Aquatic Invasions (2012) Volume 7, Issue 2: 271–275
doi: http://dx.doi.org/10.3391/ai.2012.7.2.013

Short Communication

Detection and distribution of *Craspedacusta sowerbii*: Observations of medusae are not enough

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Received: 21 November 2011 / Accepted: 31 January 2012 / Published online: 6 February 2012

Abstract

The freshwater cnidarian *Craspedacusta sowerbii*, native to the Yangtze valley, has invaded lakes and ponds throughout the world. Most distribution records have to date been based on observations of the medusa (jellyfish) stage, including numerous recent publications. We aimed to determine whether polyps are widespread in lakes, and geographical areas, outside of where medusae have been observed, and whether constructed waters are more easily invaded than natural waters. Our results show that *C. sowerbii* is more common and widespread than is apparent from observations of medusae. We argue that observed occurrences of medusae provide little useful information regarding the distribution of this species, and that published records of new jellyfish occurrences provide unreliable estimates of the timing of introduction, establishment or spread of *C. sowerbii* in new regions. We found no evidence that constructed waters were more readily invaded than natural waters. Overall, accurate determination of *Craspedacusta* occurrence and distribution requires systematic surveys of the polyp stages.

Key words: freshwater jellyfish, polyps, species detection, constructed waters

Introduction

Craspedacusta sowerbii Lankester is a small freshwater hydrozoan cnidarian (medusa <25 mm). As with most Hydrozoa, the life cycle of *C. sowerbii* includes both an attached polyp and swimming medusa (jellyfish) stage. First recorded and described from the 'Victoria regia' (*Victoria amazonica*) tank at the Royal Botanic Society's Gardens in Regent's Park, London, it was immediately recognised as non-indigenous to the United Kingdom (Lankester 1880a, b). A Yangtze valley origin was later inferred due to the presence of both sexes in the river and its floodplain lakes there, in contrast to populations elsewhere that are almost invariably either all male or female (Kramp 1950). Since its initial discovery the species has been recorded widely, having established in every continent except Antarctica, and on numerous islands (Bushnell and Porter 1967; Dumont 1994). This puts *Craspedacusta* among the most widespread of freshwater invaders globally, despite it not having been intentionally introduced anywhere. Several early authors noted that the occurrences of *Craspedacusta* were primarily from constructed water bodies (e.g., concrete fish ponds, abandoned quarries, gravel pits and dams; Pennak 1956; Lytle 1960). That constructed waters facilitate the establishment and spread of aquatic species has gained recent attention (e.g., Johnson et al. 2008; Banks and Duggan 2009). *Craspedacusta* medusa do not appear to have great effects on the lakes they are recorded from (Dodson and Cooper 1983; Boothroyd et al. 2002a; Janowski et al. 2005), and these effects are further limited due to their sporadic occurrence and the short period of jellyfish blooms in any water body. Despite this, *C. sowerbii* has been the topic of numerous papers, likely a result of the unusual sight of jellyfish in lakes, their unpredictable occurrence, and their prevalence in a water body during bloom. Most studies, however, have simply provided new distributional records based on observations of medusae. For example, numerous recent publications have included new records for larger regions, such as Mexico (Moreno-Leon and Ortega-Rubio 2009) and Patagonia (Figueroa and de los Rios 2010), or from individual lakes within regions where they are already known (e.g., Stefani et al. 2010; Aysel et al. 2011).

Craspedacusta sowerbii was first observed in New Zealand in 1956 from Lake Taupo, and further observations were made later that same year in Lake Tarawera (both in the central North Island; Fish 1971). Since this time there have been a number of additional sightings from a wide geographical range in New Zealand. However, wild records have exclusively been of medusa, and their appearance is irregular both spatially and temporally. Published records of medusae are restricted to north of approximately Taupo, the site of initial observation, in the centre of the island. There appears to be a strong distributional disjunction, with reports of the species from two lakes in the lower South Island (Boothroyd et al. 2002a). Despite the jellyfish stage being observed only occasionally, this species will typically exist as polyps on the bottom of lakes throughout the year. However, outside of an aquarium in Dunedin, this life stage has not been recorded in New Zealand, and is rarely considered elsewhere. Our aim was to explore whether polyps exist in lakes, and geographical areas, outside of where medusa have been observed (for example, in North Island sites south of Taupo). We also aimed to determine whether constructed waters are invaded at greater rates than natural lakes.

