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Food quality matters

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Food quality matters: interplay among food quality, food quantity and temperature affecting life history traits of *Aurelia aurita* (Cnidaria: Scyphozoa) polyps

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Abstract

Understanding the interaction between organisms' life history traits and environmental factors is an essential task in ecology. In spite of the increasing appreciation of jellyfish as an important component in marine ecosystem, there are still considerable gaps in understanding how the phase transition from the benthic polyp to the pelagic medusa stage is influenced by multiple environmental factors, including nutrition. To investigate survival, growth, and phase transition of *Aurelia aurita* polyps, we designed a factorial experiment manipulating food quantity (20 µg C, 5 µg C and 1.5 µg C polyp⁻¹ every other day), food quality (*Artemia salina* and two dietary manipulated *Acartia tonsa*), and temperature (13 °C, 20 °C, and 27 °C). Temperature was the key factor determining phase transition of polyps and negatively affecting their survival rate and

growth at 27°C, which reflected a summer heatwave scenario. Furthermore, at polyps' optimum tolerance temperature (20°C) in our study, budding reproduction benefits from high food concentrations. Interestingly, polyps fed with food containing high level highly unsaturated fatty acid (HUFA) were able to compensate for physiological stress caused by the extreme temperature, and could enhance budding reproduction at optimum temperature. Moreover, benthic-pelagic coupling (strobilation) was determined by temperature but affected significantly by food conditions. Mild temperature together with optimum food conditions contributes to inducing more polyps, which may potentially bring about great ephyrae recruitments during overwintering. In contrast, heatwave events can potentially regulate plankton community structure accompanied by changes of nutritional conditions of primary and secondary producers and thus, negatively affect the population dynamics of polyps. We suggest a novel polyp tolerance curve, which can help to understand jellyfish population dynamics in different seasons and ecosystems. This sets up a baseline for understanding how anticipated global warming and food conditions may affect the population size of benthic polyps and consequently pelagic medusae.

Keywords: life history, multiple stressors, asexual reproduction, phase transition, tolerance curve, jellyfish

1. Introduction

Dense aggregations and population outbreaks of jellyfish have been reported from several coastal areas (Kawahara et al., 2006; Daryanabard and Dawson, 2008; Licandro et al., 2010), which may cause environmental and socio-economic problems (Purcell, 2012; Boero, 2013). Most of the reports on jellyfish bloom refer to the class Scyphozoa. In general, this group exhibits a metagenic life cycle (Arai, 1997), involving pelagic stages (ephyra, medusa, and planula) and benthic stages (polyp, strobila, and podocyst). Take the moon jelly *Aurelia aurita* for example, matured medusae release planula larvae, which then settle on hard substrates and develop into polyps. Benthic polyps can expand the population size *via* budding reproduction and produce pelagic juvenile medusae (ephyrae) through strobilation. Polyp population size, strobilation rate and ephyra production of each strobila can directly contribute to medusa recruitment. Recently, benthic polyp stage of scyphozoans has attracted increasing attentions (reviewed by Lucas et al., 2012), as their recruitment success is considered to play a critical role in massive population occurrence of medusae in summer (Gröndahl, 1988a; Lucas, 2001). Moreover, population size of polyp varies greatly with changing environments (Liu et al., 2009; Purcell et al., 2009; Han and Uye, 2010). Among a variety of environmental factors, temperature and food conditions have been revealed to be principle factors determining polyps' fitness and asexual reproduction (Willcox et al., 2007; Purcell et al., 2012).

In the literature on polyp ecology, the relative importance of food conditions has been subject to considerable discussion (Han and Uye, 2010; Wang et al., 2015). However, most of the experiments preferentially used *Artemia sp.* as the major food source (e.g., Feng et al., 2015; Han and Uye, 2010; Wang et al., 2015), which does not reflect the natural food type. For example, the biochemical composition of prey, e.g., vitamin content (such as thiamin) and fatty acids (FAs), as food quality determinants, have received little attention in jellyfish polyp studies so far. Thiamin is involved in several metabolic pathways, e.g. as a cofactor in production of

Acetyl Coenzyme A, which is in turn essential in carbohydrate metabolism and FAs synthesis (Lonsdale, 2006; Manzetti et al., 2014). In contrast, the impact of thiamin on life history traits and biochemical cycles has been largely overlooked (Giovannoni, 2012). In addition, some essential ω 3 polyunsaturated fatty acids, including the highly unsaturated fatty acids (HUFA) eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), play important roles for many aquatic organisms, such as sustaining membrane fluidity or serving as precursors for tissue hormones (Müller-Navarra, 2008). Thus, HUFA play a critical role that enable organisms to achieve optimal health and reproduction (Arts et al., 2009). Moreover, HUFA as essential dietary components could flow in food webs *via* trophic transfer (Brett and Müller-Navarra, 1997). The ecological implications of using HUFA content to indicate overall food quality, which in turn is used to estimate proper functioning drivers of ecosystem stability, encompass two aspects. First, the biosynthesis ability of HUFA and its transfer efficiency to higher trophic levels vary in different primary producers (Taipale et al., 2013; Strandberg et al., 2015). Second, HUFA content of the same species has seasonal and spatial shifts regulated by temperature and stoichiometry (Hartwich et al., 2012; De Moura, 2016; Brett et al., 2000, Brett et al., 2000). Thus, alterations of HUFA in primary producers will consequently alter herbivores' growth and reproduction *via* changing community structure and bio-chemicals composition (Jónasdóttir, 1994; Müller-Navarra and Huntley, 2013). The same processes will potentially affect development at higher trophic levels, such as fishes (e.g., Sargent et al., 2002).

The objective of the present study was to address knowledge gaps in the ecological role of food quality involved in life history strategy of scyphozoans, especially in their benthic life stages. Furthermore, we studied the combined effects of food quality and food quantity under different temperature regimes on the overall outcome of benthic-pelagic coupling.

We hypothesized that higher food quality can 1) improve polyps' survival rates under extreme

temperatures such as heatwaves; 2) contribute to larger individual size; and 3) affect budding reproduction and strobilation. To test these hypotheses, we designed a factorial feeding experiment on polyps of a cosmopolitan species, *A. aurita* (Linnaeus, 1758), under different temperature and food regimes, the latter differing in quality and in quantity.

