

## Environmental responses of jellyfish polyps as drivers of medusa populations off the coast of Namibia

L. Ziegler and M.J. Gibbons

### Abstract

Jellyfish populations in the southeastern Atlantic off the coast of Namibia have increased subsequent to the decline of small pelagic fisheries at the end of the 1960s, although the environment there has also become warmer and the waters off Walvis Bay have become richer in zooplankton in recent years. Laboratory experiments were conducted with the scyphozoan jellyfish *Chrysaora fulgida* to investigate the effects of food density (0, 30, 70, 100 or 150 *Artemia nauplii* 200 ml<sup>-1</sup>), feeding frequency (once daily or once every third day) and water temperature (12, 16 or 20 °C) on the asexual reproduction, growth and development of polyps. The results of a generalised linear mixed-effects model reveal that all variables impacted asexual reproduction, with greater polyp production attained at higher food concentrations, increased feeding frequencies and increased temperatures. The most common mode of asexual reproduction was by lateral budding. These laboratory results suggest that polyps of *C. fulgida* may have proliferated off Namibia in recent times, which would contribute to increased numbers of jellyfish there.

### Introduction

Jellyfish populations off Namibia appear to have increased in size subsequent to the overfishing of small pelagic fishes there at the end of the 1960s (Venter 1988; Roux et al. 2013), though the jellyfish populations at present may be relatively stable (Flynn et al. 2012). In 2003, the biomass of jellyfish (i.e. *Chrysaora fulgida* [Reynaud, 1830] and *Aequorea forskalea* [Péron & Lesueur, 1810]) in the northern Benguela Current ecosystem was estimated to exceed that of all commercial finfish (Lynam et al. 2006).

Increases in jellyfish populations have been noted in a number of ecosystems around the world (e.g. Brotz et al. 2012; Richardson et al. 2012), although whether these are sustained increases or simply increases associated with natural cycles is yet unclear (Condon et al. 2013; Gibbons and Richardson 2013). A number of anthropogenic drivers have been proposed to explain the recent increases in jellyfish abundance, such as overfishing, cultural eutrophication, alien introductions, the proliferation of hard substrata, and climate change (Purcell et al. 2007). In the Namibian situation, two of these may be important: overfishing and climate change. Roux et al. (2013) eloquently articulated the case for the former, and it is likely that overfishing created the initial

'space' for jellyfish to move into (Bakun and Weeks 2006). Since 1980, however, the marine ecosystem off Namibia has become warmer (Salvanes et al. 2015), and there has been an increase in the abundance of copepods off Walvis Bay, with changes in size composition favouring smaller copepods (Verheye et al. 2016).

Scyphozoans (and many hydrozoans) have a metagenic life cycle, wherein there is an alternation between generations of free-swimming medusae and (generally) a benthic polyp phase. The medusae reproduce sexually and the fertilised eggs develop into planula larvae that (typically) settle onto a hard substrate, whereas the polyps reproduce asexually to produce ephyrae and new polyps. Though temperature (Hansson 1997; Widmer 2005) and food (Olesen et al. 1996) can influence the growth of ephyrae, and likely too adult medusae, how these variables may quantitatively affect planula production and the size of future medusa populations is unknown. However, in the case of benthic polyps it is clear that both temperature and food can influence polyp population sizes (Lucas et al. 2012) and, by likely extent, subsequent medusa populations. At least, both food supply and temperature have been implicated as causative factors leading to jellyfish blooms elsewhere in the world (Purcell et al. 2007).

Our understanding of the factors that influence the polyps of Namibian jellyfish, especially scyphozoans, is presently non-existent as none have ever been observed *in situ*. However, we recently managed to culture some polyps of *Chrysaora fulgida* in the laboratory, following the methods of Widmer (2008a), and we used these to investigate the effects of water temperature, food density and feeding frequency on polyp growth and development.

## **Materials and methods**

Polyps of *Chrysaora fulgida* were derived from planulae collected in 2013 from the lagoon at Walvis Bay, Namibia. Polyps were plated on plastic Petri dishes and maintained in shallow, flow-through aquaria in the laboratory at the University of the Western Cape, South Africa, at a salinity of 35 (natural seawater). Ambient temperature was maintained at a constant 14 °C, and animals were exposed to a 12 h dark:12 h light regime. Polyps were fed with newly hatched *Artemia* nauplii, *ad libitum* once weekly, and re-plated on an *ad hoc* basis, when necessary.

