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Source: African Invertebrates, 54(1) : 161-170

Published By: KwaZulu-Natal Museum

URL: https://doi.org/10.5733/afin.054.0110

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African Invertebrates Vol. 54 (1): 161–170 Pietermaritzburg 14 May 2013

Observations on the bloom-forming jellyfish *Crambionella stuhlmanni* (Chun, 1896) in the St Lucia Estuary, South Africa

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ABSTRACT

Opportunistic observations made in the St Lucia estuarine lake, mainly during the period 1991 to 2000, show that the rhizostomatid scyphozoan *Crambionella stuhlmanni* often forms aggregations with densities in excess of 1 ind.m^{-3}. Its salinity tolerance varies in the range of 12–65 ‰, with the highest jellyfish concentrations often observed at hypersaline levels of 40–65 ‰. Considering that the species has persisted in the system under the present closed mouth conditions, it is suggested that it is capable of completing its life cycle within the estuarine lake. Its role in the ecosystem needs to be investigated, with emphasis on its potential ability to remove suspended sediment particles from the water-column.

KEY WORDS: Scyphozoa, *Crambionella stuhlmanni*, iSimangaliso Wetland Park, St Lucia, estuarine lake, jellyfish, salinity tolerance.

INTRODUCTION

Scyphozoan jellyfish are conspicuous because of their relatively large size and ability to form dense blooms at seasonal intervals (Brusca & Brusca 2003). Recently, jellyfish blooms have been reported with increased frequency from several parts of the world and it has been suggested that this phenomenon might be related to over-fishing and other human activities that are driving marine ecosystems off balance (Pauly *et al*. 1998). Although this view has been contested by some researchers (Condon *et al*. 2012, 2013), it has contributed to the formulation of the "fishing down the food chain" hypothesis (Pauly *et al*. 1998), which is based on the assumption that the reduction in fish populations and of other large marine predator populations is promoting the growth of organisms from lower levels of the food chain (Graham 2001). Ecological support for this idea is based on the concept of eutrophication potentially increasing the food supply to jellyfish, overfishing decreasing predation and competition for resources, and rising temperatures promoting jellyfish reproduction and growth (Mills 2001; Schrope 2012).

Despite their apparent importance for marine ecosystems, and their potential use as key indicators of ocean health, jellyfish have not been adequately investigated yet. Little is known about their population dynamics, taxonomy and natural variability. This has been attributed not only to the complexity of their life cycles, but also to difficulties encountered when collecting and studying most of the species (Schrope 2012). Moreover, the considerable phenotypic plasticity and crypsis that many species exhibit complicates their identification as well as attempts to carry out research on them (Dawson 2005; Neethling *et al*. 2011).

Only three species are known at present for the genus *Crambionella* Stiasny, 1921, and all appear to be restricted to the Indian Ocean (Neethling *et al*. 2011). *Crambionella stuhlmanni* (Chun, 1896) (Fig. 1), originally described from the Quelimane River mouth in central Mozambique, was recently reassessed using both molecular and morpho-

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Fig. 1. Large specimen (≈16 cm bell diameter) of *Crambionella stuhlmanni* in the shallows of Charter's Creek. (Photo Nicola K. Carrasco, 29 May 2008)

logical characters of specimens collected in the St Lucia Estuary (Neethling *et al*. 2011). No ecological or behavioural information was, however, included either in the work of Neethling *et al*. (2011) or in the studies conducted prior to this. *C. stuhlmanni* is apparently endemic to the East African coastline and has been recorded in the St Lucia Estuary since the very earliest surveys conducted there. Apart from St Lucia, the currently known distribution for the species includes the coasts of Mozambique and Madagascar (Neethling *et al*. 2011).

The St Lucia Estuary is the largest estuarine lake in Africa and forms a crucial part of South Africa's first UNESCO World Heritage Site, the iSimangaliso Wetland Park (Whitfield & Taylor 2009). It consists of three major lake basins (False Bay, North Lake

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Fig. 2. Map of the St Lucia estuarine lake, showing the main basins and stations within the system.

and South Lake), which are generally connected to the Indian Ocean through a narrow, long channel knows as the 'Narrows'. The estuarine lake is susceptible to periodic large-scale fluctuations in physico-chemical characteristics due to stochastic flood and drought events, and has recently experienced a prolonged period of virtually uninterrupted mouth closure since 2002 (Whitfield & Taylor 2009; Cyrus *et al*. 2011).

