Belg. J. Zool., 136 (2) : 163-166 July 2006

First record of *Craspedacusta sowerbyi* Lankester, 1880 (Cnidaria: Limnomedusae: Olindiidae) in the Proserpina Reservoir (Extremadura, SW Spain) with notes on their feeding habits

José Luis Pérez-Bote, Antonio Muñoz, Ricardo Morán, Rafael Roso and Antonio José Romero

Corresponding author : José Luis Pérez-Bote, e-mail : jlperez@unex.es

ABSTRACT. The first record of the invasive freshwater jellyfish *Craspedacusta sowerbyi* Lankester in the Proserpina Reservoir, a shallow reservoir in the Extremadura region of SW Spain is reported in this paper. *C. sowerbyi* was recorded in open water away from the immediate littoral zones. All individuals captured were females with bell diameters ranging from 7-21 mm. Tentacle numbers ranged from 218 to 398. The stomach contents included most of the taxa abundant in the zooplankton, with *Daphnia longispina* being the most abundant.

KEY WORDS : freshwater medusa, feeding habits, Iberian Peninsula

INTRODUCTION

The freshwater jellyfish *Craspedacusta sowerbyi* Lankester, 1880 is an invasive species native of China. Apart from China, *C. sowerbyi* has colonized most continents (DUMONT, 1994) but only at the end of the 19th and into the 20th century. The first records from non natural open waters correspond to the end of 19th century. It has been recorded in Italy, France, Sweden, Central Europe, Portugal (FERREIRA, 1985), U.S.A. (DEVRIES, 1992), Canada (MCALPINE et al., 2002), Hawaii, South Australia (THOMAS, 1950), New Zealand, Philippine Islands, China, Japan, Central Asia, South America (ACKER, 1976) and Africa (RAYNER, 1988), as well as in Spain (in Cordoba and Madrid provinces, M. Villena, pers. comm., Fig. 1).

The life cycle of *C. sowerbyi* includes both a polyp and a medusa stage. It belongs to the Order Hydroidea; Suborder Limnomedusae, which have only a tiny and solitary polyp. *Craspedacusta sowerbyi* produce free-swimming medusae, which bud off from the side of the polyp (BARNES, 1980; PEARSE et al., 1987). The active medusa stage of cnidarians is the sexually reproducing stage. The polyp is rarely encountered, despite its ability to withstand long periods of food shortage and tolerate extreme variations in temperature and light conditions by encysting as resting bodies consisting of a ball of cells surrounded by a membrane (ACKER, 1976; ACKER & MUSCAT, 1976).

Although freshwater medusae have been known for more than 100 years (LANKESTER, 1880) (in China for centuries) and much literature is available, our knowledge (systematic, ecological) of these animals is unsatisfactory (DUMONT, 1994). This paper presents the results of a study of the spatial distribution, population size structure, and diet of the medusae in the Proserpina Reservoir, in the south-western Iberian Peninsula.

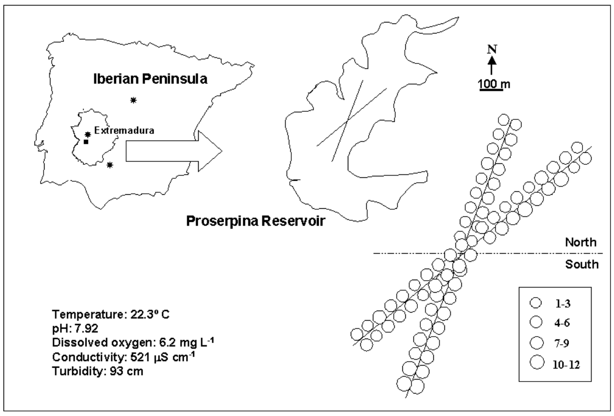

Fig. 1. – Location of the study site with water characteristics on the sampling day, and location of the two sampling transects (solid line). Abundance of *C. sowerbyi* is expressed in number of specimens per square meter. Asterisks indicates other localizations of *C. sowerbyi* in Spain.

