J. Mar. Biol. Ass. U.K. (2006), **86**, 699–703
Printed in the United Kingdom

European hydromedusa *Eleutheria dichotoma* (Cnidaria: Hydrozoa: Anthomedusae) found at high densities in New South Wales, Australia: distribution, biology and habitat

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Eleutheria dichotoma, a hydrozoan not previously recorded from the southern hemisphere, was found at high densities at several locations along the coast of New South Wales (NSW), Australia, between August and November 2005. The identity of the species was confirmed by morphological and molecular (16S rDNA) comparisons with European specimens. Local densities, distribution and habitat (algal substrate) were examined. The medusae were found along a 400 km stretch of coastline between Bateau Bay (33°23′S 151°29′E) and Pebbly Beach (35°35′S 150°43′E), primarily on the green alga *Ulva*, at mean densities of more than 50 individuals per 10 cm^2 plot. The species is probably a recent introduction to Australia.

INTRODUCTION

Introduced species are one of the greatest contemporary threats to marine environments (Bax et al., 2001), particularly those that become pests (Hutchings & Glasby, 2004). Nonindigenous organisms have the capacity to destabilize native ecosystems by several mechanisms, including resource depletion, predation, and disease transmission (Coles & Eldredge, 2002), and their early detection is vital in controlling or preventing potential invasions (Hutchings & Glasby, 2004). Not all introduced species are problematic, however, and control measures require an understanding of whether the species is truly nonindigenous, how it arrived, and its population dynamics (Bax et al., 2001).

Eleutheria dichotoma Quatrefages, 1842 (family Cladonematidae), a hydrozoan with a crawling medusa, has not previously been recorded from the southern hemisphere. Originally described from the English Channel, it has since been recorded from many locations along the Atlantic coast of Europe (up to Norway), from the Mediterranean and Black Sea (Schuchert, in press), and from Belize, in the Caribbean (Spracklin, 1982). The species is generally found on algae such as *Ulva*, *Cystoseira* and *Gelidium* (Schuchert, in press).

Eleutheria dichotoma was found at several locations along the coast of New South Wales (NSW), Australia, between August and November 2005. The identity of the species was confirmed by morphological and molecular comparisons with European specimens. Sampling was carried out to determine densities, distribution and habitat.

MATERIALS AND METHODS

Samples were collected between August and November 2005, along the coast of NSW, eastern Australia. Each was obtained by scraping algae (*Ulva*, *Enteromorpha*, *Sargassum* and *Corallina*) from a 10 cm^2 area of intertidal rock platform. Samples were fixed in 7% formalin and preserved in 80% ethanol. Algae were shaken thoroughly and removed. Specimens of *Eleutheria dichotoma* in the residual ethanol were counted. This methodology is similar to that used by Hirano et al. (2000). Algae from the samples were air-dried and weighed.

Live medusae were photographed using a Nikon D70 digital camera, with a micro Zeiss Lumina 25 mm lens. Specimens for scanning electron microscopy (SEM) study were dehydrated in ethanol, critical point dried, covered with 20 nm of gold and examined under a Leo 435VP scanning electron microscope.

To determine the distribution of *E. dichotoma* in NSW, samples of *Ulva* were collected from the following locations: the headland between Shelly Beach and Bateau Bay Beach (33°23′S 151°29′E), 23 October 2005; the central rock platform of Mona Vale Beach (33°41′S 151°18′E), 31 August and 30 October 2005; the northern rock platform of Maroubra Beach (33°57′S 151°15′E), 8 October 2005; Barrack Point, Shellharbour (34°36′S 150°54′E), 15 October 2005; and the northern rock platform of Pebbly Beach (35°35′S 150°43′E), 16 October 2005 (Figure 1). Voucher specimens were deposited in the collections of the Australian Museum (G.17068, G.17117-22, G.17124-26).

To estimate the population density of *E. dichotoma*, 11 samples of exposed *Ulva* were randomly collected from Maroubra, 8 October 2005. To compare densities on different substrata, four samples each of exposed *Ulva*, sheltered (rockpool) *Ulva*, and exposed *Sargassum*, *Enteromorpha*, and *Corallina*, were randomly collected from Mona Vale, 30 October 2005.

