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Spreading factors of a globally invading coastal copepod

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Abstract

The Mediterranean Sea is one of the most affected areas by alien invasions, which are continuously increasing due to the intense human activities and environmental changes that favor the introduction of species previously unable to colonize the basin. This is the case of the copepods of the genus *Pseudodiaptomus*, first described in the Indian Ocean and considered as one of the most resistant to unfavorable conditions but never recorded in the Mediterranean until 2011 though present in adjacent seas. *Pseudodiaptomus marinus*, in particular, is common in shallow marine-brackish waters and is one of the species often found in ballast waters and in aquaculture plants. Native of Japan, it has started spreading since 1950s, and its populations have established in several harbors, eutrophic inlets, and lagoons along the coasts of the Pacific and Indian Oceans. In the last few years, *P. marinus* has been increasingly reported in European Seas (Mediterranean Sea and North Sea).

In this article, we review the invasion history of this species with a special emphasis on its records in the Mediterranean Sea, and its occurrence and establishment in Sicilian waters. We also compare the biological traits and population dynamics of *P. marinus* with those of other representative of the genus and discuss about the possible mechanisms of introduction in new environments. The aim of this work is to understand the reasons of successful invasion of *P. marinus* and the environmental and biological factors that may lead to its further biogeographic expansion.

Keywords: Copepods*, Pseudodiaptomus marinus,* Invasion, Eutrophication, Aquaculture, Mediterranean.

Introduction

The Mediterranean Sea is a region of intense invasions (Galil, 2009; Zenetos *et al*., 2010). The high diversity in its marine ecosystems (reviewed by Coll *et al*., 2010) is both due to the co-occurrence of species that have colonized the area in the past (Streftaris *et al*., 2005) and to a number of species introduced recently (Costello *et al*., 2010). Recent improvements of sampling methods, increasing interest of alien species study, and the continuous introduction of new species have led to a growing number of recorded invasive species at a rate never experienced before (Zenetos *et al.*, 2010). Crustaceans rank second in terms of abundance after Mollusks (Zenetos *et al*., 2012); among them, decapods are the prevalent group followed by copepods. Alien representatives of this latter group are mostly thermophilic species, having their native range in the Indo-Pacific Ocean (86%) (Zenetos *et al*., 2010).

Most of the copepod invasions, indeed, take place in the Levantine basin through Lessepsian migration (Por, 1978; Galil, 2009), as the eastern Mediterranean presents environmental characteristics that favor the establishment of species of Indo-Pacific origin (Galil, 2009; Zenetos *et al*., 2010). This process is further enhanced by the tropicalization of the region (Galil, 2009). Conversely, the western Mediterranean is more likely exposed to the introduction of alien species by vessels (e.g., ballast waters, fouling) and aquaculture/mariculture (Galil, 2009; Zenetos *et al*., 2012). The areas most impacted by non-indigenous species in the Mediterranean Sea are the coastal zones, estuaries, and harbors, which are sites of intense human pressure, eutrophication, and pollution (Zenetos *et al*., 2010).

The genus *Pseudodiaptomus* is very common in coastal zones. It is particularly abundant in transitional areas, inhabiting fresh to hyper saline waters (e.g., estuaries, coastal lagoons, neritic areas, and rivers) and is characterized by a pronounced vertical migration (Walter, 1986a). This genus is particularly interesting from the ecological and zoogeographical point of view since it is possible to follow its spreading history accurately (Grindley, 1984). Indeed, most of its species have a restricted distribution, that is, less than 1 mile along a continental coastline, and usually do not live or are rare below the 10 m isobath (Fleminger & Hendrix Kramer, 1988). In addition, no resting stages have been reported for the family Pseudodiaptomidae (Grindley, 1984), making the dispersal of the species unlikely through currents.

The genus *Pseudodiaptomus* originated supposedly in the Indo-Malayan region of the Indo-Pacific basin (Walter, 1986b). The speciation was originally due to allopatric reasons determining, as an example, an Americanus group, clearly derived by continental drift, and for this reason it is similar to the African species (Grindley, 1984). Several species of the genus are endemic to coast of America (Walter, 1986a), while only a few species occur along the African coasts, where the lowest diversity of the genus has been recorded (Walter, 1986a). Further spreading and speciation of this genus was consequently due to human activities. Madhupratap & Haridas (1986) outlined the peculiarity of few representatives of this genus (e.g., *P. marinus, Pseudodiaptomus nankaurensis, Pseudodiaptomus andamanensis, Pseudodiaptomus masoni*) inhabiting both coastal zones and oceanic islands, suggesting the effect of human activities (e.g., ballast waters and aquaculture) in the further spreading of this genus.

The genus *Pseudodiaptomus* comprises today 80 species, five of which have been described in the last 10 years (e.g., Nishida & Rumengan, 2005; Sakaguchi & Ueda, 2010; Srinui *et al*., 2013). Most of them are distributed in the Indo-Pacific area, occupying a few restricted regions, and the majority (~60 species) occupies only one geographical area or two adjacent ones (Table 1 in the Supplementary material). Nevertheless some of the species are considered highly invasive, such as *Pseudodiaptomus forbesi* and *Pseudodiaptomus inopinus*, for which a comprehensive literature on their invasion history is available, particularly on US coasts (e.g., Cordell *et al.,* 2007; Bollens *et al*., 2012, and references therein). However, these two species have remained confined to few areas along the coasts of the Pacific Ocean. The genus *Pseudodiaptomus* has started colonizing the Mediterranean basin only recently, reported for the first time in 2011 (De Olazabal & Tirelli, 2011). *Pseudodiaptomus serricaudatus* and *Pseudodiaptomus salinus* are present in the Red Sea but have never crossed the Suez Canal (Grindley, 1984).

Among the numerous congeners, *P. marinus* is the most widespread species; it is present at higher latitudes and has a longer invasion history (literature on its invasions started in 1950), occupying 10 different areas (Razouls *et al.,* 2005–2015) (Table 1 in the Supplementary material). It is an estuarine-coastal species of Asian origin (Sato, 1913), likely native of the eastern sector of the Indo-Malayan region (Grindley & Grice, 1969). It was first recorded in embayment on the west coast of Japan (Sato, 1913), and since 1950s, it has increasingly spread in new environments (Brylinski *et al*., 2012 and references therein) including recently the Mediterranean Sea (Zenetos *et al*., 2012) where it is, the only representative of the genus *Pseudodiaptomus*. To date, *P. marinus* is included in a list of potential “next pests” in Australia owing to its high invasive potential (Hayes *et al*., 2005), as well as in the alert list of the species that could invade Swedish coastal areas, based on the records in the North Sea (http://www.frammandearter.se/).

In this article, we will review the invasion history of this species and the biological, ecological, and biogeographical traits that may allow *P. marinus* to colonize new environments. We will report about its occurrence and successful establishment in Lake Faro (Sicily, Southern Italy, and Tyrrhenian Sea) and will analyze how the specific adaptations this species has evolved to thrive in this peculiar area. We will also discuss about its recent introduction in the Mediterranean Sea and in other sites along the Italian coasts. Finally, we will compare the biological traits and population dynamics of *P. marinus* with those of other representatives of the genus *Pseudodiaptomus*.

Pseudodiaptomus marinus: ecological, biological, and behavioral traits

P. marinus is a small species (average total body length: 1.1–1.8 mm; Table 1) inhabiting shallow marine environments like coastal lagoons and estuaries where food supply is generally abundant (Lawrence *et al.,* 2004). This species was extensively investigated in the Inland Sea of Japan, where it was first recorded (Sato, 1913) and occurs as a perennial species (Hirota, 1962, 1964; Uye *et al*., 1982). The numerical development of

Table 1: Average values of total body length values (and prosome length, when measured) for adult *Pseudodiaptomus marinus* females recorded by the different authors in native and invaded areas. References are listed in chronological order.

