



# DISTRIBUTION OF THE GENUS OPHRYOTROCHA (POLYCHAETA) IN ITALY: NEW RECORDS AND COMMENTS ON THE BIOGEOGRAPHY OF MEDITERRANEAN SPECIES

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# DISTRIBUTION OF THE GENUS *OPHRYOTROCHA* (POLYCHAETA) IN ITALY: NEW RECORDS AND COMMENTS ON THE BIOGEOGRAPHY OF MEDITERRANEAN SPECIES

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POLYCHAETES  
COSMOPOLITAN SPECIES  
NON INDIGENOUS SPECIES  
REMNANT POPULATIONS  
SAMPLING EFFORT

**ABSTRACT.** – A number of intensive surveys were performed from 2002 to 2008 to implement the distribution data of the genus *Ophryotrocha* in Italian harbour and lagoon environments. The occurrences of *O. hartmanni*, *O. l. labronica*, *O. macrovifera*, *O. p. puerilis*, *O. robusta* and *O. japonica* were confirmed, and the first records of *O. adherens* in Italy and *O. diadema* in Europe were documented. The three most common *Ophryotrocha* were *O. l. labronica*, *O. japonica* and *O. p. puerilis*. The other species were rarer. Data were integrated with literature records, and some hypotheses which were proposed to justify the wide, patchy distribution of most Mediterranean *Ophryotrocha* were discussed. It was previously suggested that isolated populations could be remnants of a wider continuous distribution, the result of anthropogenic dispersion by means of sea traffic, and/or the by-product of a heterogeneous sampling effort in different biogeographic areas. It appeared that the last two hypotheses and the dispersion through waves, currents and/or storms could explain the distribution patterns of certain species. The high incidence of the most common species in the investigated area and the scant information outside the Mediterranean suggested that the distribution of *Ophryotrocha* species could be wider and more continuous than that recognized today.

## INTRODUCTION

During the last century, polychaetes belonging to the genus *Ophryotrocha* Claparède et Mecznirow, 1889, have proven to be valid model organisms in several fields of biological sciences, to such a degree that Paxton & Åkesson (2007) consider *Ophryotrocha* “the *Drosophila* equivalents of the polychaete literature”. The ease with which they can be reared and transported among laboratories, the availability of “reference” laboratory cultures, the short generation time, the occurrence of various forms of sex strategies within the genus (gonochorism, sequential and simultaneous hermaphroditism), and the considerable behavioral, reproductive, and karyological differentiation between species appear the most important reasons for the attractiveness of *Ophryotrocha* (Dahlgren *et al.* 2001, Simonini 2002, Paxton & Åkesson 2007 and references therein). The interest in these small worms (the most investigated species are less than 50 mm in length) has increased in the last decade, when more than 30 papers focused on *Ophryotrocha* have been published in international journals with impact factor (ISI Web of Knowledge<sup>SE</sup>). A key publication was the redescription of two of the most studied species, *O. puerilis* Claparède & Mecznirow, 1889 and *O. labronica* La Greca & Bacci, 1962, which has removed the confusion and uncertainty surrounding the identity of these two species that have been raised since the end of 19<sup>th</sup> century (Paxton & Åkesson 2007). Further research concerned the reconstruction of the phylogeny of *Ophryotrocha* (Dahlgren *et al.* 2001,

Heggøy *et al.* 2007), the evolutionary changes in annelid musculature (Bergter *et al.* 2008), the role of cytokine in aging physiology of invertebrates (Franchini & Ottaviani 2007), and the evolution of sex strategies (Prevedelli *et al.* 2006, Lorenzi & Sella 2008, Lorenzi *et al.* 2008).

The considerable number and variety of investigations performed on laboratory cultures appear to be in strong contrast with the relatively scant amount of papers on *Ophryotrocha* biogeography and ecology “in the field” (Sella & Ramella 1999), perhaps because of the patchy distribution, the small size and the occurrence of a number of sibling species within the genus (Åkesson 1975, 1984, Simonini 2002, Simonini & Prevedelli 2003, Åkesson & Paxton 2005, Prevedelli *et al.* 2005, Paxton & Åkesson 2007).

