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Eudiaptomus gracilis in Italy: how, where and why

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ABSTRACT

Eudiaptomus gracilis*, one the most widely distributed calanoid copepod species in Europe, was not reported in Italy prior to the late 1980s. Since then,* E. gracilis *has spread to an increasing number of Northern Italian water bodies where an indigenous calanoid copepod,* E. padanus*, was commonly present and abundant. In some instances, the former species has displaced the latter. Morphological and ecological similarities between the two species suggest that competitive exclusion may explain this substitution. The establishment of* E. gracilis *seems to be limited to relatively small, eutrophic water bodies, which represent the majority of floodplain lakes in Northern Italy. The very recent colonization of oligo-mesotrophic Lake Maggiore - one of the largest Italian lakes - may allow for an examination both of the invasion process and its consequences for the abundant* E. padanus *population. Establishment of* E. gracilis *in Lake Maggiore could accelerate the spread of the species to other lakes in the region. Indeed, due to its high connectivity, Lake Maggiore could become an invasion hub in a manner consistent with that reported for other invaders in lakes around the world.*

Key words: freshwater calanoids, non-indigenous species, endemic species, species replacement, geographic distribution

1. INTRODUCTION

Until the last decades of the past century, the Alps and the Mediterranean Sea seemingly represented an efficient barrier against the entrance of non-indigenous species (NIS) species in Italian inland water bodies, thus enabling several endemic species to maintain themselves in their native environments. With the exponentially increasing rate of human-mediated introductions of NIS all over the world, natural barriers no longer provide effective protection (e.g., Rahel 2007), and any environment is potentially receptive to NIS invasions. An increasing number of non-indigenous zooplankton species have being reported in Italian freshwater bodies since the 1980's (e.g., Ferrari *et al*. 1992; Rossetti *et al*. 1996; Riccardi *et al*. 2004; Margaritora 2005; Stoch 2005). Some of these species were only occasionally found, such as the freshwater calanoid *Boeckella triarticulata* (Ferrari *et al*. 1992; Ferrari & Rossetti 2006), others seemingly failed to establish successfully after a few years (e.g., *Daphnia parvula*; Riccardi *et al*. 2004; Riccardi, unpublished data), while others successfully established permanent populations and extend their distribution to more water bodies. The freshwater calanoid copepod *Eudiaptomus gracilis* is a member of the latter group (Rossetti *et al*. 1996; Riccardi & Giussani 2007).

The differential success of invaders is not surprising since one of the main conclusions that has emerged from invasion studies is that the successful establishment of a NIS is an improbable event, and that many failed attempts occur for every successful one (Williamson 1996). Indeed, once introduced into a new habitat, an invader has to pass through sequential "filters" in the invasion sequence (e.g., Williamson & Fitter 1996; Muirhead & MacIsaac 2005) before becoming successfully established. The second filter encompasses environmental tolerance to ambient physical and chemical conditions. Finally, the success of invasions depends strongly on community characteristics, including the diversity of the resident species pool (e.g., Case 1990; Tilman 1997; Levine 2000; Louette *et al*. 2006). This finding is consistent with the classical theory that linked environment stability to community diversity. It also represents successful integration of the NIS into the biological community of the novel habitat. Integration requires that the NIS sustain predation and competition with existing native species. Given the complexity of processes that underlie biological invasions, many hypothesis have been formulated, each of which has been shown to help explain some invasions (Alpert 2006). A central role is often recognized to species life history traits by the many ecological hypotheses based on niche trade-off models (e.g., Hutchinson 1951; Tilman 2004), while stochastic effects (i.e., propagule abundances and introduction pressure) are mostly invoked by neutral models (e.g., Hubbell 2001; Alonso *et al*. 2006) to predict invasion dynamics and species invasiveness. In particular, according to classical trade-off based niche theories, the outcome of competition can produce niche partitioning, leading to coexistence of NIS and native species, or displacement of either the NIS or native species. In this view, Riccardi & Giussani (2007) suggested that the freshwater copepod *Eudiaptomus padanus*, one of the most common calanoid spe-

Tab. 1. The distribution of *Eudiaptomus gracilis* in Italian water bodies and the year of the first finding of this species.

