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Clytia hummelincki (Hydroidomedusae: Leptomedusae) in the Mediterranean Sea

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The inconspicuous hydrozoan Clytia hummelincki, *first recorded from the Mediterranean Sea in 1996, is presently widespread throughout the middle Mediterranean Sea and the Adriatic Sea. Two surveys carried out in 2003 and 2004 along the coast of the Salento Peninsula, Italy, showed that this species inhabits a belt between 0.5 and 2 m depth in sea urchin barrens and in areas damaged by date mussel fisheries. The comparison between the two surveys indicates that the frequency of the alien increased from 2003 to 2004. The life cycle of* C. hummelincki *is described for the first time.*

Keywords: *Clytia hummelincki*, Mediterranean Sea

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INTRODUCTION

The Mediterranean Sea is highly susceptible to biological invasions for several reasons: placement within or near the Atlantic, Erythrean, and Pontic regions, busy maritime traffic, high density of aquaculture farms (Galil & Zenetos, 2002). Intrinsic reasons for biological invasions of the Mediterranean Sea are linked to its physical features: temperatures are almost tropical in shallow waters in the summer, and temperate in the winter; the recent tendency to global warming is leading to the tropicalization of the basin (Boero, 2002). This may provide greater colonization opportunities for tropical species. Extrinsic reasons for biological invasion are linked to human activities: (a) the opening of the Suez Canal in 1869 allowed entry of Indo-Pacific and Erythrean biota (Boero, 2002; Galil & Zenetos, 2002); (b) shipping activities transporting species in both fouling and ballast waters (CIESM, 2002); (c) escape of exotic species, used to enhance aquaculture yields, from culturing grounds (CIESM, 2002). In particular, the study of lessepsian immigration from the Red Sea to the Mediterranean Sea through the Suez Canal originated a wealth of information about Indo-Pacific species entering the basin (e.g. Por, 1978; Spanier & Galil, 1991). A first list of species that had newly entered the Mediterranean basin via the Suez Canal was compiled by Por (1978). Lately, investigations on the Suez Canal revealed an intensification of the Erythrean invasion (Halim & Messih, 1999). Shipping is probably the largest vector for the movement of non-indigenous marine species across the globe (Ruiz *et al.*, 1997), and the Mediterranean Sea, with its high-volume shipping routes and degraded habitats, is clearly highly susceptible to ship-transported bioinvasions (CIESM, 2002). Zenetos *et al.* (2005) assembled an annotated list of 963 alien marine species in the Mediterranean Sea. With over 300 species, the Erythrean alien contingent is mainly confined to the eastern part of the basin (Galil & Zenetos, 2002). At present the entrance of new species is well-monitored and new records of conspicuous species, usually belonging to popular groups such as fish, molluscs, crustacea or to groups that form blooms like dinoflagellates, scyphozoan jellyfish and ctenophores, are continuously published (Boero *et al.*, 2003).

Most Hydrozoa are inconspicuous, both in the hydroid and the medusa stage, and are easily overlooked by non-specialists. The group comprises hundreds of species in the Mediterranean Sea (Bouillon *et al.*, 2004); some are well represented both in coastal environments and in ship fouling communities.

In particular, the genus *Clytia* has a global distribution and includes many species (Govindarajan *et al.*, 2006). The life cycle of *Clytia* includes both polyp and medusa stages. Bouillon *et al.* (2004) report 12 species of *Clytia* from the Mediterranean, but for only three of them the life cycle is known (*C. hemisphaerica*, *C. linearis* and *C. viridicans*) (Pagliara *et al.*, 2000; Lindner & Migotto, 2002). At present, two species of Mediterranean *Clytia* are recognized as aliens: *C. linearis* and *C. hummelincki* (Boero *et al.*, 2005). *Clytia linearis* was firstly recorded from the basin in the 1950s, but has been overlooked as an alien until recently, whereas *C. hummelincki* was firstly recorded in 1996 from the coast of Calabria (Ionian coast of Italy) (Boero *et al.*, 1997). The polyp of *C. hummelincki* is redescribed and developmental stages of the medusa are described herein. The aim of the present study was to estimate the distribution of *C. hummelincki* in the Mediterranean and to focus on the spread of the species along approximately 150 km of coast by *in situ* observations. Preliminary observations at several sites along the Salento

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Peninsula (Ionian coast of Apulia, south-coast Italy) showed that this species thrives only in summer, forming dense carpets at 0.5–2 m depth, on rocks covered by encrusting coralline algae that are intensively grazed by sea urchins (Boero *et al.*, 2005).

MATERIALS AND METHODS

Hundreds of hydroid colonies were collected by SCUBA diving along the Ionian coasts of Apulia, Italy (Figure 1A). Rearing experiments were made on fertile colonies of *Clytia hummelincki* collected in September 2004 along the shallow subtidal coasts of Santa Caterina (40°08.430′N 17°58.828′E), Ionian Sea (Figure 1A). Colonies were reared in glass containers filled with 0.45 μm filtered natural seawater until medusa liberation. Temperature and photoperiod were regulated to match the natural cycle. *Artemia* nauplii were provided for food every two to three days; water was changed after each feeding session. Colonies were examined daily to detect medusa buds. When buds started to develop, the colonies were fed daily. Colonies kept in the laboratory under controlled temperature conditions (25°C) produced medusae in September. Released medusae (6) were divided into two groups of three individuals each: the first group was reared under the same conditions as the hydroid colony (25°C), while the second was kept at 12°C (preliminary observations showed that gonad development was faster at lower temperatures). All medusae were fed daily and reared until their death. All stages of development were recorded with a video camera connected to either a stereo or a compound microscope.

