



Growth and age determination of the tropical Australian cubozoan *Chiropsalmus* sp.

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Abstract

Chiropsalmus sp. medusae collected in this study ranged from 3 to 71 mm diagonal bell width and displayed growth best described by the following equation: size (mm) = $74.9 \times \exp(-\exp(0.041(\text{time since metamorphosis (day)} - 35.6674)))$. Growth rates of up to 7 mm week⁻¹ increase in diagonal bell width are theoretically possible, with animals able to reach sexual maturity in approximately 70 days. Correlation of the number of rings on the statoliths with the predicted age of the individual from the field produced a relationship that indicates the growth rings are laid down daily and as such could be used to infer age of the medusae. Over the 1998–1999 season, there were four influxes of juvenile cohorts, each occurring approximately 14 days after a major rainfall event.

Introduction

Cubozoans, or box jellyfish, are common inhabitants of Australia's tropical coasts during the warmer months of the year (Barnes, 1965, 1966; Brown, 1973; Hartwick, 1987, 1991; Burnett et al., 1996). Adult medusae die off at the end of the season (usually early May) with juvenile medusae budding from asexual polyps in November at the start of the season in at least *Chironex fleckeri* (Southcott) (Hartwick, 1991). Presently this is assumed to be similar for other Australian chirodroids, or multi-tentacled cubozoans. There is considerable confusion over the taxonomic identity of a second species, *Chiropsalmus quadrigatus* (Haeckel), also found commonly in these waters. These two species form the major component of the Australian chirodroids.

Descriptions of population structure in Australian chirodroids is limited to those of Barnes (1966), who indicated that, while cubomedusae are typically uniform in size within populations,

marked differences in size are evident between populations. Juveniles originate asexually from polyps and increase in size rapidly (Hartwick, 1987, 1991; Hamner et al., 1995), reaching sexual maturity late in the season (Barnes, 1966; Hartwick, 1991); however, data quantifying these changes within populations are lacking. In comparison, data for scyphozoans are plentiful, and field studies have indicated that a typical growth pattern includes rapid growth to maturity, with growth at a decreased rate thereafter (Arai, 1997). This pattern is often best described by the von Bertalanffy growth curve (Schnute & Fournier, 1980; Gibbons & McCarthy, 1984; Pauly, 1984; Ryser, 1988; Bigelow et al., 1995; Mohammed, 1996; Platz et al., 1997); however, a logistic curve (Nigmatullin et al., 1995; Dimlich & Hoedt, 1998) or the Gompertz growth equation (Arkhypkin, 1997) may provide a better estimation of growth.

In parallel with a lack of data on population structure is a lack of a reliable means of aging

jellyfish. As many cnidarians are able to undergo growth and degrowth (Arai, 1997), the use of size to represent age in field populations may be inherently flawed. However, at least in one species of cubomedusae, daily growth rings found in the statoliths may prove to be a reliable indicator of age (Ueno et al., 1995, 1997), as it is in many species of fishes and cephalopods.

This paper examines the growth rate of *Chiropsalmus* sp., using modal progression of cohorts, to develop a growth curve and to determine if *Chiropsalmus* sp. has a single influx of juveniles per season or several. It also examines the validity of using growth rings of statoliths as a tool for determining the age of individual medusae.

Methods

The original description of *Chiropsalmus quadrigatus* describes the gonads as 'cox comb' in shape (Haeckel, 1879). The species of *Chiropsalmus* (Fig. 1) in Australia does not have 'cox comb' gonads, but has a cluster of eight grape-like gonads within the bell, suggesting it is probably a different species from that described by Haeckel; it is thus referred to as *Chiropsalmus* sp. in this study. Voucher specimens are housed at James Cook University, Cairns campus.

Specimen collection

Weekly sampling between early November 1998 and late April 1999 was done at Port Douglas, North Queensland, Australia, using a 30 m monofilament beach seine with a mesh of 10 mm. Sampling was conducted between the water's edge and 20 m from the shoreline, between 0600 and 0900 h. All *Chiropsalmus* sp. caught were removed and preserved in 4% seawater formalin. The diagonal bell width (dbw, the distance between diagonally opposite pedalia) of each specimen was recorded to the nearest millimetre with specimens in their natural, cuboidal shape. Five millimetre size classes were defined, with class 1 containing individuals 0–5 mm dbw.