Reference	Site	Mean length	Mean prosome length
NATIVE REGION			
Sato (1913)	Inland Sea of Japan, Japan	1.3-1.6 mm	-
Uye *et al.* (1982)	Fukuyama harbour, Japan	1.25-1.5 mm	-
Liang & Uye (1997b)	Tomo Bay, Japan	-	0.76-0.95 mm
INVADED REGIONS			
Jones (1966)	Ala Wai Canal, Oahu, Hawaii	1.08-1.31mm	-
Grindley & Grice (1969)	Port Louis harbour, Mauritius	1.28-1.31mm	-
De Olazabal & Tirelli (2011)	Rimini and Trieste, Italy		0.67-0.76 mm
Brylinski *et al*. (2012)	Gravelines and Calais harbour, France	Max 1.8 mm	-
Sabia (2012)	Lake Faro, Italy	1.24-1.58 mm	0.93 mm

P. *marinus* in Fukuyama Harbor (Inland Sea of Japan) seems to depend on temperature, with peaks (15.6 × 10^3 ind. m^{-3}) in summer at 20–25 °C (Liang & Uye, 1997a; Uye *et al.*, 1983), and lows in winter at about 7 °C (Uye & Kasahara, 1983). The species is epibenthic during the day, while at night it swims vertically up into the water column (Valbonesi & Harada, 1980; Fleminger & Hendrix Kramer, 1988; Liang & Uye, 1997a). This species was first described as neritic (Jones, 1966) living in waters of reduced salinity (Grindley & Grice, 1969). Field studies confirmed this observation indicating that this copepod dwells in environments where salinity usually ranges between 30 and 37, though being able to survive and reproduce in lower salinity environments (Table 2).

In *P. marinus,* the eggs are carried by the female in a single sac attached to the genital somite (Grindely & Grice, 1969; Uye *et al.,* 1982). The egg carrying strategy leads to very high survival rates from egg to NIII (~ 94%) (Liang & Uye, 1997b). In Tomo Bay (Japan), the daily egg production rate was continuously high from May to October (12.1 eggs $female^{-1}$ d^{-1}) and low from January to March (2.3 eggs $female^{-1}$ d^{-1}) (Liang & Uye, 1997b). The egg production peaked at 20–25 °C, which corresponded to the optimal temperature range for the highest population growth in laboratory (Uye & Kasahara, 1983). Not being limited by food availability, the egg production rate is only temperature dependent, following a linear function (Liang & Uye, 1997b). In Fukuyama Harbor, the egg production rate of *P. marinus* was lowest with respect to other co-occurring copepod species (Liang & Uye, 1997b). The developmental time from egg to adult is on an average 13 days, short enough for the species to rapidly increase its abundance under favorable environmental conditions (Huang *et al.*, 2006).

P. marinus was observed creating feeding currents (Sabia, personal observation) and is reported as herbivorous and detritivorous (Uye & Kasahara, 1983). During the day, due to its epibenthic habit, the species is able to feed on organic detritus settled at the bottom (Uye & Kasahara, 1983), while at night, it moves along the water column likely exploiting different prey (Uye & Kasahara, 1983). The feeding behavior is similar for both adult sexes, but it differs from the copepodite and nauplii stages (Uye & Kasahara, 1983). Feeding activities do not show diel periodicity, as suggested by the same number of fecal pellets collected both at day and at night (Uye & Kasahara, 1983).

The swimming behavior of *P. marinus* is characterized by an alternation of active movements and periods of inactivity (Sabia *et al.*, 2012). The typical behavior displayed by the representatives of the family Pseudodiaptomidae, that is, remaining attached to the substrate for most of the time (Fancett & Kimmerer, 1985; Dur *et al.*, 2010), is displayed more frequently by *P. marinus* females than males (Sabia *et al.*, 2014). Sticking to the substrate may be a winning strategy for hiding from visual predators while creating feeding currents to acquire detrital food items. In fact, females are larger than males, and are even more visible and vulnerable when they carry the egg sac. By contrast, males show more explorative searching modalities presumably aimed at scanning the water volume to increase the encounter probability with a female (Sabia *et al.*, 2014).

Table 2: salinity range of the locations where *Pseudodiaptomus marinus* was detected, recorded by the different authors. References arranged in increasing salinity ranges order.

Reference	Site	Salinity Range	Temperature Range
Orsi & Walter (1991)	Sacramento San Joaquin estuary, California USA	2.5-18.9	-
Jones (1966)	Ala Wai Canal, Oahu, Hawaii	18	-
Delpy *et al.* (2012)	Berre Lagoon, France	23.0-35.0	3.4-28.2 °C
Liang & Uye (1997b)	Fukuyama Harbour, Inland Sea of Japan, Japan	28.6-32.3	8.9-28.2 °C
Lee *et al.* (2012)	Asan Bay, Korea	29.0-32.0	5-25°C
Villate (pers. comm.)	Estuary of Bilbao, Bay of Biscay, Spain	30	-
De Olazabal & Tirelli (2011)	Rimini and Trieste, Italy	29.9-37.5	16-25.3°C
Hsu *et al.* (2008)	Tapong Bay, Japan	30.0-35.0	20-31°C
Fleminger & Hendrix Kramer (1988)	Mission Bay and Agua Hedionda Lagoon, Southern California, USA	33.0-34.0	14-22°C
Jiménez-Pérez & Castro-Longoria (2006)	Todos Santos Bay, Baja California, Mexico	33.0-34.0	-
Brylinski *et al.* (2012)	Gravelines and Calais harbor, France	33.1-34.2	5.6-19°C
Greenwood (1976)	Moreton Bay	33.8-34.6	15-25.8 °C
Pansera *et al.* (2014)	Lake Faro, Messina, Italy	34.0-37.0	15-25°C
Mahadik &Mazzocchi (unpubl)	Gulf of Naples and Fusaro Lake, Italy	35-38.05	13-28°C

Biogeography of *Pseudodiaptomus marinus*

After the first description in the Inland Sea of Japan (Sato, 1913), *P. marinus* was recorded in different regions of the same basin (Brodskii, 1950; Shen & Lee, 1963; Tanaka, 1966) until it appeared in 1964 in the brackish waters of Hawaii (Jones, 1966). In the same years, the species was found and re-described in the harbor of Port Louis in the Island of Mauritius (Indian Ocean) (Grindley & Grice, 1969). These specimens were compared with those from Japan and Hawaii and reported as ecophenotypes of *P. marinus* based on minor morphological differences among populations from different oceans (Grindely & Grice, 1969). *P. marinus* was reported in 1963 for the first time in Australian waters in Moreton Bay (Greenwood, 1976).

The occurrence of *P. marinus* in Mission Bay and Agua Hedionda lagoon (California) was reported as the first discovery of this species in the United States (Fleminger & Hendrix Kramer, 1988), though the entrance in these environments could not be precisely dated. The establishment of *P. marinus* was concurrent with the disappearance of the native *Pseudodiaptomus euryhalinus* from both water bodies, though no direct association between the two events could be clearly established (Fleminger & Hendrix Kramer, 1988). In the Agua Hedionda lagoon, *P. marinus* became the numerically dominant copepod in late spring (Fleminger & Hendrix Kramer, 1988). During the same time, *P. marinus* was recorded even farther north on the coast of California (Orsi & Walter, 1991) and was still present among the numerous alien species of the San Francisco estuary 10 years later (Choi *et al*., 2005). In 1998, *P. marinus* was detected for the first time in the coastal area of Todos Santos Bay (Baja California, Mexico), and further surveys in 2002 confirmed that the species was established in this area (Jiménez-Pérez & Castro-Longoria, 2006).

