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ORIGINAL ARTICLE

The challenge of life history traits: a small cladoceran, *Ceriodaphnia rigaudi*

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Abstract

Using accurate and precise species-specific parameters in mechanistic models can lead to better predictions of population dynamics and ecosystem function (e.g. nutrient cycling) across a range of environmental conditions. Zooplankton are important in the aquatic food web and for nutrient cycling but are highly diverse, and there is only limited information on specific species. Knowledge of species-specific attributes is patchy. In particular, tropical species are underrepresented in this regard. Here, we gather all the known information about a wide-spread tropical zooplankton member, *Ceriodaphnia rigaudi*, and add new information from lab and field experiments. We determine feeding rate across a range of food concentrations and food-dependent population growth rate of *C. rigaudi*. Additionally, we use 16 years of occurrence data from rock pools in Jamaica to explore environmental characteristics of the habitat in which *C. rigaudi* live. We compare our data to worldwide records of the species attributes and create a reference map of its occurrence.

Keywords Ceriodaphnia · Species traits · Life history

Introduction

Functional traits are morphological–physiological aspects of a species that impact fitness (Violle et al., 2007); often functional traits are also traits of the organisms that directly interact with (sensu effect traits Hébert et al., 2017; Lavorel and Garnier, 2002) the environment. Functional traits are important for two reasons: (1) making model predictions involving a specific species of interest (e.g. van der-Meer,2006; (2) enabling classifications of species into functional groups for classic trait-based models (e.g. Vogt et al., 2013). Trait-based models may be particularly important in aquatic systems due to high species richness (e.g. phytoplankton) and the desire for species-specific models (e.g. fisheries). Aquatic systems are well-suited to trait-based methods due to a long history of modelling (Robson, 2014) and combining of high species richness into subgroups (e.g. phytoplankton: Litchman et al. 2010; zooplankton: Litchman et al. 2013). Yet, despite advances in data amalgamation for aquatic species (e.g. Hèbert et al., 2016; Robson et al., 2018) more information is always needed for additional species to expand the usefulness of trait-based methods.

Zooplankton represent a large and important part of aquatic systems and yet species specific information is limited. Zooplankton classifications are usually based on size and feeding strategy. However, size may not be a good predictor of traits of interest (e.g. grazing) outside of temperate regions (Pinheiro-Silva et al., 2020) which may be a larger problem than currently realized because tropical species tend to be underrepresented (e.g. Hèbert et al., 2016; Rizo et al., 2017). One challenge is the limited scope of studies on life history that makes it impossible to tell if species traits are consistent throughout their range. With more resolved life history information, more informed and nuanced decisions for trait-based classifications should be easier. Here, we provide additional information for a small, tropical cladoceran, *Ceriodaphnia rigaudi*.

Cladocerans are a second crucial link between lower trophic levels (microbial) and upper trophic levels (fish) of the freshwater food web (Burns & Schallenberg, 2001), alter algal production and community structure (Sommer et al., 2001), and impact nutrient cycling (e.g. Migal, 2011). However, most cladoceran species have little life history information; a meta-analysis by Hébert et al. (2016) found that the genus Daphnia comprises half of all known cladoceran

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information. Despite a known 620 unique cladoceran species (Litchman et al. 2010), a meta-analysis found species trait information on less than 70 (Hébert et al., 2016) which is concerning for the ubiquitous use of species traits in aquatic modelling. Gathering more information on smaller cladocerans will help identify when size is or is not a good proxy for traits of interest.

Ceriodaphnia rigaudi is a small cladoceran commonly found throughout tropical freshwater ponds. Originally thought to be distinguished from *Ceriodaphnia cornuta* by the absence of head, shoulder and tail spikes, this classification turns out potentially to be based solely on predation and not a true physiological characteristic (Rietzler et al., 2008). However, recent genetic tests do in fact place *C. rigaudi* as a separate species from *C. cornuta* (Sharma & Kotov, 2013). *C. rigaudi* have been considered for use as a water quality indicator species and as such have been used in some toxicology experiments (e.g. Raymundo et al., 2019; Mohammed, 2007), and may be important community indicators (Márquez et al., 2016). Because *C. rigaudi* is also widespread and may play a dominant role in some systems, understanding its traits and distribution could be important for nutrient cycling and food web models in specific locations. However, little is known about their life history traits. Here, we amalgamate all data on the life history and geographical spread of the species and add information from our own laboratory experiments and field observations.