Surveys of the Salento coast

A first survey along 250 km of the Salento Peninsula, from Torre Specchia to Torre Lapillo (Figure 1A), at 0–5 m depth, was carried out between June and July 2003; a second survey was carried out between June and July 2004, following the sampling-protocol reported in Table 1. Each station was inspected visually by a SCUBA diver along a 100 m horizontal transect, parallel to the coastline, in the depth-range optimal for *Clytia hummelincki*, to detect the frequency (in terms of presence/absence) of the species. If present at two adjacent stations, the species was considered as being continuously present along the stretch of coast delimited by the two stations. The same procedure was adopted in the case of absence. The distribution of *C. hummelincki* hydroids was calculated using ArcGis 8.1.

RESULTS

Description of *Clytia hummelincki* (Leloup, 1935)

HYDROID

Colony stolonal, hydrorhiza reticular and anastomosed. Hydrotheca short and wide, ~0.35 mm high and ~0.30 mm wide; hydrothecal rim smooth (Figure 2A). Hydrothecal pedicel long, with several distal annulations (generally three) and four proximal ones; sub-hydrothecal spherule present; diaphragm oblique; hypostome peduncled; hydranth with 22 amphicoronate filiform tentacles. Gonotheca on hydrorhiza, sessile to shortly stalked, truncate, tapering below, 0.8 mm in height and maximum diameter 0.28 mm, with two basal annulations (Figure 2B); only one medusa bud per gonotheca.

Cnidome: small microbasic b-mastigophores on both tentacles and hydranth body.

BEHAVIOUR OF HYDROID

Hydranths feed passively: their feeding space coincides with the volume covered by the extended tentacles, and they wait for prey to collide with tentacles. Tentacles with a prey (*Artemia* nauplii) bend towards the mouth. Up to two prey items can be usually ingested at a time. New ingestions occur about 25 minutes after the preceding one. Every mechanical stimulus is a ‘disturbance’ that causes hydranth retraction into the theca, a typical behaviour of Leptomedusan hydroids (Miglietta *et al.*, 2000).

Medusa reared at 25°C

Three medusae were reared at 25°C for 11 days, but gonad development was not observed.

NEWLY RELEASED (FIGURE 2C,D)

Bell almost spherical, 1.24 mm in diameter, 0.85 mm high; manubrium 0.27 mm long, mouth quadratic, with four lobes; four radial canals, eight bulbs (four large, pyriform, perradial and tentacular ones; four small, rounded and

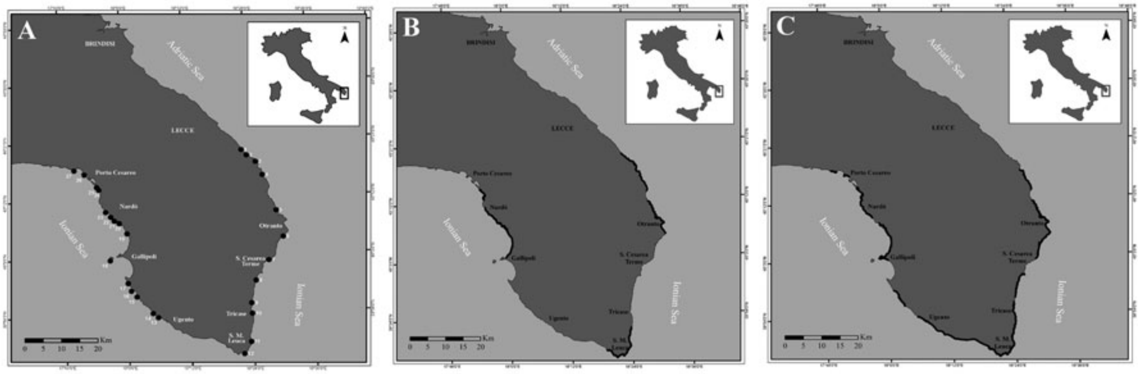

Fig. 1. (A) Map showing the sampling area in the northern Ionian Sea (Lecce, Apulia, Italy); (B) records of *Clytia hummelincki* colonies in 2003 survey; (C) records of *Clytia hummelincki* colonies in 2004 survey.

Table 1. Sampling-programme with the indications of presence/absence of the *Clytia hummelincki* species.