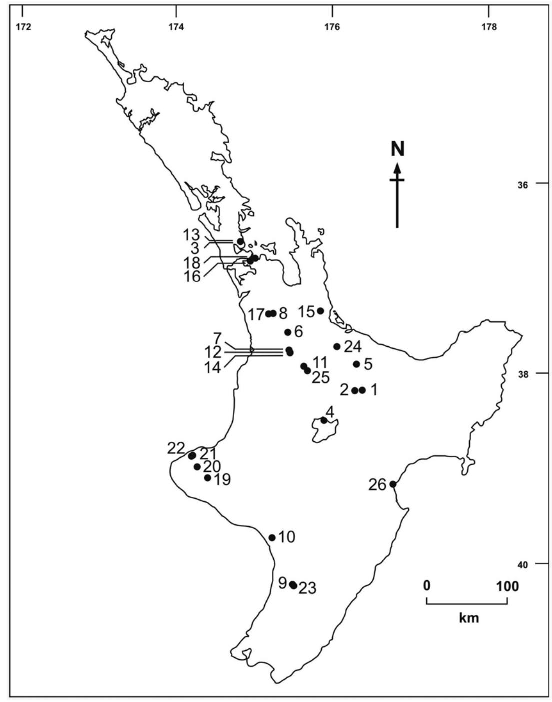

Figure 1. Map of the North Island, New Zealand, showing sites sampled for *Craspedacusta* polyps. Numbers refer to site codes provided in Table 1.

Methods

We visited 26 locations throughout the North Island, New Zealand, in the austral summers of 2009/2010 and 2010/2011 (Figure 1). Of these, 8 were sites where medusae had previously been sighted, based on published reports and our own observations, while for the remaining 18, records are not known (Table 1). Eleven lakes were natural, while fifteen were constructed. Sampling methods were guided by Acker and Musckat (1976). By wading, we collected randomly encountered stones, ranging from coarse gravel to small cobble in size. Ten to fifteen stones were collected between a depth of 0.1 and 1.0 m, typically along a 50-100 m transect at an accessible site in each lake. Samples were placed gently into 5 L buckets filled to approximately 75% of capacity with ambient lake water.

In the laboratory stone samples were placed in 1 L glass beakers, and incubated at 25°C using a 16:8 light:dark cycle in lake water from where the sample was collected. Stones were then examined on all sides under a dissecting microscope, at magnifications between 20× and 60×, up to four times over two weeks to ascertain whether there were polyps present. Stones were turned using as little handling as was practicable, by holding the stones at their longest edges. Extra lake water was added to offset evaporative losses. Once the polyps were found at a site, the sample was no longer monitored.

Results

Of the eight lakes that had previous sightings of *Craspedacusta sowerbii* medusae, we recorded the polyps from seven (= 88%; Table 1). Of the remaining 18 lakes, from which medusae had never been observed, polyps were recorded from eleven (= 61%), including three of eight (38%) south of Lake Taupo (Table 1, Figure 1). Lake Virginia, an urban lake in Wanganui, was the most southern record in our survey. Polyps were detected in nine of eleven natural lakes (= 82%), while they were observed in nine of the fifteen (= 60%) constructed lakes (Table 1).

Table 1. Lakes and ponds surveyed, including origin (Natural = N; Constructed = C), previous records of medusa (Y = Yes; N = No), whether polyps were observed during this survey, date sampled and site geo-reference.

