of medusae (Goldstein & Riisgård, 2016). Prey removal has previously been suggested as a 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 a common scyphozoan jellyfish population. Such changes include enhanced boom and bust dynamics and shorter generation times. We show that jellyfish blooms are a natural consequence of complex life cycles and emphasize the key role of benthic polyps in ensuring long-term survival (Boero et al., 2008; Lucas, Graham, & Widmer, 2012), particularly when food is scarce. Extended polyp life-spans along with reduced rates of asexual reproduction under low food levels further suggest a trade-off between survival and reproduction (Stearns, 1976). In the common jellyfish, increased food levels are associated with boosted population growth rates and dramatic life history shifts, 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 insight into the consequences of habitat eutrophication in context with jellyfish blooms, as investigated food levels are motivated by eutrophic to hypereutrophic conditions (cf. Riisgård, Jensen, & Rask, 2008) in our study areas Kerteminde Fjord/Kertinge Nor (Nielsen, Pedersen, & Riisgård, 1997; Olesen, Frandsen, & Riisgård, 1994) and Limfjorden (Møller & Riisgård, 2007; Riisgård, Madsen, Barth-Jensen, Purcell, 2012).

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 (cf. Lucas, 2001). A transition probability of 0.001 $month^{-1}$ from larva to polyp that matches well previous estimates for *A. aurita* (Xie, Fan, Wang, & Chen, 2015) was found during calibration of our presented matrix models for low and high food conditions. Our resulting stable population under low food levels (λ = 1 $month^{-1}$) 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 (Goldstein & Riisgård, 2016; Nielsen, Pedersen, & Riisgård, 1997; Olesen, Frandsen, & Riisgård, 1994; Riisgård, Barth-Jensen, & Madsen, 2010). 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 (Goldstein & Riisgård, 2016; Möller, 1980) or in Limfjorden (Hansson, Moeslund, Kiørboe, & Riisgård, 2005; Møller & Riisgård, 2007). In Limfjorden, *A. aurit*a may currently experience the process of being outcompeted by the invasive ctenophore *Mnemiopsis leidyi* (Riisgård, Goldstein, Lundgreen, & Lüskow, 2015). This implies additional factors regulating polyp, ephyra and medusa density in less protected ecosystems. According to our matrix projection for high food levels, a pronounced increase in polyp mortality to 0.3 day^{-1} (cf. Xie, Fan, Wang, & Chen, 2015, Table 1 therein; i.e. a survivorship of 2.3×10^{-5} $month^{-1}$) would decrease population growth rates only marginally from 1.63 $month^{-1}$ to 1.44 $month^{-1}$. In contrast, reduced medusa survival to 0.1 $month^{-1}$ (corresponding to a mortality of 0.07 day^{-1}; Xie, Fan, Wang, & Chen,

2015) 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 λ = 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 above-mentioned estimates and the results of our life table response experiment analysis suggest that besides successful metamorphosis of planula larvae, 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.

Besides prey abundance, food quality, intra- and inter-specific competition, predation, substrate availability, hydrodynamic currents and extreme environmental conditions (Arai, 2005; Chi, Mueller-Navarra, Hylander, Sommer, & Javidpour, 2018; Hansson, 1997; Hernroth & Gröndahl, 1985; Johnson, Perry, & Burke, 2001; Kakinuma, 1975; Lucas, Graham, & Widmer, 2012; Xie, Fan, Wang, & Chen, 2015) should be considered as important constraints for the development of jellyfish blooms. In particular, population density-dependent mechanisms controlling individual size (Goldstein & Riisgård, 2016; Lucas, 2001; Riisgård, Barth-Jensen, & Madsen, 2010; Schneider & Behrends, 1994) could play a major role for the demography of *A. aurita*. Size-structure should hence be taken into account for future population models (cf. Bordehore et al., 2015) to evaluate the importance of size-specific traits for the development of jellyfish blooms. Although the temporal and spatial patterns of abundance in each life stage may vary according to jellyfish species (Lucas, Graham, & Widmer, 2012; Scorrano, Aglieri, Boero, Dawson, & Piraino, 2016) and subspecies (Lucas, 2001), our observations on the common jellyfish

are likely not unique. We hope they will help to reveal general trends in population stage structure and dynamics of metagenic scyphozoans in response to variable food supply.