In 2015, a series of experiments were conducted to investigate the effects of feeding frequency (once daily or once every third day), water temperature (12, 16 or 20 °C) and food density (at 0, 30, 70, 100 or 150 newly hatched *Artemia* nauplii 200 ml<sup>-1</sup>) on polyp growth and development, comprising 30 different treatments in total. Experiments were conducted over a 30-day period during September– October. Experimental polyps (8–17 tentacles, non-strobilating) were isolated from the main culture, plated on plastic Petri dishes (four per plate) and acclimated (in 350-ml glass beakers) to each experimental temperature for five days, without food, at a salinity of 35 and under a 12 h dark:12 h light regime. The glass beakers were suspended below the surface in aquaria wherein the water temperature was maintained at experimental levels using thermostat-controlled

heaters or chillers. The seawater within each glass beaker was replaced daily and observations were made on individual polyps immediately prior to feeding. The observations included a count of the number of daughter polyps and the modes of reproduction, with the latter identified following the descriptions of Adler and Jarms (2009) and Schiariti et al. (2014).

Data on the numbers of polyps produced were analysed using a generalised linear mixed-effects model (GLMM; with log-link), with temperature, food density and feeding frequency as fixed effects, and tank number and polyp (per individual) as random effects. Daily population growth rate ( $r$ ) was calculated as:

$$\text{Daily growth rate}(r) = \frac{N_t}{N_{t-1}} \quad (1)$$

and

$$\text{Standardised daily growth rate } (X) = \left[ \frac{N_t}{N_0} \right]^{1/(t-t_0)} \quad (2)$$

where  $N_t$ ,  $N_{t-1}$  and  $N_0$  refer to the numbers of polyps at times  $t$ ,  $t - 1$  and 0, respectively. The effect of temperature, food density and feeding frequency on the standardised daily growth rate ( $X$ ) was determined using three-way factorial ANOVA, and the effect of density on the daily growth rates was examined using regression techniques. Probability values for all tests were considered significant at a 0.05 level.

## Results

Asexual reproduction was observed in all treatments. This took the form of: (i) lateral budding by means of stolons (ST); (ii) podocysts (POD); (iii) strobilation; and (iv) lateral budding (LB) (*sensu* Adler and Jarms 2009). Although 70% of all polyps produced lateral stolons (Figure 1), fewer than 2% of these developed buds on the stolons. The number of stolons produced varied with food density and feeding frequency, but not temperature (Table 1).

Lateral budding was the most prevalent method of asexual reproduction by which new polyps were generated (Figure 1) and was first noticeable as a unilateral protrusion appearing at the junction of the polyp calyx and stalk. Soon thereafter, a stolon formed. The bud could be distinguished from the stolon on day 1, by the presence of a slight depression distally, surrounded by premature tentacles. Day 2 presented a bud with a defined mouth opening, and one or two well-developed tentacle primordia: the stolon had extended rapidly to attach to the Petri dish. From day 3 onwards, the bud was fully formed and able to feed. Daughter polyps detached themselves from the parent polyp by means of the new stolon, thereby moving away from the parent location.

Ephyrae were produced by only two polyps during the course of the experiment: both at 12 °C and at low food densities (i.e. 30 *Artemia* nauplii 200 ml<sup>-1</sup>, fed daily; 70 *Artemia* nauplii 200 ml<sup>-1</sup>, fed every third day); the number of ephyral discs observed was eight and five, respectively. Podocysts were produced in low numbers at all temperatures, though more were produced at lower food densities (30 or 70 *Artemia* nauplii 200 ml<sup>-1</sup>) than at higher ones (100 or 150 *Artemia* nauplii 200 ml<sup>-1</sup>). No podocysts were produced by starved polyps, and no excystment was observed during the course of the experiment.