ID	Latitude	Longitude	Site	Survey 2003	Survey 2004
1	40° 9.321′	18° 2.855′	Torre Specchia	A	A
2	40° 8.460′	18° 3.828′	San Foca	A	A
3	40° 7.412′	18° 5.531′	Roca	A	A
4	40° 5.332′	18° 6.757′	Sant'Andrea	P	P
5	40° 9.769′	18° 9.164′	Nord di Otranto	P	P
6	40° 5.626′	18° 0.341′	Nord S. Emiliano	A	P
7	40° 2.078′	18° 7.413′	Santa Cesarea Terme	A	A
8	39° 8.965′	18° 4.779′	Marina di Andrano	A	P
9	39° 5.477′	18° 3.780′	Tricase Sud	A	P
10	39° 3.851′	18° 3.827′	Sud T.re Tiggiano	P	P
11	39° 9.448′	18° 3.447′	Gagliano	P	P
12	39° 7.600′	18° 2.039′	Santa Maria di Leuca	P	P
13	39° 3.637′	18° 5.756′	Scoglio Tondo	P	P
14	39° 4.311′	18° 4.783′	Madonna della Luce	A	A
15	39° 6.948′	18° 1.767′	Porto Racale	A	P
16	39° 7.086′	18° 4.105′	Torre Suda	P	P
17	39° 9.081′	18° 0.159′	Marina di Mancaversa	A	A
18	40° 2.701′	17° 6.855′	Isola di S. Andrea	A	P
19	40° 6.790′	18° 0.260′	T.re dell'Alto Lido	A	P
20	40° 8.430′	17° 8.828′	Santa Caterina	P	P
21	40° 8.839′	17° 7.885′	Punta della Lea	A	A
22	40° 3.130′	18° 8.662′	Grotta Corvine	P	P
23	40° 0.215′	17° 6.265′	Punta Longa	P	P
24	40° 3.700′	17° 5.096′	S. Isidoro	P	P
25	40° 4.021′	17° 4.696′	Penisola della Strea	A	P
26	40° 6.128′	17° 2.406′	Isola della Malva	P	P
27	40° 6.803′	17° 0.445′	Torre Lapillo	P	P

A, absence; P, presence.

interradial); eight statocysts along circular canal, with one statolyth each; velum ~0.16 mm wide; gonads absent; tentacular tips clavate.

Cnidome: atrichous ishorizas, microbasic mastigophores, on tentacles and manubrium.

Descriptions of further growth stages report on features that were absent or different in previous stages.

FIVE-DAY-OLD MEDUSA

Bell flatter than the previous stage, 1.26 mm high and 3.28 mm in diameter; manubrium 0.41 mm high; 16 bulbs (four large, pyriform, perradial, tentacular; four small, rounded and interradial; eight adradial).

EIGHT-DAY-OLD MEDUSA

Bell almost hemispherical, 3.73 mm in diameter and 1.60 mm high; manubrium 0.42 mm long; mouth quadratic, with large ondulate lobes.

ELEVEN-DAY-OLD MEDUSA (FIGURE 2E,F)

Bell hemispherical, 3.97 mm in diameter and 2.23 mm high. Manubrium 0.48 mm long; mouth quadratic with four large ondulate lobes; 24 bulbs (four tentacular, pyriform, perradial ones; the others small, rounded: four interradial and 16 adradial).

TWELVE-DAY-OLD MEDUSA

Bell hemispherical; 28 bulbs.

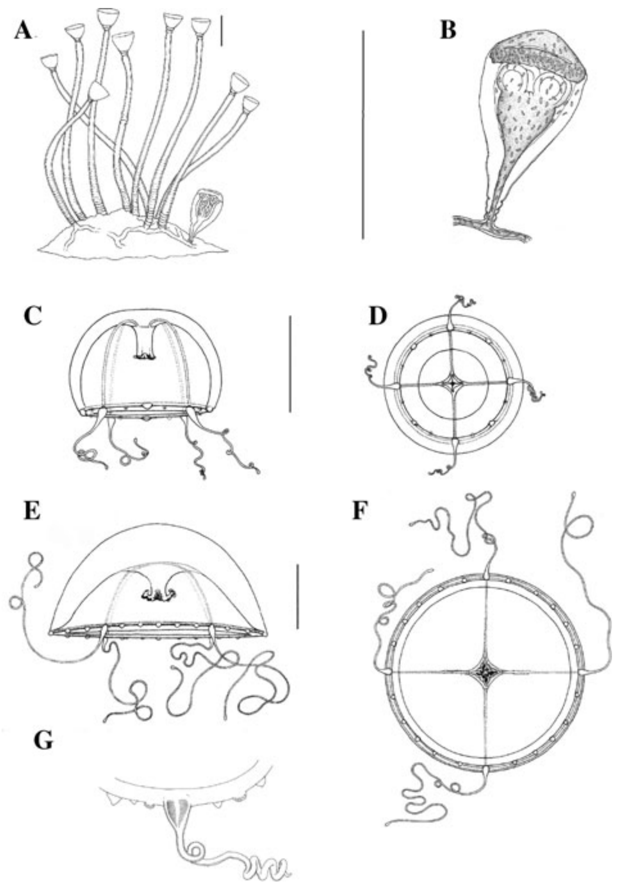

Fig. 2. *Clytia hummelincki* reared at 25°C: (A) colony with gonotheca; (B) gonotheca with a medusa-bud; (C, D) new born medusa, frontal and oral view; (E, F) 11-day-old medusa, side and oral view; (G) 15-day-old medusa, enlargement of tentacled and atentaculate bulbs, and statocysts. Scale bars: A, 500 μm; B–G, 1 mm.

FIFTEEN-DAY-OLD MEDUSA (FIGURE 2G)

Bell hemispherical, 4.02 mm in diameter and 2.54 mm high; 38 bulbs, eight tentacles and eight statocysts. No gonads.