2. Materials and methods

2.1. Polyp preparation

A. aurita polyps were obtained from permanent cultures of the Christian-Albrechts University, Kiel (Germany); they were originally collected from the North Sea population (Helgoland, Germany), and kept at 20 °C with a salinity of 30. Prior to the experiment, polyps were fed with newly hatched *A. salina* nauplii, and water was changed with filtered seawater (0.2 µm filter) twice a week. In preparation for the experiment, polyps were detached carefully from their substrate with forceps and were placed individually in each well (growth area: 8,87 cm², volume: 4 ml) of 6-well polycarbonate culture plates. To allow polyps to attach to the plates, they were kept in climate cabins at 20 °C for 5 days without any feeding or water exchange. Polyps were kept under dark conditions during both the acclimation time and the entire of the experiment, as light influences polyps' asexual reproduction (Custance, 1964; Liu et al., 2009).

2.2. Temperature manipulation

The experiment consisted of three temperature levels, 13 °C, 20 °C, and 27 °C, ensured through temperature-controlled climate cabins. The temperatures 13 °C and 20 °C represented late autumn/early spring and common summer temperatures in the study area, respectively (Wiltshire and Manly, 2004). The highest temperature, 27 °C, served as an unusual summer heatwave scenario (Meehl and Tebaldi, 2004; Garrabou et al., 2009). Polyps were randomly distributed in climate cabins, and were acclimated by increasing or decreasing 1 °C d⁻¹ to the test temperatures. During the experiment, water was exchanged every second day with filtered and autoclaved North Sea water. After water exchange, polyps were fed with the respective prey

items.

2.3. Food quality manipulation

Three types of food were chosen to perform this treatment: a) *Artemia salina* nauplii (thereafter as *Art*); b) copepodites of *Acartia tonsa* (thereafter as *Aca*⁽⁺⁾) that were fed with standard *Rhodomonas baltica* stock, in a culture medium modified after Provasoli (1963) (thereafter *Rhodo*⁽⁺⁾); and c) *A. tonsa* (thereafter as *Aca*⁽⁻⁾) fed with *R. baltica* cultures that lacked thiamin (vitamin B₁) in their medium (thereafter *Rhodo*⁽⁻⁾). *R. baltica* were cultured at 20 °C and under 100 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ light condition. To manipulate *A. tonsa*'s food quality as prey for polyps, newly hatched nauplii were cultured in separate buckets in a climate room under 20 °C, and were fed daily with the two types of algae *Rhodo*⁽⁺⁾ and *Rhodo*⁽⁻⁾, respectively. All food concentrations were adjusted to be above the food limitation level for this copepod species, i.e. > 600 $\mu\text{g C L}^{-1}$ (Kjørboe et al., 1985). Similar size of copepodites were collected for feeding polyps. Thus, in summary, the experiment consisted of three food quality treatments for polyps, i.e. polyps fed with *Art* (thereafter $\text{pol}_{(\text{Art})}$), polyps fed with *Aca*⁽⁻⁾ (thereafter $\text{pol}_{(\text{Aca}^-)}$), and polyps fed with *Aca*⁽⁺⁾ (thereafter $\text{pol}_{(\text{Aca}^+)}$).

Thiamin analysis was conducted with a high-performance liquid chromatography (HPLC) according to the method by Pinto et al. (2002), with modifications according to Sylvander et al. (2013). FAs in the samples were analyzed as FA methyl esters (FAMES) using a gas chromatograph (GC; Thermo Fisher Scientific, Germany) described in detail by Chi et al. (2018).

2.4. Food quantity

For each food quality, three levels of high (20 $\mu\text{g C polyp}^{-1}$), medium (5 $\mu\text{g C polyp}^{-1}$) and low (1.5 $\mu\text{g C polyp}^{-1}$) food concentrations were offered every other day based on previous studies (Han and Uye, 2010; Wang et al., 2015). Detailed calculation regarding the number of individuals given per treatment is provided in Suppl. Table 1. The highest food concentration provided an excess food supply to polyps, and remaining food was removed during water

exchange. The medium food concentration was representative of polyps' average food level, and the low food concentration represented starvation conditions. These food concentrations ensured that some food items were left over at high concentration, while all preys were consumed before the next feeding event at medium and low food concentrations.

Each combination of food quality, food quantity, and temperature involved 12 replicates. As polyps' strobilation was expected to occur at 13 °C, causing a loss of some individuals for the final assessments, we added 6 more replicates in both food quality and food quantity at 13°C, resulting in a total of 18 replications at this specific temperature, and leading to a total of $n = 378$. When all polyps had attached to the plates, their initial diameters (1.04 ± 0.26 mm) were measured under a microscope equipped with a camera and scaling system, and we started to feed and change water as described above. The experiment lasted for 30 days.

2.5. Data collection

Following each feeding time, polyps' status was checked. Those polyps had decomposed were recorded as dead and survival rates were calculated based on the number of vital polyps. The diameters of the polyps' cone-shaped calyxes were measured every 6th day to denote somatic growth. To avoid disturbances on polyps, diameters were measured by taking photos before feeding and water exchange. An average of the maximum and minimum dimensions of the calyx was calculated if it was not round. Before each time feeding and water exchange, a total number of buds were counted. In our study, we refer to "buds" as individuals produced by mother polyps in the form of "polyp-to-polyp" (Schiariti et al., 2014). To avoid any intraspecific competition, new buds produced during the treatments were recorded and removed from the original cultures. When signs of strobilation occurred, polyps were regarded as strobilae and were no longer included in calyx diameter measurements. Numbers of ephyrae released by each strobila were recorded as well.

2.6. Statistical methods

Data were checked for outliers, homogeneity, and collinearity in both response and explanatory variables before applying statistical models (Zuur et al., 2010). Generalized linear models (GLMs) were used to analyze response variables, namely survival rate, somatic growth, budding reproduction, and strobilation rate, separately. The explanatory variables, temperature, food quality, food quantity, and time (only for survival rate) were included in the GLMs, and treated as factorial variables. We first fitted GLMs regarding different response variables with all explanatory factors and their interactions, and then selected the optimum models by applying a stepwise backward selection method *via* an Akaike information criterion (AIC) index (Zuur et al., 2009). For the survival rate data, time was included in the GLM, taking a binomial family distribution into account. Somatic growth data were fitted with Gaussian family distribution. Because a relatively large number of polyps that were fed low food quantity did not produce buds, we treated budding reproduction data in two ways, first by modeling presence/absence data and fitting it with a binomial distribution, and secondly by taking the numbers of produced buds in the GLM, and fitting a Poisson distribution. Strobilation success occurred in different food treatments, so we modeled strobilation rate data by applying binomial family distribution in the GLM, while ephyrae production of each strobila was described by mean $\pm$ SD. Tukey's post-hoc test was applied when explanatory variables had a significant effect on responses. All GLMs, data explorations, and data visualizations were performed using R software, version 3.3.3. (R Core Team, 2017).