The results of the GLMM (Table 1) revealed that all the variables impacted asexual reproduction, and that greater polyp production was generally attained at higher food concentrations, increased feeding frequencies and increased temperatures (Figure 2). Warmer temperatures and higher food concentrations also tended to be associated with a slightly earlier start to polyp proliferation. The number of new polyps grew exponentially (Figure 2) after an initial lag period of 23 days.

Standardised daily growth rates ( $X$ ) varied between 1.012 and 1.063 polyps per polyp per day when fed daily, or between 1.002 and 1.027 when fed once every three days (Table 2). As noted by the results of the GLMM on polyp numbers, the results of the three-way factorial ANOVA reveal that the standardised daily growth rate ( $X$ ) was impacted by all three predictor variables (Table 3). The overall model was significant (adjusted  $R^2 = 0.55$ ,  $F = 6.072$ ,  $p < 0.001$ ), though none of the predictors were, in any combination (Table 3). The relationship between time and standardised daily growth rate ( $X$ ) was positive and linear at lower temperatures, food densities and feeding frequencies, but approximately S-shaped at higher food densities and temperatures (data not shown). When all data were pooled, an exponential curve best fitted the relationship between polyp population size and standardised daily growth rate ( $X$ ) ( $R^2 = 0.86$ ), which stabilised at between 1.11 and 1.13 polyps per polyp per day following an observed density of approximately 15 polyps per clone. This appears to represent the maximum standardised growth rate that could be observed in the experimental population (Figure 3a). The slight negative relationship between daily population growth rate ( $r$ ) and population density was not significant ( $R^2 = 0.03$ ) (Figure 3b).



**Figure 1:** Changes in the proportional contribution of the different modes of asexual reproduction (i.e. typical lateral budding – LB, lateral buds by means of stolons – ST, and podocysts – POD) in comparison to stolon formation, as exhibited by polyps of *Chrysaora fulgida* through time in the different experimental treatments. Feeding frequency 1 (once daily) is indicated by solid lines, and feeding frequency 2 (once every third day) by broken lines

## Discussion

The most frequently displayed method of asexual reproduction by polyps of *Chrysaora fulgida* was typical lateral budding (*sensu* Adler and Jarms 2009). This form of asexual reproduction is common in Scyphozoa, having been reported for, among other species, *Sanderia malayensis*, *C. hysoscella* (Chuin 1930), *Aurelia aurita* (Han and Uye 2010), *A. coerulea* and *A. relictata* (Hubot et al. 2017). Lateral budding by means of stolons has previously been reported for other members of the genus *Chrysaora* (see references in Adler and Jarms 2009), and Hubot et al. (2017) noted that it was more commonly employed by polyps of *A. coerulea* and *A. relictata* at a higher temperature (i.e. 21 °C). While the polyps of *C. fulgida* observed here produced stolons, and some few of these stolons developed buds, the buds never developed into polyps themselves, and it appeared as though the stolons were used for stabilisation and movement. These observations are in contrast to those regarding many other *Chrysaora* species, which are known to favour lateral budding by means of stolons as a means of asexual reproduction (e.g. Condon et al. 2001; Adler and Jarms 2009), or, in the case of *C. fuscescens*, by podocysts (Widmer 2008b). Although

podocysts were produced by some of the *C. fulgida* polyps under all experimental conditions when fed, in no instance did these excyst and develop into polyps. All of these results merely support the fact that scyphozoan scyphistomae display a variety of modes of asexual reproduction (Adler and Jarms 2009)

**Table 1:** Summary of results from the generalised linear mixed-effects model; z-values and *p*-levels are shown for all fixed variables. None of the interactions were significant, and are thus not included in the table

