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Research Article

First observations of the freshwater jellyfish *Craspedacusta sowerbii* Lankester, 1880 in Ireland coincides with unusually high water temperatures

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Abstract

The freshwater hydrozoan *Craspedacusta sowerbii* was observed for the first time in Ireland at five localities in two separate river catchments (Shannon and Erne) during the summer of 2013. All collected medusae from Lough Derg on the Shannon catchment were female. Analysis of water temperature data for the period 2001–2015 found that water temperatures greater than 21°C were only recorded in 2013. The occurrence of medusae in three distinct areas during this unusually warm summer suggests that it may have been present in its polyp form for some years, or even decades. While it is not known when the species arrived in Ireland, the spread of this species may have involved different pathways. With climate warming, further appearances of the medusa-stage may be expected.

Key words: polyp, medusa, cryptogen, lake, bloom

Introduction

Craspedacusta sowerbii Lankester, 1880 is considered to be a non-indigenous hydrozoan species that is widely distributed within a range of freshwater habitats on all continents, except Antarctica (Fritz et al. 2007; Smith and Alexander 2008). It is the only member of its genus that is so widely distributed (Jankowski 2001). It was first recognised and described from specimens obtained in Regents Park in London based on specimens associated with an imported Brazilian aquatic plant (Lankester 1880), suggesting a South American origin. Nevertheless, there have been many separate descriptions of *Craspedacusta* in China, generally accepted as representing three species: *C. sowerbii*, *C. sinensis* Gaw and Kung, 1939 and *C. kiatingi* Gaw and Kung, 1939 and there is some uncertainty about the status of *C. ziguiensis* He and Xu, 1985 (Zang et al. 2009). However, Jankowski (2001), in a detailed review, considers *C. kiatingi* to be a form of *C. sowerbii*. A further species *C. iseanum* Oka and Hara, 1922 known from Japan, from an old well, is now thought to be extinct (Dumont 1994). In addition, Jankowski (2001) refers to a further species *C. sichuanensis* He and Kou, 1984 whose status is unclear. However, it is generally accepted that the species, *C. sowerbii* originates from China, being abundant in the Yangtze River catchment and with both sexes recurring annually (Kramp 1951; Smith and Alexander 2008). Elsewhere, however, most records reveal only single sex medusa blooms (Pennak 1989). In China *C. sowerbii* is frequently found in shallow pools and this is consistent within many of the records from within invaded world regions.

There are records *C. sowerbii* from North and South America (Dean 1962; Galarce et al. 2013; Moreno-Leon and Ortega-Rubio 2009; Ringuelet 1950), Australia (Thomas 1950; Greenwood 1966;

Ling and Duggan 1962), Africa (Rayner 1988) and Eurasia (Kanaev 1949; Stephani et al. 2010, Fritz et al. 2007, Ferreira 1985, Pérez-Bote et al. 2006, Lundberg and Svensson 2003; Farkašova and Stloukal 2007; Jakovčev-Todorović et al. 2010). It has been recorded in natural and artificial, and in oligotrophic and eutrophic water bodies. It has been recorded from tanks, ponds, quarries, reservoirs, lakes (Pérez-Bote et al. 2006; Zang et al. 2009; Figueroa and de los Ríos 2010) and from slow moving rivers and streams (DeVries 1992). It is unable to tolerate brackish or marine conditions (Gophen and Shealtiel 2012; Wang et al. 2006). *C. sowerbii* is known to occur on islands, such as the Azores (Raposeira et al. 2011), Guam (Belk and Hotaling 1971), Hawaii (Matthews 1963), New Zealand (Boothroyd et al. 2002) as well as in Britain (Anon 1977; Van Someren 1933; Green 1998). The worldwide distribution includes many first time records since 2000 (Väinölä 2002; Arbačiauskas and Lesutienė 2005; Peréz-Bote et al. 2006; Saadalla 2006; Stefani et al., 2010; Gasith et al. 2011; Raposeira et al. 2011; Galarce et al. 2013; Gomes-Pereira and Dionisio 2013; Karaouzas et al. 2015), suggesting a continued expansion of its range. In the Americas the species is known to range from the Laguna Illahuapa region in Patagonia at 40° S (Galarce et al. 2013) to 46° N in Canada (McAlpine et al. 2002). In Europe the species extends as far north as 61° N in Finland (Väinölä 2002). The ability of this species to become so widespread has been linked to its complex life history stages that include drought-resistant podocysts and frustules (Reisinger 1957; Matthews 1966).