Determination of cohorts

To determine if *Chiropsalmus* sp. has one or several influxes of juveniles into the population during the season, and whether influxes were correlated with rainfall, the number of individuals caught per 100 m of seine drag on each sampling occasion was calculated. Specimens less than 20 mm dbw were defined as juveniles. These data were plotted against time since 1 October, as was the amount of rain (recorded from Port Douglas meteorological station). The date at which rainfall



Figure 1. An adult specimen of *Chiropsalmus* sp., captured at Southern Four Mile Beach, Port Douglas, Australia.

was recorded was advanced 14 days to allow alignment of the peaks in cohort influxes with the peaks in rainfall.

Growth curve determination

Size-percent frequency histograms were produced. Modal class intervals were determined for each sample and, using the criteria described by Kaufmann (1981), the specific growth rate was calculated. Regression analysis of specific growth rate against both natural logarithm of the geometric mean dbw and reciprocal mean dbw was performed to determine the most appropriate growth curve. The resulting growth equation was calculated using a minimum medusae size of 1 mm, as Hartwick (1987) reported the size of newly produced medusae of a closely related species, *C. fleckeri*, to be between 1.2 and 1.4 mm immediately following metamorphosis. Regression analysis of the linear component of the resulting growth curve against time was used to produce a growth rate estimate.

Statolith ring correlation

Two statocysts from each of 24 individuals were removed. The statoliths were embedded in epoxy and ground using fine emery paper and toothpaste. Each statocyst was viewed under a light microscope using oil immersion and the number of rings in each statolith was counted (Fig. 2). The mean number of rings in the two statoliths (the difference was never $> 5\%$) was regressed against the theoretical age of the medusa using the calculated growth equation. The use of tetracycline as a vital stain for statoliths caused rapid mortality in medusae.

Results

A progression through the modal size classes was observed, individuals becoming larger as the season progressed. Three distinct cohorts were observed over the 1997/1998 medusae season, with an additional influx having occurred prior to 9 November (Fig. 3). All four influxes occurred

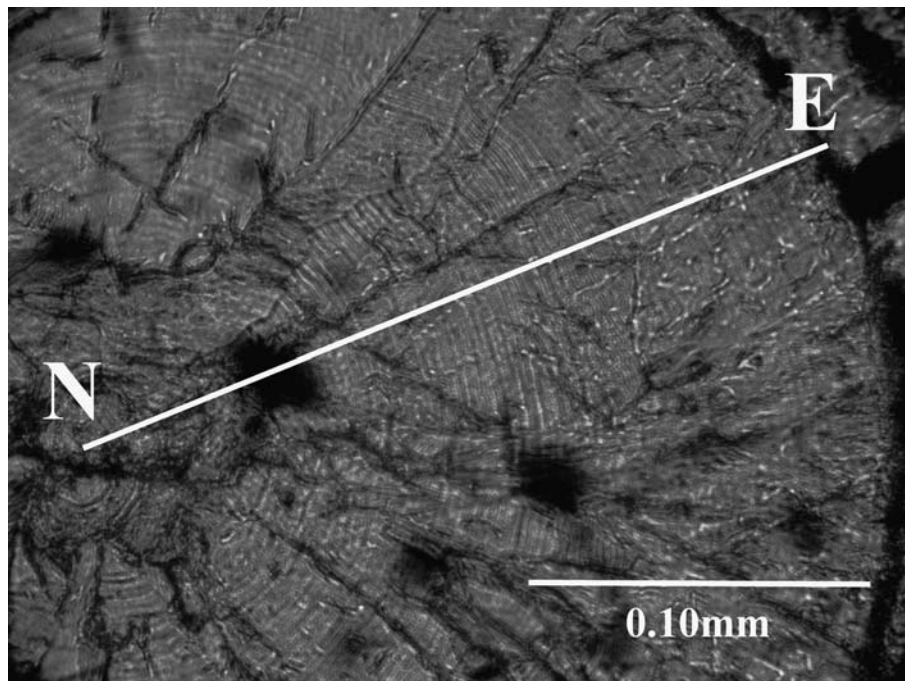


Figure 2. A sectioned statolith from *Chiropsalmus* sp. viewed through a compound light microscope. (N) nucleus or centre of statolith, (E) edge of statolith.