Methods

All analyses were completed in R. Data and codes are available: https://github.com/jwerba14/Ceriodaphnia.

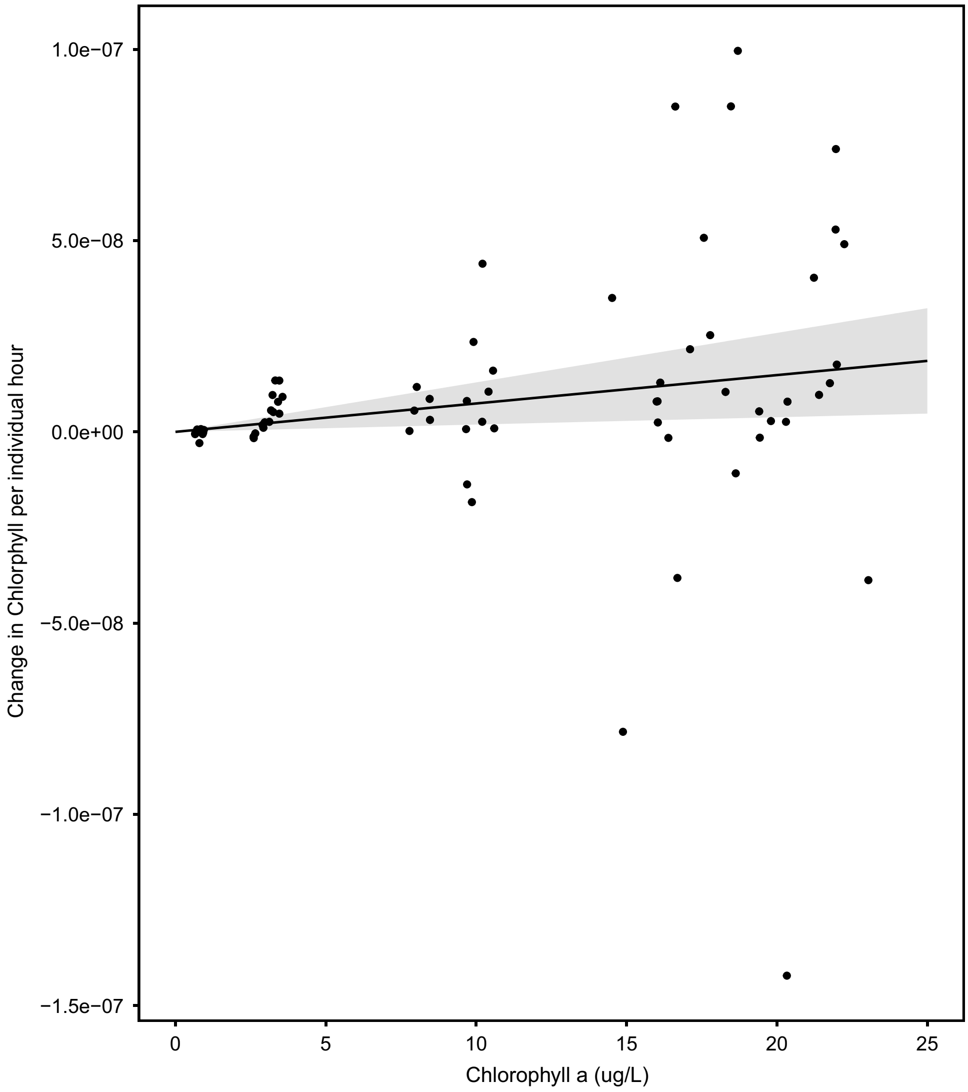

Fig. 1 Feeding rate of *C. rigaudi* individuals per hour

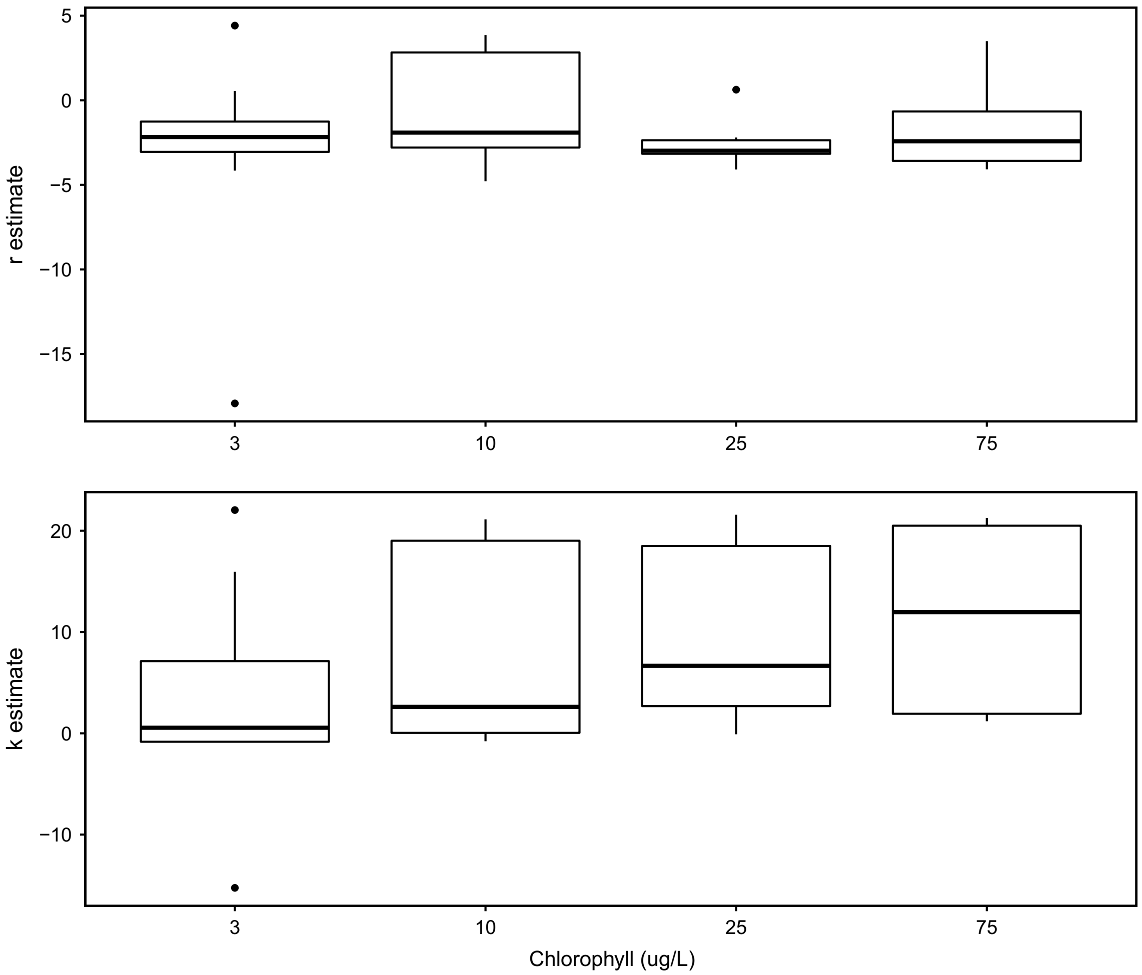

Fig. 2 Estimates of r and k for *C. rigaudi* populations at different constant food treatments; estimates are on the log scale

Laboratory conditions

Ceriodaphnia rigaudi has been maintained in our laboratory continuously for several years. All individuals used in our experiments came from our laboratory population and were randomly removed for experiments. The colony originated from Jamaican rock pools. Water temperature of the stock cultures varied from 17–22 °C.