The short-lived medusa stage of the fresh-water hydrozoan *Craspedacusta sowerbii* is the most noticeable stage of the life history of this species. Occurrences of this pelagic stage are sporadic, lasting only a few weeks usually in the late summer and autumn. This medusa stage alternates with a small, long-lived, asexual and inconspicuous polyp stage that attaches to firm substrata (Stanković and Ternjej 2010) and so occurrences are usually based on the presence of medusae. Nevertheless, appearances of medusae provide an indication as to where the polyp stage may reside and enable insights into the ecological requirements of this elusive life-history stage.

Here we discuss the first observations of the medusa stage of *C. sowerbii* in Ireland, at five locations, in two separate river catchments during an unusually warm summer in 2013. We discuss the likely cause of the appearances in Ireland and how the species might have spread to, and within, Ireland.

Study sites

The Shannon River is navigable for most of its length, and to some extent on some of its large tributary rivers. This river has an overall length of 360 km and its largest and most downstream lake is Lough Derg. This lake has an area of 188 km^2 with deep troughs to >30 m and shallow bays along its margins. Several rivers discharge to the lake on either side and two on the west side are navigable. These are the Scarriff and Rossmore Rivers (Figure 1).

The town of Roosky on the River Shannon is situated >100 km upstream from Lough Derg (Figure 1) and this river section lies immediately below two shallow lakes, Loughs Boderg and Bofin.

The Erne River catchment has two predominant lakes, Upper and Lower Lough Erne, connected by a broad slow moving river section (Figure 1). Upper Lough Erne is a complex of a series of interconnected shallow water lakes studded with islands that drains into Lower Lough Erne and passes by Carrybridge. The Erne catchment is linked to the Shannon by means of sixteen locks via the Shannon-Erne Canal.

Methods

Scarriff Harbour, upriver from Lough Derg (Figure 1), was visited on 23 August 2013 following reports of medusae sightings. A vertical net of 95 cm diameter with a 3 mm bar mesh was hauled from a depth of 2.7 m. The following day, a hand net with a mesh of ~1 mm was used to collect medusae close to the water surface. On 25 August a pole mounted scraper was used to sample hard surfaces in the Harbour with the aim of collecting the polyp stage. On 28 August 2013, three surface horizontal tows with a 0.4 m diameter and 200 µm mesh net were deployed in Scarriff Harbour from a boat. Horizontal net tows were conducted midway along the channel entrance to Scarriff Harbour, at the entrance to Scarriff Harbour, at Rossmore Bay and in Dromineer Bay. During each tow, visual observations of the water surface for the presence of jellyfish were also made by an observer on either side of a boat. Single horizontal net tows were conducted over deep water at a number of locations in Lough Derg (Figure 1) on 29 August and sampling using a hand net from a boat was conducted in the shallow water at Rossmore and Dromineer. In addition, the Woodford River on the west side of Lough Derg (Figure 1) was sampled. Further sightings of *C. sowerbii* were verified having been actively sought through the media (Table 1).