The first questions about the biogeography and the causes of distribution of *P. marinus* rose in 1960s (Jones, 1966). The Island of Mauritius and the Hawaii were too far from the speciation center of the species and from the other sites of recordings in the Indian and Pacific Oceans. Thus, the arrival through ocean currents was unlikely as the time required would have exceeded the life span of the individual (Fleminger & Hendrix Kramer, 1988). Both for the Hawaii (Jones 1966) and for the Mauritius specimens (Grindley & Grice, 1969), it has been hypothesized that *P. marinus* had most likely migrated through ballast waters or adhered to the algae or fouling attached to the hull of the vessels. For the introduction of *P. marinus* in Mission Bay and Agua Hedionda lagoon, the possibility of oceanic transportation of resting stages was excluded because they have not been reported in this calanoid so far (Fleminger & Hendrix Kramer, 1988; Mauchline, 1998). In addition, ballast waters as vehicle of transportation were disregarded because the two sites are shallow and closed to transoceanic ship traffic, and the species was not present in any nearby port (Fleminger & Hendrix Kramer, 1988). Aquaculture was thus proposed as the means of introduction because in the previous years, the lagoon had been the site of experimental aquaculture of shellfish from Japanese coastal waters (Fleminger & Hendrix Kramer, 1988). Whereas, in the case of San Francisco estuary, ballast waters were the most plausible source of introduction of *P. marinus*, as this species was found among zooplankters in ballast waters examined from several ships arriving in the area (Choi *et al.*, 2005).

P. marinus expanded its invasion area to Europe and the Mediterranean Sea only in recent years. It is present in the estuary of Bilbao along the Atlantic coast of Spain since 2010 (Villate, personal communication). It was signaled further north in the Bay of Biscay, near the Gironde estuary (France) (Brylinski *et al*., 2012) (Fig. 1) and in the North Sea, that is, in the harbor of Calais (France) (2010) and along the coast off Gravelines (France) (2011) (Fig. 1) (Brylinski *et al.*, 2012). The species was recorded in the afore mentioned sites in different periods of the year; however, to date it is not possible to assess whether *P. marinus* is still present there. In all these cases, the ballast waters were considered the most probable vehicle of introduction (Brylinski *et al.*, 2012). Recently, the presence of *P. marinus* has been reported in additional sites in the North Sea (Jha *et al.*, 2013), in particular, in the southern North Sea along routes sampled with the Continuous Plankton Recorder, and further north in the German exclusive economic zone (Jha *et al.*, 2013) (Fig. 1). In the latter case, samples were always taken around sunset, in agreement with the diel migratory behavior of the species. The authors hypothesized that *P. marinus* might have originated from Calais and transported in the North Sea through the intense along-coast currents. These may favor additional invasion of the eastern North Sea and the Baltic Sea by this species (Jha *et al.*, 2013). These are to date the highest latitude records for *P. marinus*.

In the Mediterranean Sea, *P. marinus* has been recorded to date only in the western sector, that is, in Italian waters and in the Berre Lagoon (Marseille, France), where it was recorded few years ago (Delpy *et al.,* 2012) (Fig. 1). The species has not yet been recorded in the eastern Mediterranean, and is still not found in the Saronikos Gulf (I. Siokou, personal communication).

Establishment of *Pseudodiaptomus marinus* in Italian waters

As recently reviewed by Occhipinti-Ambrogi *et al.* (2011), Italian seas have been the site of intense biological invasions with 165 records between 1945 and 2009, most frequently introduced by shipping and aquaculture. It is worth noting that Italian inland waters also host a number of non-indigenous species, as discussed in Gherardi *et al.* (2008).

P. marinus was first signaled along the Italian coast of the northern Adriatic Sea in November 2007, and in a cooling channel in the Monfalcone harbor near Trieste

Fig. 1: European distribution of the invasive calanoid copepod *Pseudodiaptomus marinus*. ○: Gravelines (France) (Brylinski *et al.*, 2012); ♦: Calais (France) (Brylinski *et al.*, 2012); ◖: Bay of Biscay (France) (Brylinski *et al.*, 2012); □ and ■: Southern North Sea (Jha *et al.*, 2013); ⊙: North Sea (German exclusive economic zone) (Jha *et al.*, 2013); ⊗: Rimini (Italy) (De Olazabal and Tirelli, 2011); ♦: Monfalcone (Italy) (De Olazabal & Tirelli, 2011); ✶: Berre Lagoon (France) (Delpy *et al.*, 2012); ★: Lake Faro and Lake Ganzirri (Italy) (present work); **O**: Gulf of Naples (Italy) (two sites: St. LTER-MC and an offshore sampling site) (present work); ●: Lake Fusaro (Italy) (present work); : Marina di Carrara (Italy) (present work); ■: Gulf of Trieste (Italy) (St. LTER-C1); ✚: Bilbao (Spain) (present work). Coastline data: NOAA National Geophysical Data Center, Coastline extracted: WLC (World Coast Line), Date Retrieved: 08 January, 2013, http://www.ngdc.noaa.gov/mgg/shorelines/shorelines.html.

(northeastern Adriatic) in May 2009 (De Olazabal & Tirelli, 2011) (Fig 1). Afterwards, it was not possible to assess whether the species had successfully survived in the area as no more samplings in the same area have been performed. In this case, it was hypothesized that *P. marinus* had arrived more likely through aquaculture rather than ballast waters (De Olazabal & Tirelli, 2011). At that time, *P. marinus* had not yet been recorded in the nearby St. LTER-C1 in the Gulf of Trieste (as discussed in De Olazabal & Tirelli, 2011). Later on, the species has been found in several other Adriatic coastal sites between 2011 and 2013, as well as at station LTER-C1 in the Gulf of Trieste (Tirelli, personal communication).

Since July 2014, a few individuals of *P. marinus* have been found as a rare species in samples collected in the upper 50 m layer at St. LTER-MC in the Gulf of Naples (Tyrrhenian Sea) (Mazzocchi, personal observation). It was also found in December 2013 and April 2014 in the central Gulf of Naples (Tyrrhenian Sea), in the upper 50 m water column over the ~ 100 m isobaths (Mahadik & Mazzocchi, unpublished data) (Fig. 1). These are the first records of *P. marinus* in exclusively planktonic habitats. Though only a very few specimens were collected, they were just adult healthy females which suggests a further invasive ability of this copepod that may have evolved a planktonic behavior to survive in offshore environments. A few specimens of *P. marinus* were also occasionally found in March 2011 in the Lake Fusaro, a shallow coastal pond near Naples, along the Tyrrhenian coast (Mazzocchi, personal observations) (Fig. 1). This pond is characterized by a salinity of 35–38 (Sarno *et al.,* 1993) and in that period by intense aquaculture, which is supposed to be the means of introduction of the species into it.

In the central Tyrrhenian Sea, *P. marinus* was found only once along the Tuscany coast in December 2008 (Cruscanti, personal communication) at a site located about 1 km from the coast and over the 10 m isobaths in close proximity of the mouth of the Marina di Carrara port (Fig. 1).

In October 2008, *P. marinus* was found for the first time in Lake Faro (Fig. 2), a small coastal pond (surface area: 0.26 km^2, diameter: 500 m, max depth: 28 m, salinity: between 34 and 37, and temperature: between 10 and 28 °C Ferrarin *et al.,* 2013) located in the north-eastern tip of Sicily, where in 3 years, it has become the fourth copepod species in a rank order of abundance (Pansera *et al.*, 2014). In recent years, the lake was characterized by a consistent decrease in biodiversity of the zooplankton community (Zagami & Brugnano, 2013), and by the introduction of potentially invasive species (e.g., the polychaete *Linopherus canariensis*; Cosentino & Giacobbe, 2011). The whole area of the Strait of Messina is mostly impacted by the alien species introduced by shipping activities (Katsanevakis *et al.*, 2014). However, in this case, the introduction of *P. marinus* by means of ballast waters or by attachment to ship hulls must be excluded because the lake is shallow and non-navigable, but could be due to aquaculture, which is extensively carried out in the lake. In Lake Faro, *P. marinus* follows the same seasonal cycles recorded in its original sites (e.g., Liang & Uye, 1997a; Lee *et al.*, 2012), with a major peak of abundance in June–July (~4×10^3 ind. m^{-3}) and lowest abundance in winter (4 ind. m^{-3}) (Pansera *et al.*, 2014). Furthermore, the specimens in Lake Faro seem to be quite resistive to parasites present in the pond. In fact, in the same period other copepod species in Lake Faro, such as *Acartia tonsa*, were infested by external parasites, while *P. marinus* was not (Sabia, personal observation).