Winter warming and jellyfish blooms

Warm temperature can lead to enhanced asexual reproduction and has therefore been associated with increased numbers of medusae for most temperate scyphozoan species (Purcell, 2005). Our findings support that increased water temperature can boost the booms and busts of jellyfish blooms (Richardson, Bakun, Hays, & Gibbons, 2009; Xie, Fan, Wang, & Chen, 2015). Winter warming has pronounced effects on the growth of *A. aurita* populations due to seasonal changes in population composition and structure. Our winter warming scenario caused a general trend towards more medusae and less polyps but did not reveal the potential to shift the population structure from polyp- to medusa-dominated *A. aurita* populations as observed under increased food conditions. Winter warming however can increase the net reproductive rate of temperate jellyfish populations, particularly in regions with limited food availability. Due to enhanced strobilation periods and increased numbers of released ephyrae per polyp (Holst, 2012), warmer winter temperatures may thus shorten the generation time under low food conditions drastically. Based on recent climate analyses, rises in sea surface temperature by 5 °C are expected within the next 100 years (Belkin, 2009). Our results indicate a maximum increase in jellyfish density by 2.75 during this hypothetical warming period, while regionally observed increases in food level (1:10) are likely to boost jellyfish proportions by a factor 12.3. Climate warming has previously been pointed out to benefit the population size of temperate scyphozoan species, but not tropical or boreal species

(Holst, 2012; Purcell et al., 2012). Further taking into account that a cold trigger is necessary to stimulate strobilation in many scyphozoans (Holst, 2012; Lotan, Fine, & Ben-Hillel, 1994; Purcell, White, Nemazie, & Wright, 1999) and that more frequent and long-lasting heatwave events may negatively affect the population dynamics of jellyfish (Chi, Mueller-Navarra, Hylander, Sommer, & Javidpour, 2018), we suggest winter warming may promote the outbreak potential of certain temperate scyphozoans but should generally be considered a much less powerful driver of jellyfish blooms than increased food availability.

Conclusions

Our study highlights that food availability drives and specifically shapes the booms and busts of jellyfish blooms. We suggest that for most temperate scyphozoans predicted changes in water temperature may cause less dramatic increases in jellyfish density than already established food concentrations in several eutrophic regions around the world. The importance of natural competitors and predators for keeping jellyfish blooms in check needs further exploration, but our findings might serve as a promising starting point. We conclude that a combination of environmental triggers, such as habitat eutrophication, overfishing, artificial settlement substrates and climate change, can promote jellyfish outbreaks severely. Our findings emphasize the fundamental importance of an integral, quantitative view on jellyfish life histories. We believe such perspective, comprising species-, life stage- and age-specific traits, is an inevitable prerequisite in providing visions for future management of jellyfish blooms and other mass occurrences.

Authors' contributions

US and JG conceived the ideas and designed the methodology, JG collected the data and led the writing of the manuscript; JG and US analyzed the data. Both authors contributed critically to the drafts and gave final approval for publication.

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Supporting Information

Additional Supporting Information is available online in the supporting information tab for this article.

Tables

Table 1. *Aurelia aurita*. Life table response experiment (LTRE) analysis for the sensitivity of the population growth rate λ to changes in monthly transitions including survivorship t_{ii}, transition probability t_{ij} and fecundity $F_{ii/ij}$ of the stages larva (L), polyp (P), ephyra (E) and medusae (M) when comparing low and high food conditions (1:10).

Monthly transition	Sensitivity of λ					
	$t_{PP} + F_{PP}$	F_{PE}	t_{EE}	t_{EM}	t_{MM}	$F_{ML} \times t_{LP}$
Jan–Feb	0.00121	0	0	0.00007	0.00003	0
Feb–Mar	0.00238	0.00997	0	0	0.00005	0
Mar–Apr	0.00151	0.01068	0.00257	0.07712	0.00016	0
Apr–May	0.00081	0.00444	0	0.13628	0.07727	0
May–Jun	0.00072	0	0	0.01065	0	0
Jun–Jul	0.00049	0	0	0	0	0
Jul–Aug	0.00043	0	0	0	0.03890	0
Aug–Sept	0	0	0	0	0.02894	0.06808
Sept–Oct	0	0	0	0	0.00820	0.05629
Oct–Nov	0	0	0	0	0	0.05401
Nov–Dec	0.00649	0	0	0	0	0.05046
Dec–Jan	0.00484	0.00007	0	0	0.00001	0