Medusa reared at 12°C

Three medusae reared at 12°C developed gonads in 12 days.

FIVE-DAY-OLD MEDUSA (FIGURE 3A)

Bell almost spherical, 1.48 mm in diameter and 1.12 mm high; eight bulbs (four large tentacular, pyriform, perradial ones; four rounded and interradial); eight statocysts along circular canal.

EIGHT-DAY-OLD MEDUSA

Bell 1.98 mm in diameter and 1.57 mm high; mouth quadratic; eight bulbs arranged as in five-day-old medusa.

TWELVE-DAY-OLD MEDUSA (FIGURE 3B)

Bell almost spherical, 2.52 mm in diameter and 2.03 mm high; mouth quadratic, with four large ondulate lobes; eight bulbs; eight statocysts along circular canal; four male oval gonads in the upper side of radial canals.

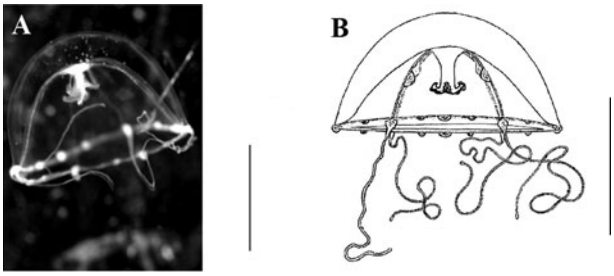

Fig. 3. *Clytia hummelincki* reared at 12°C: (A) five-day-old immature medusa; (B) male mature medusa (12-day-old). Scale bars: A, 1 mm; B, 2 mm.

BEHAVIOUR

The medusa catches prey (*Artemia* nauplii) during swimming, so being a cruising predator (Mills, 1981). Captured prey is brought to mouth by tentacle contraction. *Clytia hummelincki* needs water currents to remain suspended in the water column: this is a problem in rearing because if medusae lie on the bottom they soon die probably due to loss of ability to catch prey. The medusa is very voracious: in a few days specimens ingest up to seven prey with an increasing ingestion of 1–3 prey. Well-fed medusae release captured prey.

REMARKS

The present description does not cover the whole development of the medusa, since gonad maturation and spawning were not observed. The medusae did not grow easily under laboratory conditions and, probably, their natural diet has much different requirements than what is available in an *Artemia*-based diet. This is, however, the most complete description of the life cycle of this species.

Survey results

FIRST SURVEY (2003)

A total of 217 out of 250 km of the Salento Peninsula coast is rocky, the remainder is characterized by sandy and muddy substrata (Fanelli *et al.*, 1994). *Clytia hummelincki* colonies were present in half of the surveyed sectors of the Salento Peninsula (125 out of 250 km, 58% of the rocky substrates), from Torre Specchia to Torre Lapillo (Table 1; Figure 1B). The species was particularly abundant in full light, on bare substrates covered by encrusting corallines, being absent on sandy and muddy ones.

SECOND SURVEY (2004)

Clytia hummelincki hydroids were present in about 74% of the sites (185 out of 250 km, 85% of the rocky coast) (Table 1; Figure 1C).

Distribution of *Clytia hummelincki* in the Mediterranean Sea (Figure 4)

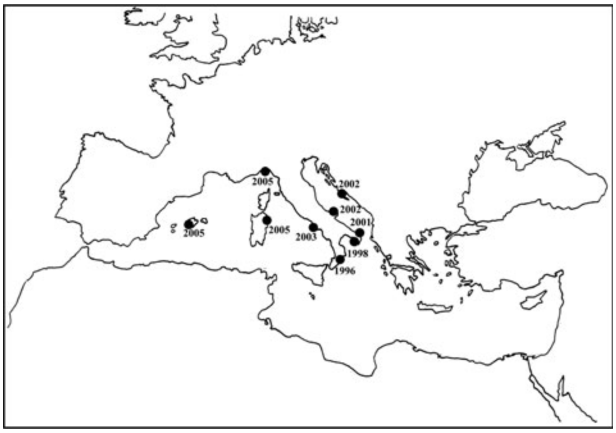

Fig. 4. Records of *Clytia hummelincki* hydroid colonies in the Mediterranean Sea.

The first Mediterranean record of *C. hummelincki* was from Copanello (Calabria, Ionian Sea), in 1996 (Boero *et al.*, 1997). After its discovery, this species has been widely recorded along the Apulian coast: Tremiti Isles in the Adriatic Sea (S. Fraschetti, unpublished data); Torre del Serpe, Torre Inserraglio and Porto Cesareo in the Apulian Ionian Sea. Colonies of *C. hummelincki* were recorded from the Croatian coast (C. Di Camillo, unpublished data), Ponza (Naples) (A. Terlizzi, unpublished data), Capo Figari (north-east Sardinia) (P. Guidetti, unpublished data), Portofino (C. Cerrano, unpublished data) and from Majorca Island (P. Schuchert, unpublished data).