This introduction is particularly interesting if we consider the bathymetry of Lake Faro: it varies considerably, with bottom depths of 1–5 m near the shore and a steep slope towards the center of the lake, with a maximum depth (29 m) in a slightly decentered position (Saccà *et al.*, 2008). With no river inputs and only marginal connections to the Strait of Messina and eventually with the Ionian Sea by two artificial canals (De Domenico, 1987) (Fig. 2), the lake is meromictic with consistent variations of the dissolved oxygen content along the water column, ranging from a maximum of 8.3 mg L^{-1} to almost complete anoxia near the bottom in the hypolimnion, characterized by the presence of hydrogen sulfide (H_2S) and with red-waters metalimnion (De Domenico, 1987). During the same year, the aerobic epilimnion had a maximum depth of about 15 m with large seasonal variations.

While *P. marinus* is reported as epibenthic during the daytime and migrates upward in the water column only at night, in Lake Faro the copepod has changed its typical habit remarkably, becoming truly planktonic, likely owing to the presence of the anoxic bottom. In the center of Lake Faro, *P. marinus* is concentrated in the upper 15 m of the water column, which is the only oxygenated layer. Semi-quantitative samples collected in summer along the shore of the lake, where the depth is a few meters only and water column is not anoxic, revealed that differently from the other copepod species that are uniformly distributed in these few meters, *P. marinus* was much more abundant near the bottom than at the surface (Sabia, 2012).

The presence of some individuals of *P. marinus* has been very recently recorded in the neighboring Lake Ganzirri (Zagami, personal observations), which is connected with Lake Faro through the Margi Canal, but is characterized by different hydrological properties, such as shallower bottom (7 m max depth) and lower salinity (30–35) (Leonardi *et al.*, 2009; Ferrarin *et al.*, 2013). Despite the water exchange with the sea (Ferrarin *et al.,* 2013), *P. marinus* has not been recorded in the neighbor-

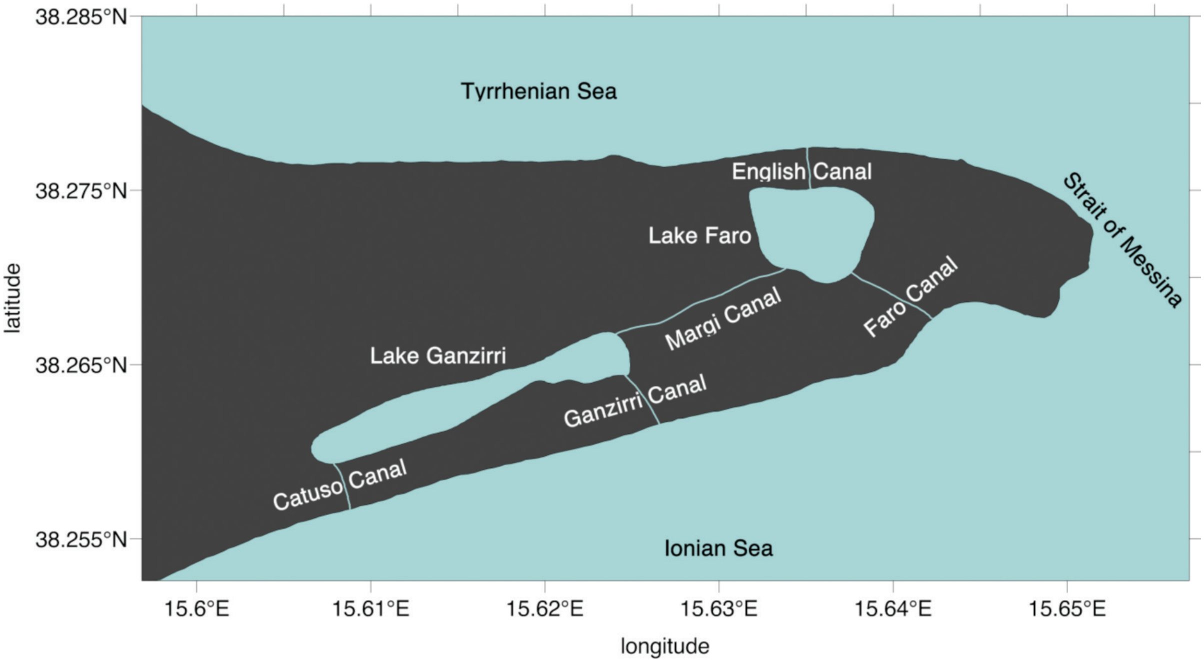

Fig. 2: Coastline of Sicily in the area of the Strait of Messina, showing the location of Lake Faro, Lake Ganzirri and their relative canals.

ing Ionian coast (Zagami, personal observation). A plausible explanation lies in the different dynamic regimes of these areas: the enclosed embayment where *P. marinus* has settled and established are characterized by weaker hydrodynamics, while the typical turbulent motions of the coastal areas may be disadvantageous for this species, as suggested by rearing experiments in the laboratory that have demonstrated that intense turbulence affects the population negatively (Sabia, 2012).

Discussion

The presence of non-indigenous species introduced by the human activities (e.g., ship fouling, ballast waters, aquaculture, and mariculture) in coastal areas is considered as one of the main descriptors for the definition of the ecological status of coastal areas in the Marine Strategy Framework Directive (E.C., 2010). The increasing reports of biological invasions are strictly linked to the numerous effects brought by global environmental changes (Occhipinti-Ambrogi & Savini, 2003; Occhipinti-Ambrogi, 2007). Almost 69% of the aquatic species successfully established in European countries are known for their ecological impact (Simberloff *et al.*, 2013), but this value can be an underestimation because of the difficulties in accessing and sampling all habitats adequately (Simberloff *et al.,* 2013). As an example, epibenthic species are present in the water column only occasionally or during night-time due to diel vertical migration (Zagami & Brugnano, 2013). This may be the cause of a possible underestimation of the abundance of *P. marinus* (De Olazabal & Tirelli, 2011; Brylinski *et al.*, 2012; Delpy *et al.*, 2012) although in the North Sea, the strong tidal currents should guarantee a constant homogenization of the water column and a constant re-suspension of suprabenthic species (Brylinski *et al.*, 2012; Jha *et al.*, 2013).

Invasion dynamics of Pseudodiaptomus marinus

As outlined by Carlton (1996), different processes may favor the introduction of new species, such as the progressive degradation of the coasts worldwide that occurred in recent years (Zenetos *et al.*, 2012). In this case, this phenomenon may have caused a change in the recipient region and favored the genus *Pseudodiaptomus*, which feeds on detritus and lives commonly in the turbidity maximum zone (Shang *et al.*, 2008). A particular role could have been played by the emergence of new vectors from the region of origin (e.g., Eastern Malayan region, China seas, and Japan) because of the great economic growth it underwent. One or a combination of these scenarios may have favored the introduction of *P. marinus* in the Mediterranean Sea.