Site number	Lake/Pond	Origin	Previous record of medusae	Polyps present	Date sampled	Geo-reference
1	Lake Rerewhakaaitu	N	Y	Y	1 Dec 2009	38°17′18″S - 176°30′04″E
2	Lake Okaro	N	Y	Y	1 Dec 2009	38°17′52″S - 176°23′40″E
3	Lake Pupuke	N	Y	Y	7 Jan 2010	36°46′54″S - 174°45′37″E
4	Lake Taupo	N	Y	Y	19 Jan 2010	38°46′40″S - 176°04′00″E
5	Lake Rotoiti	N	Y	Y	6 Jan 2011	38°02′12″S - 176°29′11″E
6	Lake Kainui	N	Y	N	12 Feb 2011	37°40′39″S - 175°14′06″E
7	Lake Rotoroa	N	N	Y	25 Nov 2009	37°47′53″S - 175°16′41″E
8	Lake Hakanoa	N	N	Y	7 Jan 2010	37°33′16″S - 175°09′51″E
9	Hokowhitu Lagoon	N	N	N	19 Jan 2010	40°21′60″S - 175°37′51″E
10	Lake Virginia	N	N	Y	19 Jan 2010	39°54′51″S - 175°01′56″E
11	Lake Te Koutu	N	N	Y	10 Feb 2010	37°53′18″S - 175°28′18″E
12	Chapel Lake	C	Y	Y	20 Nov 2009	37°47′18″S - 175°18′54″E
13	Quarry Lake	C	Y	Y	7 Jan 2010	36°46′57″S - 174°45′35″E
14	Turtle Lake	C	N	Y	20 Nov 2009	37°48′19″S - 175°18′14″E
15	Lake Gilmour	C	N	Y	4 Dec 2009	37°23′42″S - 175°50′59″E
16	Western Springs	C	N	Y	7 Jan 2010	36°51′59″S - 174°43′24″E
17	Lake Puketirini	C	N	Y	7 Jan 2010	37°34′06″S - 175°07′57″E
18	Auckland Domain Pond	C	N	N	7 Jan 2010	36°51′33″S - 174°46′26″E
19	Stratford Pond	C	N	Y	19 Jan 2010	39°20′18″S - 174°17′21″E
20	Lake Mangamahoe	C	N	Y	19 Jan 2010	39°07′18″S - 174°07′28″E
21	Pukekura Park Pond	C	N	N	19 Jan 2010	39°03′54″S - 174°04′44″E
22	Lake Rotomanu	C	N	N	19 Jan 2010	39°02′25″S - 174°06′48″E
23	Massey Campus pond	C	N	N	19 Jan 2010	40°23′11″S - 175°36′60″E
24	Lake McLaren	C	N	Y	10 Feb 2010	37°48′37″S - 176°02′36″E
25	Lake Karapiro	C	N	N	10 Feb 2010	37°55′48″S - 175°32′35″E
26	Anderson Park Pond	C	N	N	10 Feb 2011	39°31′18″S - 176°52′07″E

Discussion

Our results show that *Craspedacusta sowerbii* is more prevalent and widespread in New Zealand than is apparent from observations of medusae, and can be found in geographic areas where medusae have never been observed (in this case, lakes south of Lake Taupo). We argue that the observed presence of medusae from lakes and ponds provides little useful information regarding the distribution of this species in an area. In addition, as medusae have not been observed in a number of the lakes where we observed polyps, we consider that published records of jellyfish occurrences provide unreliable estimates of the timing of introduction or establishment of *C. sowerbii* in new lakes or regions, or of the rate of spread of the species across landmasses. Lag times between polyp establishment and medusa detection are potentially long (e.g., Parent 1982). Despite this, there is continued publication of distribution records based solely on medusae. Systematic surveys of polyp distribution are rare and mostly historic (e.g., Michigan, USA; Bushnell and Porter, 1967), and collection sites have to date been mainly from lakes where medusae have already been recorded (e. g., Payne 1925). Overall, new records of medusae may be useful for elucidating patterns or cues of medusa production from polyps, but they provide little information useful for invasion biology.

We found no evidence that constructed waters were more readily invaded by *Craspedacusta* than natural waters. In fact, natural waters appeared to have been invaded at a higher rate than constructed waters in New Zealand (82% vs 60%, respectively). Although some early reports of *Craspedacusta* invasion documented this phenomenon in the United States (e.g., Pennak 1956; Lytle 1960), this was subsequently disputed by Acker and Muskat (1976), as many later records there were from natural water bodies. Despite this, a high frequency of occurrence in constructed waters is still noted in some areas (e.g., in the Middle East, by Gasith et al. 2011). It is possible that constructed waters may provide environmental conditions in some areas that preferentially allows for medusa production and bloom formation (e.g., more stable conditions allowing the fragile medusae to persist), leading to higher jellyfish observation rates. However, the polyps seemingly have no such preference. Alternatively, due to its widespread presence we can not rule out that constructed waters may have provided establishment sites at the invasion front, which have subsequently acted as hubs for invasion of natural sites (*sensu* Havel et al. 2005); the invasion of this species is perhaps too historical in New Zealand, and many areas elsewhere, to now accurately elucidate such a pattern. Observations of polyps were less common for sites south of Lake Taupo, the southernmost site medusae have been observed in New Zealand. This may indicate that the polyps prefer warmer climates, or that the process of spread is still occurring in New Zealand.