The most widely studied *Ophryotrocha* species live in the fouling communities of harbours and lagoons (Simonini 2002). Crossing experiments between strains from different localities worldwide suggested that a number of species may be considered to be cosmopolitans, but their distribution is often extremely fragmented (Paavo *et al.* 2000, Simonini 2002, Åkesson & Paxton 2005). In some cases, the crosses led to the identification of several sibling species and sub-species, which represents various stages of a speciation process based on reproductive isolation (Åkesson & Paxton 2005 and references therein). The results of crosses were confirmed by molecular investigations that recognized as true species (or sub-species) not only the morphologically distinct taxa, but also the reproductively-isolated groups of sibling species (Pleijel

& Eide 1996, Dahlgren *et al.* 2001, Heggøy *et al.* 2007). Yet, some other broadly-distributed *Ophryotrocha* species did not exhibit significant reproductive isolation when strains from different continents were crossed (Levinton 1983, Paavo *et al.* 2000, Simonini 2002, Simonini & Prevedelli 2003). The wide, discontinuous distribution of *Ophryotrocha* species contrasts with their apparent limited dispersal capability due to scant adult motility and lack of pelagic larvae (Åkesson 1973, Simonini 2002) and with the rather continuous distribution of some species on a regional scale. The latter emerged in a previous survey of 11 localities along the northern and central Italian coasts, which highlighted the occurrence of six species: *O. hartmanni* (Huth 1933), *O. labronica*, *O. sp. macrovifera* (Åkesson 1975), *O. puerilis*, *O. sp. robusta* (Åkesson 1975) and *O. sp. japonica* (Pleijel & Eide 1996), which was recorded for the first time in Europe (Simonini 2002). Interestingly, some species were quite widespread along the coast (i.e. *O. labronica* and *O. japonica*) and their distribution appeared to be quite continuous, at least on a regional scale, while other species were quite uncommon and occurred at only a few localities (i.e. *O. macrovifera* and *O. puerilis*) (Simonini 2002). The differences in the geographical distribution of each species, and the new reports of *O. japonica*, suggested that the investigation should be extended, not only to find new species but also to map the distribution of the hitherto reported species in greater detail and on different spatial scales.

The first aim of this paper is to complement the distribution data of the genus *Ophryotrocha* provided in Simonini's work (2002), with new observations collected during a number of intensive surveys performed over the recent years (2002-2008) along the Italian coasts. These data, integrated with those based on literature records, were then used to reconstruct the biogeography of the Mediterranean *Ophryotrocha* species and discuss the main hypotheses which were proposed to explain the complex and patchy distribution patterns encountered in these polychaetes.

## MATERIALS AND METHODS

**Study area, sampling and identification techniques:** In the 2002-2008 survey, a total of 40 localities were investigated (Fig. 1), at least one for each of nine biogeographic sectors (BS) surrounding the Italian peninsula (Italian Society of Marine Biology <http://www.sibm.it/CHECKLIST/principalechecklist-fauna.htm>; Bianchi 2007). The BS are numbered as: 1) the Ligurian Sea (north-western Mediterranean); 2) the North Tyrrhenian Sea and the Sea of Sardinia (central-west Mediterranean); 3) the South Tyrrhenian Sea and the Strait of Sicily (central-west Mediterranean); 4) the Strait of Messina; 5) the South-east Sicily and Pelagian Islands (south-east Mediterranean); 6) the Ionian Sea (central-East Mediterranean); 7) the South Adriatic; 8) the Central Adriatic; 9) the Northern Adriatic Sea (Fig. 1). Most of the