MATERIAL AND METHODS

The Proserpina Reservoir is located in the centre of Extremadura (SW Spain, Fig. 1), and covers an area of 42.15 ha at an altitude of 290 m a.s.l. Its maximum length is 1177 m, maximum width 726 m, and maximum water depth about 8 m. However the reservoir is not thermally stratified. The aquatic vegetation includes *Chara* spp., *Ranunculus* spp., and *Potamogeton pectinatus*, with *Phragmites* spp. and *Typha angustifolia* along the shores. The site is surrounded by *Quercus rotundifolia* woodland, which has been cleared in the region of the dam wall, and some limited areas of non-irrigated agriculture have been developed. No data on water quality of the reservoir exist.

Collections of *C. sowerbyi* were performed during daylight hours on 7 October 2004. Climatic conditions during the summer in the Extremadura region are generally hot (mean September air temperature at the study site is 30.1º C), with a September mean rainfall of 23 mm (mean annual rainfall is 624 mm). No further temporal sampling was undertaken to measure population growth and development. Densities of *C. sowerbyi* in the surface waters were estimated at 20 m intervals along two bisecting transect of the lake (Fig. 1). Counts were made within a 60 s period of the numbers of medusae visible in 1 m^2 of surface water (n = 76) on both sides of each transect. Samples for measurement and gut analysis were collected by lowering a 50 μm mesh net to the lake bottom and rowing approximately 5 m, hauling the net diagonally to the surface. Samples were preserved with 70% ethanol. Zooplankton samples were also collected. Temperature, pH, dissolved oxygen, conductivity, and Secchi depth were measured at 11 :00 h from surface water (n = 1).

The umbrellar diameter, gonad length, and number of tentacles were determined from medusae randomly selected from the net samples (n = 172). Sex of *C. sowerbyi* was determined by examining the gonadal tissue under a microscope. Mature females have eggs clearly visible as relatively large round cells embedded in the gonad surface (visible already under intermediate magnification of the dissecting microscope), usually in clusters. Juvenile females still usually have small immature eggs, distinguishable as cells significantly larger than most of the tissue, whereas males have much more uniform sized gonadal cells which are all fairly small. Sperm cells are usually present in mature male gonads. However, they are very small, distinguishable only under high magnification in the microscope (A. Petrusek, pers. comm.). Measurements were made using a stereomicroscope fitted with a calibrated ocular micrometer one day after the captures.

A random sub-sample of 41 medusae was used to identify and count prey items within the gastrovascular cavity. Items were identified under a compound microscope, and the diet was expressed as the percent frequency of occurrence (%FO) of each prey, and the percent of total stomach content number (%N) of each prey according to HYSLOP (1980).

Prey selection of the more commonly eaten prey was examined by PEARRE'S (1982) prey selection index (V) :

$V = (a_d b_e - a_e b_d) (abde)^{1/2}$

The significance of V was tested with a χ^2 evaluation ($\chi^2 = (a_d b_e - a_e b_d)^2 n / abde$), where a_d and a_e are the numbers of a given prey taxon in the diet and in the environment, respectively; b_d and b_e are the numbers of all other prey taxa in the diet and environment respectively; and $a = a_d + a_e$, $b = b_d + b_e$, $d = a_d + b_d$, $e = a_e + b_e$, and $n = a_d + a_e + b_d + b_e$. Values of V can range from -1 to +1, representing complete avoidance and high selection, respectively, whereas 0 implies no selection.

RESULTS

A total of 374 individual medusae were counted in the two transects across the reservoir (density = 2.52 ind./m^2). Patches of *C. sowerbyi* were recorded in open water away from the immediate littoral zones. The number of medusae did not differ between transects (chi-square test, $\chi^2 = 20.81$, $P < 0.05$). However, there were significantly more in the south part of transects (chi-square test, $\chi^2 = 0.1723$, $P = 0.6782$). Mean umbrellar diameter was 14.75 mm (S.D. = 3.47, n = 172), minimum 7 mm and maximum 21 mm. Mean tentacle number was 320 (S.D. = 47.03, n = 172), minimum 218 and maximum 398. All the medusae examined were females, and had a typical number of four gonads. The percentage of medusae containing prey was 63.4%. The number of prey items per

TABLE 1

Diet of *C. sowerbyi* expressed as frequency of occurrence (%FO) and percentage of prey (%N).