Numbers of medusae in each sample were compared between algal substrates by one-factor analysis of variance,

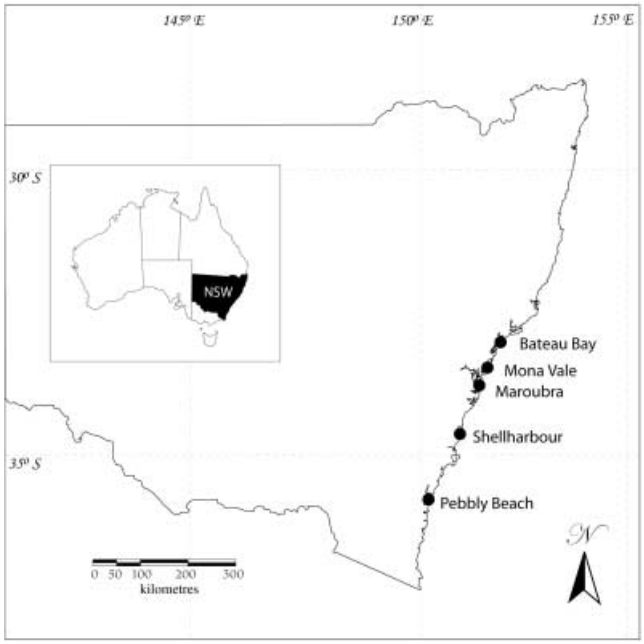

Figure 1. Distribution of *Eleutheria dichotoma* along the New South Wales (NSW) coast. Black spots mark the locations at which *E. dichotoma* was collected during this study.

using the statistical software MINITAB. Fisher's least significant difference test was used to determine where differences lay.

The 16S DNA sequence of several ethanol-fixed specimens from Maroubra Beach was determined for comparison with European material. DNA extraction, amplification of about 600 base pairs of the 16S gene and sequencing followed Schuchert (2005). The sequence of the Australian *E. dichotoma* was deposited in the European Molecular Biology Laboratory (EMBL) database (Accession no. AM159500). Voucher specimens from Maroubra were deposited in the Muséum d'Histoire Naturelle de Genève (MHNG INVE37416). The 16S sequence was compared to those of *E. dichotoma* originating from the Mediterranean: two haplotypes from Banyuls-sur-Mer (Accession nos. AY512538 and AM088485), as well as several sequences from western Mediterranean populations reported by Ender (1997).

SYSTEMATICS

Order ANTHOMEDUSAE Haeckel, 1879
Suborder CAPITATA Kühn, 1913
Family CLADONEMATIDAE Gegenbaur, 1857
Genus *Eleutheria* Quatrefages, 1842
Eleutheria dichotoma Quatrefages, 1842
(Figure 2)

Eleutheria dichotoma—Bouillon et al., 2004: 89. Figure 48g–h; Schuchert, in press: figures 19A–C, 20, synonymy.

Diagnosis of medusa

Normally six (rarely five or seven) bifurcated tentacles, with a distal adhesive disk on the lower branch and an upper branch with a terminal knob of stenotele and desmoneme nematocysts. Simple mouth without nematocyst knobs, bell margin with a thick nettle ring. Brood chamber located above the manubrium. Medusae buds on exumbrella.

Remarks

This species is well characterized by previous authors (Bouillon et al., 2004; Schuchert, in press) and only some comments about the morphology of the Australian populations are included here. Most medusae had six bifurcating tentacles (Figure 2A,B&D). Some medusae with seven (Figure 2C) or five tentacles were found; although those with five had most probably lost a tentacle during life, given the arrangement of the five remaining.

All specimens from NSW were pale orange, with conspicuous red ocelli at the base of each tentacle (Figure 2A,B), whereas previous records have described *E. dichotoma* as olive cream with red to brown abaxial ocelli (Schuchert, in press). Umbrella diameters measured less than 0.5 mm, consistent with other studies (e.g. Schierwater, 1989; Hadrys et al., 1990).

Walking motion occurs by expansion and contraction of the tentacles. The distal adhesive pads are able to cling to the surface by sucking, apparently achieved by variation in the pressure of internal liquid in the tentacular canal (Figure 2A). The pads are verrucose, with a large surface area (Figure 2G,H), assisting in the force of adhesion.

No polyp was found during this study, but medusae with buds at different developmental stages, as well as laboratory-reared sexually mature specimens, were examined. Most specimens collected bore up to six buds, attached to the margin of the exumbrella, arranged between the ocelli in the interradial areas of the ring canal (Figure 2A–C&E).