Response variable	Fixed effects	z-value	<i>p</i> -value
Total no. of polyps produced	Temperature	2.981	0.003
	Frequency	-2.626	0.009
	Food density	-2.314	0.020
	Time	7.313	0.001
	Temperature : Time	-2.532	0.011
	Frequency : Time	2.098	0.036
	Food density : Time	3.945	0.001
Cumulative no. of stolons	Temperature	1.507	0.132
	Frequency	-1.920	0.054
	Food density	-8.372	0.001
	Time	17.940	0.001
	Temperature : Time	-0.865	0.387
	Frequency : Time	1.964	0.049
	Food density : Time	10.223	0.001
Cumulative no. of buds from stolons	Temperature	-0.989	0.323
	Frequency	-0.197	0.844
	Food density	0.623	0.533
	Time	4.539	0.001
	Temperature : Time	1.623	0.105
	Frequency : Time	0.249	0.803
	Food density : Time	-0.112	0.910
Cumulative no. of buds from polyps	Temperature	4.915	0.001
	Frequency	-4.503	0.001
	Food density	-12.502	0.001
	Time	12.332	0.001
	Temperature : Time	-4.238	0.001
	Frequency : Time	4.579	0.001
	Food density : Time	14.763	0.001
Cumulative no. of podocysts	Temperature	0.461	0.645
	Frequency	-1.995	0.001
	Food density	-4.340	0.001
	Time	1.273	0.203
	Temperature : Time	-0.359	0.719
	Frequency : Time	2.189	0.001
	Food density : Time	4.811	0.001

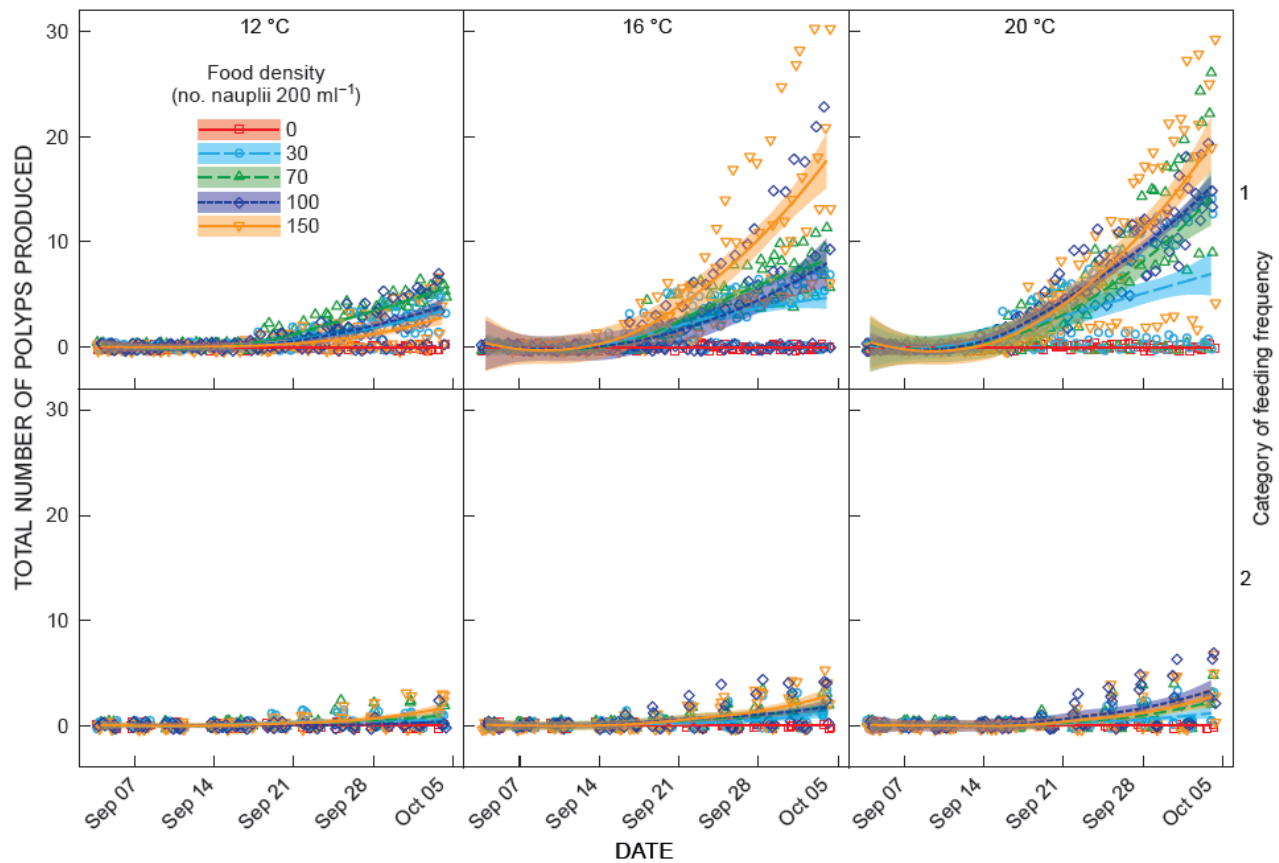
and our understanding of which method is employed by which species and under which set of circumstances is at present unclear, especially as it may vary with population

density (Schiariti et al. 2015). We cannot comment on strobilation by *C. fulgida* in the laboratory at this stage, because the data collected here are scant, and the study was not designed to examine strobilation.