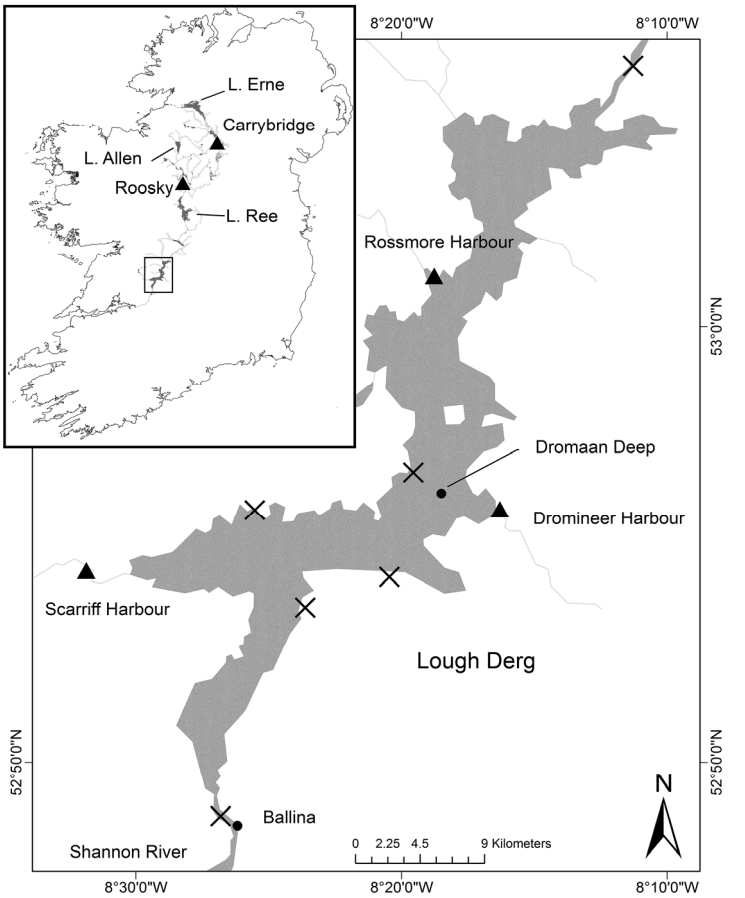


Figure 1. Localities where medusae were found (triangles) and where none were located (X). Inset: Lough Derg.

Table 1. Localities where sampling and observations of medusae took place during 2013.

Date	Location	Latitude/ longitude	Abundance	Depth	Notes
01/08/13	Scarriff Harbour	52°54′20″N 08°31′43″W	1	<3m	P. Joyce notices a single jellyfish
06/09/13	Scarriff Harbour	52°54′20″N 08°31′43″W	100s	<3m	P. Joyce notices 100s of small medusae at and below water surface
01/08/13 04/08/13	Scarriff Harbour	52°54′20″N 08°31′43″W	100s	<3m	T. Cassells notices 100s of medusae
06/08/13	Portlick Harbour	53°06′27″N 08°10′26″W	0	~2m	Not observed (DM)
07/08/13	Castlelough Harbour	52°53′46″N 08°23′25″W	0	2m	Not observed (DM)
19/08/13	Dromaan Harbour	52°56′36″N 08°19′54″W	0	2m	Not observed (DM and RB)
25/08/13	Scarriff Harbour	52°54′20″N 08°31′43″W	0	<3m	Not observed (DM)
26/08/13	Scarriff Harbour	52°54′20″N 08°31′43″W	~20	<3m	Collected using dip-net (DG and CW)
26/08/13	Scarriff Harbour	52°54′20″N 08°31′43″W	14	<3m	Collected using dip-net (DM)
28/08/13	Ballina Marina Harbour	52°48′45″N 08°26′50″W	0	2m	Not observed (DM)
28/08/13	Scarriff Harbour	52°54′20″N 08°31′43″W	1	<3m	Collected by dip net (DM and JC)
28/08/13	Mountshannon	52°55′44″N 08°25′47″W	0	<3m	Not observed (DM)
28/08/13	Rossmore	53°01′10″N 08°18′52″W	2	~1m	Collected by dip-net (DG)
28/08/13	Dromineer Harbour	52°55′52″N 08°16′43″W	8	2m	Collected by dip-net (DG, TD, DM)
29/08/13	Garrykennedy	52°54′18″N 08°20′32″W	0	4m	Not observed (DM)
29/08/13	Dromaan Harbour	52°56′36″N 08°19′54″W	0	2m	Not observed (DM)
20/08/13	Roosky	53°50′01″N 07°54′53″W	several	3m	Stephan Kinahan
06/09/13	Carrybridge	54°17′01″N 07°32′49″W	several	<3m	J. C. pers. com.