Here we report on findings for *C. stuhlmanni*, mostly obtained during a decade of opportunistic observations made in the St Lucia estuarine lake, between 1991 and 2000. Data were gathered during routine monitoring surveys undertaken mainly by the regional conservation body, Ezemvelo KwaZulu-Natal Wildlife (EKZNW).

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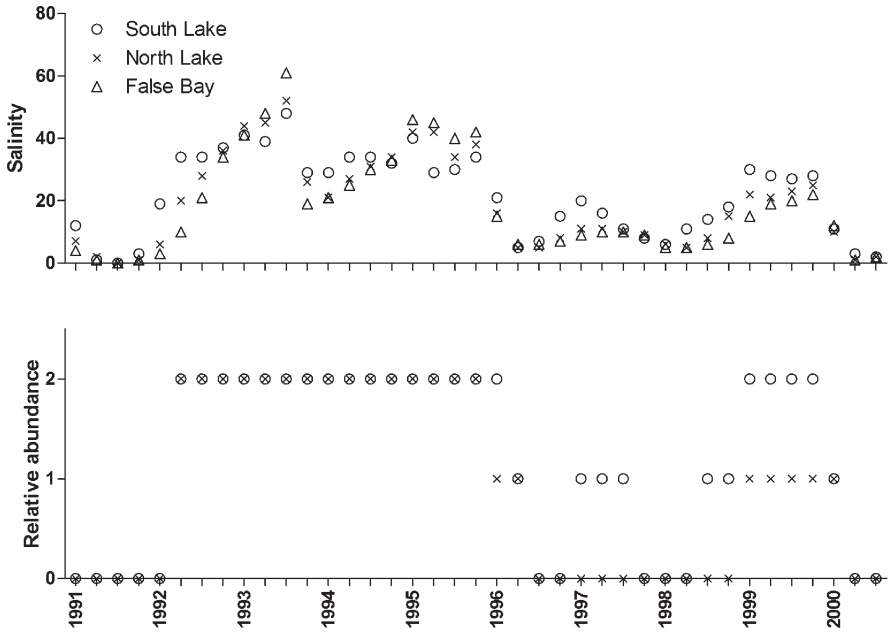


Fig. 3. Salinity and relative abundance of *Crambionella stuhlmanni* recorded in the St Lucia Estuary from 1991 to 2000. Abundance: 0 – absent, 1 – present, 2 – abundant.

MATERIAL AND METHODS

The occurrence of *C. stuhlmanni* in St Lucia was estimated qualitatively every quarter for the period 1991 to 2000 at two of the main lake basins, viz. North Lake and South Lake (Fig. 2). On each occasion, jellyfish were noted as "absent", "present", or "abundant" (Fig. 3) by the same EKZNW team while crossing the entire lake by motorboat. Surface salinity measurements were made in conjunction with the jellyfish observations.

The only quantitative information available for this species in St Lucia was gathered in January 1987 and May 2008, when specimens were collected using a "gate net" and a hyperbenthic sled-net, respectively. The first sampling occasion (January 1987) coincided with a wet phase at full lake levels and under open mouth conditions. The second (May 2008), in contrast, was characterized by persistent mouth closure and dry conditions, when extensive desiccation was occurring throughout the lake surface (Whitfield & Taylor 2009; Carrasco *et al*. 2010; MacKay *et al*. 2010; Cyrus *et al*. 2011). The gate net consisted of a rectangular aluminium frame 4.9 m wide by 1.1 m high, which was mounted on skids to prevent it from sinking into the muddy substratum during trawling. The netting was approximately 4 m deep with 25 mm stretch mesh and was designed specifically for the prawn fishery operating in the estuary at the time (Forbes & Forbes 2013). The hyperbenthic sled-net, on the other hand, was fitted with a 200 µm mesh net and towed in shallow waters for a distance of about 30 m. The mouth of the net was semi-circular in shape (r = 18.5 cm) and was mounted on the sled, so that the net was raised 7.5 cm above the sediment surface. In both cases, when using either the gate net or the hyperbenthic sled, the volume of water filtered was calculated by multiplying

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the area of the net mouth by the distance towed. Specimens collected were counted, measured (umbrella diameter in mm) and generally released.