PREY CATEGORY	(%) F	(%) N
COPEPODA		
Megacyclops viridis	30.77	11.43
Acanthocyclops robustus	23.08	8.57
Tropocyclops sp.	15.38	5.71
Cyclops sp.	11.54	4.29
CLADOCERA		
Daphnia longispina	61.54	22.86
Daphnia magna	26.92	10.00
Bosmina longirostris	19.23	7.14
ROTIFERA		
Brachionus sp.	23.08	8.57
Keratella cochlearis	19.23	7.14
Lecane lunaris	15.38	5.71
Asplachna sp.	7.69	2.86
Trichocerca sp.	15.38	5.71

TABLE 2

Prey-selection indices as calculated from the number of prey in the gut of *C. sowerbyi* in relation to numbers of prey found in Proserpina Reservoir on 7 October 2004. ***, $P < 0.001$; *, $P < 0.05$ for χ^2-test.

PREY CATEGORY	V
COPEPODA	
Megacyclops viridis	0,11***
Acanthocyclops robustus	0,07***
Tropocyclops sp.	0,03*
Cyclops sp.	0,01*
Eucyclops serrulatus	-0.01
Diaptomus spp.	-0.01
CLADOCERA	
Daphnia longispina	0,12***
Daphnia magna	0,09*
Bosmina longirostris	0,04*
Diaphanosoma spp.	-0.02
Ceriodaphnia spp.	-0.04
ROTIFERA	
Brachionus sp.	0,01*
Keratella cochlearis	0,02*
Lecane lunaris	0,01*
Asplachna sp.	0,07***
Trichocerca sp.	0,01*
Anuraeopsis fissa	-0.05
Filinia spp.	-0.03
Polyarthra spp.	-0.02

medusa varied from 1 to 4 (mean S.D.= 2.69 ± 0.23). Most of the animal taxa found in the gut contents were common components of the zooplankton community of the lake, with the most frequently (Table 1) occurring prey items being *Daphnia longispina*, *Megacyclops viridis,* and *D. magna*. The same prey also dominated in absolute number. Other zooplankton species found in Proserpina Reservoir but not found as prey were the copepods *Eucyclops serrulatus* and *Diaptomus* spp., the cladocerans *Diaphanosoma* spp., and *Ceriodapnia* spp., and the rotifers *Anuraeopsis fissa*, *Filinia* spp., and *Polyarthra* spp. No nauplii were found in gut contents.

PEARRE's (1982) prey selection indices are presented in Table 2. *M. viridis* and *D. longispina* corresponded to the highest positive prey selection indices.

DISCUSSION

This study represents the first attempt to characterize morphometric characteristics and feeding biology of *C. sowerbyi* in the Iberian Peninsula. The size ranges of the medusae found in the Proserpina Reservoir were within the ranges recorded elsewhere. PENNAK (1956) noted that the medusae are often not noticed until they are over 10 mm in diameter, although smaller size ranges have been recorded (BYERS, 1945; BECKETT & TURANCHIK, 1980; RAYNER, 1988). In a temporal study in Louisiana, ZISER & BURKE (1984) found that the size range of medusae during each month of summer (April–October) was highly variable (1–17 mm), although they observed a general trend toward an increasing mean medusa diameter over their study period. In New Zealand, the umbrellar diameter of *C. sowerbyi* ranged between 3.2 and 16.8 mm (BOOTHROYD et al., 2002).

C. sowerbyi medusae were found only in open water in the Proserpina Reservoir. This is a common feature of *C. sowerbyi* medusae, which occur in surface and deeper waters as reported by BYERS (1945) and ZISER & BURKE (1984). KIMMEL et al. (1980) found *C. sowerbyi* mid-lake in Broken Bow Reservoir with no additional sightings near shore, while in the Ohio River medusae were recorded at the surface and as deep as 3 m both day and night (BECKETT & TURANCHIK, 1980). The abundance of *C. sowerbyi* medusae in the Proserpina Reservoir was lower than the range reported by ANGRADI (1998) and BOOTHROYD et al., (2002), but higher than reported by SPADINGER & MAIER (1999) or DAVIS (1955). However, the number of medusae per m^2 was probably underestimated in our study due to the water's turbidity.