Feeding rates

To determine how quickly *Ceriodaphnia rigaudi* cleared *Haematococcus sp.* from the system, we used five treatments of chlorophyll-a concentration (mean ± SD: 0.778 ± 0.0985µg—Chla/L, 3.11 ± 0.321µg—Chla/L, 9.43 ± 1.01 µg—Chla/L, 16.7 ± 1.24 µg—Chla/L, 20.9 ± 1.27 µg—Chla/L) with five replicates each. Temperature was kept at (mean ± SD) 20.7 ± 1.1. These chlorophyll-a environments were chosen to span a range of lake trophic states from oligotrophic to eutrophic (Kratzer & Brezonik, 1981). Each replicate had an average of 75 individuals. We measured chlorophyll-a after six hours. We did not expect discernible growth in the *Haematococcus sp.* population over six hours, but we did include three replicates without any *Ceriodaphnia* for each chlorophyll treatment to account for any growth or death of algae unrelated to grazing to be used as a reference. We subtracted the average change of the controls, by treatment, from the experimental replicates. We ran a linear model across food treatment to determine average uptake rate.

Population growth

For population growth, we began colonies in 1.1 L of water with 30 individuals of *Ceriodaphnia rigaudi* each at four chlorophyll-a treatments (mean ± SD: 2.93 ± 0.905µg—Chla/L, 9.39 ± 22.5µg—Chla/L, 22.3 ± 6.32µg—Chla/L, 65.5 ± 10.1 µg—Chla/L) with six to nine replicates each. Temperature of tanks between (mean ± SD) 21.6 ± 0.5 °C As in the feeding experiment concentrations was chosen to represent a range of trophic states. Everyday either algae or distilled water was added to bring the tanks back to the chlorophyll concentration level; chlorophyll-a was measured using an AquaFlor fluorometer. *Ceriodaphnia rigaudi* was counted weekly in eight 50-mL sub-samples. Replicates were ended when *C. rigaudi* where extirpated or 50 days from initiation had passed. We fit a logistic growth curve (1) to each replicate separately using `nlxb` (Nash & Murdoch, 2021) and then ran a linear regression of each parameter (r,k) against the food treatment.

$$N_t = \frac{k}{1 + \frac{k-N_0}{N_0} e^{(-rt)}} \tag{1}$$

where k is the population asymptote, r is the growth rate and N_0 is initial population size

Literature search

A Google Scholar search on April 23, 2020, for "Ceriodaphnia rigaudi" resulted in 523 hits. We downloaded those papers that had survey data or had life history information for a total of 196 papers. Of those, we found 94 with either geographical information (92) or life history information (3 papers). After confirming geographical coordinates, we accepted 137 records as sufficiently reliable.

Distribution

We mapped *C. rigaudi* with the `maps` package (code by Richard A. Becker et al., 2021); the map includes 138 locations (one is our own data). Whenever possible, we mapped the exact sampling locations (considered exact if the coordinates were reported in the manuscript or we found the body of water mentioned). We did not consider any river an exact location (unless coordinates were given). All coordinates are the closest we could establish based on the location description found in the paper.

Jamaican data and Habitat

Rock pools are located on the west coast of Discovery Bay, Jamaica. Fifty out of over 200 pools were sampled annually from 1989–2006, (except 2004) (Hammond et al., 2020). We also obtained salinity and oxygen concentrations as well as pH and temperature from each pool. To determine which if any environmental factors were associated with the presence or absence, or level of abundance of *C. rigaudi*, we ran a hurdle model with a zero inflated negative binomial error distribution in `glmmTMB` package (Brooks et al., 2017).

Results

Feeding rate Individual *C. rigaudi* took up marginally more chlorophyll-a per hour as chlorophyll-a availability increased (Estimate: 7.42e−10, $p = 0.009$, Fig. 1).