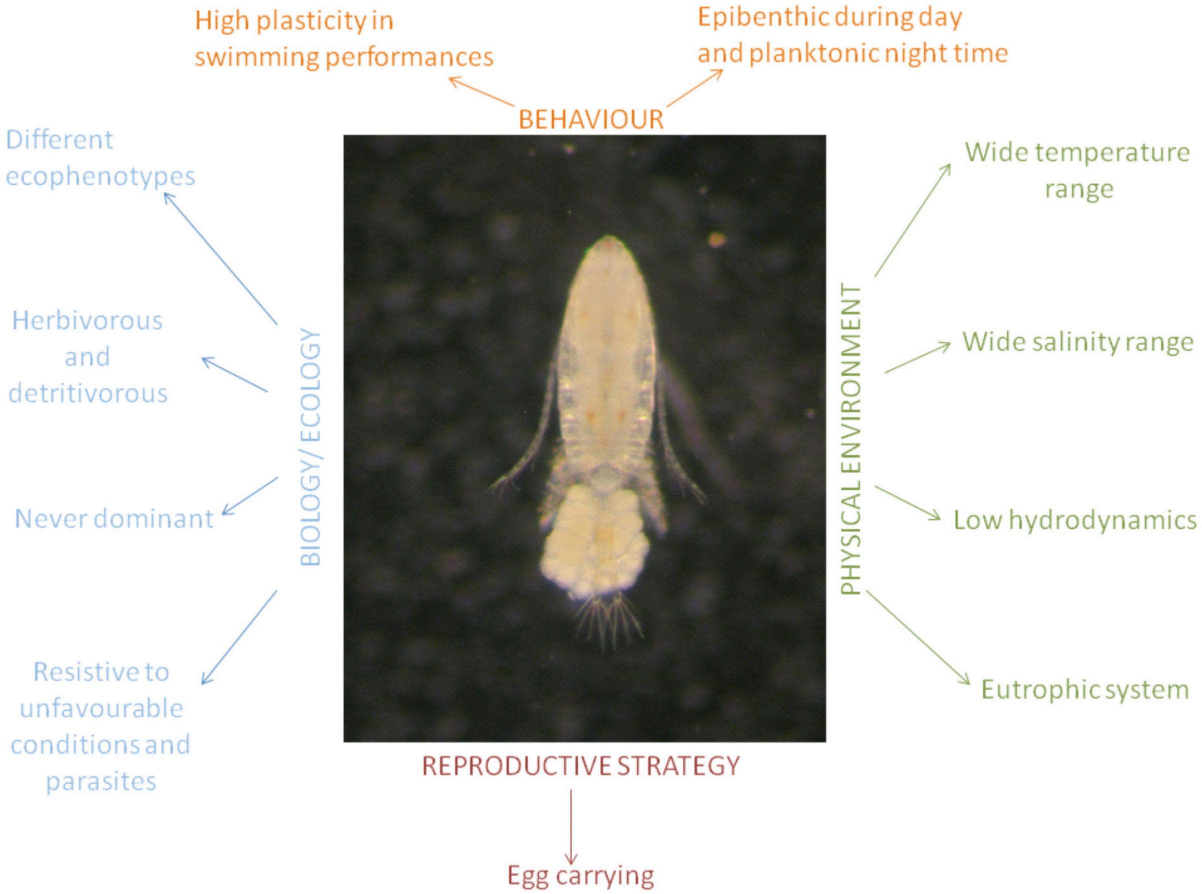

***Fig. 3**:* Schematic representation of the biological, ecological, and behavioral characteristics, which may determine the invasion success of *Pseudodiaptomus marinus.*

P. marinus possesses several biological and ecological traits that might explain its invasiveness (Fig. 3). It is resistant to unfavorable conditions and tolerant to a wide range of salinity and temperature (summarized in Table 2). This evidence highlights the strong adaptability of *P. marinus* to very diverse environments, and underlines the invasive ecology of this small calanoid in Mediterranean areas. *P. marinus* inhabits shallow, low turbulent, eutrophic environments using an epibenthic behavior, which might represent an optimal behavioral strategy to reduce predation risk. It is also able to feed both on detritus and suspended matter, widening its feeding spectrum and thus being more adaptable to different food conditions. In addition, the occurrence of different ecophenotypes with different body sizes (Table 1) suggests that different populations can take advantage of diverse characteristics in each place which allows them to inhabit new areas and thus enlarge their distributional areal.

P. marinus is characterized by great plasticity in its demersal nature, shifting to a more strictly planktonic behavior when conditions do not allow it to live on the bottom. This has been observed in Lake Faro where the species moves to the water column to avoid the bottom anoxic layer and in the offshore Gulf of Naples where they were found in the upper layer, as the bottom is too deep to allow a demersal behavior of the copepod. Behavioral plasticity can represent a crucial factor in driving the outcome of a new invasion (Wolf & Weissing, 2012), and provides a basis to possibly predict which species have the potential to become established (Carere & Gherardi, 2013). In this light, *P. marinus* can be depicted as one of the species with highest invasive potential. Behavior is an important part of the immediate response of an individual to its environment, and consequently it is crucial for understanding how populations respond to environmental change (or to a different environment), thus affecting population stability, persistence, and invasion capability (Wolf & Weissing, 2012).

Two different models have been proposed for the invasive dynamics of *P. marinus* (Barry & Levings, 2002; Rajakaruna *et al.*, 2012). A first simulation (Barry & Levings, 2002) established the risk of *P. marinus'* massive invasion using life history data. This model indicated that the most important factors influencing population outbursts are the initial population abundance and distribution and the transport rate, while high reproductive rate and physiological and ecological tolerance of conditions in the recipient environment contribute to the invasive success (Barry & Levings, 2002). The results of these models are supported by the evidence that invasion of *P. marinus* often occurs in areas characterized by weak hydrodynamic conditions with some exceptions such as the recording of *P. marinus* in the North Sea (Brylinski *et al.*, 2012; Jha *et al.*, 2013). However, in this case the high number of individuals arrived by ship tanks may have favored the flourishing of this species despite the unfavorable intense hydrodynamics of the area.

A different model was implemented based on the net reproductive rate (R_0) as a function of temperature (Rajakaruna *et al.*, 2012). The model limited the habitats that can be potentially invaded by *P. marinus* to a temperature range between 11 and 23 °C, assuming that other environmental factors are suitable for the numerical growth of the population. Based on these results, the areas that might be therefore potentially invaded by *P. marinus* have been mapped (Rajakaruna *et al.*, 2012). Despite the entire Mediterranean Sea was included in the map, the recorded number of *P. marinus* is still relatively low and restricted to the western sector of the basin (Delpy *et al.,* 2012; present work) and to the north Adriatic Sea (De Olazabal & Tirelli, 2011). Also, the occurrence of *P. marinus* in the North Sea (Brylinski *et al.,* 2012; Jha *et al.,* 2013) is compatible with the distribution thus depicted (Rajakaruna *et al.,* 2012).

The absence of records, however, might not be due to the absence of the species but to inadequate sampling owing to *P. marinus* demersal attitude, and considering that typically coastal samplings are performed during the day.

None of the two above discussed models (Barry & Levings, 2002; Rajakaruna *et al.*, 2012) included the effect of salinity on the fitness of *P. marinus*. In the Mediterranean Sea, this species has been recorded in areas with salinity lower than the basin average, although in the Gulf of Naples, salinity reaches a value of 38. The absence of this species in the Levantine basin where salinity is ≥38.5 (Malanotte-Rizzoli & Hecht, 1988) might probably indicate that salinity ≥38.5 limit recorded so far (Table 2) is an environmental barrier to the diffusion and establishment of *P. marinus*.

