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Effects of temperature on growth of north-east Pacific moon jellyfish ephyrae, *Aurelia labiata* (Cnidaria: Scyphozoa)

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The effects of ten different water temperatures on the growth of newly released ephyrae of *Aurelia labiata* were explored. Ephyrae grown at 21°C showed the greatest growth, increasing in bell diameter from about 4.0 mm to 14.5 mm in 14 days and remained in good condition for the duration of the experiment. Ephyrae subjected to other temperatures grew at different rates. Ephyrae maintained at 8°C gradually decreased in size during the experiment, shrinking in bell diameter from about 4.0 mm to 3.8 mm by day 14, but remained in apparent good condition. Ephyrae reared at 22.5°C and above everted their bells, were in poor condition, and were unable to feed or swim effectively by about day ten. In this study the optimal temperature range for rearing *A. labiata* ephyrae was 12°C–21°C, which corresponds with the reported range for this species.

INTRODUCTION

Jellyfish are popular display animals at public aquariums due to their charismatic nature and general crowd appeal. At the Monterey Bay Aquarium (Monterey, California, USA) *Aurelia labiata* (Chamisso & Eysenhardt) are displayed as examples of common scyphomedusae native to Monterey Bay. These jellyfish may also be found inhabiting near shore surface waters year-round from Prince William Sound, Alaska to San Diego, California (Wrobel & Mills, 1998; Gershwin, 2001).

Medusae of *A. labiata* play important roles in their ecosystems and at times have significant impacts on human activities. Seasonally they form blooms that can clog seawater intakes, foul fishing gear and may compete for food with commercially important fish (Mills, 2001; Purcell & Sturdevant, 2001). Factors influencing the size and frequency of jellyfish blooms are poorly understood for most jellyfish species, especially for large surface cruising scyphomedusae of the north-east Pacific ocean which are likely to be affected by El Ninos and increasing sea surface temperatures (SST) (Lau & Weng, 1999).

Surprisingly little published information exists regarding the effects of temperature on growth and development on any stage of the life cycles for scyphomedusae of the north-east Pacific ocean (Arai, 1997). Most work concerning growth of scyphomedusae ephyrae has been limited to only a few hardy 'lab rat' species such as *Chrysaora quinquecirrha*, *Aurelia aurita* and *Cyanea capillata* (Olesen et al., 1996; Bamstedt et al., 1997; Bamstedt et al., 2001, respectively).

Medusae of *A. labiata* may be found in the surface waters of Monterey Bay year round but foul weather and patchy distribution often prevent successful collections. This study explores propagation techniques and optimal growth parameters for ephyrae of *A. labiata* in an attempt to minimize collecting pressures on wild populations and to ensure a steady and reliable source of medusae for exhibits and research. The purpose of this paper is to report on the effects of ten different temperatures on the growth and development of newly released *A. labiata* ephyrae.

MATERIALS AND METHODS

Subjects

Mature *Aurelia labiata* medusae were collected with a hand net from the surface waters of Monterey Bay, California, from February to May 2003, aboard the RV 'Plankton Boat'. Medusae were transported to the jellyfish culture laboratory at the Monterey Bay Aquarium (Monterey, California) within two hours. To start new cultures of scyphistomae a pipette was used to remove brooded planulae from mature female medusae. The planulae were placed into 4" diameter glass culture dishes filled with 5 μm filtered seawater. Culture dishes were exposed to overhead lighting (Sylvania Octron, 3500K, 32W) and maintained at 15°C. Resultant polyps were fed daily with Selco-enriched *Artemia salina* nauplii to saturation. Strobilation occurred under laboratory conditions after about five months.

Procedure

Ephyrae that released from their strobilae within 48 hours were used to start all experiments. Each treatment consisted of three replicate plastic 2-l beakers containing 15 ephyrae and 5 µm filtered seawater (34 ppt.). The ephyrae in the three 2-l beakers were statistically treated as one group in all treatments, due to a lack of significant differences between beakers (analysis of variance (ANOVA) $P>0.05$). Selco-enriched *Artemia* nauplii were provided in excess (~410 nauplii $ml^{-1} \times 20$ ml d^{-1}) so that food availability was not a limiting factor. Food and water were changed every day for 14 days. Experimental beakers were gently mixed using an aeration system consisting of a single airline tube with a small lead weight affixed per beaker. The bubble rate in the beakers was approximately 4–6 bubbles per second. The beakers were submerged in ten temperature controlled seawater baths held at 8, 10, 12, 15, 17, 21, 22.5, 24, 26 and 28°C. Controlled bath temperatures were checked three times daily. Specific temperatures were selected on the basis of what temperatures *Aurelia labiata* ephyrae experience in their range distributions during spring and summer (SST data from NOAA website) www.noaa.org.