Figures

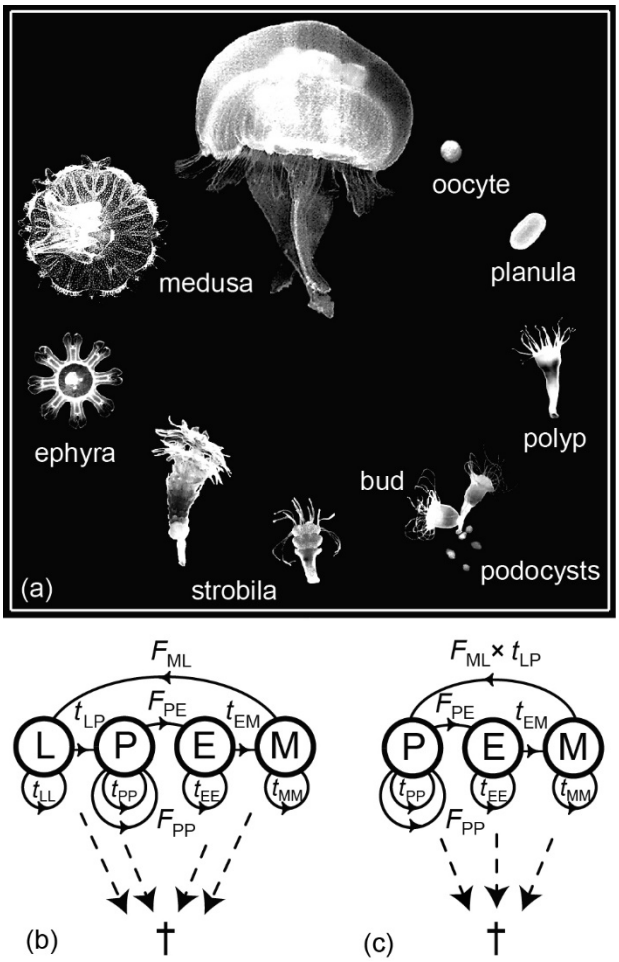

Fig. 1. Life history of the common jellyfish *A. aurita* (Scyphozoa, Cnidaria). (a) Metagenic life cycle with alternation of generations between the sexually reproducing medusa and the asexually reproducing polyp stage. (b) Life cycle graph for *A. aurita*, including transition probability *t*, fecundity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

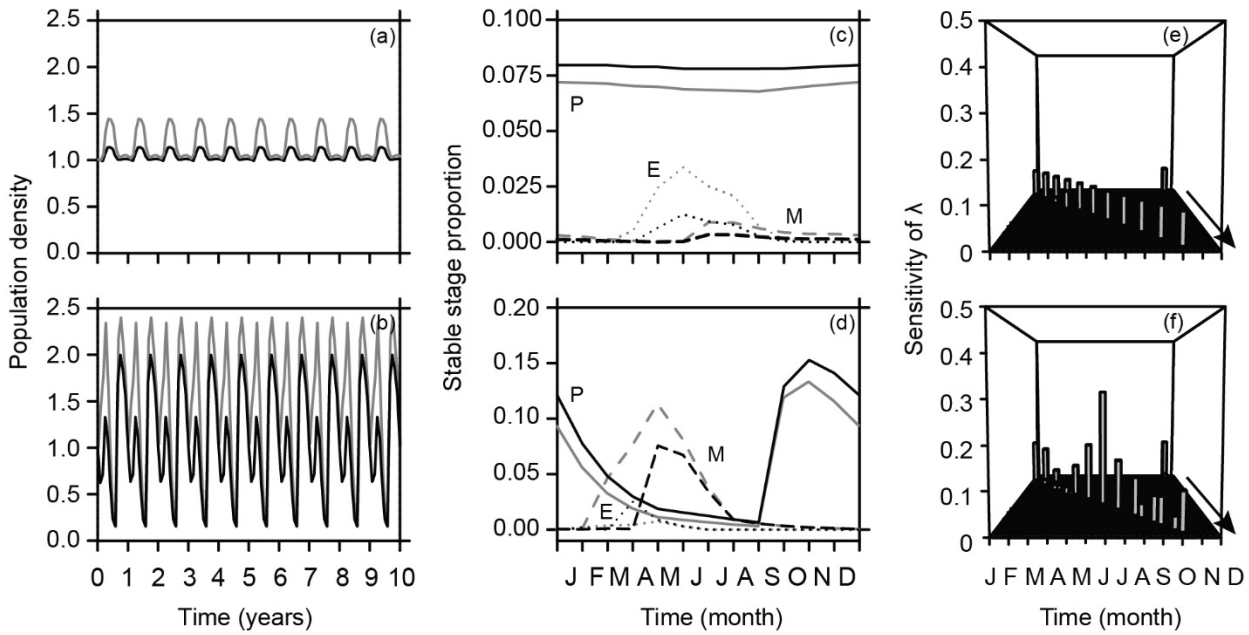

Fig. 2. Population matrix model for *A. aurita* under low (upper panels) and high (lower panels) food conditions (1:10). (a−b) Matrix projection over a 10-year period, standardized to the long-term effects of population growth rates $\lambda = 1$ month^{-1} and $\lambda = 1.63$ month^{-1}, respectively,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