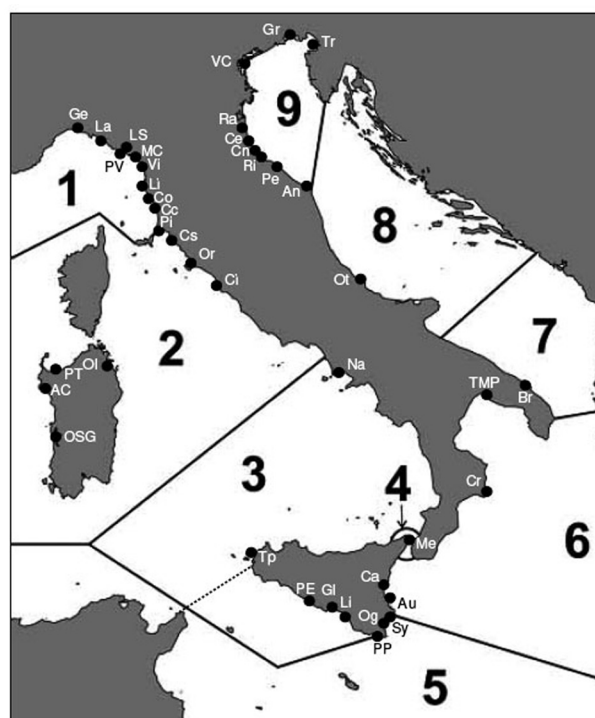


Fig. 1. – Localities sampled for the study of *Ophryotrocha* species distribution in Italy. Numbers refer to the main biogeographic sectors (BS). The dotted lines represent the eastern and southern limits of the Ionian Sea ecoregion. (see text for further details). Abbreviations of localities (from BS1 to BS9): Ge = Genoa; La = Lavagna; LS = La Spezia; PV = Porto Venere; MC = Marina di Carrara; Vi = Viareggio; Le = Leghorn; Co = Castiglione; Cc = Cecina; AC = Alghero/Calich; PT = Porto Torres; OSG = Oristano/Santa Giusta; Ol = Olbia; Pi = Piombino; Cs = Castiglione; Or = Orbetello; Ci = Civitavecchia; Na = Naples; Tp = Trapani; PE = Porto Empedocle; Gl = Gela; Li = Licata; Me = Messina; PP = Porto Palo; Og = Ognina; Sy = Syracuse; Ca = Catania; Au = Augusta; Cr = Crotone; TMP = Taranto/Mar Piccolo; Br = Brindisi; Ot = Ortona; Ra = Ravenna; VC = Venice/Chioggia; Ce = Cervia; Cn = Cesenatico; Ri = Rimini; Ps = Pesaro; Gr = Grado; An = Ancona; Tr = Trieste.

B.S. lay within single ecoregions (Spalding *et al.* 2007): the BS 7, 8 and 9 belong to the Adriatic ER; the BS 6, the northern section of BS 5 and the southern portion of BS 3 (the Sicilian coasts facing the Strait of Sicily) fit into the Ionian ER; the BS 1, 2 and the rest of BS 3 belong to the Western Mediterranean ER (Fig. 1). Sampling localities included all harbours and lagoons considered by Simonini (2002) and the places investigated before 1999 by other authors. The only exception was the Naples harbour, for which only historical information was available (Åkesson & Paxton 2005). At least two sites (100 m-2 km away from each other) were sampled for each locality. The samplings were repeated at least twice for each site, for a total of more than 100 surveys.

Samples of fouling were collected by scraping hard surfaces, such as banks and wharves, between the normal low tidal level and 1-1.5 m in depth, using a steel net with a cutting edge and extendible handle. Each sample consisted of at least eight replicates weighing 1 kg each, which were placed into small aquaria (capacity of 2.5 dm<sup>3</sup>) filled with seawater. The aquaria were taken to the laboratory and kept at room temperature under

Table I. – Main morphological and reproductive traits of the different *Ophryotrocha* species found along the Italian coast. Quotes to species name: 1 = first record for Italy; 2 = first record for Europe. \* = traits which can be appreciated only from live specimens. 2n = diploid number of chromosomes.

| species                         | prostomium shape             | ants; palps*    | eyes*; pigment strand* | adult jaws                  | max. length [mm] | form of sexuality*           | shape of egg masses*    | egg size [ $\mu$ m]* | 2n |
|---------------------------------|------------------------------|-----------------|------------------------|-----------------------------|------------------|------------------------------|-------------------------|----------------------|----|
| <i>O. adherens</i> <sup>1</sup> | triangular; prostomial gland | present present | present absent         | K type, not bifid           | 2-4              | simultaneous hermaphroditism | loose jelly             | 100-110              | 10 |
| <i>O. diadema</i> <sup>2</sup>  | triangular                   | present absent  | present present        | p-type                      | 4-5              | simultaneous hermaphroditism | fusiform                | 145-180              | 8  |
| <i>O. hartmanni</i>             | triangular                   | present absent  | absent absent          | K type, both forceps bifid  | 4-5              | simultaneous hermaphroditism | fusiform                | 170-175              | 10 |
| <i>O. sp. japonica</i>          | roundish                     | present absent  | present absent         | K type, right forceps bifid | 5-6              | gonochorism                  | tubular or spoon-shaped | 145-160              | 6  |
| <i>O. l. labronica</i>          | triangular, elongate         | present absent  | present present        | K type, right forceps bifid | 3-5              | gonochorism; sex dimorphism  | tubular                 | 120-125              | 6  |
| <i>O. sp. macrovifera</i>       | triangular                   | present absent  | present present        | K type, right forceps bifid | 3-5              | gonochorism; sex dimorphism  | tubular                 | 150-180              | 6  |
| <i>O. p. puerilis</i>           | triangular                   | present present | present absent         | K type, not bifid           | 11-13            | sequential hermaphroditism   | loose jelly             | 100-110              | 8  |
| <i>O. sp. robusta</i>           | roundish                     | present absent  | present absent         | K type, right forceps bifid | 5-6              | gonochorism sex dimorphism   | tubular                 | 120-125              | 10 |