Population growth rate We were unable to estimate a nonzero slope across feeding treatments for either r or k ($p > 0.05$). Food treatment did not explain much of the variance in either parameter ($R^2 < 0.1$). The range of r and k estimates for each treatment was very variable by replicate (Fig. 2).

Environmental correlates We find, in the Jamaican rock pools, that as pH, oxygen and salinity increase, the probability of *C. rigaudi* being present declines ($p < 0.05$, Fig. 3). Decreases in pH and salinity increase the abundance of *C.rigaudi* ($p < 0.05$, Fig. 3). We are unable to detect an effect ($p > 0.05$) of temperature on either presence or abundance of *C. rigaudi*.

Map of species distribution We were able to find 138 records of *C. rigaudi* in survey data. We see clusters in southern Brazil. Otherwise, records spread throughout Africa, south Central Asia and parts of central America (Fig. 4), while *C. rigaudi* is generally thought of as a tropical species; we found records outside the tropics or subtropics, in the United States and southern Europe.

Life history information from literature Three papers provided some measurement of life history information about *C. rigaudi*. These papers supplied information about either fecundity, clutch size or time to maturity. No papers provided information about feeding or excretion rates (Table 1).

Discussion

We find that feeding rate increases very little as food concentration increases. As far as we are aware, this is the first study of *C. rigaudi* feeding rate. Estimating population growth rate was challenging, and our fits gave wide possible ranges for k and r. Due to the high variation among replicates, we could not identify a pattern across food concentration for either parameter. Likely some of this variation is due to the fact that experiments contained a range of size and developmental stages of individuals. Interestingly, higher food concentrations did not give reliably higher