Ephyrae were measured from lappet tip to lappet tip to determine bell diameter size. Individual ephyrae were placed on a glass dish using a wide-mouthed pipette, allowed to relax and then measured using a dissecting stereomicroscope and a grid with 1 mm gradations. Measurements for each ephyra were completed in less than one minute. Ephyrae were measured three times, on days one, seven and 14. The growth rate was calculated (% d^{-1}) with the following equation using increments of diameter after Bamstedt et al. (1997) where D1 and D2 are the mean diameters from each treatment group, measured from lappet tip to lappet tip, at two consecutive analyses, t1 and t2 (days), respectively.

$$\% \text{ growth } d^{-1} = \ln[(D_2/D_1)^3]/(t_2 - t_1) \times 100 \quad (1)$$

This equation was used rather than ones based on ash free dry weight, as it takes into account the gradual development from ephyra to medusa (Bamstedt et al., 1997) and does not require destruction of the specimen.

Statistics

One-way ANOVA tests were carried out to determine the significance of temperature on growth. The assumption of normality was verified using a normal probability plot. The assumption of homoscedasticity was checked using a Hartley's F-test (Hartley, 1950). It was necessary to transform the data with the natural log to meet the assumption of homoscedasticity.

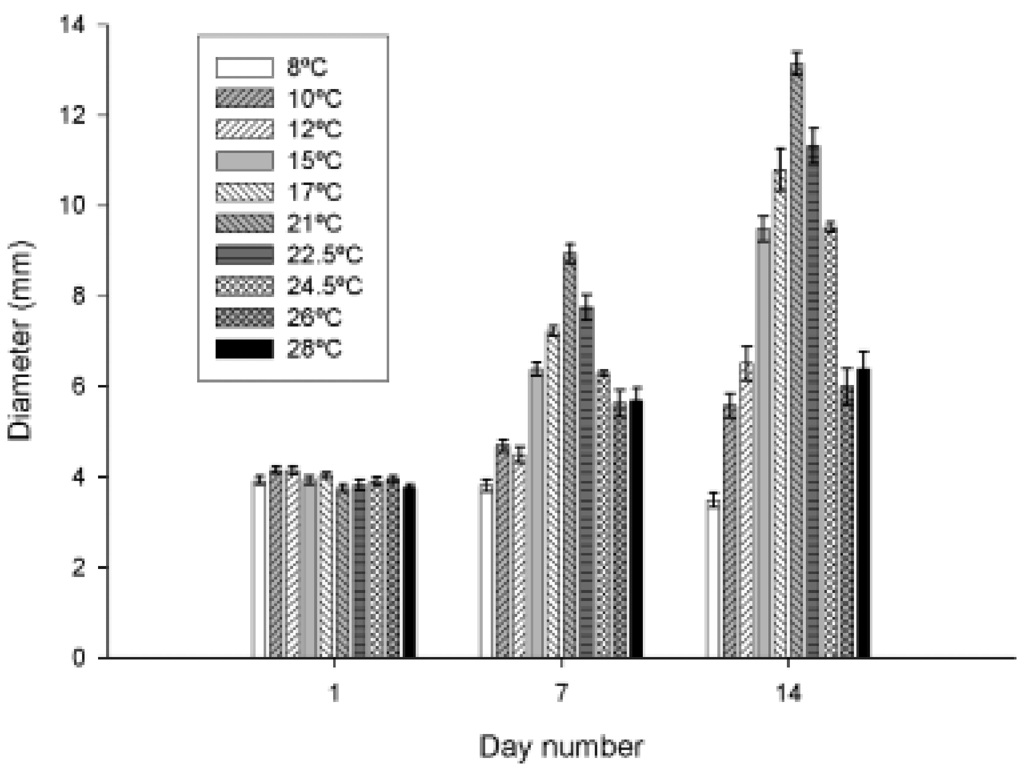

Figure 1. Effects of temperature on the growth of *Aurelia labiata* ephyrae, N=45 in each treatment.