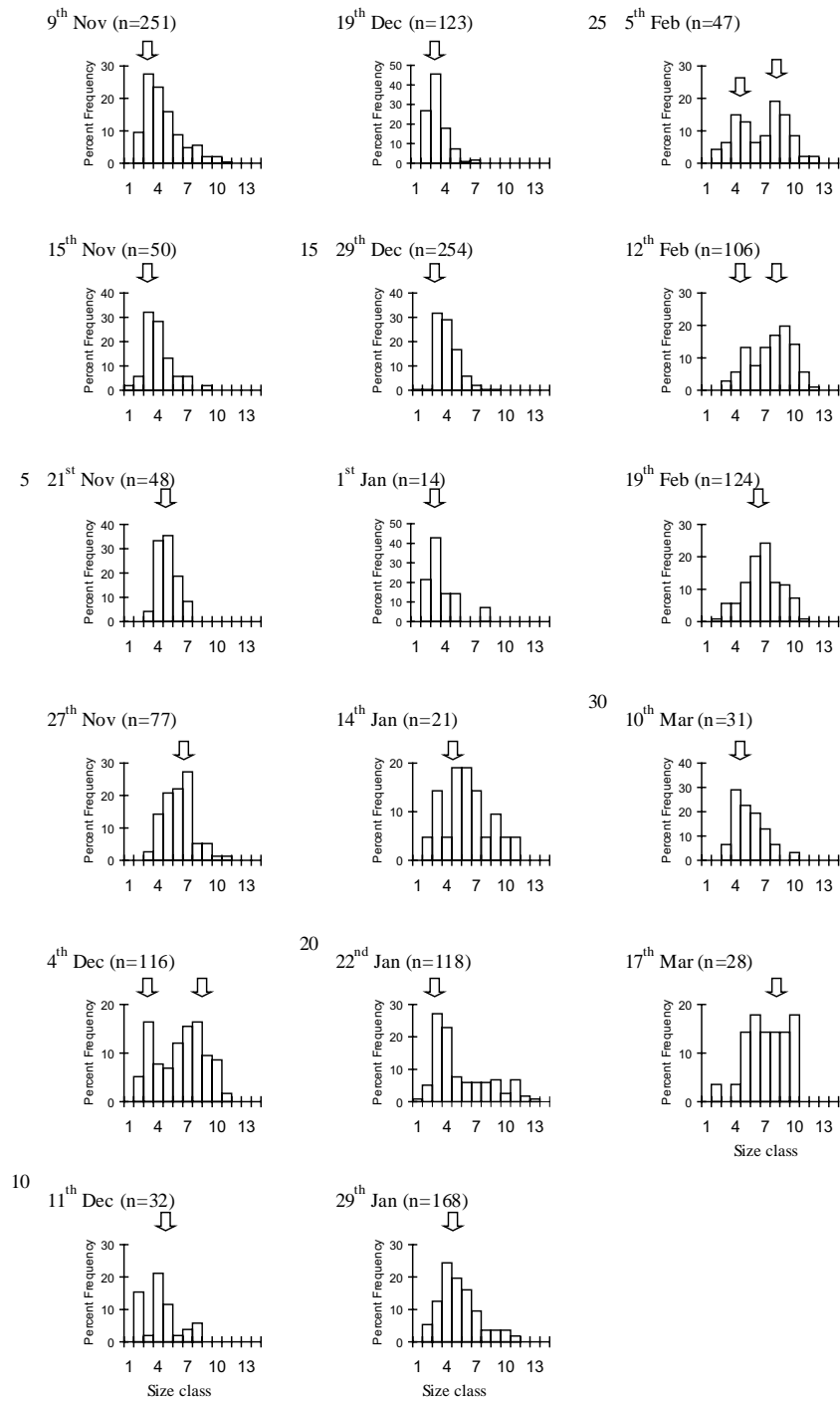


Figure 3. Modal progression of individuals of *Chiropsalmus* sp. sampled from Four Mile Beach, Port Douglas (⇩ = mode).

approximately 14 days after a rainfall event. Notably, no juveniles were found in October, even though a rainfall event occurred prior to that

month. Likewise, from early April (day 182 onwards), no further influx of juveniles was recorded, even though a rainfall event occurred (Fig. 4).