Although our method of polyp survey greatly increased the detection rate for *Craspedacusta* over medusa observations, our detection rate was not perfect, as we did not observe polyps in one of the eight lakes where medusae have been recorded previously (i.e., we had an 88% detection rate). Our detection rate might be improved by increasing the sample size at each site (i.e., collecting more stones), or by selecting substrates from a greater variety of areas and depths around the lakes (e.g., Harvey et al. 2009). For example, while we examined shallow depth ranges similar to Acker and Muskat (1976), authors such as Hubschman and Kishler (1972) have recorded polyps on stones as deep as ~9 m in Lake Erie. However, it is possible that the site we did not detect polyps from, Lake Kainui, could have a very limited population, or they may have been extirpated since detection of the medusa in 1986; Lake Kainui is highly eutrophic (Boothroyd et al. 2002b). *Craspedacusta*, in contrast, are generally thought to prefer more oligotrophic than eutrophic conditions, while polyps prefer areas without heavy sedimentation or rock surfaces with heavy algal growth (Acker and Muskat 1976; although see Hubschman and Kishler 1972). Polyps were recorded from a lower percentage of lakes where medusae had not been recorded previously (61%), indicating that the species may be less likely to occur where medusa have not been recorded. We commonly did not detect polyps on our first examinations of stones following incubation. Acker and Muskat (1976) note that following feeding, polyps shrink to half their normal size, while if starved they can grow to twice their normal size. Incubating stones as we did, without supplying new food, may therefore have enhanced the probability of observing polyps through time. However, small invertebrates were commonly observed crawling on the stones, indicating prey availability for polyps, while the incubation temperature of 25°C was within the optimal range for polyp development and growth (McClary 1959; Acker and Muskat 1976), which also may have facilitated the ease of detection. We recommend further testing of methods that might maximise detection probability, including studies on seasonality to determine the most effective timing for sampling. For example, most sites where polyps were deemed absent were sampled in late-January and February.

In conclusion, *Craspedacusta* are far more widely dispersed than observations of medusae suggest, and a more accurate determination of distribution requires surveys of the polyp stages. Although polyps are more rarely observed than the medusae, they are far more widespread and common. Records of *Craspedacusta* polyps have, to date, been rare globally, as have studies on benthic microfauna in general (especially for attached species). However, in most of its non-indigenous range globally, the polys are unlikely to be mistaken for any other species, making surveys relatively simple (although moderately time consuming). Trophic interactions have focussed primarily on the medusa stage. The polyp stage is known to prey on a variety of planktonic and benthic organisms, in particular small arthropods (Bushnell and Porter 1967), but also larval fish (Dendy 1978). Greater attention should therefore be given to this stage, which dominates the life history of this species (Acker and Muskat 1976). Overall, we recommend systematic surveys for polyps, and of their effects, including areas where medusae have not been recorded to date.

Acknowledgements

KRE was supported by a University of Waikato Summer Research Scholarship.

References

Acker TS, Muscat AM (1976) The ecology of *Craspedacusta sowerbii* Lankester, a freshwater hydrozoan. *The American Midland Naturalist* 95: 323–336, http://dx.doi.org/10.2307/2424397

Aysel B, Memet V, Bulent G (2011) A new record of the freshwater jellyfish *Craspeducusta sowerbii* Lankester, 1880 (Hydrozoa) in Southeastern Anatolia (Turkey). *Chinese Journal of Oceanography and Limnology* 29: 366–368, http://dx.doi.org/10.1007/s00343-011-0047-1

Banks CM, Duggan IC (2009) Lake construction has facilitated calanoid copepod invasions in New Zealand*. Diversity and Distributions* 15: 80–87, http://dx.doi.org/10.1111/j.1472-4642.2008.00524.x

Boothroyd IKG, Etheredge MK, Green JD (2002a) Alien predator: freshwater jellyfish in New Zealand. *Water & Atmosphere* 10: 16–17

Boothroyd I KG, Etheredge MK, Green JD (2002b) Spatial distribution, size structure, and prey of *Craspedacusta sowerbii* in a shallow New Zealand lake. *Hydrobiologia* 468: 23–32, http://dx.doi.org/10.1023/A:1015206320300

Bushnell JH, Porter TW (1967) The occurrence, habitat and prey of *Craspedacusta sowerbyi* (particularly polyp stage) in Michigan. *Transactions of the American Microscopical Society* 86: 22–27, http://dx.doi.org/10.2307/3224420

Dendy JS (1978) Polyps of *Craspedacusta sowerbyi* as predators on young striped bass. *The Progressive Fish-Culturist* 40: 5–6, http://dx.doi.org/10.1577/1548-8659(1978)40[5:POCSAP]2.0.CO;2

Dodson SI, Cooper SD (1983) Trophic relationships of the freshwater jellyfish. *Craspedacusta sowerbyi* Lankester 1880. *Limnology and Oceanography* 28: 345–351, http://dx.doi.org/10.4319/lo.1983.28.2.0345

Dumont HJ (1994) The distribution and ecology of the fresh- and brackish water medusa of the world. *Hydrobiologia* 272: 1–12, http://dx.doi.org/10.1007/BF00006508