World distribution of *Clytia hummelincki*

The type locality of this species is the West Indies (Leloup, 1935); it has also been recorded from the Gulf of Mexico (Deevey, 1954), Ghana (Buchanan, 1957), South Africa (Millard, 1966, 1975), Papua New Guinea in 1986 (F. Boero & J. Bouillon, unpublished data), Bonaire, the Netherlands Antilles (Bermuda) (Calder, 1991), Brazil (Haddad, 1992; Migotto, 1996; Kelmo & Attrill, 2003), North Sulawesi, Indonesia in 2001 (C. Di Camillo, unpublished data), the Galapagos Islands (Calder *et al.*, 2003), and the Mediterranean. These records suggest that this species is circumtropical.

Taxonomic remarks

Leloup (1935) described this species as *Laomedea hummelincki* due to the features of the hydroid that, having a subhydrothecal spherule, was clearly not a *Clytia*. Leloup's material, however, was infertile. Millard (1966) described the gonotheca for the first time, reporting it as containing a developing medusa bud. The presence of a medusa in the life cycle is a clear feature of *Clytia*, the only campanulariid genus with medusae (besides the very peculiar ones of *Obelia*). Millard (1966) considered the presence of a medusa in the life cycle as having more generic weight than the subhydrothecal spherule and thus transferred the species to *Clytia*. Cornelius (1982) considered the shared feature of a subhydrothecal spherule as a convergence between *Clytia* and *Campanularia*–*Laomedea*. Moreover, the hydrorhiza of *Clytia hummelincki* is reticular and anastomosed, a typical character of another campanulariid, *Orthopyxis*. This character, overlooked by Millard (1966, 1975) in a colony growing on the surface of *Lepas* sp. from South Africa, might be a functional specialization of the hydroid stage that occurs in many genera (Boero & Sarà, 1987). Govindarajan *et al.* (2006), in a molecular revision of the Campanulariidae, found that *C. hummelincki* is clearly a member of the clade comprising all the examined *Clytia* species, having the basalmost position in the clade. From a morphological point of view, the species is clearly referable to *Campanularia* in the hydroid stage and to *Clytia* in the medusa stage, constituting a case of 'inconsistent evolution' (*sensu* Boero & Bouillon, 1987), resolved by Govindarajan *et al.* (2006) with a molecular approach.

DISCUSSION

Clytia hummelincki is likely a recent introduction into the Mediterranean Sea (Boero *et al.*, 1997). It is highly improbable, in fact, that such a distinctive species, living in such an easily reachable habitat, passed unobserved in the two centuries of Hydrozoan studies in the Mediterranean. The species is present both in the Atlantic and the Pacific Oceans, and it is difficult, at present, to establish if it entered either from Suez or from Gibraltar (Boero, 2002; Boero *et al.*, 2005).

The temperature of the Mediterranean Sea has increased due to global warming. Since the mid-1950s, in fact, an average warming of 0.31°C from the surface to 300 m depth of the world ocean has been recorded (Levitus *et al.*, 2000; Purcell, 2005), possibly favouring tropical species such as the present one. In general, tropical invasive species gain a distinct advantage over the native Mediterranean fauna (Galil & Zenetos, 2002).

Most species studied by Galil *et al.* (2002) and Golani *et al.* (2002) have been recorded only a few times because their destiny is usually local extinction, but some species are able to replace similar indigenous species.

At present, *C. hummelincki* can be considered as a successful invader due to its high frequency at 0.5–1 m depth in sea urchin barrens where it forms a 'belt' along the Apulian coast. Boero *et al.* (2005) hypothesized that the rapid expansion of *C. hummelincki* might be the result of efficient dispersal of the medusa stage mainly obtained by displacement with currents.

Unfortunately, for the moment, its true distribution in the eastern Mediterranean basin is unknown, probably because this species can be easily overlooked by non-specialists. A phylogeographical approach based on DNA sequences might be used to trace the origin of *C. hummelincki* in the Mediterranean.

The ecological importance of hydrozoan species resides in the feeding habits of their medusae. Purcell (1989, 1990, 1991a,b, 1997, 2003), Purcell *et al.* (1987, 1994) and Purcell & Arai (2001) stressed the role of *Aequorea victoria*, a hydrozoan species, in the predation on zooplankton of many coastal plankton communities. Jellyfish are potentially important as predators of fish eggs and larvae, as well as being competitors for zooplankton prey with fish larvae and zooplanktivorous fish (Purcell, 2003).

Clytia hummelincki, like other Hydroidomedusae, might play an important ecological role, since it is of the right size to predate on fish eggs and larvae and on their prey too, copepods and larvae, acting as both competitor and predator (Boero *et al.*, 2005). The numerous colonies of *C. hummelincki* probably produce many relatively large medusae. In the Mediterranean Sea, this species might play an important ecological role in the success of fish recruitment by competing with fish by predating on their prey, i.e. zooplanktonic crustacea, possibly feeding also on fish eggs and larvae (Boero *et al.*, 2005). The arrival of a new predator not coevolved with the resident species may have a strong impact on local communities, with both competition and predation on species of commercial interest, just as it happened for *Mnemiopsis* in the Black Sea (CIESM, 2002).