In Proserpina Reservoir, *C. sowerbyi* did not show any regular distribution, as has been reported in other studies as well. BOOTHROYD et al. (2002) found a patchy distribution of *C. sowerbyi* in a New Zealand lake. They suggest that the patchy distribution occurred as a result of feeding, reproductive, or defensive activities, or possibly a wind-driven current system in the lake. Likewise, ANGRADI (1998) found a highly localized distribution of medusae in a reservoir, and suggests that the distribution of medusae may result from the pattern of dispersion from a location determined by the habitat requirement of the polyp. We have not analysed the factors affecting the distribution of *C. sowerbyi* in the Proserpina Reservoir. However, we suspect that the wind direction (from the northwest) may have been the principal factor affecting that distribution.

Craspedacusta sowerbyi tentacles consist of three sets of variable length (PAYNE, 1924), with shorter tentacles for food capture, and longer tentacles acting as stabilizers during swimming and predatory behaviour (PENNAK, 1956). Tentacle numbers increase with age and maturity (BOOTHROYD et al., 2002), with a clearly greater number of tentacles in mature medusae (348, PAYNE, 1924; 350, FERREIRA, 1985; 200-400, JANKOWSKI, 2001; 497, BOOTHROYD et al., 2002).

Craspedacusta sowerbyi medusae reach sexual maturity after 5–6 weeks, and occur more frequently in late summer (ACKER & MUSCAT, 1976; ZISER & BURKE, 1984). Estimates of optimum growth temperatures vary in the literature (25º C, MCCLARY, 1959; 19-23º C, ACKER, 1976), but are generally considered to be lower for polyps than for medusae. ACKER & MUSCAT (1976) found that the polyps disintegrated at temperatures of 30º C. Medusae of *C. sowerbyi* have been reported from waters >30º C (PENNAK, 1956; ZISER & BURKE, 1984). Medusae of *C. sowerbyi* have generally only been recorded during summer in most temperate countries. Most records of polyps have also been during summer (DEVRIES, 1992), indicating increased growth and reproductive activity during warm periods. The presence of medusae of *C. sowerbyi* in the Proserpina Reservoir in summer is consistent with the widely-reported observation of *C. sowerbyi* occurring at times of high water temperatures, although water level and food abundance (LYTLE, 1962) have also been suggested as regulating mechanisms.

A common feature of records of *C. sowerbyi* has been the lack of encounters of male and female medusae together. Outside China, a very few observations have been made of populations with medusae of both sexes (PAYNE, 1924; RICE, 1958; DEACON & HASKELL, 1967). Some studies report only female medusae (e.g., PENNAK, 1956; ZISER & BURKE, 1984), although in other areas populations composed exclusively of males have also been found (BYERS, 1945; FISH, 1971; BOOTHROYD et al., 2002; LUNDBERG et al., 2005).

The present observation of the diet of *C. sowerbyi* is similar to previous reports. It includes a variety of cladocerans, copepods, and rotifers (e.g., DODSON & COOPER, 1983; SPADINGER & MAIER, 1999; BOOTHROYD et al., 2002). Medusae are active predators, and when moderately abundant can be a key factor influencing the population dynamics of other zooplankton (MATSAKIS & CONOVER, 1991; GOPAL SARMA & CHAKRABARTI, 2000). Thus, predation by *C. sowerbyi* causes significantly lower abundances of bosminids and cyclopoid copepods (JANKOWSKI & RATTE, 2000; JANKOWSKI, 2004).

Similarly to other published data (BOOTHROYD et al., 2002), nauplii were not recorded in the gut content of *C. sowerbyi* in the Proserpina Reservoir. Whether this was because they were not preyed upon, or because they were more rapidly digested and thus were missed in the analysis, is uncertain. DODSON & COOPER (1983) found in laboratory experiments that nauplii were consumed at high rates by *C. sowerbyi*. In our study, *C. sowerbyi* fed on five rotifer taxa, whereas in New Zealand (BOOTHROYD et al., 2002) only *Asplanchna* was recorded in jellyfish stomachs. DODSON & COOPER (1983) also demonstrated that *C. sowerbyi* selected large and predaceous rotifers such as *Asplancha,* and avoided small rotifers.