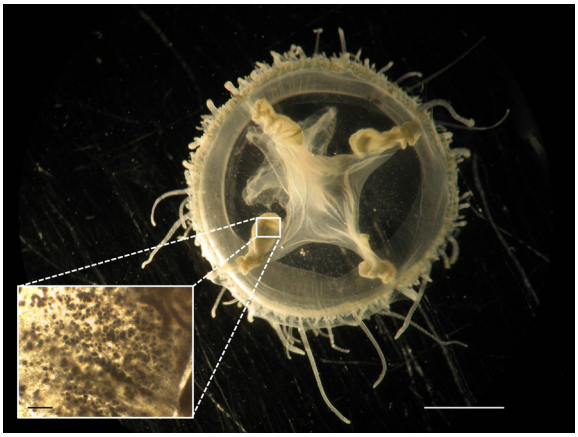


Figure 2. Female medusa (scale bar 5mm) with insert showing gonads. See eggs within inset (scale bar 20µm). Photographs by Thomas Doyle.

Temperature was recorded using a continuous recording probe at a fixed station, from a depth of 30 cm, located at the southern end of Lough Derg at Ballina. A further probe was attached to the keel of a boat at a depth of 70 cm. This vessel travelled the mid- and lower Shannon River during the summer of 2013. A hydrographic reversing thermometer was used to obtain measurements at a depth of 0.3 m in various shallow bays and at greater depths. This same thermometer was used for collecting measurements over the years 2001 to 2015 at weekly intervals.

Female medusae were identified from the presence of large egg cells which are conspicuous in the gonads under low magnification.

A one-way analysis of variance (ANOVA) was used to test the hypothesis that there was a significant difference in water temperature between years (using the fixed station temperature data). These data were checked for normality and homogeneity of variance (Levene's test). A *post hoc* Tukey test was used to investigate pairwise comparisons.

Results

The medusa was the only life history stage of *C. sowerbii* recovered; no polyps were found. Most medusae were recorded at Scarriff Harbour which has a low exchange of water with the adjacent river. This Harbour is 3 km upstream of Lough Derg. The medusae were collected by hand net and a single specimen from four net tows. No medusae were captured in the river downstream of the harbour nor near to where the river enters the Lough Derg. Medusae ranged 13 to 22 mm in relaxed bell diameter (Table 1; Figure 2). Medusae were also obtained in Lough Derg from the Dromineer Marina 17 km to the ENE, and the Rossmore Delta 24 km to the NE, of Scarriff Harbour (Figure 1; Table 1). Sampling elsewhere in the lake, to depths of over 20m, failed to recover specimens (Table 1, Figure 1). All medusae in Scarriff Harbour and Lough Derg examined were female.

Elsewhere medusae were seen on the Shannon River at Roosky, upstream from Lough Derg, and in the river section betwen Upper and Lower Lough Erne. These records, and those from Lough Derg and Scarriff Harbour were all from depths of < 4m.

Water temperatures

Boat keel temperatures were greatest when within shallow water areas. During mid-July water temperatures recorded from this probe in shallow areas of the lake varied between 22° and 25 °C. A maximum temperature of 27.5 °C was recorded during this sampling period upstream and north of Roosky within a small navigable lake. In Lough Derg both the keel temperatures and the fixed station to the south of the lake attained 25 °C, although briefly (Figure 3). In the days following 21 July water temperatures declined rapidly. From 6 August until the end of August, water temperatures remained between 17.5 and 19.5 °C. The highest mid-lake water temperatures recorded, at a depth of 5 m, were 22.2 to 22.5 °C on 16 July. The vessel passed Roosky on 8 and 12 July, with corresponding keel temperatures of 19.5 to 22 °C and 25 to 26 °C respectively (Figure 3), with a sighting of medusae eight days later on 20 July.

The highest temperature recorded at the fixed temperature station at Lough Derg at Ballina was 24.5 °C (11 to 14th July and the 20th July 2013). In all other years, the temperature was always below 20 °C (except on one occasion in 2006 when it attained 20.2 °C). A one-way ANOVA revealed a significant difference in water temperatures between years: $F_{(12, 132)} = 2.821$, $P < 0.05$. *Post hoc* comparisons using the Tukey's test showed the mean water temperature for 2013 was significantly higher than during both 2002 and 2011 (which had the lowest mean water temperatures). There were no other significantly different comparisons.

Following 2013 the 2014 temperatures attained 21 °C at the Dromaan Deep (Figure 4) but no medusae were observed during this summer. During the summer of 2015 temperatures at the same station only reached 18 °C.