Temperature, food density and feeding frequency all affected the growth and asexual reproduction of polyps of *C. fulgida*. This is not new information *per se*, as a number of authors have shown that, as food availability and ambient water temperature increase, the number and asexual development of polyp clones (number of polyps and buds in the clonal colony) and individual polyps (number of buds per active polyp), increase significantly (e.g. Han and Uye 2010). Nevertheless, the standardised daily growth rates reported here for *C. fulgida* are among the highest recorded for polyps of any jellyfish species in culture. For example, the standardised growth rate of a polyp of *C. fuscescens* has been measured at 1.017 (Widmer et al. 2008b), whereas Purcell (2007) has shown that polyps of *A. labiate* have standardised growth rates of 1.011–1.016. Our data therefore suggest that polyp populations of *C. fulgida* can expand rapidly—even under cool temperatures and ‘relatively low’ food concentrations.

The lack of a significant relationship between daily population growth rate and population density suggests an absence of density-dependent controls on growth at the densities studied. This result contrasts with those of Melica et al. (2014) and Schiariti et al. (2015), who noted that increases in density led to reductions in growth rate. Indeed, the results of both those studies imply that polyp populations (in the laboratory) may be regulated around a carrying capacity, and Schiariti et al. (2015) intriguingly suggest that, at very high densities, polyps may switch their mode of asexual reproductive to facilitate emigration. Carrying capacities were not attained in the present study, which perhaps simply implies that the experiments were not conducted for long enough.

Caution should be exercised in extrapolating the present data to the field, because even the lowest prey density used here (30 *Artemia* nauplii 200 ml<sup>-1</sup>) exceeds the highest recent *in situ* estimates off Walvis Bay (Verheye et al. 2016).



**Figure 2:** Cumulative number of polyps produced from parent polyps of *Chrysaora fulgida* reared under varying food densities, temperatures and feeding frequencies (1 = once daily; 2 = once every third day), across the four-week experimental period. Shaded areas around fitted lines indicate 95% confidence intervals

**Table 2:** Means (standard deviation) of the standardised daily population growth rates of *Chrysaora fulgida* polyps (polyps per polyp per day), calculated after 30 days in the laboratory, under different combinations of water temperature, food density (no. *Artemia* nauplii 200 ml<sup>-1</sup>) and feeding frequency; in all instances,  $n = 4$

Feeding frequency	Temperature (°C)	Food density				
		0	30	70	100	150
Once daily	12	1 (0)	1.019 (0.025)	1.03 (0.0316)	1.018 (0.0265)	1.012 (0.0229)
	16	1 (0)	1.033 (0.0396)	1.042 (0.0412)	1.026 (0.0428)	1.056 (0.0511)
	18	1 (0)	1.042 (0.0487)	1.046 (0.0523)	1.063 (0.0496)	1.056 (0.0531)
Once every third day	12	1 (0)	1.013 (0.0165)	1.011 (0.0179)	1.002 (0.0072)	1.014 (0.0199)
	16	1 (0)	1.012 (0.0205)	1.022 (0.0231)	1.021 (0.0285)	1.025 (0.0281)
	18	1 (0)	1.011 (0.0203)	1.017 (0.0228)	1.027 (0.0311)	1.018 (0.0288)

Nonetheless, polyps of *Chrysaora fulgida* clearly have a capacity to respond even to what are likely to be considered *ad libitum* concentrations of prey. Type-II feeding responses are typically exponential at food concentrations above a baseline threshold (Begon et al. 2006) and flatten towards satiation.