As in other studies (DODSON & COOPER, 1983; BOOTHROYD et al., 2002), a positive selection by *C. sowerbyi* towards copepods and cladocerans was observed in Proserpina Reservoir. However the calculated selectivity values should be interpreted with caution since *C. sowerbyi* can follow particular day-night vertical migrations (SPADINGER & MAIER, 1999), and sampling in the present study was restricted to daytime only. Thus our results may underestimate predation if it occurs at other times of the 24-h period.

ACKNOWLEDGEMENTS

We thank Inés María Pavón for providing information on the presence of medusae in Proserpina Reservoir, and M. Villena (Museo Nacional de Ciencias Naturales, Madrid) for providing information on the presence of *C. sowerbyi* in Spain. We also thank Adam Petrusek (Department of Ecology, Charles University, Prague) for help in sex determination of medusae.

REFERENCES

ACKER, T.S. (1976). *Craspedacusta sowerbyi* : an analysis of an introduced species. In : MACKIE, G.O. (ed), *Coelenterate Ecology and Behavior.* Plenum Press, New York : 219–226.

ACKER, T.S. & A.M. MUSCAT (1976). The ecology of *Craspedacusta sowerbyi* Lankester, a freshwater hydrozoan. *Am. Midl. Nat*., 95 : 323–336.

ANGRADI, T.R. (1998). Observations of freshwater jellyfish, *Craspedacusta sowerbyi* Lankester (Trachylina : Petasidae) in a West Virginia Reservoir. *Brimleyana*, 25 : 34-42.

BARNES, R.D. (1980). *Invertebrate Zoology.* Holt-Saunders, Japan.

BECKETT, D.C. & E.J. TURANCHIK (1980). Occurrence of the freshwater jellyfish *Craspedacusta sowerbyi* Lankester in the Ohio River. *Ohio J. Sci*., 80 : 95–96.

BOOTHROYD. I.K.G., M.K ETHEREDGE & J.D GREEN (2002). Spatial distribution, size structure, and prey of *Craspedacusta sowerbyi* Lankester in a shallow New Zealand lake**.** *Hydrobiologia*, 468 : 23–32.

BYERS, C.F. (1945). The fresh-water jellyfish in Florida. *Proceedings of the Florida Academy of Sciences*, 7 : 173–180.

DAVIS, C.C. (1955). Notes on the food of *Craspedacusta sowerbyi* in Crystal Lake, Ravenna, Ohio. *Ecology,* 36 : 364–366.

DEACON, J.E. & W.L. HASKELL (1967). Observations on the ecology of the freshwater jellyfish in Lake Mead, Nevada. *Amer. Midl. Nat*., 78 : 155-166.

DEVRIES, D.R. (1992). The freshwater jellyfish *Craspedacusta sowerbyi* : a summary of its life history, ecology and distribution. *J. Freshwat. Ecol*., 7 : 7–16.

DODSON, S.I. & S.D. COOPER (1983). Trophic relationships of the freshwater jellyfish *Craspedacusta sowerbyi* Lankester 1880. *Limnol. Oceanogr*., 28 : 345–351.

DUMONT, H.J. (1994). The distribution and ecology of the fresh- and brackish-water medusae of the world. *Hydrobiologia*, 272 : 1–12.

FERREIRA, M.T. (1985). Occurrence of the freshwater medusa *Craspedacusta sowerbyi* Lank, 1880 (Hydrozoa : Olindiidae) in Portuguese reservoirs. *Bol. Soc. Port. Cienc. Nat*., 22 : 41–46.

FISH, G.R. (1971). *Craspedacusta sowerbyi* Lankester (Coelenterata : Limnomedusae) in New Zealand lakes. *New Zealand J. mar. Freshwat. Res*., 9 : 573-574.

GOPAL SHARMA, J. & R. CHAKRABARTI (2000). Seasonal occurrence of freshwater medusa *Limnocnida indica* Annandale (Cnidaria : Limnomedusae) in a lake associated with the river Yamuna, India. *Aquatic Ecology,* 34 : 205–207.