3. Results

3.1. Meeting food quality assumptions

We analyzed the biochemical composition (i.e., thiamin and FA content) of phytoplankton and zooplankton. Thiamin contents were higher in *Rhodo*⁽⁺⁾ stock cultures (average 36.74 ± 4.86 pmol mg C⁻¹), than in *Rhodo*⁽⁻⁾ (15.33 ± 2.04 pmol mg C⁻¹, $F_{(1,4)} = 59.9$, $p < 0.005$), indicating that the food quality manipulation was successful. Thiamin levels also tended to be higher in

Aca⁽⁺⁾ (60.02 ± 9.61 pmol mg C⁻¹) than *Aca*⁽⁻⁾ (45.27 ± 11.38 pmol mg C⁻¹), although not significantly different ($F_{(1,4)} = 2.82, p = 0.17$). On the other hand, the HUFA content in our study was not only significantly different between the two manipulated *R. baltica* (ANOVA, $F_{(1,4)} = 26.8, p < 0.01$), but also among the three types of zooplankton prey (ANOVA, $F_{(2,6)} = 64.6, p < 0.001$). For the detailed fatty acid composition of phytoplankton and zooplankton, please see the previous publication of Chi et al. (2018). In general, HUFA content was higher in *Rhodo*⁽⁺⁾ ($26.7 \pm 0.2\%$) and *Aca*⁽⁺⁾ ($48.8 \pm 7.8\%$), than in *Rhodo*⁽⁻⁾ ($18.2 \pm 4.7\%$) and *Aca*⁽⁻⁾ ($32.8 \pm 2.9\%$), while *Art* contained the least HUFA ($4.2 \pm 0.3\%$). Thus, the manipulations of three food types involving different HUFA content levels guaranteed different food quality for feeding polyps. The three food quality treatments in this experiment denote three HUFA content levels from low to high, i.e., HUFA levels of *Art* < *Aca*⁽⁻⁾ < *Aca*⁽⁺⁾.

3.2. Survival

Polyp survival was affected significantly by experimental temperature, food quality, food quantity, experimental time, and the interaction of food quality and quantity (Table.1). Temperature was the main factor that determined survival rate of polyps. At low and intermediate temperatures, all polyps survived (100 %), independent of food quality or quantity. However, survival rate dropped at the highest temperature (27 °C), though it was interestingly food dependent (Fig. 1). In general, polyps fed low food concentration had a higher survival rate than those fed medium (Tukey's test, $z = -2.9, p = 0.01$) and high concentrations (Tukey's test, $z = -3.4, p = 0.002$), with no significant differences between high and medium concentrations (Tukey's test, $z = -0.5, p = 0.86$). Pol_(Art) had a lower rate of survival than pol_(Aca-) (Tukey's test, $z = 3.1, p = 0.005$) and pol_(Aca+) (Tukey's test, $z = 2.9, p = 0.009$). Survival rates were not significantly different between pol_(Aca-) and pol_(Aca+) (Tukey's test, $z = -0.5, p = 0.88$) over the experimental time. However, critical mortality at high temperature treatments occurred from the 12th experimental day onwards (Tukey's test, $z = -3.1, p = 0.015$). Surprisingly, the

mortality rate in $\text{pol}_{(\text{Aca-})}$ was somewhat lower (16.7%) than $\text{pol}_{(\text{Aca+})}$ when fed at medium and high food concentration. At the end of this experiment, the lowest survival rate (8.3 %) occurred at $27\text{ }^{\circ}\text{C} \times \text{high food concentration} \times \text{pol}_{(\text{Art})}$ treatment.

3.3. Somatic growth

Temperature had a negative effect on polyps' growth (Table. 1, Fig. 2). Polyps cultured at high temperature grew to significantly smaller diameters ($0.93 \pm 0.25\text{ mm}$) compared to those at medium ($1.55 \pm 0.33\text{ mm}$, Tukey's test, $z = -4.7$, $p < 0.001$) and low temperature ($1.81 \pm 0.33\text{ mm}$, Tukey's test, $z = -4.8$, $p < 0.001$). An overall significant effect of food quality on growth could be detected (Table. 1). However, pair-wise comparisons between food quality treatments were not significantly different. Diameters of $\text{pol}_{(\text{Aca+})}$ ($1.52 \pm 0.46\text{ mm}$) and $\text{pol}_{(\text{Art})}$ ($1.70 \pm 0.36\text{ mm}$) ultimately grew to similar sizes, while $\text{pol}_{(\text{Aca-})}$ grew to relatively smaller sizes ($1.42 \pm 0.48\text{ mm}$); however, the size difference was not statistically significant. Food quantity had a positive effect on growth, as expected (Table. 1, Fig. 2), i.e. polyps grew to larger diameters at high food concentration ($1.86 \pm 0.45\text{ mm}$) than at medium ($1.46 \pm 0.35\text{ mm}$, Tukey's test, $z = 5.5$, $p < 0.001$) or at low concentration ($1.30 \pm 0.35\text{ mm}$, Tukey's test, $z = 6.6$, $p < 0.001$). The interactions among these three factors showed significant effects on growth (Table. 1). At the end of the experiment, noticeably larger diameters could be observed in polyps fed a high food concentration of these three prey items at $13\text{ }^{\circ}\text{C}$, while smaller diameters were observed in polyps fed a low food concentration at $27\text{ }^{\circ}\text{C}$.

3.4. Budding reproduction

Temperature, food quality, and food quantity influenced budding reproduction (Table. 1). Budding reproduction was limited at high temperature ($1.1 \pm 1.7\text{ ind polyp}^{-1}$), but was favored at low ($3.7 \pm 2.7\text{ ind polyp}^{-1}$, Tukey's test, $z = -3.1$, $p = 0.006$) and intermediate temperatures ($4.8 \pm 3.6\text{ ind polyp}^{-1}$, Tukey's test, $z = -3.4$, $p = 0.002$). Overall, the number of buds produced was dependent on food quality (Table.1, Fig. 3). $\text{Pol}_{(\text{Aca+})}$ produced significantly more buds on

average (4.2 ± 3.3 ind polyp⁻¹) compared to pol_(Aca-) (3.0 ± 2.8 ind polyp⁻¹, Tukey's test, $z = 3.2$, $p = 0.004$) and pol_(Art) (2.7 ± 3.0 ind polyp⁻¹, $z = 6.0$, Tukey's test, $p < 0.001$); budding reproduction of the latter two treatments was also significantly different from each other (Tukey's test, $z = 3.4$, $p = 0.004$). Food quantity had a positive effect on budding production (Table. 1, Fig. 3), leading to a significantly higher bud production when polyps were fed high food concentration (5.5 ± 3.5 ind polyp⁻¹) than when fed medium (3.4 ± 2.3 ind polyp⁻¹, Tukey's test, $z = 7.2$, $p < 0.001$) or low (1.0 ± 1.2 ind polyp⁻¹, Tukey's test, $z = 8.9$, $p < 0.001$) food concentrations. Moreover, two-way interactions of temperature, food quality, and quantity showed significant effects on the number of bud production (Table. 1). Overall, the most buds were produced by pol_(Aca+) that were fed the high food concentration at 20 °C (10.1 ± 3.1 ind polyp⁻¹), while pol_(Art) fed the low food concentration at 27 °C had no budding success.