RESULTS

During the January 1987 survey, the size of the jellyfish specimens collected ranged from approximately 100 to 150 mm (bell diameter), which is well within the recognized size range for the species of 62–200 mm (Chun 1896; Stiasny 1922; Neethling *et al*. 2011). Jellyfish densities were on average about 0.3 ind.m^{-3}, with denser blooms in the north-eastern part of North Lake approaching levels of 1 ind.m^{-3}. Salinity data for this time period showed levels of about 30–35‰ virtually throughout the lake region.

Densities of 1.3 ind.m^{-3} were obtained during May 2008 at Lister's Point, after the mouth of the estuary had been closed uninterruptedly for almost 10 months and the desiccating lake had reached hypersaline levels of about 44‰.

As regards the qualitative quarterly surveys undertaken between 1991 and 2000 in the South and North lakes, jellyfish relative abundance peaked during the years 1992–1995, when salinity levels were in the range of 20–60‰ (Fig. 3). A secondary, smaller peak was also attained during the first nine months of 1999, but this appeared to be restricted to the South Lake, where salinity at the time was between 25 and 30‰. When abundance indexes are compared with salinity levels during the entire 10-year period, the range of tolerance for this species as determined in Lake St Lucia is seen to be from 12 to 65‰ (Fig. 3). Although densities of individuals per unit volume of water were not measured during this period, under peak conditions dense blooms were regularly observed in the lake. Large numbers of jellyfish were found washed up on the sand and mud along the lake shores (Fig. 4), where a long fetch prevailed and a wind had been blowing constantly for several hours. This occurred mainly when the jellyfish were sluggish (or dead), floating and carried by wind/wave action, but not while they were actively swimming.

The specimens used in the taxonomic study of Neethling *et al*. (2011), i.e. 48 specimens collected by dip-netting during December 2005 and three more specimens collected by hand during September 2008, were found after 3.5 and one year of persisting mouth closure, respectively.

DISCUSSION

An accurate identification to species level of the jellyfish recorded regularly in the St Lucia estuarine lake has only been provided recently, through the combined molecular and morphological study of Neethling *et al*. (2011). Although Day *et al.* (1954) did not specifically mention the species in their report on the first St Lucia scientific survey, their reference to the occurrence of "large numbers of Rhizostomid jellyfish all over the estuary" leaves very little doubt as to their identity. The same jellyfish were also abundant at the time of the second survey conducted by the University of Cape Town team, during the years 1964–1965 (Millard & Broekhuysen 1970). Grindley (1982) noted large numbers (the species was erroneously identified at that time as *Crambionella orsini*; see Neethling *et al*. 2011), particularly in the region of the Narrows during a long-term investigation spanning the years 1948 to 1980.

More recently, *C. stuhlmanni* has been collected repeatedly in substantial numbers, even under conditions of prolonged mouth closure of the estuary. Similarly, the con-

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Fig. 4. Swarming *Crambionella stuhlmanni* washed up on the shore of Catalina Bay. (Photo Ricky H. Taylor, Dec. 2005)

centrations of 1.3 ind.m^{-3} obtained in this study at Lister's Point during May 2008 were recorded 9 months after the re-closure of the mouth. Occasional occurrences have been recorded at least until November 2011 at Catalina Bay, well over four years since the

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mouth was last breached by storm activity from the ocean side (March–August 2007). Although nothing is yet known about the life cycle of *C. stuhlmanni*, this is evidence that it may be completed inside the estuarine lake, rather than requiring a "seeding population" from the ocean. The species probably has a polyp stage capable of forming resting cysts under unfavourable conditions (e.g. hypersalinity and lake desiccation during droughts or limnetic phases following floods) and of strobilating when suitable conditions prevail again (Barnes *et al*. 2001; Schrope 2012). Unrelated faunal species have been observed developing in large numbers inside Lake St Lucia under closed mouth conditions and favourable salinity levels, only to disappear completely once major salinity changes occur (Carrasco & Perissinotto 2012). In some cases, resting forms have been positively identified, for instance of the ciliate *Fabrea* cf. *salina* (Carrasco *et al*. 2013).

Virtually no information is currently available on the role that *C. stuhlmanni* plays in the ecosystems it inhabits. Although jellyfish are often regarded as trophic dead-ends (Lynam *et al*. 2006), worldwide at least 124 fish and 34 other animal species are known to utilize jellyfish in their diet (Pauly *et al*. 2009; Richardson *et al*. 2009). There is not as yet any direct evidence of consumption of jellyfish by predators in the St Lucia Estuary. It seems likely that large fish and some birds, generally observed in the estuarine lake, would be able to ingest *C. stuhlmanni* of appropriate sizes. A single jellyfish (identified as *Eupilema inexpectata*, probably erroneously) was recorded in the stomach of a crocodile, *Crocodylus niloticus*, during the study by Leslie (1997) at Lake St Lucia. Globally, predation on jellyfish is mainly by fish, turtles, seabirds and even a few invertebrates, with some species actually regarded as obligate jellyfish predators (e.g. the ocean sunfish *Mola mola* and the leatherback turtle *Dermochelis coriacea*; Pauly *et al*. 2009).