Site	Type	Year	Reference
1 Lake Sirio	Small, meso-eutrophic	1980	de Bernardi *et al.* 1984
2 Lake Lugano	Large, eutrophic	1988	Polli & Simona 1992
3 Lake Candia	Shallow, eutrophic	1989	Riccardi & Giussani 2007
4 Lanca del Rottone	Backwaters, Ticino River	1990	Cazzalini & Sconfietti 1993
5 Lanca del Topo	Backwaters, Ticino River	1990	Cazzalini & Sconfietti 1993
6 Lake Isola Giarola	Quarry lake, Po River	1991	Rossetti *et al.* 1996
7 Lake Endine	Relatively large , eutrophic	1994	Verga 2003
8 Cava Vecchia	Sand pit	2000	Rossetti *et al.* 2003b
9 Terzo Casone	Sand pit	2001	Rossetti *et al.* 2003a
10 Brusa Vecchia	Sand pit	2001	Rossetti *et al.* 2003a
11 Lake Pusiano	Relatively large, eutrophic	2002	Osservatorio dei laghi Lombardi 2005
12 Po River	Potamal river segment	2003	Ferrari *et al.* 2006
13 Cà Stanga	Sand Pit	2004	Tavernini & Rossetti (unpublished)
14 Lake Maggiore	Large, oligo-mesotrophic	2006	Visconti *et al.* 2007

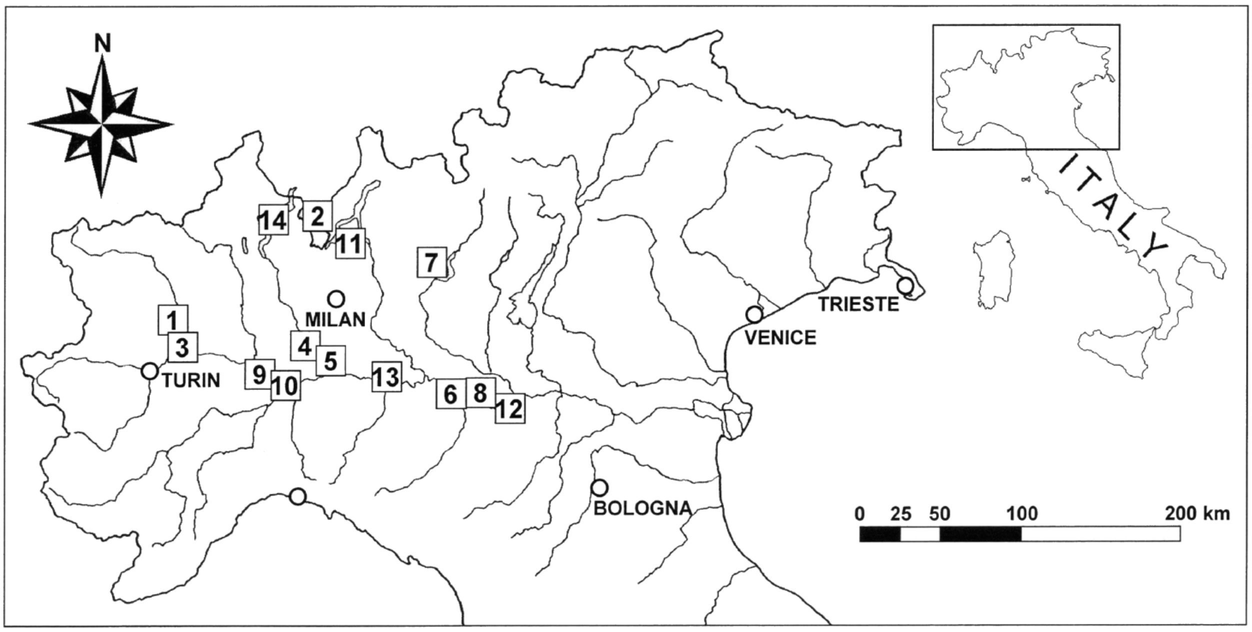

Fig. 1. Map showing the distribution of *Eudiaptomus gracilis* in Italy (updated from Stoch 2005). Sites numbered as in table 1.

cies both in the prealpine Italian regions (subspecies *padanus padanus*) and in the peninsular area (subspecies *padanus etruscus* and *etruscosexsetosus*) (Stella 1984; Dussart & Defaye 2002), might have been competitively displaced by the closely related *E. gracilis* in an increasing number of environments in Northern Italy.

The present study aims to assess the available information on the ecology of both the native and invading copepod species, and on the actual distribution of *E. gracilis* in Italy in the attempt to evaluate the potential for future range expansion and its consequences for the endemic freshwater taxa.

2. RESULTS AND DISCUSSION

Current knowledge on the distribution of *E. gracilis* in Italy is summarized in table 1 and figure 1. The first records date to 1980, in which the species was described in the small (0.3 km^2), meso-eutrophic (mean total phosphorus concentration 73 $\mu g\ L^{-1}$; Regione Piemonte 2004) Lake Sirio. The most recent record of introduction is for 2006 with reference to the large (212 km^2) oligo-mesotrophic (mean total phosphorus concentration 10-11 $\mu g\ L^{-1}$; Regione Piemonte 2004) Lake Maggiore. During this time interval several other waterbodies have been successfully colonized, most of which are represented by gravel pits, river pools and backwaters or eutrophic lakes. *Eudiaptomus padanus* was previously present in four of these water bodies and it is still present in the most recently colonized Lake Maggiore.