3.5. Strobilation

Temperature, food quality and quantity all affected strobilation success (Table. 1). In the present study, strobilation only occurred at 13 °C, as expected (Fig. 4a). Interaction of food quality and quantity also influenced strobilation success (Table. 1). Pol_(Aca-) and pol_(Art) strobilated at medium (44.4 % and 38.9 %, respectively) and low (72.2 % and 38.9 %, respectively) food concentrations, whereas pol_(Aca+) strobilated with 27.8 % success when fed at a high concentration. The number of ephyrae released from each strobila differed between food sources and food concentrations (Fig. 4b). Maximum production of ephyrae (21.4 ± 6.0 ephyrae polyp⁻¹) was recorded in pol_(Aca+) fed a high food concentration. Pol_(Aca-) released 11.6 ± 1.1 and 10.9 ± 2.4 ephyrae polyp⁻¹ at medium and low food concentrations, respectively. Meanwhile, pol_(Art) released 16.4 ± 2.1 and 8.3 ± 3.5 ephyrae polyp⁻¹ at medium and low food concentrations, respectively.

3.6. Podocyst

Podocysts were found at 27 °C treatments when we analyzed the photographic data (Suppl. Fig.

1). Some of them hatched into new polyps, which were subsequently removed from the cultures and were not included in budding reproduction. We didn't collect podocysts, or measure their production and hatching rates.

4. Discussion

Prior studies have noted the importance of temperature and food concentration on jellyfish polyps' life history traits and phase transition (Ishii and Watanabe, 2003; Purcell, 2007; Han and Uye, 2010). However, there have been very few empirical investigations studying the importance of food quality on this benthic-pelagic coupling process (but see Purcell et al., 1999). Our results suggest that polyps' survival was independent of food conditions at temperatures prevailing in late autumn/early spring and at common summer temperatures within the experimental time, but did under heatwave scenarios. It is somewhat surprising that polyps could compensate part of the stress when fed with elevated HUFA containing food (*Aca*⁽⁺⁾ and *Aca*⁽⁻⁾). Although high HUFA containing food could not significantly contribute to somatic growth, but promoted polyp asexual reproduction (buds' production). This finding verifies an earlier experimental study indicating that polyp produced more buds when fed ciliates compared to fed *Artemia sp.*, while polyps' growth was not affected (Kamiyama, 2013). These results imply that we should re-discuss the outcome of previous experiments measuring asexual reproduction that only applied *Artemia sp.* as a major food source. In addition, further empirical studies are required considering prey food quality to understand its effect on polyps' life history traits enabling us to predict physiological performances in fluctuating and multifactorial environments.

4.1. Polyp survival and somatic growth

In our study the overall survival rate of polyps was 100 % at 13°C and 20°C regardless of food conditions during the experimental time, but not at the highest temperature of 27°C. Polyp's survival, thus, seems to be independent of their nutritional state within the experimental duration.

However, fewer polyps survived when facing an extreme heatwave scenario, indicating that this high temperature was close to the polyps' maximum tolerance range and that polyps suffered from physiological stress. Interestingly, detrimental effects of high temperatures on survival were eased by high HUFA containing food when comparing $\text{pol}_{(\text{Art})}$ with $\text{pol}_{(\text{Aca-})}$ and $\text{pol}_{(\text{Aca+})}$. It is somewhat surprising that a slight difference in the survival rate between $\text{pol}_{(\text{Aca-})}$ and $\text{pol}_{(\text{Aca+})}$ was noted in the last day of the experiment. Therefore, a note of caution is due since we did not control other sources of bias such as bacterial activities under elevated temperature.

Heatwaves might have negative effects on polyp populations especially in shallow temporal coastal waters where heating is most pronounced during summer season. A recent study reported that heatwaves will become very frequent and extreme under global warming (Frölicher et.al., 2018). Irreversible changes in organisms may result under extreme heatwaves because of decreasing dissolved oxygen (Matear et. al., 2000), immunocompetence or HUFA content of organisms (Roth et.al., 2010). To manipulate the nutritional states of the prey, we altered the level of thiamin in phytoplankton which changed the HUFA contents in the zooplankton prey. The mechanism of how heatwaves would affect different nutritional levels in food webs has been rarely quantified. For example, it is known that the thiamin profile in phytoplankton is affected by temperature and species composition (Sylvander et al., 2013; Fridolfsson et al., 2018) and it has been suggested that thiamin deficiency can be a wide-spread phenomenon in several of bird and fish populations in the Northern Hemisphere (Balk et al., 2016). It was also approved that HUFA content generally decreased with warming temperature (Thompson, 1996; Sushchik et al., 2003). Thus, not only polyps would suffer from heatwaves directly, but they will face lower food quality in terms of FA profile under warming scenarios (Fuschino et al. , 2011), which may reduce their survival significantly. Thus, the combined effect of lower prey quality and increased temperature would play a crucial role in population performance of jellyfish (especially scyphomedusae) as consequences of heatwaves. It is worth

noting that effects of heatwaves on organism's physiology are multidimensional. For example, besides negative effects on nutritional conditions found in this study, depletion of dissolved oxygen or elevated bacterial activities may also be critical for polyps' survival (Ishii et al., 2008). Once polyps attach to substrates, they feed and ingest prey to support individual somatic growth. The fact that polyps survived and grew to larger diameters at lower temperatures well agrees with previous studies (Han and Uye, 2010). As polyps in temperate zones are known to be the overwintering phase, they are pre-adapted to cold conditions. Large body size potentially contributes to greater performance and fitness of organisms in general (Kingsolver and Huey, 2008). In this study, high food quantity guaranteed polyps obtaining sufficient energy to support somatic growth, while high HUFA containing food didn't improve somatic growth. It, therefore, implies that HUFA content of food was not the direct factor determining polyps' somatic growth.