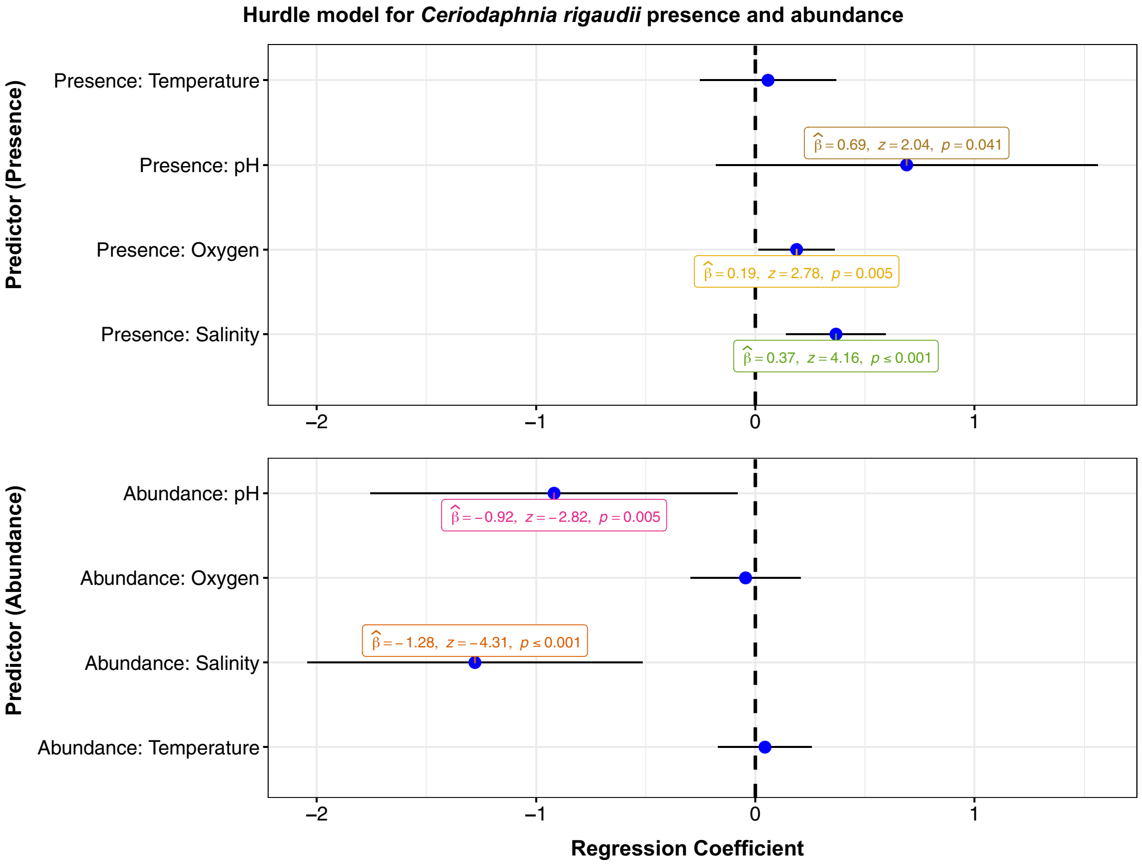

Fig. 3 Environmental factors contributing to the presence (**a**) and abundance (**b**) of *C. rigaudi* presence in Jamaican rock pools based on a hurdle model