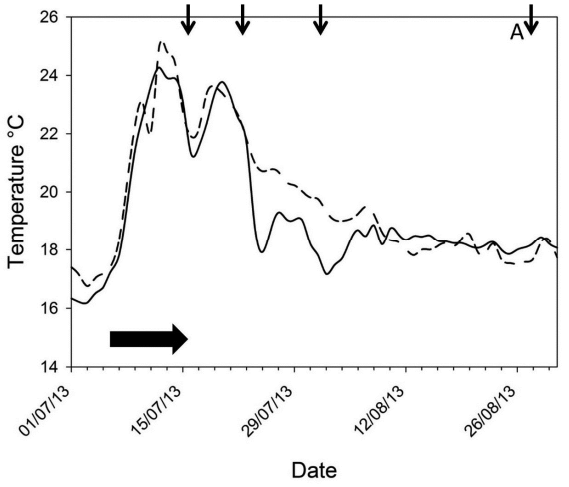


Figure 3. Temperature data from boat keel and Ballina data loggers. Horizontal arrow indicates the duration of a visit by the boat to the Roosky region. Black arrows indicate sampling dates. 'A' indicates benthic sampling for polyps.

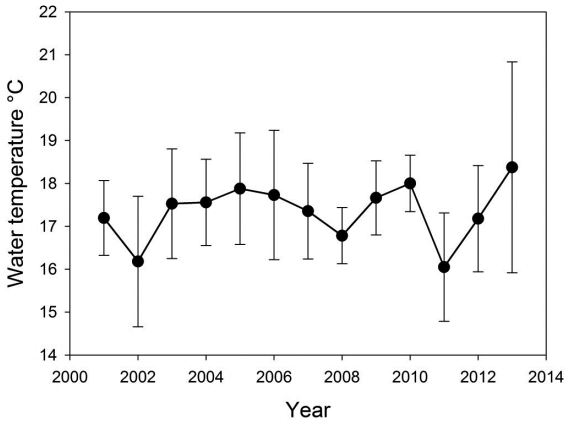


Figure 4. Temperature ranges at the southern end of Lough Derg 2001 to 2013 for June to August.

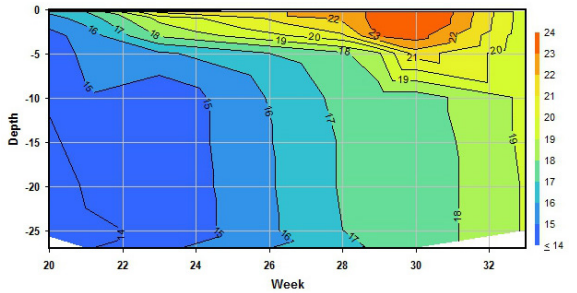


Figure 5. Lough Derg (Dromaan Deep Station) water temperatures, July/August 2013.

Discussion

The concurrent appearance of *C. sowerbii* medusae at three geographically separate regions in Ireland (Loughs Derg, Bofin (Roosky) and Erne) as well as at three separate localities within Scarriff Harbour and Lough Derg indicates that elevated temperatures are a general trigger for their production. All records were from shallow water where temperatures were generally higher. In Lough Derg the specimens were collected over depths of <3 m. In the shallow bays of Lough Derg, water temperatures ranged from more than 20 °C to over 25 °C. Such elevated temperatures are considered necessary for the formation of medusae (Kato and Hirabayashi 1991; Dodson and Cooper 1983). Notably, recorded water temperatures in Lough Derg were greater in 2013 than in July and August of other years over the period 2001 to 2013, when maximum temperatures seldom exceed 20 °C (Figure 4).

Blooms of medusae world-wide have been generally infrequent and sporadic. These either arise from long established colonies of polyps or as a result of a recent introduction (Fish 1971). The polyps are generally <2 mm while the medusa buds range from 0.5 to 1 mm in diameter. The small size of both life history stages may have led to individuals being overlooked (DeVries 1992); but as the medusae increase in size they become more easily recognised. In a study by Duggan and Eastwood (2012) in New Zealand, polyps were recorded in lakes more widely than where medusae have been observed. In this study the medusae attained 22 mm in bell diameter, larger than those reported in the review by Jankowski (2001). Conditions that trigger medusa blooms are not fully known, although temperature is probably an important contributory stimulus, as it is known to be a trigger for a number of marine jellyfish species (Mills 2001; Purcell 2005). Water levels and food abundance may also be involved (Pennak 1956; Deacon and Haskell 1967; Acker and Muscat 1976; Lytle 1961). In some studies the abundance of medusae was greater during years when water temperatures were above average (Acker and Muscat 1976), and usually when water temperatures were >21 °C. In Sweden, medusae are normally observed during warm summers (Lundberg et al. 2005).