Table 2 summarizes the main ecological characteristics of *E. padanus* and *E. gracilis*. The former has a very narrow geographic distribution, while the latter is broadly distributed throughout Europe and into North America, Siberia, China and Israel (Gaviria 1998; Dus-

Tab. 2. Geographic distribution and ecological characteristics of *Eudiaptomus padanus padanus* and *E. gracilis*.

	E. padanus padanus	*E. gracilis*
Distribution	limited to Northern Italy	broad geographic distribution: Europe, North America, Asia
Habitat characteristics:		
Water body type	Large and small floodplain water bodies (lakes, perifluvial pools and backwaters)	Large and small lowland and mountain water bodies (lakes, rivers, perifluvial pools and backwaters)
Trophic state	Oligo- to eutrophic	Oligo- to eutrophic
Sensitivity to eutrophication	Reduction until elimination from highly eutrophic lakes	Highly tolerant
Dietary items	unknown	Phytoplankton, bacteria, detritus
Seasonal cycle	Eurythermic, perennial with continuous recruitment	Eurythermic, perennial with continuous recruitment

sart & Defaye 2002). Both species inhabit a wide variety of habitat typologies, but only *E. gracilis* is found in slow-flowing rivers and in mountain lakes.

Both *E. padanus* and *E. gracilis* seem to be tolerant to a wide range of trophic conditions. However, *E. padanus* was reported to be eliminated from lakes undergoing severe eutrophication, including Lake Lugano, Italy (e.g., Ravera 1977). Conversely, *E. gracilis* seems tolerate highly eutrophic conditions, a characteristic which enabled this species to colonize Lake Lugano about forty years after *E. padanus* had been eliminated.

No information is available on the diet requirements of *E. padanus*, but like most calanoid copepods it has generally been considered as essentially herbivorous. Even though a similar herbivorous diet characterizes *E. gracilis*, the latter can survive for long periods of time feeding on bacteria and organic detritus (Nauwerk 1962). Both species are eurythermic and perennial with egg production throughout the year (e.g., Elster 1954; Ravera 1954, 1955; Hofmann 1979; Santer *et al.* 2000). In Lake Candia the two species displayed substantially similar seasonal patterns and reproductive cycles (Riccardi & Giussani 2007). However, *E. padanus* has greater clutch size of smaller sized eggs relative to *E. gracilis*. Although total reproductive output (egg volume × clutch size) was higher in *E. padanus* than in *E. gracilis*, the ratio of clutch volume to female body volume is similar in the two species, indicating that energy investment in reproduction is the same on a weight-specific basis. Since the rate of clutch production might be expected to be similar, interspecific differences in developmental rates and/or juvenile mortality have been suggested as a reason for the observed species replacement (Riccardi & Giussani 2007). The lower death rate and higher adult/egg ratio of *E. gracilis* observed in Lake Candia seems to support this hypothesis. Moreover, a comparison of temperature dependent development rates of *E. padanus* (Ravera, unpublished) with those of *E. gracilis* (Munro 1974) indicates that the latter species develops at twice the rate from egg to adult.

Invasion by *E. gracilis* is broadly consistent with expectations based on life-history. Among the traits that characterize a good invader, a high dispersal capacity and a type *r* demographic strategy, along with the physiological capacity to tolerate and reproduce in a wide range of environmental conditions, are considered essential (e.g., Ehrlich 1986; McMahon 2002). Even though *E. gracilis* lacks diapausing eggs (e.g., Santer *et al.* 2000; Bohonak *et al.* 2006), which are known to enhance dispersal potential (e.g., Bilton *et al.* 2001; Panov *et al.* 2004), at least for short distances (Zeller *et al.* 2006), its wide distribution throughout different continents in water bodies of different typologies (Gaviria 1998; Dussart & Defaye 2002) indicates a high dispersal ability as well as an ability to adapt to different local conditions. Data on the recent colonization of Northern Italian water bodies seem to provide further and strong evidence of its wide ecological tolerance. Indeed, it succeeded in establishing permanent populations in lakes and water bodies (e.g., lakes Lugano, Endine and Pusiano) in which trophic and/or physico-chemical conditions appeared to be unsuitable for calanoid copepod survival. While eutrophication was the most likely reason for the elimination of calanoid copepods (*Eudiaptomus padanus* and *Mixodiaptomus laciniatus*) from Lake Lugano (Ravera 1981), a high calcium concentration was hypothesized to be the reason for the lack of calanoid copepods in lakes Endine and Pusiano (e.g., Bonomi *et al.* 1967; Vighi 1977). *E. gracilis* establishment in marginal habitats, including river backwaters and slow-flowing river stretches, provides further support of its ability to tolerate even extremely harsh conditions. By contrast, the narrow distribution range of *E. padanus* suggests that it should have a very limited dispersal capacity (at least over long distances), while the comparatively limited set of environmental conditions which seem to enable *E. padanus* survival gives evidence of its narrower tolerance limits.