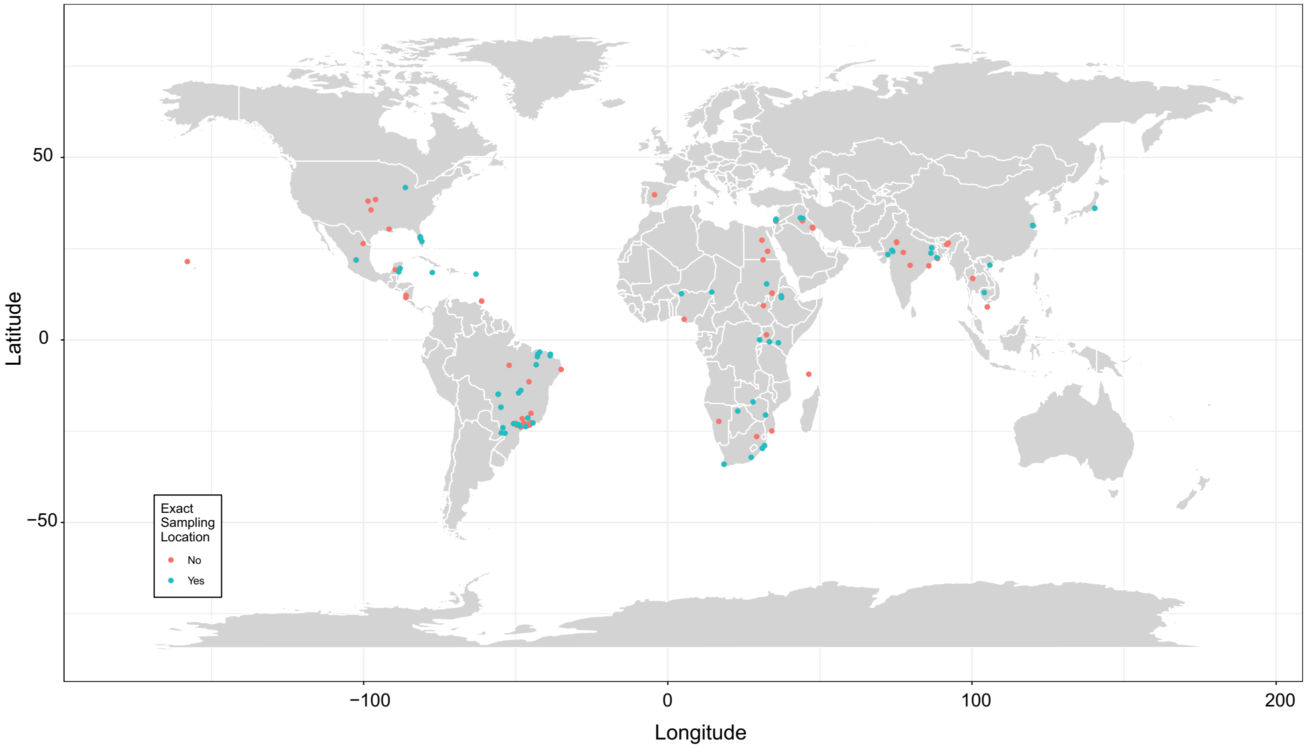

Fig. 4 All reported sightings of *C. rigaudi* in published works

Table 1 Data summaries from the literature review

Trait(s) measured	Independent variable	Summary	Study
Sexual maturity (d)		2	Mohammed (2009)
Survival (d)		10–15	
Average clutch size		4	
Average clutch size	Food type and temperature	Largest with *P. subcapitata*, 25°C 2.9–6.6 (min–max)	Martinez-Jeronimo and Ventura-Lopez (2011)
Total offspring	*Ankistrodesmus falcatus*, *Pseudokirchneriella subcapitata*, *Chlorella vulgaris*	Most with *A. falcatus*, 25°C 9.8–40.8 (min–max)	
Number of clutches		Most with *A. falcatus* at 20°C 2.9–11 (min–max)	
First reproduction (d)	20 and 25°C	Shortest with *A. falcatus* at 20°C 4–12 (min–max)	
Survival (d)		Longest with *A. falcatus* at 20°C 15.2–48.7 (min–max)	
Average clutch size	Month	1.5–3.2 (min–max)	Burgis (1973)
Body size (μm)		329–465 (min–max)	
Total offspring	Harmful cyanobacteria (0, 20, 40, 60, 80, 100%)	Decreased 0–1.7 (min–max)	Gu et al. (2020)*
First reproduction (h)		Increased 1–5 (min–max)	
Survival(d)		Decreased 10–12 (min–max)	

*Likely a different species, in paper referred to as *C. cornuta*, but the complex is difficult to differentiate and likely has many of the same traits

populations at the end of eight weeks, suggesting that either our algal species (*Haematococcus sp.* mixed with *Scenedesmus sp.*) were not favoured food or that other factors were limiting their growth (Fig. 5). Previous studies have shown clutch size, survival and day to first reproduction to vary with different food type and concentrations (all data in our metafile; summary provided in Table 1; Burgis, 1973; Mohammed, 2007; Martinez-Jeronimo and Ventura-Lopez, 2011). Excretion and uptake rates of nutrients for *C. rigaudi* would be helpful additional traits to measure.

While we find *C. rigaudi* throughout the tropic and subtropic regions (Fig. 4), some of the records are quite old and may no longer be accurate. For example, we did not include a record from Garças Reservoir, Sao Paulo, Brazil (Di Genaro et al., 2015), because the most recent paper did not find any *C. rigaudi*, and it appears to have disappeared since 1997. However, it is unclear if this was seasonal and the species will return or if it is in fact extirpated. Many of our records are quite old (e.g. Jones, 1958; Egborge, 1987) and or/ single sightings (e.g. Hart and Boane, 2004) and thus make any extrapolation about continued presence or changes over time impossible.

Tropical freshwater species are understudied. *Ceriodaphnia rigaudi* is a widespread species that may be useful as a water quality indicator species, but more information about the species is critical. Here, we provide some of the needed information. It is important to continue to learn about tropical species for water quality and toxicity because their responses may be quite different than temperate species (Mohammed, 2007).

Trait-based approaches are powerful tools for understanding community assembly (Cornwell & Ackerly, 2009), species distributions (McGill et al., 2006), and the impact of particular species on the environment (Lavorel & Garnier, 2002). However, trait-based methods require a large database of information about a wide array of species. Furthermore, our experiments indicate that the estimates of crucial parameters prerequisite for the quantitative evaluation of *C. rigaudi* role in aquatic systems are difficult to obtain even under controlled conditions and considerable time investment. Superimposed on the possible regional variation, this difficulty may limit the range of predictions that trait-based models involving zooplankton species will be able to make. At the same time, our observations highlight a need for further research into the variation of r and k and conditions explaining such variation.