Figueroa D, de los Rios P (2010) First report of *Craspedacusta sowerbii* (Cnidaria) (Lankester, 1880) for Patagonian waters (38 degrees S, Chile): a possible presence of invasive species and its potential ecological implications. *Brazilian Journal of Biology* 70: 227–228, http://dx.doi.org/10.1590/S1519-69842010000100032

Fish GR (1971) *Craspedacusta sowerbyi* Lankester (Coelenterata: Limnomedusae) in New Zealand lakes. *New Zealand Journal of Marine and Freshwater Research* 5: 66–69, http://dx.doi.org/10.1080/00288330.1971.9515368

Gasith A, Gafny S, Hershkovitz Y, Goldstein H, Galil BS (2011) The invasive freshwater medusa *Craspedacusta sowerbii* Lankester, 1880 (Hydrozoa: Olindiidae) in Israel. *Aquatic Invasions* 6, Supplement 1: S147–S152, http://dx.doi.org/10.3391/ai.2011.6.S1.033

Harvey CT, Qureshi SA, MacIsaac HJ (2009) Detection of a colonizing, aquatic, non-indigenous species. *Diversity and Distributions* 15: 429–437, http://dx.doi.org/10.1111/j.1472-4642.2008.00550.x

Havel JE, Lee CE, Vander Zanden MJ (2005) Do reservoirs facilitate invasions into landscapes? *Bioscience* 55: 518–525, http://dx.doi.org/10.1641/0006-3568(2005)055[0518:DRFIIL]2.0.CO;2

Hubschman JH, Kishler WJ (1972) *Craspedacusta sowerbyi* Lankester 1880 and *Cordlophora lacustris* Allman 1871 in western Lake Erie (Coelenterata*). The Ohio Journal of Science* 72: 318–321

Jankowski T, Strauss T, Toni Ratte H (2005) Trophic interactions of the freshwater jellyfish *Craspedacusta sowerbii. Journal of Plankton Research* 27: 811–823, http://dx.doi.org/10.1093/plankt/fbi055

Johnson PTJ, Olden JD, vander Zanden MJ (2008) Dam invaders: impoundments facilitate biological invasions into freshwaters. *Frontiers in Ecology and the Environment* 6: 359–365, http://dx.doi.org/10.1890/070156

Kramp PL (1950) Freshwater medusae in China. *Proceedings of the Zoological Society of London* 120: 165–184, http://dx.doi.org/10.1111/j.1096-3642.1950.tb01469.x

Lankester ER (1880a) On a new jelly-fish of the order trachomedusae, living in freshwater. *Science* 1: 34, http://dx.doi.org/10.1126/science.os-1.4.34

Lankester ER (1880b) On *Limnocodium (Craspedacustes) sowerbii,* a new trachomedusa inhabiting fresh water. *Quarterly Journal of Microscopical Science* 20: 351–371

Lytle CF (1960) A note on distribution patterns in *Craspedacusta*. *Transactions of the American Microscopical Society* 79: 461–469, http://dx.doi.org/10.2307/3224130

Moreno-Leon MA, Ortega-Rubio A (2009) First record of *Craspedacusta sowerbyi* Lankester, 1880 (Cnidaria: Limnomedusae: Olindiidae) in Mexico (Adolfo Lopez Mateos reservoir), with notes on their feeding habits and limnological dates. *Biological Invasions* 11: 1827–1834, http://dx.doi.org/10.1007/s10530-008-9361-8

McClary A (1959) The effect of temperature on growth and reproduction in *Craspedacusta sowerbii*. *Ecology* 40: 158–162, http://dx.doi.org/10.2307/1929945

Parent GH (1982) Une page d'histoire des sciences contemporaines: un siecle d'observations sur la meduse d'eau douce *Craspedacusta sowerbyi* Lank. *Bulletin Mensuel de la Société Linnéenne de Lyon* 51: 47–63

Payne F (1925) The hydroid of *Craspedacusta rydei,* in Kentucky. *Science* 62: 421, http://dx.doi.org/10.1126/science.62.1610.421

Pennak RW (1956) The fresh-water jellyfish *Craspedacusta* in Colorado with some remarks on its ecology and morphological degeneration. *Transactions of the American Microscopical Society* 75: 324–331, http://dx.doi.org/10.2307/3223963

Stefani F, Leoni B, Marieni A, Garibaldi L (2010) A new record of *Craspedacusta sowerbii*, Lankester 1880 (Cnidaria, Limnomedusae) in Northern Italy. *Journal of Limnology* 69: 189–192, http://dx.doi.org/10.4081/jlimnol.2010.189