16S sequence data

Although the 16S DNA of the Australian specimens was derived from a pool of several animals, the resulting sequences showed no polymorphies. Those from Maroubra Beach differed only in two out of 588 base pairs from the two other published sequences (AY512538, AM088485) originating from Banyuls-sur-Mer. These three haplotype sequences, in turn, differ in up to six positions from other haplotypes of the same population described in Ender (1997). There was, however, no exact match among the latter sequences.

Distribution and density

Eleutheria dichotoma was found at all sites sampled during this study (Figure 1). Density of medusae averaged 51.45 individuals per 10 cm^2 plot of exposed *Ulva* (standard error (SE)=9.45) at Maroubra, 8 October 2005. Variation in the weight of algae from these samples was small, with a mean weight of 3.44 g and a SE of 0.44.

Algal substrate

The abundance of *E. dichotoma* differed significantly ($F=7.30$, $P<0.002$) between algal substrates at Mona Vale Beach. Medusae were present in significantly higher numbers on exposed *Ulva* than on any other algal substrate sampled, but no significant difference was found between *Ulva* from sheltered (rockpool) locations, *Sargassum*,

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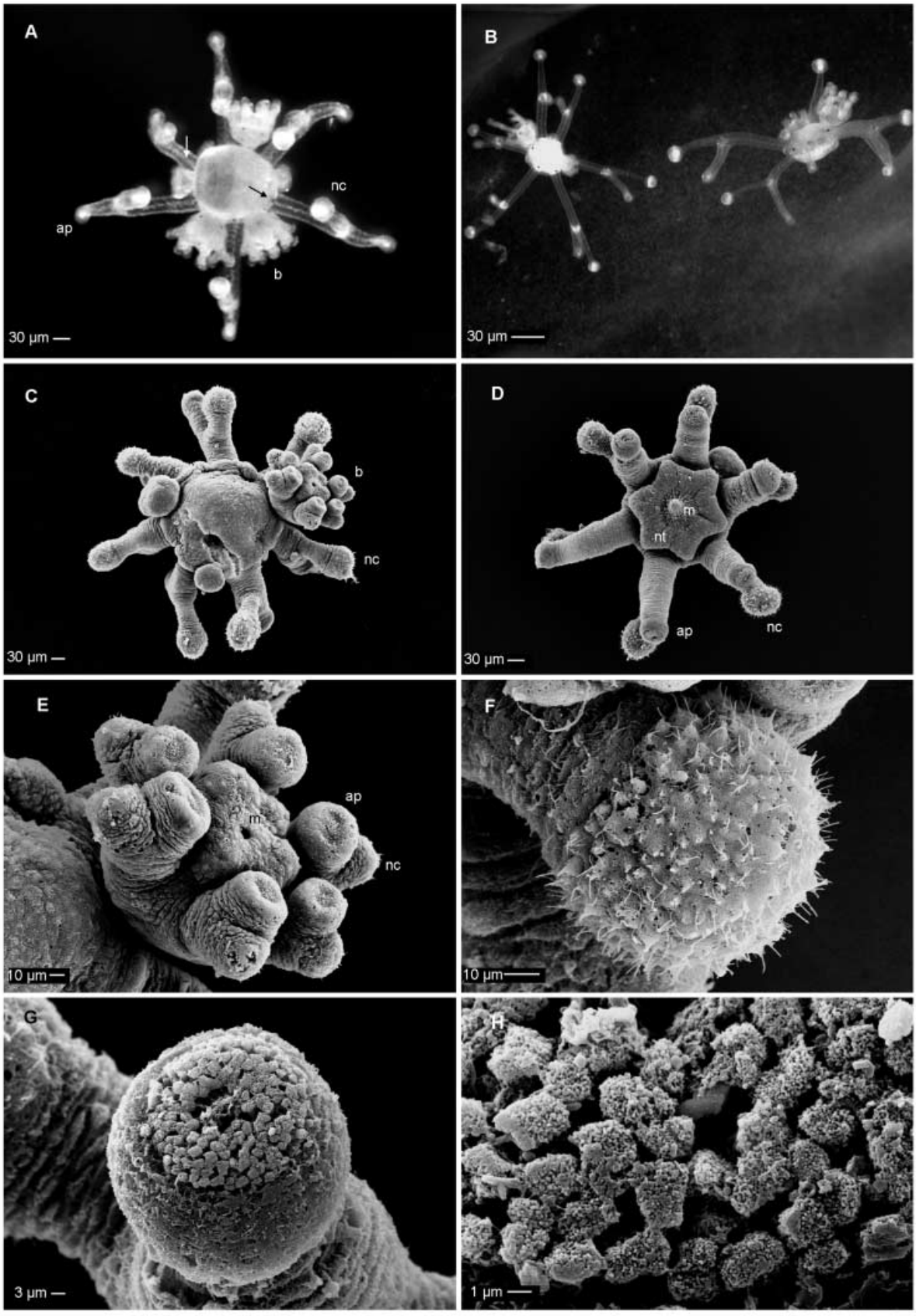