Like most other scyphozoan jellyfish, *Crambionella* species presumably feed on zooplankton (Eiane *et al*. 1999; Flynn & Gibbons 2007). In the process of collecting food and transporting it to the oral cavities, suspended sediment particles would also be incorporated in the bolus. The discarded parts would form 'pseudofaeces', which sink rapidly to the bottom (Fortier *et al*. 1994). Under bloom conditions, *C. stuhlmanni* is thus likely to play a significant role in reducing water turbidity in the St Lucia system by removing silt particles that are notoriously abundant and easily resuspended in this estuarine lake (Carrasco *et al*. 2007; Whitfield & Taylor 2009; Stretch *et al*. 2013).

C. stuhlmanni is a broadly euryhaline species, having been found at salinity levels ranging from 12 to 65 ‰, with the highest recorded densities associated with the upper salinity ranges. Thus, it appears to be well-adapted to the fluctuating conditions that currently prevail in the St Lucia system (Whitfield & Taylor 2009; Carrasco *et al.* 2010) and the bloom formations reported here are, therefore, not surprising. In recent years, jellyfish 'outbreaks' worldwide have increasingly been ascribed to biological invasions, over-fishing, eutrophication and climate change (Mills 2001; Purcell 2005; Hay 2006) and have, therefore, become almost symptomatic of degradation of coastal marine ecosystems (Dybas 2005). However, the early records of *C. stuhlmanni* occurrence in bloom density at St Lucia date back more than half a century, when most of these anthropogenic impacts were virtually non-existent and the system was still in quasi-pristine condition (Whitfield & Taylor 2009). It has been suggested lately that worldwide oscillations with approximately a 20-year periodicity may be occurring in jellyfish populations (Condon *et al.* 2013).

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'Outbreaks' of jellyfish seem to be a natural phenomenon in St Lucia and may be associated with the variability in physical conditions experienced by the system and the resulting rapid switching of ecological states. As a consequence, successional pathways within the system are often curtailed, resulting in shortened food webs (Carrasco & Perissinotto 2012). Thus, this could be a natural type of population increase, similar to what occurs under 'down-fishing' conditions, where the food web is dominated by fast-growing primary producers and r-selected consumers that are able to rapidly increase their growth and take advantage of the favourable conditions (Dawson & Hamner 2009; Hamner & Dawson 2009).

During the recent freshwater deprivation crisis (2002–2011), the St Lucia system has undergone profound changes. In particular, water levels became shallower (<0.9 m throughout most of the lake basins), and the lake region more sensitive to heating/evaporation and prone to the regular occurrence of hypersaline conditions (Perissinotto *et al*. 2013). Although information on the natural baseline dynamics of *C. stuhlmanni* is still lacking, it is possible that these changes may have contributed to the patterns described in this report.

It is not known to what extent these extreme events, which have already resulted in large-scale ecosystem change (Taylor 2006; Whitfield & Taylor 2009; Carrasco & Perissinotto 2012), may be impacting on the ability of *C. stuhlmanni* to continue its successful occupation of the estuarine lake. There is a need to undertake more detailed studies on *C. stuhlmanni* in the St Lucia estuarine lake, in particular to investigate its life cycle, its diet and feeding rates, and its potential contribution to the removal of suspended sediments from the water-column.

ACKNOWLEDGEMENTS

This work was carried out under a research agreement with the iSimangaliso Park Authority for the project registered under the title "Climate Change and the Management of KZN Estuaries: St Lucia Estuary", with a Marine and Coastal Management collection permit in terms of Section 83 of the Marine Living Resources Act, 1988. We are grateful to the management and staff of the iSimangaliso Wetland Park and Ezemvelo KZN Wildlife for administrative, logistical and operational support for this study. Funding was provided by the National Research Foundation (NRF, Pretoria), the World Wide Fund (WWF-SA, Stellenbosch) and the University of KwaZulu-Natal (UKZN, Durban).

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