Invasive and non-invasive congeneric species: a comparison

The comparison of biological and ecological traits of *P. marinus* with three species of the same genus might help understanding why this particular species is so widespread across the world (Table 3). As mentioned in the Introduction section, *P. forbesi* and *P. inopinus* are well-documented invasive species, whereas *Pseudodiaptomus annandalei* has never been reported as established outside its native range and a good amount of literature is present for this species too. All four species are epibenthic and as observed in *P. marinus*, they might use vertical migrations to increase the possibility of invading new areas. The temperature and salinity ranges to which *P. marinus* is adapted, however, are the largest compared to the others. This species, moreover, is never dominant (with the exception of Agua Hedionda Bay, as reported by Fleminger & Hendrix-Kramer, 1998) differently from the other three species (Uye & Kasahara, 1982). The egg carrying strategy, which is common to the four species, has been considered among the favorable factors affecting the inva-

Table 3: Comparison of bioecological traits of four species of the genus *Pseudodiaptomus*. Information for *Pseudodiaptomus inopinus* are taken by: Cordell *et al*. (2007); Shang *et al*. (2008); Razouls *et al*. (2005–2015)–for *Pseudodiaptomus forbesi*: Bollens *et al*. (2012); Shang *et al.* (2008); Orsi & Walter (1991) - for *Pseudodiaptomus marinus*: Uye & Kasahara (1982, 1983); Rajakaruna *et al.* (2012); Razouls *et al.* (2005–2015); Orsi & Walter (1991); De Olazabal & Tirelli (2011) - for *Pseudodiaptomus annandalei*: Chen *et al.* (2006); Shang *et al.* (2008).

	P. inopinus	***P. forbesi***	***P. marinus***	***P. annandalei***
Temperature range	6.4-21°C	5-12°C	5-28°C	15-33°C
Salinity range	0-12	0-16	2.5-38	5-20
Period of peak	August-September	October-November	June-July and October	not available
Max abundances	>10^5 ind. m^{-3}	2.2×10^4 ind. m^{-3}	1.5×10^4 ind. m^{-3}	not available
Gravid females	perennial	abundant from June to December	perennial	perennial
Feeding habits	herbivourous-detritivourus	herbivorous and protozoans	herbivourous-detritivourous	mainly protists and herbivorous
Ecology	dominant	dominant	never dominant	dominant
Behaviour	epibenthic	epibenthic	epibenthic	epibenthic
Means of introduction	ballast water	ballast water	ballast water-aquaculture	non invasive species
Hydrodynamic realm	turbulent environments	turbulent environments	lentic environments	turbulent environments

sion process in cases of low copepod abundances (as for *P. marinus*) with respect to free spawning ones (as outlined in the simulations by Barry & Levings, 2002). Following this hypothesis, the nauplii hatched from egg sacs remain positioned more closely together, reducing the risk of each individual to be preyed upon and thus increasing the survival rate (Barry & Levings, 2002 and references therein).

Over the last 30 years, evidence has been accumulated on the role of ballast waters as transfer mechanism of alien species (Carlton, 1985; Davidson & Simkanin, 2012). Copepods are the most abundant representatives of zooplankton in ballast waters (Choi *et al.*, 2005), and among them, *P. marinus* scores as one of the most frequent (Choi *et al.*, 2005; Cordell *et al.*, 2008; Lawrence & Cordell, 2010; Kasyan, 2010), as well as *P. inopinus* and *P. forbesi* (Cordell *et al.*, 2007; Cordell *et al.*, 2008). The invasion history of *P. marinus*, though, suggests aquaculture as additional vector of introduction (Fleminger & Hendrix-Kramer, 1988; De Olazabal & Tirelli, 2011), which increases the possibilities of this species to spread into new environments compared to *P. inopinus* and *P. forbesi*. Conversely, *P. annandalei* has neither been reported in ballast waters nor in any other vector of introduction. All these factors taken together build up a specific framework for *P. marinus*, explaining its wide distributional area, the largest among all *Pseudodiaptomus* species (Table 1 in the Supplementary material).

The behavioral plasticity discussed for *P. marinus* might be an additional advantage in the successful invasion of new areas. To the best of our knowledge, no reports are available for the swimming behavior of *P. inopinus* and *P. forbesi*, making an interspecific comparison impossible. The motion pattern of *P. marinus* shows some peculiarities compared to *P. annandalei*, with higher mean swimming speeds but showing a simpler swimming pattern, without looping and sinking behavior. These factors allow them to have room for an evolution of the motion (Sabia *et al.*, 2014).

Being *P. marinus,* the species with a wider tolerance range to environmental factors and the higher number of the above discussed "invasive parameters," it may be the forerunner of the genus that is slowly spreading in new areas. Such a dynamic was observed in San Francisco Bay, where the first invader of the genus was *P. marinus* in 1986, followed by *P. forbesi* in 1987, and by *P inopinus* in 1990 (Cordell *et al.*, 2008). It is not improbable that in a near future other species of the genus *Pseudodiaptomus* will be introduced in the Mediterranean Sea.

Concluding remarks

It is undeniable that *P. marinus* deserves our attention and should be listed as a potential invader in the Mediterranean Sea. Particular attention should be devoted to this species, also taking into account the difficulty in correctly sampling it, given its epibenthic nature. Its introduction and establishment in the coastal areas of Europe, is a recent and ongoing process whose consequences are not yet predictable. Further data on the abundance and relative importance of *P. marinus* in the zooplankton assemblages in already invaded sites will allow acquiring more numerous and precise information on its ecological role in confined environments and some hints on the possible effect of its settling and on the factors that may sustain the invasion of other Mediterranean areas.

The criticality of European coastal waters has already been highlighted for an adequate prevention policy to minimize alien species introduction (Boxshall, 2007; Zenetos *et al.*, 2010), indicating the need of a regular monitoring effort. In addition, the use of molecular analyses integrate the taxonomical approaches in identifying unreported alien species and may unveil the genetic relationships among populations inhabiting different areas, as well as the mechanisms of introduction (Zenetos *et al.*, 2010).

Conflict of interest

The authors declare that they have no competing interests.

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References

Barry, K.L., Levings, C.D., 2002. *Feasibility of using the RAMAS-Metapopulation model to assess the risk of a non-indigenous copepod (Pseudodiaptomus marinus) establishing in Vancouver Harbour from ballast water*. Canadian Technical report of Fisheries and Aquatic Science, WestVancouver, Canada, 25 pp.

Bollens, S.M., Breckenridge, J.K., Cordell, J.R., Bollens G. R., Kalata. O., 2012. Invasive copepods in the Lower Columbia River Estuary: seasonal abundance, co-occurrence and potential competition with native copepods. *Aquatic Invasions,* 7,101-109.

Boxshall, G.A., 2007. Alien species in European coastal waters. *Aquatic Invasions*, 2, 279-280.

Brodskii, K.A., 1950. Calanoida of the Far Eastern Seas and Polar Basin of the U.S.S.R. *Opredeliteli Po Faune SSSR,* 35, 1-442.

Brylinski, J.M., Antajan, E., Raud, T., Vincent, D., 2012. First record of the Asian copepod *Pseudodiaptomus marinus* Sato, 1913 (Copepoda: Calanoida: Pseudodiaptomidae) in the southern bight of the North Sea along the coast of France. *Aquatic Invasions*, 7, 577-584.

Carere, C., Gherardi, F., 2013. Animal personalities matter for biological invasions. *Trends in Ecology & Evolution*, 28, 1, 5-6.

Carlton, J.T., 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. *Oceanography and Marine Biology Annual Review*, 23, 313-371.

Carlton, J.T., 1996. Pattern, process and prediction in marine invasion ecology. *Biological Conservation*, 78, 97-106.

Choi, K.H., Kimmerer, W., Smith, G., Ruiz, G.M., Lion, K., 2005. Post-exchange zooplankton in ballast water of ships entering the San Francisco Estuary. *Journal of Plankton Research*, 27, 707-714.

Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Ben Rais Lasram, F. *et al.* 2010. The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. *PLoS ONE*, 5, e11842.

Cordell, J.R., Bollens, S.M., Draheim, R., Sytsma, M., 2008. Asian copepods on the move: recent invasions in the Columbia-Snake River system, USA. *ICES Journal of Marine Science,* 65, 753-758.