Moreover, the environmental status of the receiving area is a fundamental pre-requisite for the colonization success of alien species. The pre-existing instability of the *Posidonia oceanica* endemic ecosystem, for example, facilitated the spread of the tropical algae *Caulerpa* in the north-western basin of the Mediterranean Sea in relation to stress of both natural and anthropogenic origin (Occhipinti-Ambrogi & Savini, 2003). Therefore, human intervention caused long-term modifications in the Mediterranean Sea environment, preparing a fertile ground for mass bioinvasions of alien species that might alter the original dynamics of the resident communities.

The results of the present study showed that *C. hummelincki* is particularly frequent on bare substrates, and its propagation, along the Apulian coast, coincides with the frequency of rocky coastal stretches damaged by date mussel fisheries (Fanelli *et al.*, 1994, 1999; Fraschetti *et al.*, 1999), and, therefore, might be caused by the indiscriminate fishing of *Lithophaga lithophaga* which give rise to barren grounds. Probably the effects of date mussel (*Lithophaga lithophaga*) collection, and the lack of recolonization due to sea urchin grazing (Fanelli *et al.*, 1994, 1999), heavily damaged hundreds of kilometres of the Salento rocky coasts, transforming them into suitable substrate for *C. hummelincki* colonies.

In addition, the study of the life cycle of *C. hummelincki* confirms the relevant role of the temperature on the medusa generation in hydrozoan species (Schierwater & Hadrys, 1998; Carré & Carré, 2000). Moreover, the stage of maturation reached by *C. hummelincki* medusae under different temperatures, concurs with the observations reported by Hincks (1868) for *Clytia hemisphaerica*. The specimens reared at low temperatures lived shorter lives than those kept at higher temperatures, showing a faster gonad development (Table 2). The same has been observed by Boero & Sarà (1987) for *Clytia linearis*.

Table 2. Features of *Clytia hummelincki* medusae reared at 25°C and 12°C. Diameters of umbrella are in mm. Unchanged characters are not repeated.

	Newly released	5-day-old	8-day-old	11-day-old	12-day-old	15-day-old
Medusae at 12°C	Almost spherical, diameter 1.24, 4 tentacles, 8 bulbs, 8 statocysts	Almost spherical, diameter 1.48	Almost spherical, diameter 1.98	Almost spherical, diameter not measured	Almost spherical, diameter 2.52, 4 male gonads (not ripe)	–
Medusae at 25°C	Almost spherical, diameter 1.24, 4 tentacles, 8 bulbs, 8 statocysts	Bell flatter than the previous stage, diameter 3.28, 16 bulbs	Almost hemispherical, diameter 3.73	Hemispherical, diameter 3.97, 24 bulbs	Hemispherical, diameter not measured, 28 bulbs	Hemispherical, diameter 4.02, 38 bulbs, 8 tentacles, 8 statocysts (no gonads)

In addition, the patterns of variation of reproduction strategy are affected by temperature in a few invasive hydrozoans (Ma & Purcell, 2005). The flexible strategy might promote alien invasions and the establishment of populations in new habitats.

The case of the Hydrozoa in general, and of *Clytia* species in particular, shows that the understanding of ecosystem functioning in terms of species roles is needed for a proper evaluation of biodiversity structure and function. In particular, this species might play an important ecological role in a short time window in a key period of fish population dynamics.

General predictions are not yet available to assess the interactive effects of various environmental and biological factors on invasion success (Carlton & Geller, 1993; Boero, 2002). Furthermore, Boero (2002) and Boero & Bonsdorff (2007) suggested that the number of variables pertinent to new invaders, and to ecosystem functioning in general, is so great that it is almost impossible to build up predictive models based on insufficient factual information. Moreover, it will be necessary to test for correlations between patterns of invasion and associated environmental data (Ruiz & Carlton, 2003), investigating the changes in ecosystem functioning and in food web structure caused by alien species.

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REFERENCES

Boero F. (2002) Ship-driven biological invasions in the Mediterranean Sea. In Briand F. (ed.) *CIESM Workshop Monographs, Instanbul, 6–9 November 2002. Alien marine organisms introduced by ships in the Mediterranean and Black Seas.* Monaco: CIESM Publishers, pp. 87–91.

Boero F. and Bonsdorff E. (2007) A conceptual framework for marine biodiversity and ecosystem functioning. *Marine Ecology* 28, 134–145.

Boero F. and Bouillon J. (1987) Inconsistent evolution and paedomorphosis among the hydroids and medusae of the Athecatae/Anthomedusae and the Thecatae/Leptomedusae (Cnidaria, Hydrozoa). In Bouillon J. *et al.* (eds) *Modern trends in the systematics, ecology and evolution of hydroids and hydromedusae*. Oxford: Clarendon Press, pp. 229–250.

Boero F., Bouillon J., Gravili C. and Piraino S. (2003) Who cares about the Hydrozoa of the Mediterranean Sea? An essay on the zoogeography of inconspicuous groups. *Biogeographia* 24, 101–113.

Boero F., Di Camillo C. and Gravili C. (2005) Aquatic invasions: phantom aliens in Mediterranean waters. *MarBEF Newsletter* 3, 21–22.

Boero F., Gravili C., Denitto F., Miglietta M.P. and Bouillon J. (1997) The rediscovery of *Codonorchis octaedrus* (Hydroidomedusae, Anthomedusae, Pandeidae), with an update of the Mediterranean hydroidomedusan biodiversity. *Italian Journal of Zoology* 64, 359–365.