4.2. Benthic population recruitment

Budding is an important asexual reproduction mode of polyps, mainly occurring after a phase of somatic growth, to increase the population size of the benthic stage. We show here that budding production was highest under the intermediate temperature, representing summer conditions. It seems that budding can contribute to the expansion of polyp populations mainly during warmer seasons, while an extreme heatwave in summit summer could inhibit it and even cause mortality. Similar to Cargo and Schultz (1967), we found that polyps may produce inactive podocysts to survive severe heatwaves and start building a new polyp population after hatching from those cysts. On the other hand, under the representative temperature for late autumn/early spring (13 °C), budding production was inhibited, and polyps were in transit to the strobilation mode.

In line with previous studies (Han and Uye, 2010; Wang et al., 2015), our study also found that polyp budding was favored at medium and high food supply. Moreover, our study highlights the importance of food quality influencing this process besides temperature and food quantity.

More buds were produced when fed high HUFA containing food. Therefore, former studies that applied *Artemia sp.* as a food source might have greatly underestimated (ca. 34.5 %) its effect on bud production and thus the vegetative reproduction potential of the sessile stages. Thus, to better mimic food supply in the field, we suggest using copepod as experimental food supply instead of *Artemia sp.* Future research should consider species-specific and population-specific responses.

4.3. Pelagic population recruitment

Strobilation that leads to ephyrae production is a benthic-pelagic coupling process and its success directly determines the potential abundance of medusae. Although a low temperature was indicated as a positive trigger for strobilation, the optimum range is quite narrow and extremely low temperature (5 °C) in winter can inhibit strobilation (Holst, 2012). Consistent with previous studies on *A. aurita* from populations of temperate regions (Lucas, 2001), strobilation occurred only at the designed late autumn/early spring temperature (13 °C) in this study. Although temperature *per se* seems to be the important stimulus inducing strobilation, many studies find the shift of temperature, rather than a constant temperature, being the stimulus (reviewed by Lucas, 2012). Thus, it could be hypothesized for temperate regions, that strobilation is favored twice a year, i.e., at temperature decreases in autumn and increases in spring, but not under extreme winter temperatures. Further warming after spring might limit strobilation and make conditions in favor of budding mode again (Sokolowski et al., 2016).

Moreover, previous investigations highlighted the importance of nutritional preparation for strobilation success and the need for a short starvation time (Thiel, 1962; Ishii and Watanabe, 2003; Purcell, 2007). Therefore, it is no surprise that strobilation occurred at medium and low food concentrations in $\text{pol}_{(\text{Art})}$ and $\text{pol}_{(\text{Aca-})}$ in our study. Contrary to this expectation, strobilation also occurred at $\text{pol}_{(\text{Aca+})}$ fed high food concentration. We cannot fully explain why polyps did not follow the same pattern observed for $\text{pol}_{(\text{Art})}$ and $\text{pol}_{(\text{Aca-})}$ but rather start to strobilate when

given a high concentration of high HUFA containing food. Meanwhile, it is accepted that food quantity significantly affects the number of ephyrae produced by individual strobila (Hernroth and Gröndahl, 1983; Purcell et al., 1999; Wang et al., 2015), which could be verified in our study.

As found for budding, we demonstrate here that food quality and quantity can interplay in ephyra production as well. As ephyrae production showed inconsistent results when food quantity and quality combined, further investigations are needed to understand the mechanism behind it. In contrast to budding reproduction, which was significantly promoted by HUFA-rich copepod prey, strobilation was also affected by food quality; however, the interaction between food quality and quantity should be further investigated.

4.4. Tolerance curve

Polyps of *A. aurita* are highly tolerant to a wide range of environmental conditions, among which temperature plays an important role on polyps' survival and determines different phase transitions (Lucas et al., 2012). According to Shelford's Law of Tolerance, each organism tolerates a certain range of environmental factors between a minimum and maximum limit with a defined optimum range. Outside of this optimum range, organisms will suffer from physiological stress, leading to high mortality (Shelford, 1911). Based on this theory, we combined results from the current study and previous publications, put forward the hypothesis that polyps' temperature tolerance curve includes food effects (Fig. 5).

At an intermediate temperature, polyps seem to experience their performance optimum, with high survival and propagation rates *via* budding reproduction. Below and above that optimum temperature range, budding reproduction is limited, and polyps face physiological stress both under low (e.g. below 9 °C, Fitt and Costley, 1998; Höhn et al., 2017) and high temperatures (e.g. 27 °C, this study) and even more extreme temperatures, leading to high mortality (Fig. 5). Strobilation is likely to be a response to physiological stress when polyps encounter

decreasing/increasing temperatures accompanied by food scarcity before and after overwintering (Ishii and Watanabe, 2003). As temperatures increase after spring, polyps from the temperate region shift from strobilation to budding mode. At very low winter temperatures, polyps' physiological activities are limited (Höhn et al., 2017), strobilation is not induced, and high mortality may occur if temperature further decreases. Likewise, extremely high temperatures, which may prevail at summer summit, may be outside of polyps' maximum physiological tolerance and lead to high mortality. Under these circumstances, podocysts, as a resting stage of polyps, are produced as an adaptation to severe high temperatures (but see Gröndahl, 1988b) and could increase survival rate of polyp populations. However, when temperature continues to increase to even more extreme levels, podocysts will not survive (Cargo and Schultz, 1967).

According to our findings, food conditions can significantly alter the temperature tolerance curve of polyps (Fig. 5, dashed lines). Maximum experimental temperatures (for example, 27 °C in our study) combined with high food concentrations (dashed line) were likely stressful to polyps, leading to the highest recorded mortality rates. Interestingly, higher HUFA containing food could compensate for this effect and might extend the maximum tolerance range (dot-dash line). Effects of food quality/quantity on polyps' survival and asexual reproduction could not be validated by this study for the minimum temperature tolerance range; thus, further research is needed.

In addition to the general survival tolerance curve (Fig. 5), a similar tolerance curve could be defined separately for each of the benthic life stages by considering an optimum, minimum and maximum physiological stress range. As described above, polyps experience their highest budding rates within the optimum temperature range (around 20°C in this study), promoted by a high concentration of high HUFA containing food. When temperature shifts seasonally to within either the minimum or maximum range, the budding phase is limited and, strobilae (at

lower temperatures) or podocysts (at higher temperatures) will be triggered. Even though strobilation rate was irrespective of food conditions in our study, once strobilation was initiated, the ephyra production should also follow this bell-shaped curve pattern. This is exemplified in the work undertaken by Purcell (2007) on an *A. labiata* population from Puget Sound. In that study, polyps were estimated to increase ephyrae production by 8.8 % -11.3 % for each 1 °C of warming within a yearly field temperature range up to 15 °C; above this point, ephyrae production dropped by 0.4 % per 1 °C warming. Again, food availability and type seem to interplay with the temperature tolerance curve, producing a more variable pattern. For example, once strobilation is triggered within its optimum temperature range, better food conditions (higher food concentration and high food quality) could support the production of more ephyrae. Food quality affects polyp's asexual reproduction may more conspicuous under food scarce condition, e.g. overwintering, at which time zooplankton accumulate high concentration of HUFA (Hartwich et al., 2012).