Cordell, J.R., Rasmussen, M., Bollens, S.M., 2007. Biology of the introduced copepod *Pseudodiaptomus inopinus* in a northeastern Pacific estuary. *Marine Ecology Progress Series*, 333, 213-227.

Cosentino, A., Giacobbe, S., 2011. The new potential invader *Linopherus canariensis* (Polychaeta: Amphinomidae) in a Mediterranean coastal lake: colonization dynamics and morphological remarks. *Marine Pollution Bulletin*, 62, 236-245.

Costello, M.J., Coll, M., Danovaro, R., Halpin, P., Ojaveer, H., 2010. A census of marine biodiversity knowledge, resources, and future challenges. *PLoS ONE*, 5:e12110.

Davidson, I.C., Simkanin, C., 2012. The biology of ballast water 25 years later. *Biological Invasions,* 14, 9-13.

De Domenico, E., 1987. Caratteristiche fisiche e chimiche delle acque nello Stretto di Messina. *Documents et Travaux Institut Geologique Albert De Lapparent,* 11, 225-237.

De Olazabal, A., Tirelli, V., 2011. First record of the egg-carrying calanoid copepod *Pseudodiaptomus marinus* in the Adriatic Sea. *Marine Biodiversity Records,* 4, e85.

Delpy, F., Pagano, M., Blanchot, J., Carlotti, F., Thibault-Botha, D., 2012. Man-induced hydrological changes, metazooplankton communities and invasive species in the Berre Lagoon (Mediterranean Sea, France). *Marine Pollution Bulletin,* 64, 1921-1932.

Dur, G., Souissi, S., Schmitt, F., Cheng, S.-H., Hwang, J.-S., 2010. The different aspects in motion of the three reproductive stages of *Pseudodiaptomus annandalei* (Copepoda, Calanoida). *Journal of Plankton Research*, 32, 423-440.

E.C., 2010. Commission decision of 1 September 2010 on criteria and methodological standards on good environmental status of marine waters (notified under document C(2010) 5956) (Text with EEA relevance) (2010/477/EU*) Official Journal of the European Union,* L232, 14-24.

Fancett, M.S., Kimmerer, W., 1985. Vertical migration of the demersal copepod *Pseudodiaptomus* as a means of predator avoidance. *Journal of Experimental Marine Biology and Ecology*, 88, 31-43.

Ferrarin, C., Bergamasco, A., Umgiesser, G., Cucco, A., 2013. Hydrodynamics and spatial zonation of the Capo Peloro coastal system (Sicily) through 3-D numerical modelling. *Journal of Marine Systems,* 117-118, 96-107.

Fleminger, A., Hendrix Kramer, S., 1988. Recent introduction of an Asian estuarine copepod, *Pseudodiaptomus marinus* (Copepoda: Calanoida), into southern California embayments. *Marine Biology,* 98, 535-541.

Galil, B.S., 2009. Taking stock: inventory of alien species in the Mediterranean Sea. *Biological Invasions*, 11, 359-372.

Gherardi, F., Bertolino, S., Bodon, M., Casellato, S., Cianfanelli, S. *et al*. 2008. Animal xenodiversity in Italian inland waters: distribution, modes of arrival, and pathways. *Biological Invasions*, 10, 435-454.

Greenwood J.G., 1976. Calanoid copepods of Moreton Bay (Queensland) II. Families Calocalanidae to Centropagidae. *Proceedings of the Royal Society Queensland*, 88, 49-67.

Grindley, J.R., 1984. The zoogeography of Pseudodiaptomidae. *Crustaceana Supplement*, 7, 217-228.

Grindley, J.R., Grice, J.D., 1969. A redescription of *Pseudodiaptomus marinus* Sato (Copepoda Calanoida) and its occurrence at the Island of Mauritius. *Crustaceana*, 16, 125-134.

Hayes, K., Sliwa, C., Migus, S., McEnnulty, F., Dunstan, P, 2005. *National priority pests: Part II. Ranking of Australian marine pests*. Australian Government Department of the Environment and Heritage, Parkes, 94 pp.

Hirota, R., 1962. Species composition and seasonal changes of copepod fauna in the vicinity of Mukaishima. *Journal of Oceanographic Society of Japan,* 18, 35-40.

Hirota, R., 1964. Zooplankton investigations in Hiuchi-nada in the Setonaikai (Inland Sea of Japan) I. The seasonal occurrence of copepods at the three stations in Huichi-nada. *Journal of Oceanographic Society of Japan,* 20, 24-31.

Hsu, P.K, Lo, W.T., Shih, C., 2008. The coupling of copepod assemblages and hydrography in a eutrophic lagoon in Taiwan: seasonal and spatial variations. *Zoological Studies*, 47 (2), 172-184.

Huang, Y., Zhu, L., Liu, G., 2006. The effects of bis(tributiltyn) oxide on the development, reproduction and sex ratio of calanoid copepod *Pseudodiaptomus marinus*. *Estuarine, Coastal and Shelf Science*, 69, 147-152.

Jha, U., Jetter, A., Lindley, J.A., Postel, L., Wootton, M., 2013. Extension and distribution of *Pseudodiaptomus marinus*, an introduced copepod, in the North Sea. *Marine Biodiversity Records*, 6, e53.

Jiménez-Pérez, L.C., Castro-Longoria, E., 2006. Range extension and establishment of a breeding population of the Asiatic copepod *Pseudodiaptomus marinus* Sato, 1913 (Calanoida, Pseudodiaptomidae) in Todos Santos Bay, Baja California, Mexico. *Crustaceana*, 79, 227-234.

Jones, E.C., 1966. A new record of *Pseudodiaptomus marinus* Sato (Copepoda, Calanoida) from brackish waters of Hawaii. *Crustaceana*, 10, 316-317.

Kasyan, V.V., 2010. Holoplankton of ship ballast water in the Port of Vladivostok. *Russian Journal of Marine Biology*, 36, 167-175.

Katsanevakis, S., Coll, M., Piroddi, C., Steenbeek, J., Ben Rais, F. *et al*. 2014. Invading the Mediteranean Sea. Biodiversity patterns shaped by human activities. *Frontiers in Marine Science,* 1, 32, http://dx.doi.org/10.3389/fmars.2014.00032.

Lawrence, D.J., Cordell, J.R., 2010. Relative contributions of domestic and foreign sourced ballast water to propagule pressure in Puget Sound, Washington, USA. *Biological Conservation*, 143, 700-709.

Lawrence, D.J., Valiela, I., Tomasky, G., 2004. Estuarine calanoid copepod abundance in relation to season, salinity, and land-derived nitrogen loading, Waquoit Bay, MA. *Estuarine, Coastal and Shelf Science,* 61, 547–557.

Lee, D.B., Song, H.Y., Park, C., Choi, K.H., 2012. Copepod feeding in a coastal area of active tidal mixing: diel and monthly variations of grazing impacts on phytoplankton biomass. *Marine Ecology,* 33, 88-105.

Leonardi, M. Azzaro, F., Azzaro, M., Caruso, G., Mancuso, M. *et al*., 2009. A multidisciplinary study of the Cape Peloro brackish area (Messina, Italy): characterisation of trophic conditions, microbial abundances and activities. *Marine Ecology,* 30, 33-42.

Liang, D., Uye, S., 1997a. Population dynamics and production of the planktonic copepods in a eutrophic inlet of the Inland Sea of Japan. IV. *Pseudodiaptomus marinus*, the egg-carrying calanoid. *Marine Biology,* 128, 415-421.

Liang, D., Uye, S., 1997b. Seasonal reproductive biology of the egg-carrying calanoid copepod *Pseudodiaptomus marinus* in a eutrophic inlet of the Inland Sea of Japan. *Marine Biology,* 128, 409-414.

Madhupratap, M., Haridas, P., 1986. Epipelagic calanoid copepods of the northern Indian Ocean. *Oceanologica Acta,* 9, 105-117.