In at least three of the newly invaded sites (Lake Isola Giarola, Lake Brusa Vecchia and Lake Candia), *E. gracilis* establishment occurred concomitant with the reduction in abundance or elimination of the native species (Viaroli *et al*. 2002; Rossetti *et al*. 2003a; Riccardi & Giussani 2007). It is possible that similar reductions in native copepods have occurred in other recently invaded but less closely monitored lakes. Indeed, in most of the water bodies where the presence *E. gracilis* was reported, little or no information on the pre-invasion zooplankton composition is available to make appropriate contrasts. The leading hypothesis for this species replacement in Lake Candia is that *E. gracilis* is a superior competitor over native *E. padanus* (Riccardi & Giussani 2007), however other possibilities (e.g., apparent competition) cannot be dismissed. In addition, it is not clear whether environmental quality may influence the possible indirect interactions between *E. gracilis* and *E. padanus*. Laboratory investigations are necessary to confirm the possible role of competition in this species replacement, though additional data from other systems may also provide insight into interspecific competition. Studies are in progress on Lake Maggiore to confirm invader colonization throughout this large lake and to evaluate its effects on the resident species. Indeed, the probability of a coexistence through niche partitioning is likely to be higher in a large and deep lake, such as Lake Maggiore, than in small and relatively shallow water bodies as those where species replacement occurred.

A survey of the lakes laying in the Lake Maggiore watershed revealed that *E. padanus* is still present as the unique calanoid copepod (Riccardi, unpublished data), except in Lake Lugano, which drains into Lake Maggiore through the River Tresa. It is therefore very likely that the source of Lake Maggiore propagules is the population in Lake Lugano, which established in 1988. The 20 year interval that elapsed between when the species was detected in these two lakes indicates that a significant lag period may be required before *E. gracilis* is sufficiently dense as to be detected. The relatively long time taken for *E. gracilis* effective transfer to Lake Maggiore *via* direct river connection (about 21 km) seems to be in agreement with the lack of easily transportable diapausing eggs. Indeed, the transport of the active population component by water currents can be expected to be less effective than that of resting eggs because of the loss by mortality induced by the physical properties of the connecting elements. Since the Tresa is a torrent-like river, a substantial reduction of the flow of live individuals during the transport from Lake Lugano to Lake Maggiore can be reasonably predicted. The contrasting effects of changed environmental conditions and biotic resistance may have contributed to the time needed for successful establishment. Accordingly, Michels *et al*. (2001) measured a very low relative contribution of dispersing individuals to the total population size in target populations in a system of interconnected ponds, even though large numbers of individuals were transported from source populations.

Lake Maggiore has been studied for a number of years to assess whether *E. gracilis* was not present (e.g., Manca *et al*. 2006; Visconti *et al*. 2007). Analyses indicated that the species was not present despite high propagule pressure. Thus initial reports were consistent with the view that physical/chemical or biological interactions were preventing invasion in spite of high introduction effort. However, the recent observation of *E. gracilis* in the lake now provides support to propagule pressure theory (e.g., Williamson 1996; Lonsdale 1999; Kolar & Lodge 2001). Provided that *E. gracilis* will become permanently established in Lake Maggiore, this is likely to become an invasion hub facilitating further invasions owing both to natural and human-mediated connections to other water bodies in the region (e.g., Muirhead & MacIsaac 2005). Indeed, while most of the previously invaded sites are relatively unimportant sources (i.e., have few natural and human mediated connections), Lake Maggiore is one of the largest Italian lakes with a high recreational value and a high connectivity via its effluent (Ticino River) and departing boaters and anglers. Therefore, an increasing speed of *E. gracilis* diffusion could be tentatively predicted. In addition, the Lake Maggiore example also assumes a relevant predictive importance in relation to the fate of *E. padanus*. In fact, if even in this case a species replacement will occur, *E. padanus* should be considered a "fugitive species", *sensu* Elton and Hutchinson, whose distribution range is likely to become progressively restricted following the wave of *E. gracilis* expansion.

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