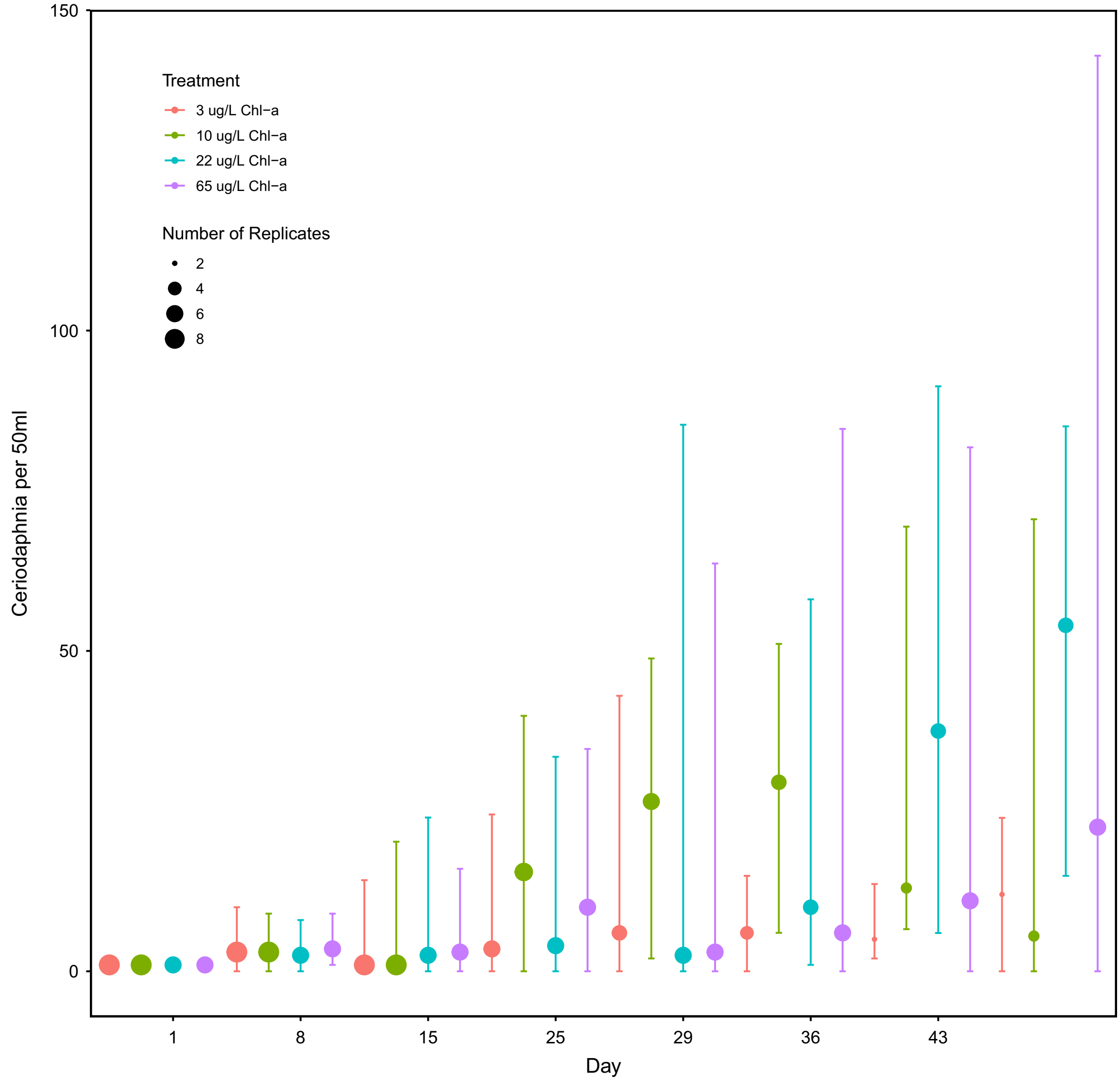

Fig. 5 *C. rigaudi* counts per 50-ml sub-samples. Colour represents food treatments. Points show means of eight sub-samples from all replicates. Error bars are 95% CI

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Declaration

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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