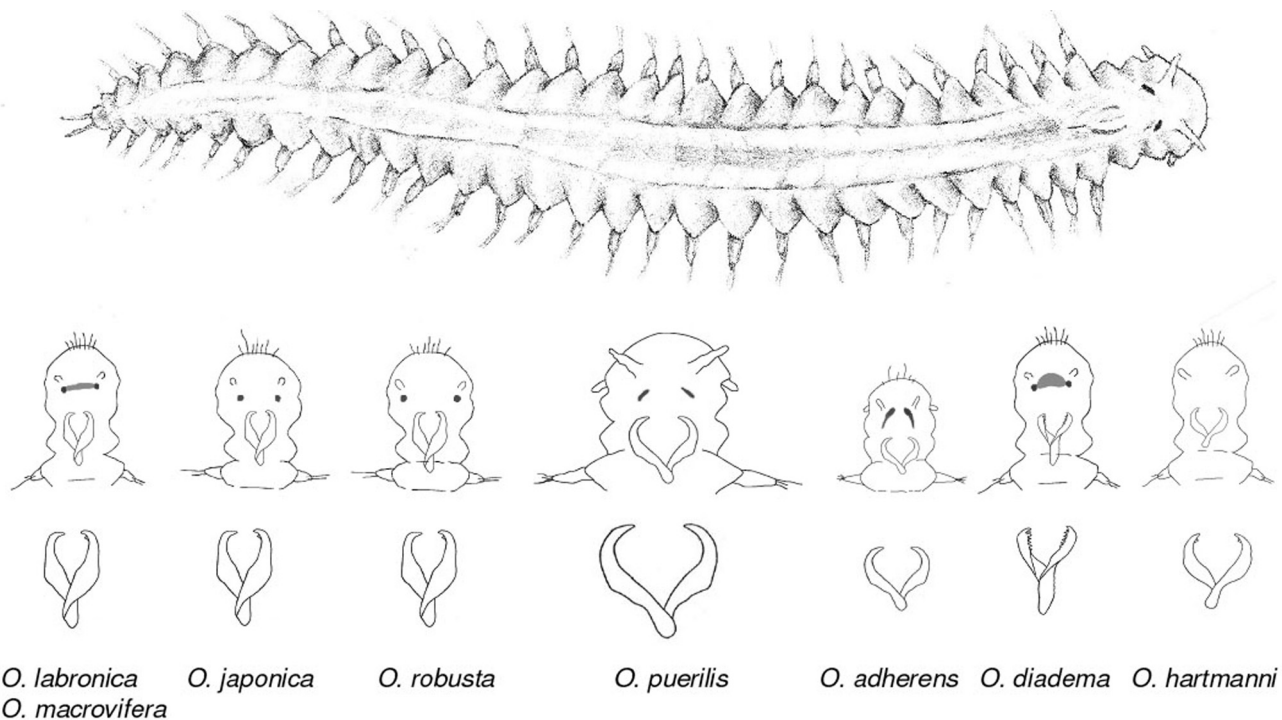


Fig. 2. – Top, *Ophryotrocha puerilis* (12 mm, ciliary bands omitted). Bottom, schematic comparison of the head and mandibles of the *Ophryotrocha* species found along the Italian coast.

exposure to light. After a few days, anoxic conditions were established at the bottoms of the aquaria, forcing the worms to climb up the walls, where the organisms were collected using a Pasteur pipette. Subsequently, the specimens of *Ophryotrocha* were sorted individually and identified to species level. Juveniles were housed in separated containers until they had assumed adult characteristics. The laboratory cultures were maintained at