Figure 2. (A&B) *Eleutheria dichotoma*, photographs. (A) Aboral view of medusa with five buds in different stages of development; (B) two medusae, on *Ulva*. (C–H) *E. dichotoma*, SEM. (C) Dorsal view of medusa with seven tentacles and buds attached to the exumbrella; (D) oral view of medusa showing the mouth, nettle ring, lower branch of tentacles and adhesive pads; (E) detail of a well developed bud; (F) detail of a nematocyst knob on the abaxial branch of the tentacle, showing the cnidocil (bristle-like expansion) of the nematocysts; (G) adhesive pad on the end of the adaxial branch of the tentacle, showing the verrucose areas; and (H) detail of some of the areas that constitute the adhesive pads. ap, adhesive pad; b, bud; m, mouth; nc, nematocyst knob; nt, nettle ring; black arrow, ocellus; white arrow, tentacular canal. [Photographs A&B: R.T. Springthorpe.]

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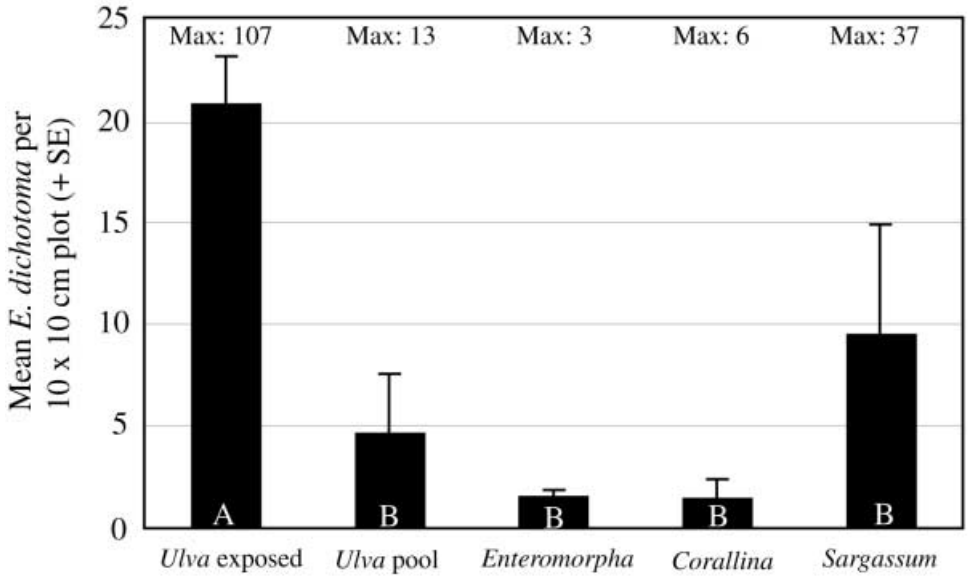

Figure 3. Mean number of *Eleutheria dichotoma* medusae on different algal substrates at Mona Vale Beach, 30 October 2005. The substrate marked 'A' (*Ulva* exposed) had significantly more medusae per 10 cm^2 plot than any other substrate, while those marked 'B' did not differ significantly in numbers of medusae. The maximum numbers, shown along the top of the chart, indicate the greatest number of *E. dichotoma* individuals from any single 10 cm^2 plot of that substrate over all sampling periods at both Mona Vale Beach and Maroubra Beach.