HYSLOP, E.J. (1980). Stomach content analysis – a review of methods and their application. *J. Fish Biol.,* 17 : 411-429.

JANKOWSKI, T. (2001). The freshwater medusae of the world – a taxonomic and systematic literature study with some remarks on other inland water jellyfish. *Hydrobiologia*, 462 : 91-113.

JANKOWSKI, T. (2004). Predation of freshwater jellyfish on Bosmina : the consequences for population dynamics, body size, and morphology. *Hydrobyologia*, 530/531 : 521-528.

JANKOWSKI, T. & H.T. RATTE (2000). On the influence of the freshwater jellyfish *Craspedacusta sowerbyi* on the zooplankton community. *Verh. Internat. Verein. Limnol*., 27 : 1-4.

KIMMEL, B.L., M.M. WHITE, S.R. MCCOMAS & B.B. LOONEY (1980). Recurrence of the freshwater jellyfish, *Craspedacusta sowerbyi* (Cnidaria : Hydrozoa), in the Little River system, Southeastern Oklahoma. *Southwestern Association of Naturalists*, 25 : 426–428.

LANKESTER, E.R. (1880). On *Limnocodium* (*Craspedacusta*) *sowerbyi*, a new trachomedusa inhabiting freshwater. *Quaterly J. Micros. Sci*., 20 : 351-371.

LUNDBERG, S., J.E. SVENSSON & A. PETRUSEK (2005). *Craspedacusta* invasions in Sweden. *Verh. Internat. Verein. Limnol*., 29 (2) : 899-902.

LYTLE, C.F. (1962). *Craspedacusta* in southeastern United States. *Tulane Stud. Zool*., 9 : 309–314.

MATSAKIS, S. & R.J. CONOVER (1991). Abundance and feeding of medusae and their potential impact as predators on other zooplankton in Bedford basin (Nova Scotia, Canada) during spring. *Can. J. Fish. Aquat. Sci*., 48 : 1419–1430.

MCALPINE, D.F., T.L. PEARD, T.J. FLETCHER & G. HANSON (2002). First reports of the freshwater jellyfish *Craspedacusta sowerbyi* (Hydrozoa : Olindiidae) from maritime Canada with a review of Canadian occurrences. *J. Freshw. Ecol*., 17 (2) : 341-344.

MCCLARY, A. (1959). Growth and differentiation in *Craspedacusta sowerbyi*. Ph.D. Thesis, University of Michigan.

PAYNE, F. (1924). A study of the fresh-water medusa, *Craspedacusta ryderi*. *J. Morphol*., 38 : 387-430.

PEARRE, S. (1982). Estimating prey preferences by predators : uses of various indices, and a proposal of another based on χ^2. *Can. J. Fish. Aquat. Sci*., 39 : 914-923.

PEARSE, V., P. PEARSE, M. BUSCHBAUM & R. BUSCHBAUM (1987). *Living invertebrates*. Blackwell Scientific Publication, California.

PENNAK, R.W. (1956). The freshwater jellyfish *Craspedacusta* in Colorado with some remarks on its ecology and morphological degeneration. *Trans. Am. Microsc. Soc*., 75 : 324–331.

RAYNER, N.A. (1988). First record of *Craspedacusta sowerbyi* Lankester (Cnidaria : Limnomedusae) from Africa. *Hydrobiologia,* 162 : 73–77.

RICE, N.E. (1958). Occurrence of both sexes of the freshwater medusa *Craspedacusta sowerbyi* Lankester in the same body of water. *Am. Midl. Nat*., 59 : 225-226.

SPADINGER, R. & G. MAIER (1999). Prey selection and diel feeding of the freshwater jellyfish, *Craspedacusta sowerbyi*. *Freshwat. Biol*., 41 : 567–573.

THOMAS, I.M. (1950). The medusa *Craspedacusta* in Australia. *Nature,* 166 : 312–313.

ZISER, S.W. & W.W. BURKE (1984). A new record of the freshwater jellyfish *Craspedacusta sowerbyi* Lankester in Louisiana. *Proc. Louisiana Acad. Sci*., 47 : 45–47.

Received: February 2, 2005
Accepted: July 7, 2006