Table 1. *Growth rate (% d^{-1}) of* Aurelia labiata *ephyrae at tested temperatures, N=45 in all treatments.*

Temperature C	Days 1–7	Days 7–14	Days 1–14
8	-1.42%	-3.77%	-2.68%
10	6.0%	7.46%	6.79 %
12	4.17%	15.9%	10.5%
15	24.1%	17.0%	20.32%
17	29.2%	17.17%	22.76%
21	43.51%	16.55%	28.99%
22.5	35.30%	16.25%	25.04%
24	32.38%	17.82%	24.66%
26	17.8%	2.72%	9.7%
28	20.62%	5.04%	12.23%

RESULTS

At the start of the experiment, *Aurelia labiata* ephyrae in all treatment groups were ~4.0 mm in diameter. By day seven, temperature effects on growth of ephyrae were visible and significant (ANOVA, $P<0.01$). At day 14, the temperature effect was further magnified and also significant (ANOVA, $P<0.01$). The general trend for the effect of temperature on ephyrae growth is shown in Figure 1.

The average growth rates, calculated from the difference in initial and final ephyrae diameters, are shown in Table 1. The temperature yielding the highest growth rate was 21°C, producing ephyrae that increased their mean diameters from ~4.0 mm to ~14.5 mm by the end of the 14-day trial. Ephyrae grown at 8°C showed a slow decrease in growth rate over time at a rate of about -2.68% overall, shrinking from ~4.0 mm to 3.8 mm by day 14 but still in apparently good condition. Ephyrae grown at 10°C and 12°C grew slowly for the first 1–7 days (Table 1) and increased their growth rates during days 7–14. Ephyrae grown at 15, 17, 21, 22.5 and 24°C had rapid growth rates for days 1–7, ranging from 24%–32%, then all had similar growth rates, 16%–17.8%, for days 7–14 (Table 1). Ephyrae grown at 26°C and 28°C had similar growth rates and developed normally during days 1–7, 17.8% and 20% respectively. However, these ephyrae everted their bells (Figure 2) and showed a decrease in growth rate during days 7–14 (Table 1).

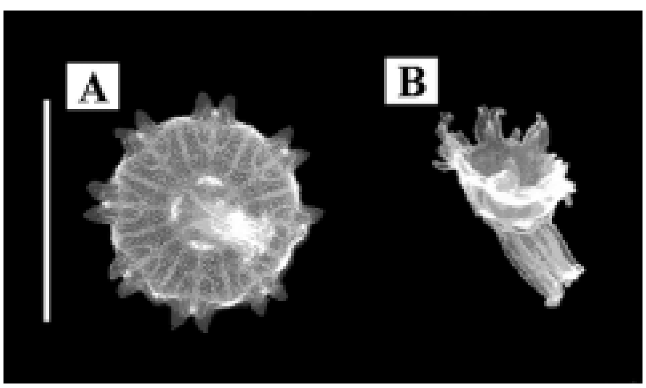

Figure 2. Day 14 *Aurelia labiata* ephyrae. (A) Reared at 17°C, this ephyra is in good condition with normal development; (B) grown at 24°C, this specimen is in poor condition with an everted bell. Scale bar: 10 mm.

DISCUSSION

General effects of temperature on jellies

The general effect of temperature on the growth of scyphomedusae is that increased temperature with a constant supply of food yields increased growth rate (Lucas, 2001). *Aurelia labiata* ephyrae in this study had excess food for the duration of the experiment, so were free to convert food to growth as quickly as possible. Of the ten temperatures tested, 21°C yielded the fastest growth for ephyrae. The effect was clear and observable at the end of day seven and was further magnified on day 14 (Figure 1). Ephyra growth rates were generally fastest for the first few days of development and gradually slowed thereafter. A similar trend was shown for ephyrae of *Aurelia aurita* (Bamstedt et al., 2001).

Aurelia labiata ephyrae raised at different temperatures had different fates. Ephyrae grown at 10°C and 12°C grew slowly for the first 1–7 days (Table 1) and increased their growth rates during days 7–14, possibly due to the development of larger guts and the subsequent ability to collect more food to put towards growth (Graham & Kroutil, 2001). Low temperatures led to decreased feeding rates for *Aurelia aurita* ephyrae (Elliot & Leggett, 1996; Bamstedt et al., 1999). The same may be the case for ephyrae of *A. labiata*, which did not appear to be active feeders at 8, 10 and 12°C although occasionally *Artemia* nauplii were found in their guts. Ephyrae grown at 8°C showed a decreasing growth rate over time, however they fed, grew well and fully recovered when added to a 0.33 m diameter

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pseudokreisel (Raskoff et al., 2003) at 15°C (C.L.W., unpublished data). Being raised at 8°C did not lead to bell deformation nor did the ephyrae become moribund. Therefore, it appears that ephyrae of wild *A. labiata* may survive for at least 14 days at 8°C, then resume growth if thermal conditions improve.