24 °C, with a 12 h light/dark photoperiod and a salinity of 30-32 psu, and they were fed with chopped spinach. In many cases, identification of the *Ophryotrocha* species could only be achieved with live animals through the analysis of some morphological, reproductive and karyological traits (Table I, Fig. 2). Hermaphroditic species often differed for one or more easily-recognizable characteristics, such as jaws (or forceps) type and

shape, body size and prostomium shape. On the other hand, most of the gonochoric species could be recognized only by studying their biological cycle and reproductive characteristics and/or by comparing and crossing them with standard strains that had been classified previously, as is the case of the “*labronica* group”, consisting of some sibling gonochoric species that are very similar to *O. labronica*. Since several of these sibling species were not formally described, we adopted their “laboratory culture name” followed by “sp.” and the references of the paper in which they were cited for the first time. Additional information on the traits relevant for the identification of the *Ophryotrocha* species can be found in Pleijel & Eide (1996).

The data on the presence/absence of each species at each locality were analyzed and integrated with those based on literature records from the investigated area, the whole Mediterranean and worldwide.

## RESULTS

The analyses of the samples of fouling collected from 40 harbours and brackish water environments during the 2002-2008 survey confirmed that the genus *Ophryotrocha* is very common along Italian coasts (Fig. 3). Eight species were recorded: *O. hartmanni*, *O. labronica*, *O. macrovifera*, *O. puerilis* and *O. robusta* were known in Italy before the 1990s, and *O. japonica* was reported just in recent years (Simonini 2002). As regards the remaining two species, the first records of *O. adherens* Paavo *et al.*, 2000 in Italy and *O. diadema* Åkesson, 1976 in Europe were documented. These species exhibited large differences in their distribution and occurrence patterns (Fig. 3, Table II).

*O. labronica* was found at about 80 % of the localities investigated and was by far the most common species. It colonized both harbours and brackish-water environments of the Western Mediterranean, Ionian Sea and Adriatic Sea (Fig. 3). All the strains collected in the investigated area belonged to the sub-species *O. l. labronica*.

*O. japonica*, which belongs to the “*labronica*” group, is regarded as a non-indigenous species (NIS) native of the Temperate Northern Pacific (Simonini 2002 Paxton & Åkesson 2005). It was recorded for the first time along the European and Mediterranean coastline in 1999. *O. japonica* has now successfully colonized the Italian harbours and lagoons, occurring at 45 % of the investigated localities and representing the second species in order of occurrence. It was common along the coast facing onto Adriatic and West Mediterranean ecoregions, especially in the northern sectors (BS 1 and 9), but it was not found on the islands of Sicily and Sardinia (Fig. 3).

The third most common species was *O. puerilis*. Simonini (2002) reported that this species occurred only at few localities (Genoa & Alghero-Calich). During the 2002-2008 surveys, *O. puerilis* was also found at a number of localities facing onto the West Mediterranean and Ionian

ecoregions (B.S 1-6, Fig. 3). An isolated population of *O. puerilis* was found in the Ancona harbour (Adriatic Sea, BS 9) (Fig. 3). All the strains collected in the investigated area were inter-fertile and belonged to the sub-species *Ophryotrocha p. puerilis*.

The other five species were rarer, occurring at less than 20 % of the localities, and were always found together with one or two of the most common species.

The presence of *O. hartmanni* in the Leghorn and Piombino harbours (Western Mediterranean) was reported by Parenti (1962) and Cognetti (1992). During the 1999-2001 survey, this species was not found (Simonini 2002). In the 2002-2008 survey, the presence of *O. hartmanni* was confirmed in Leghorn and Piombino, and in the nearby harbour of La Spezia. Two other isolated populations of *O. hartmanni* were identified at Porto Empedocle (Ionian Sea, BS 3) and Ancona (Adriatic Sea, BS 9) (Fig. 3).

*O. macrovifera* and *O. robusta* are considered to be sibling species belonging to the “*labronica*” group. The former was reported from the harbour of Genoa (Åkesson, pers comm). Yet we found *O. macrovifera* only in the Venice-Chioggia Lagoon (Adriatic, BS 9) (Fig. 3). Rolando (1982, 1984) reported the occurrence of *O. robusta* in the Genoa harbour (Western Mediterranean, BS 1) but, up to now, this species has never been collected by us from that locality. During the 2002-2008 surveys, three populations of *O. robusta* were found in Southern Sicily (Ionian Area, BS 3-5-6) (Fig. 3).