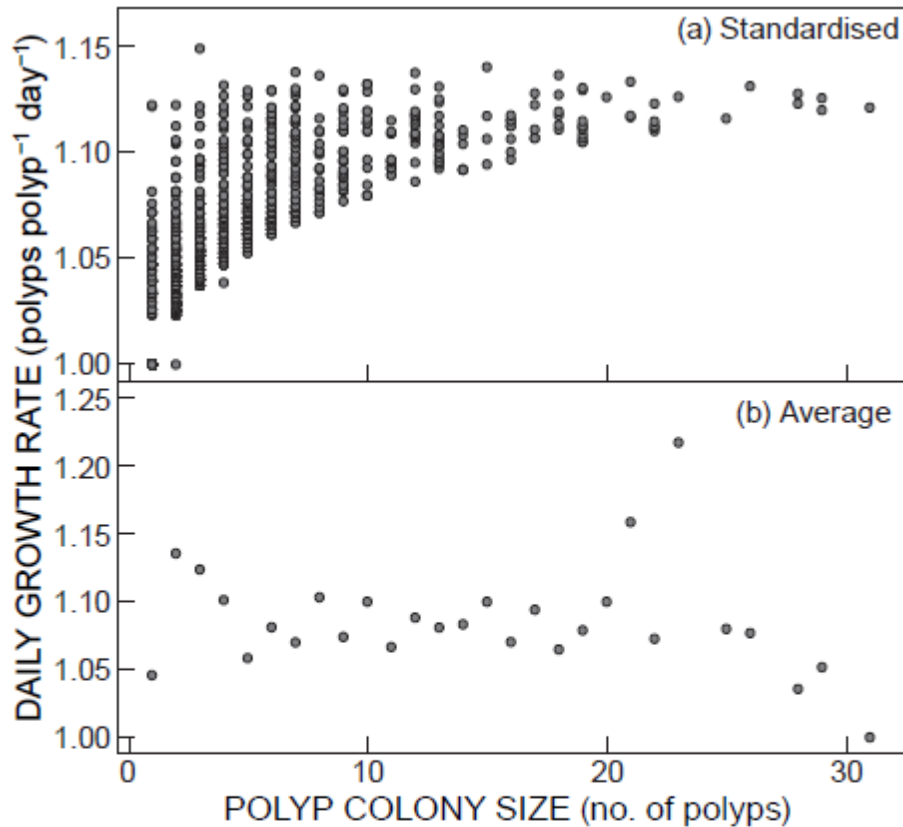
Given the response of scyphistomae of *Chrysaora fulgida* to food availability and water temperature, both of which have increased off parts of Namibia in recent decades (Salvanes et al. 2015; Verheye et al. 2016), it is not unlikely that polyp populations have expanded. Beyond the expansion that will have occurred following the increase in medusa



population sizes subsequent to the demise of pelagic fish populations (Roux et al. 2013) and the likely increase in planulae recruitment (see also Gibbons et al. 2016), it is clear that renewed efforts are merited to locate the polyp beds of *C. fulgida* off Namibia so that direct measurements (cf. Di Camillo et al. 2010) can be made on this ‘hidden’ stage in the jellyfish’s life cycle.

**Table 3:** Univariate tests of significance from a three-way factorial ANOVA to illustrate the main effects and the interactions of water temperature, feeding frequency and food density on the standardised growth rates ( $X$ ) of *Chrysaora fulgida* polyps, calculated at  $t = 30$

	SS	df	MS	F	p-value
Intercept	129.922	1	129.922	22 1575.3	0.000
Temperature	0.009	2	0.005	7.8	0.001
Feeding frequency	0.019	1	0.019	31.6	0.000
Food density	0.057	4	0.014	24.3	0.000
Temperature : Feeding frequency	0.001	2	0.000	0.5	0.629
Temperature : Food density	0.009	8	0.001	1.9	0.067
Feeding frequency : Food density	0.005	4	0.001	2.1	0.093
Temperature : Feeding frequency : Food density	0.004	8	0.001	0.9	0.527
Error	0.053	90	0.001		



**Figure 3:** The effects of *Chrysaora fulgida* polyp colony size on (a) standardised daily growth rate ( $X$ ), and (b) average daily growth rate ( $r$ )

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