Ephyrae grown at 22.5, 24, 26 and 28°C grew quickly for the first seven days but began to show signs of irreversible, deleterious heat stress. By day ten, these jellies everted their bells (Figure 2) and were unable to swim or feed effectively, which led to a decrease in bell diameters. Ephyrae grown from 22.5–28°C did not recover when added to a 0.33 m diameter pseudokreisel at 15°C (C.L.W., unpublished data) and ultimately perished, indicating that heat stressed jellies may not be able to recover if exposed for longer than 7–10 days.

Geographical range

Aurelia labiata may be physiologically and reproductively isolated from southern and northern species of *Aurelia*. Temperature affects the growth of medusae and benthic polyps, and is an important factor affecting recruitment of jellyfish from the benthic to the pelagic phase (e.g. production and development of ephyrae), and recruitment from the pelagic to appropriate benthic habitat (e.g. settlement of planulae and development of scyphistomae). Ephyrae in this study did not grow well or develop normally at temperatures found beyond the southern and northern extremes of their reported ranges.

As with many animals, jellyfish found beyond the southernmost and northernmost extents of their ranges may not be able to complete their life cycles. In this study, ephyrae maintained at 8°C gradually decreased in size, and heat-stressed ephyrae everted their bells and perished. In the field, jellyfish drifting out of ideal temperature ranges probably have a few days to return to an appropriate thermal climate. Whether *A. labiata* are able to sense and move toward optimal temperatures is presently unknown. Scyphomedusae have been shown to vertically migrate (Mackie et al., 1981), follow the sun (Hamner et al., 1994) and distantly sense food (Arai, 1991). It seems plausible that medusae may be able to migrate to appropriate temperatures. However, whether or not scyphomedusae posses this ability is presently unknown. Advancements in jellyfish tagging and tracking will certainly help elucidate the issue.

Aurelia labiata medusae are found from Prince William Sound, Alaska to San Diego, California (Wrobel & Mills, 1998; Gershwin, 2001). Sea surface temperatures in Prince William Sound, Alaska generally range between 4°C in winter and up to 15°C in summer. Sea surface temperatures in San Diego, California generally range between 15°C in winter and up to 22°C in summer (SST data from NOAA website) www.noaa.org. There is evidence for a global SST linear warming trend of about 0.1°C for the period of 1955–1997 (Lau & Weng, 1999). If SSTs continue to rise, the current range for *A. labiata* may shift northward over time due to the negative effects of prolonged exposure to excessively warm temperatures. Further, growth and development of larger medusae may occur in areas where increased temperatures are tolerable for medusae.

Ecological impact

Aurelia labiata medusae are relatively large, prey upon zooplankton and may compete with commercially important fish for food (Purcell & Sturdevant, 2001). Predation by *Aurelia aurita* medusae dramatically affected the abundance and diversity of the zooplankton community in the Keil Bight (western Baltic Sea) with the medusae seeming to exert top-down control (Schneider & Behrends, 1998). Large *Aurelia aurita* eat greater quantities and wider varieties of prey than do smaller ones (Graham & Kroutil, 2001). Provided that food is readily available, the possible effect of elevated sea surface temperatures could mean growth and development of larger *A. labiata* medusae that would eat more and possibly have a greater effect on associated commercial fisheries.

While larger jellyfish may be troublesome for some commercial fishing and other human activities, larger medusae may be beneficial to organisms that feed upon *A. labiata* medusae. A small host of pelagic organisms utilize *A. labiata* medusae as food including hyperiid amphipods (Laval, 1980), sea turtles, juvenile and adult fish, and medusae of other jellies e.g. *Phacellophora camtschatica*, *Chrysaora fuscescens*, *C. colorata* and *Aequorea victoria* (personal observations). Further, the benthic organisms *Pyconpodia helianthoides*, *Metridium senile* and *Loxorhynchus crispatus* have been observed feeding on moribund *Aurelia labiata* medusae in Monterey Bay, California (personal observations). Elevated SSTs could mean larger *A. labiata* as food for the abovementioned organisms.

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