Jellyfish bloom seems to be promoted when the combined environmental factors (mainly temperature, food quality, and food quantity) fit the polyps' optimum tolerance range that best supports-bloom conditions. Modest cooling temperatures and optimum food conditions during late autumn and early spring contribute to a long-lasting strobilation optimum, inducing polyps to produce more ephyrae at a high strobilation rate. In contrast, harsh winters and sub-optimal food conditions may lead to minimum production, resulting in the minimal or even absence of jellyfish population.

5. Conclusion

The main goal of the current study was to elucidate effects of food quality on polyps' life history traits. Our findings suggest that changes in the nutritional conditions of prey might significantly affect the survival and life history traits of polyps. Furthermore, interactions between temperature and food conditions might determine the recruitment success of pelagic medusae

from benthic polyps. Whether or not these factors have simultaneous effects on polyps and medusae recruitments depend greatly on the scale of environmental fluctuations. More importantly, under ocean warming scenarios more frequent and long-lasting heatwave events can potentially regulate plankton community structure, and may be accompanied by changes to the nutritional conditions of primary and secondary producers. Heatwaves, may thus negatively affect the population dynamics of jellyfish not only by direct physiological stress but also through the effect of food quality. To be able to fit a more generalized polyp tolerance curve, further research is needed to quantitatively examine the links between environmental factors (including, but not limited to, temperature and food conditions) and jellyfish's life history traits in consideration of different species and populations.

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References

- Arai, M.N. (1997). A functional biology of Scyphozoa. London: Chapman and Hall.
- Arts, M.T., Brett, M.T., and Kainz, M. (2009). Lipids in aquatic ecosystems. Springer Science & Business Media.
- Balk, L., Hägerroth, P.-Å., Gustavsson, H., Sigg, L., Åkerman, G., Ruiz Muñoz, Y., Honeyfield, D.C., Tjärnlund, U., Oliveira, K., Ström, K., McCormick, S.D., Karlsson, S., Ström, M., Van Manen, M., Berg, A.-L., Halldórsson, H.P., Strömquist, J., Collier, T.K., Börjeson, H., Mörner, T., and Hansson, T. (2016). Widespread episodic thiamine deficiency in Northern Hemisphere wildlife. *Sci Rep* 6, 38821.
- Boero, F. (2013). Review of jellyfish blooms in the Mediterranean and Black Sea. *Studies and Reviews. General Fisheries Commission for the Mediterranean*, 92. FAO: Rome.
- Brett, M.T., and Müller-Navarra, D.C. (1997). The role of highly unsaturated fatty acids in aquatic foodweb processes. *Freshwat Biol* 38, 483-499.
- Brett, M.T., Müller-Navarra, D.C., and Sang-Kyu, P. (2000). Empirical analysis of the effect of phosphorus limitation on algal food quality for freshwater zooplankton. *Limnol Oceanogr* 45, 1564-1575.
- Cargo, D.G., and Schultz, L.P. (1967). Further observations on the biology of the sea nettle and jellyfishes in Chesapeake Bay. *Chesapeake Sci* 8, 209-220.
- Chi, X., Javidpour, J., Sommer, U., and Mueller-Navarra, D. (2018). Tracking fatty acids from phytoplankton to jellyfish polyps under different stress regimes: a three trophic levels experiment. *Front Ecol Evol* 6, Article 118.
- Custance, D. (1964). Light as an inhibitor of strobilation in *Aurelia aurita*. 204, 2.
- Daryanabard, R., and Dawson, M.N. (2008). Jellyfish blooms: *Crambionella orsini* (Scyphozoa: Rhizostomeae) in the Gulf of Oman, Iran, 2002–2003. *J Mar Biol Assoc U K* 88, 477-483.
- De Moura, G.C., De Lucena Barbosa, J.E., Patrício, J., Nery, J.F., and Gonçalves, A.M.M.

- (2016). Seasonal and spatial shifts in copepod diets within tropical estuaries measured by fatty acid profiles. *Ecol Indicators* 69, 284-294.
- Feng, S., Zhang, G.-T., Sun, S., Zhang, F., Wang, S.-W., and Liu, M.-T. (2015). Effects of temperature regime and food supply on asexual reproduction in *Cyanea nozakii* and *Nemopilema nomurai*. *Hydrobiol* 754, 201-214.
- Fitt, W.K., and Costley, K. (1998). The role of temperature in survival of the polyp stage of the tropical rhizostome jellyfish *Cassiopea xamachana*. *J Exp Mar Biol Ecol* 222, 79-91.
- Fridolfsson, E., Lindehoff, E., Legrand, C., and Hylander, S. (2018). Thiamin (vitamin B1) content in phytoplankton and zooplankton in the presence of filamentous cyanobacteria. *Limnol Oceanogr*.
- Frölicher, T.L., Fischer, E.M., and Gruber, N. (2018). Marine heatwaves under global warming. *Nature* 560, 360-364.
- Fuschino, J.R., Guschina, I.A., Dobson, G., Yan, N.D., Harwood, J.L., and Arts, M.T. (2011). Rising water temperatures alter lipid dynamics and reduce N-3 essential fatty acid concentrations in *scenedesmus obliquus* (Chlorophyta). *J Phycol* 47, 763-774.
- Garrabou, J., Coma, R., Bensoussan, N., Bally, M., Chevaldonné, P., Cigliano, M., Diaz, D., Harmelin, J.-G., Gambi, M., and Kersting, D. (2009). Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. *Global Change Biol* 15, 1090-1103.
- Giovannoni, S.J. (2012). Vitamins in the sea. *Proc Natl Acad Sci* 109, 13888-13889.
- Gröndahl (1988a). Interactions between polyps of *Aurelia aurita* and planktonic larvae of scyphozoans: An experimental study. *Mar Ecol Prog Ser* 45, 87-93.
- Gröndahl, F. (1988b). A comparative ecological study on the scyphozoans *Aurelia aurita*, *Cyanea capillata* and *C. lamarckii* in the Gullmar Fjord, western Sweden, 1982 to 1986. *Mar Biol* 97, 541-550.