Boero F. and Sarà M. (1987) Motile sexual stages and evolution of Leptomedusae (Cnidaria). *Bollettino di Zoologia* 54, 131–139.

Bouillon J., Medel M.D., Pagès F., Gili J.-M., Boero F. and Gravili C. (2004) Fauna of the Mediterranean Hydrozoa. *Scientia Marina* 68, 1–449.

Buchanan J.B. (1957) The hydroid fauna of the Gold Coast. *Revue de Zoologie et de Botanique Africaines* 56, 349–372.

Calder D.R. (1991) Shallow-water hydroids of Bermuda. The Thecatae, exclusive of Plumularioidea. *Royal Ontario Museum Life Sciences Contributions* 154, i–iv, 1–140.

Calder D.R., Mallinson J.J., Collins K. and Hickman C.P. (2003) Additions to the hydroids (Cnidaria) of the Galapagos, with a list of species reported from the islands. *Journal of Natural History* 37, 1173–1218.

Carlton J.T. and Geller J.B. (1993) Ecological roulette: the global transport of nonindigenous marine organisms. *Science* 261, 78–82.

Carré D. and Carré C. (2000) Origin of germ cells, sex determination, and sex inversion in medusae of the genus *Clytia* (Hydrozoa, Leptomedusae): the influence of temperature. *Journal of Experimental Zoology* 287, 233–242.

CIESM (2002) Alien marine organisms introduced by ships in the Mediterranean and Black Seas. *Workshops Monographs*, no. 20, Monaco, 136 pp.

Cornelius P.F.S. (1982) Hydroids and medusae of the family Campanulariidae recorded from the eastern North Atlantic, with a world synopsis of genera. *Bulletin of the British Museum (Natural History), Zoology* 42, 37–148.

Deevey E.S. (1954) Hydroids of the Gulf of Mexico. In Galtsoff P.S. (ed.) *Gulf of Mexico. Its origin, waters, and marine life. Fishery Bulletin. Fish and Wildlife Service, United States* 55, 267–272.

Fanelli G., Giangrande A., Miglietta M.P., Morri C., Piraino S. and Rubino F. (1999) Human disturbance and biodiversity along the Apulian coast. *Biologia Marina Mediterranea* 6, 198–204.

Fanelli G., Piraino S., Belmonte G., Geraci S. and Boero F. (1994) Human predation along Apulian rocky coasts (SE Italy): desertification caused by *Lithophaga lithophaga* (Mollusca) fisheries. *Marine Ecology Progress Series* 110, 1–8.

Fraschetti S., Bianchi C.N., Boero F., Buia M.C., Della Tommasa L., Denitto F., Esposito L., Fanelli G., Giangrande A., Miglietta M.P., Morri C., Piraino S. and Rubino F. (1999) Human disturbance and biodiversity along the Apulian coast. *Biologia Marina Mediterranea* 6, 198–204.

Galil B.S., Froglia C. and Noël P. (2002) Crustaceans–decapods and stomatopods. In Briand F. (ed.) *CIESM atlas of exotic species in the Mediterranean*. Vol. 2. Monaco: CIESM Publishers, 196 pp.

Galil B. and Zenetos A. (2002) A sea change—exotics in the eastern Mediterranean. In Leppäkoski E. *et al.* (eds) *Invasive aquatic species of Europe: distributions, impacts and management*. Dordrecht, The Netherlands: Kluwer Academic Publishers, pp. 325–336.

Golani D., Orsi-Relini L., Massuti E. and Quignard J.P. (2002) Fishes. In Briand F. (ed.) *CIESM atlas of exotic species in the Mediterranean*. Vol. 1. Monaco: CIESM Publishers, 256 pp.

Govindarajan A.F., Boero F. and Halanych K.M. (2006) Phylogenetic analysis with multiple markers indicates repeated loss of the adult medusa stage in Campanulariidae (Hydrozoa, Cnidaria). *Molecular Phylogenetics and Evolution* 38, 820–834.

Haddad M.A. (1992) *Hidróides (Cnidaria, Hydrozoa) de costões rochosos do litoral sul do Estado de Paraná*. PhD thesis, Universidade de São Paulo, São Paulo, Brazil.

Halim Y. and Messih M.A. (1999) The Suez Canal revisited. changes in the ascidian fauna of the canal. *Communication read at International conference on 'Oceanography of the eastern Mediterranean and Black Sea' 23–26 February 1999. EU Report*: 367 p.

Hincks Th. (1868) *A history of the British hydroid zoophytes*, vol. 1. London: John van Voorst.

Kelmo F. and Attrill M.J. (2003) Shallow-water Campanulariidae (Hydrozoa, Leptothecatae) from Northern Bahía, Brazil. *Revista de Biología Tropical* 51, 123–146.

Leloup E. (1935) Hydraires calyptoblastiques des Indes Occidentales. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, Série 2 22, 1–73.

Levitus S., Anotonov J.I., Boyer T.P. and Stephens C. (2000) Warming of the world ocean. *Science* 287, 2225–2229.

Lindner A. and Migotto A.E. (2002) The life cycle of *Clytia linearis* and *Clytia noliformis*: metagenic campanulariids (Cnidaria: Hydrozoa) with contrasting polyp and medusa stages. *Journal of the Marine Biological Association of the United Kingdom* 82, 541–553.