*O. adherens* was recorded for the first time along the Italian coastline. It was collected at two Southern Sicily localities (Ionian ecoregion), Porto Palo di Capo Passero (BS 5) in September 2006, July 2007, and Porto Empedocle (BS 3) in September 2006, July 2007 and June 2008 (Fig. 3). The life-history and morphological traits of the specimens from both localities (Table I) perfectly fitted those reported in the original description of the species (Paavo *et al.* 2000).

*O. diadema* was reported for the first time on the European coast. It was only found at Porto Empedocle (Ionian ER, BS3, Fig. 3) in September 2006, July 2007 and June 2008. The Sicilian strains were interfertile with a laboratory culture of *O. diadema* provided by Prof Sella (University of Turin). Moreover, the wild specimens exhibited both the two-genetic markers, yellow eggs (dominant) and white eggs (recessive), which were previously documented in laboratory strains of *O. diadema* (Åkesson 1982, Simonini unpubl data, Sella pers comm).

## DISCUSSION

### *The worldwide distribution of Ophryotrocha species living in the Mediterranean*

During the 2002-2008 investigation in Italian harbours and lagoons, all the *Ophryotrocha* species that were pre-

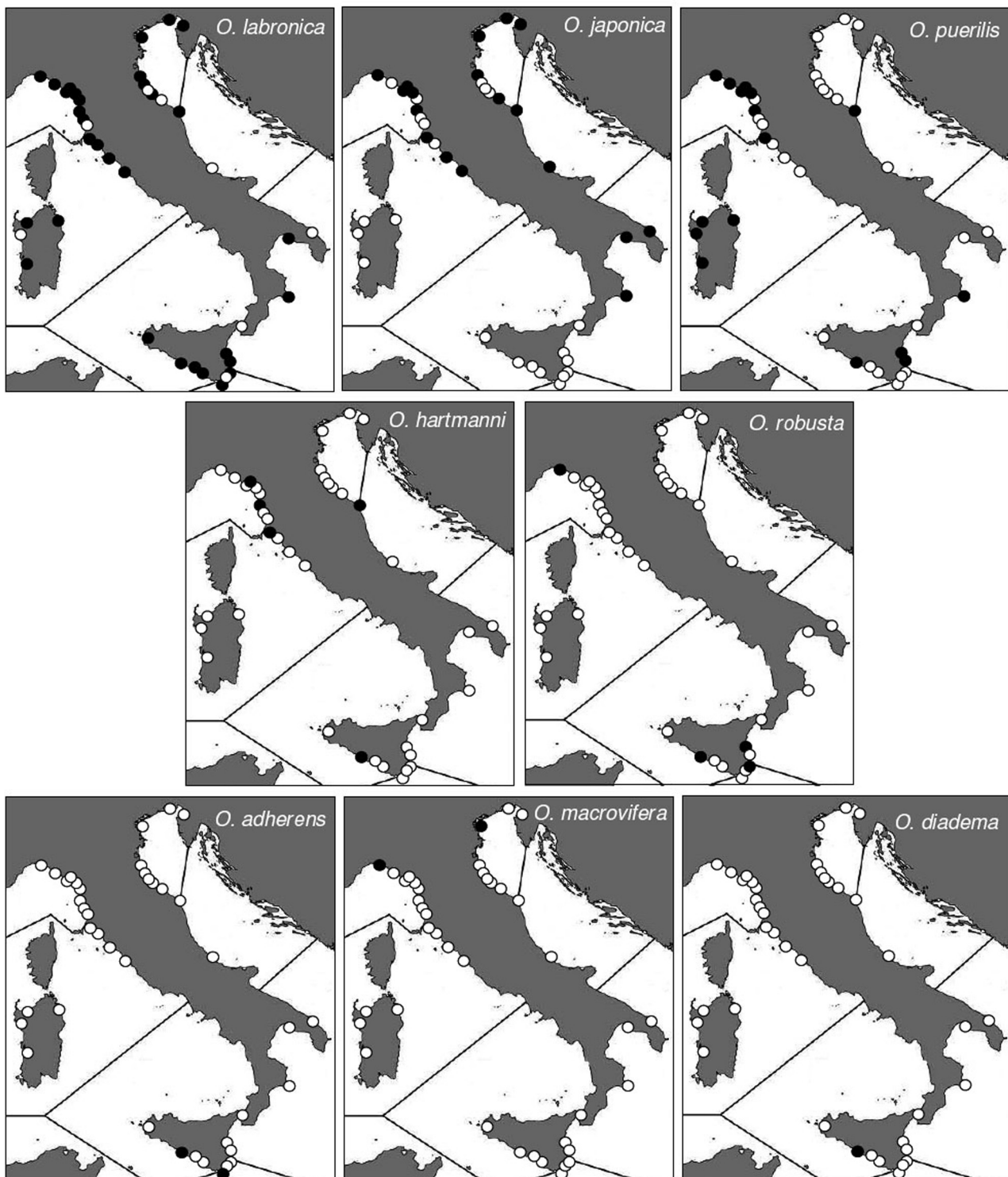


Fig. 3. – Distribution of *Ophryotrocha* species in Italy (black circle = species present; white circle = species absent).