Corallina or *Enteromorpha* (Figure 3). The maximum numbers of *E. dichotoma* from each alga illustrate the strength of the differences between substrates (Figure 3). One hundred and seven specimens were collected from one 10 cm^2 plot of exposed *Ulva* (Maroubra, 8 October 2005), 37 from one plot of *Sargassum* (Maroubra, 8 October 2005), and fewer than 15 from all other substrates sampled.

Algal habitats are three dimensional, and comparison of the dry weight of samples was expected to give an indication of the extent of intra-specific variation in the amount of each alga among replicate plots. Variation in weight was small for each algae species, with means and standard errors of: exposed *Ulva*, 3.87 g (SE=0.07); rockpool *Ulva*, 3.03 g (SE=0.24); *Enteromorpha*, 2.36 g (SE=0.40); *Corallina*, 8.18 g (SE=1.04); and *Sargassum*, 6.31 g (SE=0.41).

DISCUSSION

Eleutheria dichotoma has almost certainly been introduced to Australia. Apart from morphological similarity, the 16S DNA sequence of the Australian specimens differed by less than 0.4% from the Mediterranean specimens, which is well within the expected range of intraspecific variation. Haplotypes of *E. dichotoma* from the western Mediterranean can differ by up to six positions (1%) within a scale of 3 km (Ender, 1997). The Australian haplotype is thus well within the range of intraspecific variation observed for *E. dichotoma*. Further study of the haplotype diversity in European and Australian populations would allow more precise conclusions to be drawn about the source of the introduction, and whether it was from a single or multiple inoculations. When *E. dichotoma* arrived in Australia is not certain. The medusae could have been present for some time but gone unobserved, although this seems unlikely considering the high densities and wide distribution recorded in this study. The only other non-European record of *E. dichotoma* is from the Caribbean, based on a single polyp with seven capitate tentacles (Spracklin, 1982). As the fully grown medusa was not observed, essential for correct identification, this record is somewhat dubious.

Several anthropogenic processes have been identified as vectors of marine fauna introductions (Hutchings et al., 2002 and references therein). Planula larvae of *E. dichotoma* could have been transported in ship ballast water; medusae and/or polyps could have fouled ship hulls; or they may have been introduced via the aquarium trade, attached to algae. Whatever their mode of arrival, the presence of *E. dichotoma* in Australia raises the question of whether or not they pose an environmental threat. Although small, population densities were observed to be high, with up to 107, and an average of more than 50, individual medusae in a 10 cm^2 plot of *Ulva*. They are also widely distributed; this study sampled along a coastal distance of about 400 km and, at all locations, specimens of *E. dichotoma* were collected. The species range is likely to extend well beyond the sampled region. Specimens were collected over several months, and as the lifespan of a medusa is typically less than one month (Bouillon et al., 2004), *E. dichotoma* appears to be successfully established.

Exposed *Ulva* is the primary habitat of *E. dichotoma* medusae. Although found on other algal substrates in the rocky intertidal, they were most abundant on *Ulva* subjected to high wave action. *Ulva* has wide, flat blades that are generally free of fouling organisms (Harder et al., 2004), and may as such provide an ideal habitat for *E. dichotoma*, with a large, smooth area to cling to. The greater abundance of *E. dichotoma* on exposed rather than sheltered *Ulva* is somewhat surprising, as the medusae are easily detached by high water velocities after feeding (Schierwater & Trager, 1987), and the relative shelter of

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tidepools may thus be considered beneficial (Hirano et al., 2000). Other factors may influence the choice of substrate, such as the abundance of food.

Ulva is consumed by many fish and invertebrate species (e.g. Rogers et al., 1995; Taylor & Steinberg, 2005), and is therefore an important part of temperate Australian marine ecosystems. The presence of *E. dichotoma* in high abundances on *Ulva* could potentially affect local food webs, for example by deterring meso- or macro-grazers of *Ulva* or by depleting copepod stocks, and this could have ramifications for the wider ecosystem. Long-term monitoring would clarify the establishment, seasonality, and ecological impacts of *E. dichotoma* in Australia.

We thank the following people: Shane Ahyong, Claudia Arango and Pat Hutchings for advice, Stephen Keable for assistance with collecting, Guillermo Diaz-Pulido for identification of algae, Roger Springthorpe for live photography, and Sue Lindsay for SEM preparation and photography.

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Submitted 25 November 2005. Accepted 27 April 2006.