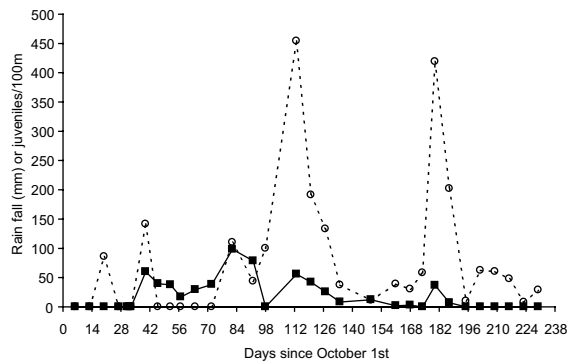


Figure 4. Recorded rainfall at Port Douglas, advanced 14 days, against time in days from October 1, 1998. Superimposed is the number (individuals/100 m) of juvenile (less than 20 mm diagonal bell width) *Chiropsalmus* sp. collected from Four Mile beach. (o) rainfall, (■) medusae numbers.

The specific growth rate of *Chiropsalmus* sp. was significantly correlated with both \ln geometric mean size ($F = 33.29$, $df = 26$, $p < 0.001$) and reciprocal mean size ($F = 23.97$, $df = 26$, $p < 0.001$). However, \ln geometric mean size explained more of the variation in specific growth rate ($r^2 = 0.554$) than \ln reciprocal mean size ($r^2 = 0.469$). In accordance with the methods of Kaufmann (1981), a Gompertz rather than a von Bertalanffy growth curve was then fitted to these data. The Gompertz growth equation had the following form:

$$S = 74.9 \times e^{-e^{-0.041(t-35.6674)}}$$

where S = size in mm at time t (in days) since metamorphosis (Fig. 5). The asymptotic (maximum theoretical) dbw for this species was calculated to be 74.9 mm. Regression analysis of the linear component of this relationship (from 30 to 70 days) ($F = 5960.95$, $df = 39$, $p < 0.001$) gave the maximum growth rate of *Chiropsalmus* sp. of 1 mm per day. Kinsey (1986) reported that the onset of sexual maturity occurs in this species at a mean size of 59 mm dbw, so, using the growth equation, medusae may reach sexual maturity after 72 days.

There was a significant and positive relationship between the theoretical age of the medusae and the number of growth rings ($F = 5.224$, $df = 1 \times 22$, $p = 0.032$, Fig. 6). The equation of this relationship was

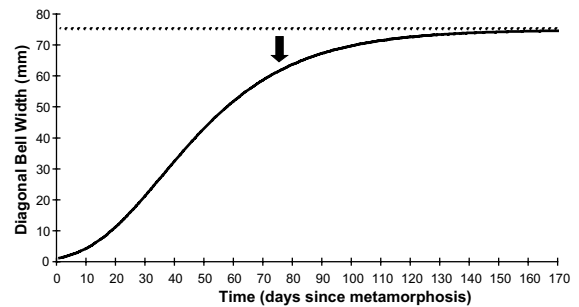


Figure 5. Gompertz growth curve for *Chiropsalmus* sp. showing the onset of sexual maturity and asymptotic diagonal bell width. ↓ mean size (mm diagonal bell width) at sexual maturity (Barnes in Kinsey, 1986), (.....) theoretical asymptotic diagonal bell width.

$$\text{number of rings} = 0.688 \times \text{dbw}(\text{mm}) + 9.89.$$

The slope of this relationship was not significantly different from 1 (95% confidence limits = 0.064–1.313).