Ma X. and Purcell J.E. (2005) Temperature, salinity, and prey effects on polyp versus medusa bud production by the invasive hydrozoan *Moerisia lyonsi*. *Marine Biology (Berlin)* 147, 225–234.

Miglietta M.P., Della Tommasa L., Denitto F., Gravili C., Pagliara P., Bouillon J. and Boero F. (2000) Approaches to the ethology of hydroids and medusae (Cnidaria, Hydrozoa). In Mills C.E. *et al.* (eds) *Trends in hydrozoan biology*. Vol. IV. *Scientia Marina* 64, 63–71.

Migotto A.E. (1996) Benthic shallow-water hydroids (Cnidaria, Hydrozoa) of the coast of São Sebastião, Brazil, including a checklist of Brazilian hydroids. *Zoologische Verhandelingen Leiden* 306, 1–125.

Millard N.A.H. (1966) The Hydrozoa of the south and west coasts of South Africa. Part III. The Gymnoblastea and small families of the Calyptoblastea. *Annals of the South African Museum* 48, 427–487.

Millard N.A.H. (1975) Monograph on the Hydroida of southern Africa. *Annals of the South African Museum* 68, 1–513.

Mills C.E. (1981) Diversity of swimming behaviors in hydromedusae as related to feeding and utilization of space. *Marine Biology (Berlin)* 64, 185–189.

Occhipinti-Ambrogi A. and Savini D. (2003) Biological invasions as a component of global change in stressed marine ecosystems. *Marine Pollution Bulletin* 46, 542–551.

Pagliara P., Bouillon J. and Boero F. (2000) Photosynthetic planulae and planktonic hydroids: contrasting strategies of propagule survival. In Mills C.E. *et al.* (eds) *Trends in hydrozoan biology*. Vol. IV. *Scientia Marina* 64, 173–178.

Por F.D. (1978) Lessepsian migration. The influx of Red Sea biota into the Mediterranean by way of the Suez Canal. *Ecological Studies* 23, i–x, 1–228.

Purcell J.E. (1989) Predation of fish larvae and eggs by the hydromedusa *Aequorea victoria* at a herring spawning ground in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 46, 1415–1427.

Purcell J.E. (1990) Soft-bodied zooplankton predators and competitors of larval herring (*Clupea harengus pallasi*) at herring spawning grounds in British Columbia (Canada). *Canadian Journal of Fisheries and Aquatic Sciences* 47, 505–515.

Purcell J.E. (1991a) Predation by *Aequorea victoria* on other species of potentially competing pelagic hydrozoans. *Marine Ecology Progress Series* 72, 255–260.

Purcell J.E. (1991b) A review of cnidarians and ctenophores feeding on competitors in the plankton. In Williams R.B. *et al.* (eds) *Coelenterate biology: recent research on Cnidaria and Ctenophora. Proceedings of the Fifth International Conference on Coelenterate Biology, 1989. Hydrobiologia* 216–217, 335–342.

Purcell J.E. (1997) Pelagic cnidarians and ctenophores as predators: selective predation, feeding rates, and effects on prey populations. *Annales de l'Institut Oceanographique* 73, 125–137.

Purcell J.E. (2003) Predation on zooplankton by large jellyfish, *Aurelia labiata, Cyanea capillata* and *Aequorea aequorea*, in Prince William Sound, Alaska. *Marine Ecology Progress Series* 246, 137–152.

Purcell J.E. (2005) Climate effects on formation of jellyfish and ctenophore blooms: a review. *Journal of the Marine Biological Association of the United Kingdom* 85, 461–476.

Purcell J.E. and Arai M.N. (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. *Hydrobiologia* 451, 27–44.

Purcell J.E., Nemazie D.A., Dorsey S.E., Houde E.D. and Gamble J.C. (1994) Predation mortality of bay anchovy *Anchoa mitchilli* eggs and larvae due to scyphomedusae and ctenophores in Chesapeake Bay. *Marine Ecology Progress Series* 114, 47–58.

Purcell J.E., Siferd T.D. and Marliave J.B. (1987) Vulnerability of larval herring (*Clupea harengus pallasi*) to capture by the jellyfish *Aequorea victoria. Marine Biology (Berlin)* 94, 157–162.

Ruiz G.M. and Carlton J.T. (2003) *Invasive species: vectors and management strategies*. Washington: Island Press.

Ruiz G.M., Carlton J.T., Grosholtz E.D. and Hines A.H. (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent and consequences. *American Zoologist* 37, 621–632.

Schierwater B. and Hadrys H. (1998) Environmental factors and metagenesis in the hydroid *Eleutheria dichotoma*. *Invertebrate Reproduction and Development* 34, 139–148.

Spanier E. and Galil B.S. (1991) Lessepsian migration: a continuous biogeographical process. *Endeavour* 15, 102–106.

and

Zenetos A., Çinar M.E., Pancucci–Papadopoulou M.A., Harmelin J.G., Furnari G., Andaloro F., Bellou N., Streftaris N. and Zibrowius H. (2005) Annotated list of marine alien species in the Mediterranean with records of the worst invasive species. *Mediterranean Marine Science* 6, 63–118.

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