Malanotte-Rizzoli, P., Hecht, A., 1988. Large-scale properties of the Eastern Mediterranean: a review. *Oceanologica Acta*, 11, 323-335.

Mauchline, J., 1998. *The Biology of Calanoid Copepods*. Academic Press, San Diego, 710 pp.

Nishida, S., Rumengan, I.F.M., 2005. A new species of *Pseudodiaptomus* (Copepoda: Calanoida: Pseudodiaptomidae) from the coastal waters of Sulawesi, Indonesia. *Plankton Biology and Ecology*, 52, 27-32.

Occhipinti-Ambrogi, A., 2007. Global change and marine communities: alien species and climate change. *Marine Pollution Bulletin,* 55, 342-352.

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

Occhipinti-Ambrogi, A., Marchini, A., Cantone, G., Castelli, A., Chimenz, C. *et al*. 2011. Alien species along the Italian coasts: an overview. *Biological Invasions,* 13, 215-237.

Orsi, J.J., Walter, C.T., 1991. *Pseudodiaptomus forbesi* and *P. marinus* (Copepoda: Calanoida) the latest copepod immigrants to California's Sacramento – San Joaquin estuary. *Bulletin of Plankton Society of Japan Special Volume,* 553-556.

Pansera, M., Granata, A., Guglielmo, L., Minutoli, R., Zagami, G. *et al*. 2014. How mesh-size selection reshape the description of zooplankton community structure in coastal lakes? *Estuarine Coastal and Shelf Science*, 151, 221-235.

Por, F.D., 1978. *Lessepsian Migration. The Influx of Red Sea Biota into the Mediterranean by Way of the Suez Canal*. Ecological Studies 23, Springer-Verlag, Berlin, 228 pp.

Rajakaruna, H., Strasser, C., Lewis, M., 2012. Identifying non-invasible habitats for marine copepods using temperature-dependent R0. *Biological Invasions,* 14, 633-647.

Razouls, C., de Bovée, F., Kouwenberg, J. Desreumaux, N., 2005-2014. Diversity and Geographic Distribution of Marine Planktonic Copepods. Available at http://copepodes.obs-banyuls.fr/en (Accessed 23 July 2014)

Sabia, L., 2012. *An integrated approach to the study of the swimming behaviour of Pseudodiaptomus marinus*. PhD thesis, University of Messina, 178 pp.

Sabia, L., Uttieri, M., Pansera, M., Souissi, S., Schmitt, F.G. *et al*. 2012. First observations on the swimming behaviour of *Pseudodiaptomus marinus* from Lake Faro. *Biologia Marina Mediterranea*, 19, 240-241.

Sabia, L., Uttieri, M., Schmitt, F.G., Zagami, G., Zambianchi, E. *et al*. 2014. *Pseudodiaptomus marinus* Sato, 1913, a new invasive copepod in Lake Faro (Sicily): observations on the swimming behaviour and the sex-dependent responses to food. *Zoological Studies* 53, 49, doi:10.1186/s40555-014-0049-8.

Saccà, A., Bruni, V., Guglielmo, L., 2008. Vertical and temporal microbial community patterns in a meromictic coastal lake influenced by the Straits of Messina upwelling system. *Hydrobiologia*, 600, 89-104.

Sakaguchi, S.O., Hueda, H., 2010. A new species of *Pseudodiaptomus* (Copepoda:Calanoida) from Japan, with notes on the closely related *P. inopinus* Burckhardt, 1913 from Kyushu Island. *Zootaxa*, 2623, 52-68.

Sarno, D., Zingone, A., Saggiomo, V., Carrada, G.C., 1993. Phyotplankton biomass and species composition in a Mediterranean coastal lagoon. *Hydrobiologia*, 271, 27-40.

Sato, F., 1913. Pelagic copepods (no. 1) Scientific Reports of the Hokkaido Fisheries. *Experimental Station* 1, 1-79.

Shang, X., Wang, G., Shaojing, L., 2008. Resisting flow laboratory study of rheotaxis of the estuarine copepod *Pseudodiaptomus annandalei*. *Marine and Freshwater Behaviour and Physiology*, 41, 109-124.

Shen, C.J., Lee, F.S., 1963. The estuarine Copepoda of Chiekong and Zaikong Rivers, Kwantung Province, China. *Acta Zoologica Sinica*, 15, 571-596.

Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D.A. *et al*. 2013. Impacts of biological invasions: what's what and the way forward. *Trends in Ecology and Evolution,* 28, 58-66.

Srinui, K., Nishida, S., Ohtsuka, S., 2013. A new species of *Pseudodiaptomus* (Crustacea, Copepoda, Calanoida, Pseudodiaptmidae) from the Prase River Estuary, Gulf of Thailand. *Zookeys*, 338, 39-54.

Streftaris, N., Zenetos, A., Papathanassiou, E., 2005. Globalisation in marine ecosystems: the story of non-indigenous marine species across European Seas. *Oceanography and Marine Biology: An annual Review*, 43, 419-453.

Tanaka, O., 1966. Neritic Copepoda Calanoida from the northwest coast of Kyusu. in: *Proceedings of Symposium on Crustacea, of Marine Biological Association of India* 1, 36-50. *Mandapam Camp, Ernakulam, January 12-15 January, 1965, India.*

Uye, S., Kasahara S., 1983. Grazing of various developmental stages of *Pseudodipatomus marinus* (Copepoda: Calanoida) on natural occurring particles. *Bulletin of Plankton Society of Japan,* 30, 147-158.

Uye, S., Iway, Y., Kasahara, S., 1983. Growth and production of the inshore marine copepod *Pseudodiaptomus marinus* in the central part of the Inland Sea of Japan. *Marine Biology*, 73, 91-98.

Uye S.-I., Iway Y., Kasahara S., 1982. Reproductive biology of *Pseudodiaptomus marinus* (Copepoda: Calanoida) in the Inland Sea of Japan. *Bulletin of Plankton Society of Japan,* 29, 25-35.

Valbonesi, A., Harada, E., 1980. The vertical distributions of some copepods and a mysid in a near-shore water of Tanabe Bay Publications of the Seto. *Marine Biological Laboratory*, XXV, 445-460.

Walter, C.T., 1986a The zoogeography of the genus *Pseudodiaptomus* (Calanoida: Pseudodiaptomidae). *Syllogeus,* 58, 502-508.

Walter, C.T., 1986b. New and poorly known Indo-Pacific species of *Pseudodiaptomus* (Copepoda: Calanoida), with a key to the species groups. *Journal of Plankton Research,* 8, 129-168.

Wolf, M., Weissing, F.J., 2012. Animal personalities: consequences for ecology and evolution. *Trends in Ecology and Evolution,* 27, 452-461.

WoRMS Editorial Board, 2015. World Register of Marine Species. Available from http://www.marinespecies.org at VLIZ. (Accessed 06 September 2014)

Zagami, G., Brugnano, C., 2013. Diel, seasonal and man-induced changes in copepod assemblages and diversity, with special emphasis on hyperbenthic calanoid species, in a Mediterranean meromictic system (Lake Faro). *Marine and Freshwater Research,* 64, 951-964.

Zenetos, A., Gofas, S., Morri, C., Rosso, A., Violanti, D. *et al*. 2012. Alien species in the Mediterranean Sea by 2012. A contribution to the application of European Union's Marine Strategy Framework Directive (MSFD). Part 2. Introduction trends and pathways. *Mediterranean Marine Science,* 13, 328-352.

Zenetos, A., Gofas, S., Verlaque, M.,Cinar, M.E., Garcia Raso, J.E. *et al*. 2010. Alien species in the Mediterranean Sea by 2010. A contribution to the application of European Union's Marine Strategy Framework Directive (MSFD). Part I. Spatial distribution. *Mediterranean Marine Science,* 11, 381-493.