Discussion

The growth of *Chiropsalmus* sp. medusae was rapid, with a maximum of 7 mm in 1 week during the summer of 1998/1999 (when mean sea water temperature was 28.6 °C). While this maximum growth rate estimate is comparable to that Guest

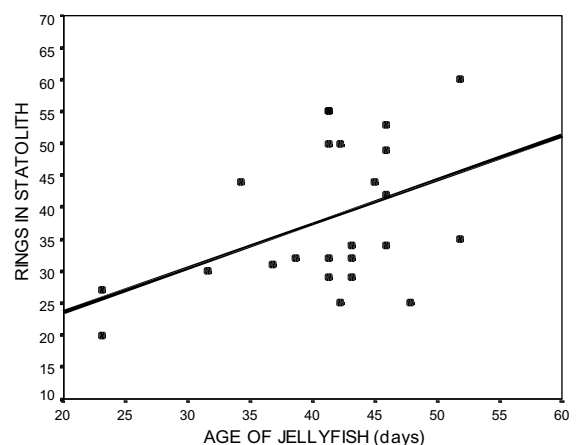


Figure 6. Relationship between the number of rings in the statolith of *Chiropsalmus* sp. and the theoretical age of the organism based on diagonal bell width. Number of rings = $0.688 \times \text{diagonal bell width (mm)} + 9.89$ ($F = 5.224$, $df = 1 \times 22$, $p = 0.032$).

(1959) provided for *Chiropsalmus quadrumanus*, it is 7–14× higher than that established for scyphozoans in similar field studies (Olesen et al., 1994; Arai, 1997).

At this rate of growth, individuals of *Chiropsalmus* sp. can reach their theoretical maximum size of approximately 75 mm dbw within 130 days, well within the average length of the medusa season of approximately 180 days (Gordon, 1998). This maximum theoretical size compares favourably to maximum size of field-collected animals reported by Barnes (1966), Sutherland (1983), and Halstead et al. (1990). Maximum sizes of 200 and 100 mm reported by Sutherland (1994) and Rifkin (1996), respectively, appear theoretically inaccurate based on these data. In these cases, specimens may have been confused with *C. fleckeri*, which is morphologically very similar but grows significantly larger (Southcott, 1960; Barnes, 1965, 1967; Keen, 1971; Marsh et al., 1986; Fenner & Williamson, 1996).

The relationship between number of rings in the statolith and theoretical age of the medusae not being significantly different from one suggests that any increase in age corresponds with a similar increase in growth rings. That is, the growth rings appear to be laid down daily. This was shown by Ueno et al. (1995, 1997) in another cubomedusa, *Carybdea rastoni*. The ability to predict the age of the medusae from the number of growth rings is important for comparisons between populations with differing environmental temperature and food resources, as size of medusae is not a reliable indication of age.

In contrast to *C. fleckeri*, with a life span thought to be the length of the medusa season (Hartwick, 1991), a number of generations of *Chiropsalmus* sp. may occur within one season. This is supported by the data collected in this study, with four influxes of juveniles during a season. The time to sexual maturity for *Chiropsalmus* sp. (72 days) is longer than the interval between juvenile influxes (~40 days). Therefore, juveniles in successive influxes cannot have arisen from the reproduction of sexually mature individuals of the previous influx. Alternatively, polyps derived from the different cohorts may produce juveniles at different times of the season. Unlike scyphozoans, which undergo strobilation and produce several medusae per polyp, cubozo-

ans are characterised by the production of only one medusa from a polyp. Consequently, the production of separate cohorts cannot be produced by continual liberation of medusae. It appears that different polyps produce medusae at different times, resulting in distinct cohorts throughout the season.

The polyps may be trading off between the potential benefits and associated hazards of undergoing metamorphosis at a particular stage of the season. What these advantages and disadvantages are is undetermined, but appear to be associated with salinity and possibly water temperature changes, as juvenile influxes show a strong relationship with rainfall events, which often lead to large variations in salinity and temperature of estuaries, where the polyps are thought to be located. To test this hypothesis, studies need to be conducted on the polyp stage of the life cycle, but unfortunately the geographic location of this species' polyps is still unknown.

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