- Han, C.-H., and Uye, S.-I. (2010). Combined effects of food supply and temperature on asexual reproduction and somatic growth of polyps of the common jellyfish *Aurelia aurita* sl. *Plankton Benthos Res* 5, 98-105.
- Hartwich, M., Martin-Creuzburg, D., and Wacker, A. (2012). Seasonal changes in the accumulation of polyunsaturated fatty acids in zooplankton. *J Plankton Res* 35, 121-134.
- Hernroth, L., and Gröndahl, F. (1983). On the biology of *Aurelia aurita* (L.) 1. Release and growth of *Aurelia aurita* (L.) ephyrae in the Gullmar Fjord, western Sweden, 1982–83. *Ophelia* 22, 189-199.
- Höhn, D.P., Lucas, C.H., and Thatje, S. (2017). Respiratory response to temperature of three populations of *Aurelia aurita* polyps in northern Europe. *PLoS One* 12.
- Holst, S. (2012). Effects of climate warming on strobilation and ephyra production of North Sea scyphozoan jellyfish. *Hydrobiol* 690, 127-140.
- Ishii, H., and Watanabe, T. (2003). Experimental study of growth and asexual reproduction in *Aurelia aurita* polyps. *Sessile Organisms* 20, 69-73.
- Ishii, Haruto, Toshifumi Ohba, and Takeshi Kobayashi. Effects of low dissolved oxygen on planula settlement, polyp growth and asexual reproduction of *Aurelia aurita*. *Plankton Benthos Res* 3.Supplement (2008): 107-113.
- Jónasdóttir, S. (1994). Effects of food quality on the reproductive success of *Acartia tonsa* and *Acartia hudsonica*: laboratory observations. *Mar Biol* 121, 67-81.
- Kamiyama, T. (2013). Planktonic ciliates as food for the scyphozoan *Aurelia aurita* (sl): effects on asexual reproduction of the polyp stage. *J Exp Mar Biol Ecol* 445, 21-28.
- Kawahara, M., Uye, S.-I., Ohtsu, K., and Iizumi, H. (2006). Unusual population explosion of the giant jellyfish *Nemopilema nomurai* (Scyphozoa: Rhizostomeae) in East Asian waters. *Mar Ecol Prog Ser* 307, 161-173.
- Kingsolver, J.G., and Huey, R.B. (2008). Size, temperature, and fitness: three rules. *Evol Ecol*

- Res 10, 251-268.
- Kjørboe, T., Møhlenberg, F., and Hamburger, K. (1985). Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration, and composition of specific dynamic action. *Mar Ecol Prog Ser* 26, 85-97..
- Licandro, P., Conway, D., Yahia, M.D., De Puellès, M.F., Gasparini, S., Hecq, J.-H., Tranter, P., and Kirby, R. (2010). A blooming jellyfish in the northeast Atlantic and Mediterranean. *Biol Lett*, rsbl20100150.
- Liu, W.-C., Lo, W.-T., Purcell, J.E., and Chang, H.-H. (2009). Effects of temperature and light intensity on asexual reproduction of the scyphozoan, *Aurelia aurita* (L.) in Taiwan. *Hydrobiol* 616, 247-258.
- Lonsdale, D. (2006). A review of the biochemistry, metabolism and clinical benefits of thiamin(e) and its derivatives. *J Evid Based Complementary Altern Med* 3, 49-59.
- Lucas, C.H. (2001). Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment. *Hydrobiol* 451, 229-246.
- Lucas, C.H., Graham, W.M., and Widmer, C. (2012). Jellyfish Life Histories: Role of Polyps in Forming and Maintaining Scyphomedusa Populations. *Adv Mar Biol* 63, 133.
- Matear, R., Hirst, A., and Mcneil, B. (2000). Changes in dissolved oxygen in the Southern Ocean with climate change. *Geochem Geophys* 1.
- Manzetti, S., Zhang, J., and Van Der Spoel, D. (2014). Thiamin function, metabolism, uptake, and transport. *Biochemistry* 53, 821-835.
- Meehl, G.A., and Tebaldi, C. (2004). More intense, more frequent, and longer lasting heat waves in the 21st century. *Science* 305, 994-997.
- Müller-Navarra, D.C., and Huntley, M.E. (2013). Bioactive Compounds Offered in Microcapsules to Determine the Nutritional Value of Copepods' Natural Diet *Mar Drugs* 11, 2459-2471.

- Müller-Navarra, D.C. (2008). Food web paradigms: the biochemical view on trophic interactions. *Int. Rev. Hydrobiol* 93, 489-505.
- Pinto, E., Pedersén, M., Snoeijs, P., Van Nieuwerburgh, L., and Colepiccolo, P. (2002). Simultaneous detection of thiamine and its phosphate esters from microalgae by HPLC. *Biochem. Biophys. Res. Commun.* 291, 344-348.
- Prieto, L., Astorga, D., Navarro, G., and Ruiz, J. (2010). Environmental control of phase transition and polyp survival of a massive-outbreaker jellyfish. *PloS one* 5, e13793.
- Provasoli, L. Growing marine seaweeds. *Proc Intl Seaweed Symp* (1963). p. 9-17.
- Purcell, J.E. (2007). Environmental effects on asexual reproduction rates of the scyphozoan *Aurelia labiata*. *Mar Ecol Prog Ser* 348, 183-196.
- Purcell, J.E. (2012). Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. *Annu Rev Mar Sci* 4, 209-235.
- Purcell, J.E., Atienza, D., Fuentes, V., Olariaga, A., Tilves, U., Colahan, C., and Gili, J.-M. (2012). Temperature effects on asexual reproduction rates of scyphozoan species from the northwest Mediterranean Sea. *Hydrobiol* 690, 169-180.
- Purcell, J.E., Hoover, R.A., and Schwarck, N.T. (2009). Interannual variation of strobilation by the scyphozoan *Aurelia labiata* in relation to polyp density, temperature, salinity, and light conditions in situ. *Mar Ecol Prog Ser* 375, 139-149.
- Purcell, J.E., White, J.R., Nemazie, D.A., and Wright, D.A. (1999). Temperature, salinity and food effects on asexual reproduction and abundance of the scyphozoan *Chrysaora quinquecirrha*. *Mar Ecol Prog Ser* 180, 187-196.
- R Core Team. R: A Language and Environment for Statistical Computing (2017). Available from: <https://www.R-project.org/>.
- Roth, O., Kurtz, J., and Reusch, T.B. (2010). A summer heat wave decreases the immunocompetence of the mesograzer, *Idotea baltica*. *Mar Biol* 157, 1605-1611.