Medusae have been reported in the water column once temperatures exceeded 20 °C (Matthews 1966; Fish 1971; Acker and Muscat 1976; DeVries 1992; Boothroyd et al. 2002) which is consistent with laboratory studies where the

threshold for the production of medusae is 21 °C (Folino-Rorem et al. 2015). The occurrence of medusae during July to September in northern latitudes, a time when water temperatures are normally greatest, also suggest that elevated water temperatures may be responsible. Some bloom events seem to occur over larger areas. For example, Lundberg and Svensson (2003) recorded medusae from several Swedish lakes during 2002 and in the same summer in Lithuania (Arbačiauskas and Lesutienė 2005). Hence the suggestion warmer summers in Ireland (and elsewhere) could result in further appearances of medusae. Indications of general warming in Irish lakes are of concern for some native species (Griffiths 2007). Already there is evidence for range shifts in freshwater environments in response to climate change at northern latitudes (Heino et al. 2009).

It is possible medusae of *C. sowerbii* may have been produced in Irish waters in previous years but were not observed or recognised. The detection from three widely separated regions at the same time is noteworthy and suggests that polyps might have been resident in these watercourses for some time and may have arisen from one or more introduction events. The elevated water temperatures in July 2013 (Figures 4 and 5) may have been the first time that conditions were suitable for the resident polyps to produce the pelagic medusa stage in Ireland. It is unknown from where, and when, the inoculating propagules originated but it will have involved a female population. Presently, we have no indication of the sex of the medusae observed at Roosky or Lough Erne as these records are based on in situ photographs. The occurrence of *C. sowerbii* in several European states since 2000 would indicate a recent spread.

There are a number of anthropogenic modes by which *C. sowerbii* could have been introduced to Ireland; but it might also have arrived naturally with birds. The species is intolerant of marine conditions, although it is unclear whether the more resistant resting stage might endure marine conditions. Transmission in ships' ballast water may be possible, as resting stages of some other biota are considered to have been transmitted in this way (Hallegraeff and Bolch 1992). Ornamental aquatic plants might also have distributed the polyp stage (in Dexter et al. 1949). There have been other invertebrate introductions such as amphipods (O'Connor et al. 1991) and snails (Moorkens 2007; Anderson 2003, 2004) as hitchhikers on ornamental aquatic plants. These may have been distributed widely within the country and to the wild from garden ponds and/or releases from aquaria (Duggan 2010).

Natural dispersal following an introduction is also likely to take place. A reported association of the polyp stage and the zebra mussel, *Dreissena polymorpha*, said to be a commensal association, has been reported by Stanković and Ternjej (2010). As there were multiple imports of used leisure craft that were fouled with zebra mussels (Pollux et al. 2003) from Britain and the continent, this is a possible vector source. That being the case, the arrival of *C. sowerbii* might be traced back to 1993, a time of more open trade within Europe and when there was a great increase in the numbers of imported leisure craft. Transmission might have been with lodged podocysts or perhaps polyps attached to zebra mussels fouling the hulls of craft imported overland and by ferry. All sites where the species was recorded are located on interconnected waterways. This might have been a separate inoculation or a spread from the Shannon system to the Erne as this was the route of spread taken by *D. polymorpha* (Rosell et al. 1999). While *D. polymorpha* is frequent at all but the Scarriff Harbour locality, recreational craft frequently visited this site following its re-development in 2004. It is highly likely that many of these craft will have had fouled hulls at this time, as this was during the 'outbreak' period when mussels extensively fouled boat hulls (Zaiko et al. 2014).

Conclusions

The medusa stage appeared in Ireland at three widely separated localities during the summer of 2013. The species may be more widely spread than is presently known. Medusae all appeared in shallow water and their production was most probably triggered by an unusual warm event in mid-July with the larger medusae surviving to the end of August-early September. With expected increases in summer temperatures during this century further bloom episodes may be expected.

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