- Sargent, J.R., Tocher, D.R., and Bell, J.G. (2002). The lipids, pp 181-257. In J.E. Halver and R.W. Hardy. [eds.], Fish nutrition, 3rd edition. Elsevier, New York.
- Schiariti, A., Morandini, A.C., Jarms, G., Von Glehn Paes, R., Franke, S., and Mianzan, H. (2014). Asexual reproduction strategies and blooming potential in Scyphozoa. *Mar Ecol Prog Ser* 510, 241-253.
- Shelford, V.E. (1911). Physiological animal geography. *J Morphol* 22, 551-618.
- Sokołowski, A., Brulińska, D., Olenycz, M., and Wołowicz, M. (2016). Does temperature and salinity limit asexual reproduction of *Aurelia aurita* polyps (Cnidaria: Scyphozoa) in the Gulf of Gdańsk (southern Baltic Sea)? An experimental study. *Hydrobiol* 773, 49-62.
- Strandberg, U., Hiltunen, M., Jelkänen, E., Taipale, S.J., Kainz, M.J., Brett, M.T., and Kankaala, P. (2015). Selective transfer of polyunsaturated fatty acids from phytoplankton to planktivorous fish in large boreal lakes. *Sci Total Environ* 536, 858-865.
- Sushchik, N., Kalacheva, G., Zhila, N., Gladyshev, M., and Volova, T. (2003). A temperature dependence of the intra-and extracellular fatty-acid composition of green algae and cyanobacterium. *J Plant Physiol* 50, 374-380.
- Sylvander, P., Häubner, N., and Snoeijs, P. (2013). The thiamine content of phytoplankton cells is affected by abiotic stress and growth rate. *Microb Ecol* 65, 566-577.
- Taipale, S., Strandberg, U., Peltomaa, E., Galloway, A.W., Ojala, A., and Brett, M.T. (2013). Fatty acid composition as biomarkers of freshwater microalgae: analysis of 37 strains of microalgae in 22 genera and in seven classes. *Aquat Microb Ecol* 71.
- Thiel, H. (1962). Untersuchungen über die Strobilisation von *Aurelia aurita* Lam. an einer Population der Kieler Förde. *Kieler meeresforsch* 18, 198-230.
- Thompson, G.A. (1996). Lipids and membrane function in green algae. *Biochim Biophys Acta, Lipids Lipid Metab* 1302, 17-45.
- Wang, N., Li, C., Liang, Y., Shi, Y., and Lu, J. (2015). Prey concentration and temperature effect

- on budding and strobilation of *Aurelia sp.* 1 polyps. *Hydrobiol* 754, 125-134.
- Willcox, S., Moltschaniwskyj, N.A., and Crawford, C. (2007). Asexual reproduction in scyphistomae of *Aurelia sp.*: effects of temperature and salinity in an experimental study. *J. Exp. Mar Biol Ecol* 353, 107-114.
- Wiltshire, K.H., and Manly, B.F. (2004). The warming trend at Helgoland Roads, North Sea: phytoplankton response. *Helgol Mar Res* 58, 269.
- Zuur, A., Ieno, E., Walker, N., Saveliev, A., and Smith, G. (2009). *Mixed Effects Models and Extensions in Ecology with R*. Statistics for biology and health.
- Zuur, A.F., Ieno, E.N., and Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1, 3-14

Table 1. Statistical outputs from GLMs selected by a stepwise backward method on different functional responses and explanation variables. (the meanings of symbols used, ~ model formulae, × inclusion of main effects plus interactions between explanatory variables, + inclusion of an explanatory variable)

Fig. 1. Survival of *A. aurita* polyps (%) under different food regimes at high temperature (27 °C) during the time of the experiment. (Note: all polyps in different food regimes survived to 100% under 13 °C and 20 °C).

Fig. 2. Final calyx diameter (mean ± SE) of *A. aurita* polyps under different food conditions and temperatures. Letters denote food quantity (a: Low, b: Medium, c: High).

Fig. 3. A total number of buds (mean $\pm$ SE) produced by *A. aurita* polyps under different food conditions and temperature regimes. Letters denote food quantity (a: Low, b: Medium, c: High).

Fig. 4. (a) Strobilation rate (%) and (b) ephyrae production (ephyrae inds polyp⁻¹, mean $\pm$ SE) of polyps at 13 °C. Numbers on top of bars represent the number of strobilae in n=18 replicates.

Fig. 5. Survival tolerance curves of polyps under different temperature regimes (solid line), food quantity (dotted line) and food quality (dot-dashed line) effects.

Table. 1. Statistical outputs from GLMs selected by a stepwise backward method on different functional responses and explanation variables. (the meanings of symbols used, ~ model formulae, × inclusion of main effects plus interactions between explanatory variables, + inclusion of an explanatory variable)

Functional Responses	Model	Family	Variables	Df	χ^2	P-value
Survival	survival ~ temperature + food quality + food quantity + time + food quality × food quantity (AIC = 290.1)	Binomial	temperature	2	245.9	< 0.001
			food quality	2	75.1	< 0.001
			food quantity	2	17.2	< 0.001
			time	5	174.6	< 0.001
			food quality × food quantity	4	11.6	0.02
Growth	diameter ~ temperature × food quality × food quantity (AIC = -45.2)	Gaussian	temperature	2	31.1	0.001
			food quality	2	1.0	< 0.001
			food quantity	2	11.6	< 0.001
			temperature × food quality	4	1.2	< 0.001
			temperature × food quantity	4	1.0	< 0.001
			food quality × food quantity	4	0.1	0.57
			temperature × food quality × food quantity	8	1.1	< 0.01
Budding	buds ~ temperature + food quality + food quantity + temperature × food quality + temperature × food quantity + food quality × food quantity (AIC = 1470.4)	Poisson	temperature	2	286.0	< 0.001
			food quality	2	48.0	< 0.001
			food quantity	2	431.9	< 0.001
			temperature × food quality	4	13.4	< 0.01
			temperature × food quantity	4	15.5	< 0.01
			food quality × food quantity	4	39.2	< 0.001
Strobilation	strobila ~ temperature + food quality + food quantity + food quality × food quantity	Binomial	temperature	2	74.2	< 0.001
			food quality	2	13.8	< 0.01

(AIC = 137.4)	food quantity	2	13.8	< 0.001
	food quality × food quantity	4	38.1	< 0.001

The statistically significant results ($P < 0.05$) are written in bold.

ACCEPTED MANUSCRIPT

Graphical abstract

Highlights

- Food quality affects polyp population and benthic-pelagic coupling.
- High food quality can compensate for physiological stress under heatwave scenarios.
- Studies using *Artemia sp.* as food might underestimate bud production.
- A novel tolerance curve for jellyfish polyps has been suggested.