viously known from Mediterranean coastal environments were found, with the addition of *O. diadema*. The eight species differed in their distribution not only in the investigated area, but also at Mediterranean and global scale (Table II and references therein).

Only *O. robusta* and *O. p. puerilis* are reported exclusively from the Mediterranean and, at present, represent

the only endemism of the genus. In fact, reports of *O. puerilis* from the eastern and western North Atlantic only referred to the sub-species *O. p. siberti*. *O. hartmanni* is known only from the Mediterranean and North Europe.

At least 4 species (*O. adherens*, *O. l. labronica*, *O. japonica* and *O. diadema*) could be considered to be

Table II. – Distribution of *Ophryotrocha* species found along the Italian coast, in other Mediterranean ecoregions and outside the Mediterranean. Quotes to species name: 1 = first record for Italy; 2 = first record for Europe. Quotes to distribution outside Italy represent the record reference: a = Åkesson 1973; b = Åkesson 1975; c = Åkesson 1976; d = Åkesson 1984; e = Levinton 1983; f = Paavo *et al.* 2000; g = Simonini 2002; h = Åkesson & Paxton 2005; i = Paxton & Åkesson 2007; j = Lee *et al.* 2006; k = Hall-Spencer *et al.* 2006; l = Pereira *et al.* 2003. Reports j, k and l refer to populations of *O. adherens* and *O. hartmanni* collected from off-shore muddy bottoms subjected to high organic enrichment. The abbreviations of biogeographic sectors (BS) and ecoregion (ER) are given in Fig. 1 legend.

| Species name                    | Italian coast       |            | Other Mediterranean ecoregions                 | Outside the Mediterranean                                                                                                                      |
|---------------------------------|---------------------|------------|------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------|
|                                 | BS                  | ER         |                                                |                                                                                                                                                |
| <i>O. adherens</i> <sup>1</sup> | 3, 5                | IS         | Levantine Sea <sup>a,b</sup>                   | Temperate Northern Atlantic (Canaries); Eastern Indo-Pacific (Hawaii) <sup>f,j</sup>                                                           |
| <i>O. diadema</i> <sup>2</sup>  | 3                   | IS         | not reported <sup>c,g</sup>                    | Temperate Northern Pacific (South California) <sup>e</sup>                                                                                     |
| <i>O. hartmanni</i>             | 1, 2, 3, 9          | WM, IS, AS | Alboran Sea <sup>b</sup>                       | Temperate Northern Atlantic (North Sea) <sup>a,k,l</sup>                                                                                       |
| <i>O. japonica</i>              | 1, 2, 3, 6, 7, 8, 9 | WM, IS, AS | not reported <sup>g</sup>                      | Temperate Northern Pacific (Japan, Southern California) <sup>g,h</sup>                                                                         |
| <i>O. l. labronica</i>          | 1, 2, 3, 5, 6, 9    | WM, IS, AS | Alboran, Aegean, Levantine Seas <sup>a,b</sup> | Western Indo-Pacific (Northern Red Sea) Temperate Northern Atlantic (Lusitanian); Temperate Australasia (Southeast Australia) <sup>a,h,i</sup> |
| <i>O. macrovifera</i>           | 1, 9                | WM, AS     | Levantine Sea <sup>b,d</sup>                   | Tropical Atlantic (Florida); Temperate Northern Atlantic <sup>e,h</sup>                                                                        |
| <i>O. p. puerilis</i>           | 1, 2, 3, 6, 9       | WM, IS, AS | Alboran Sea <sup>b,d</sup>                     | not reported <sup>i</sup>                                                                                                                      |
| <i>O. robusta</i>               | 1, 3, 5, 6          | WM, IS     | Alboran Sea <sup>b,d</sup>                     | not reported <sup>h</sup>                                                                                                                      |

cosmopolitan, but they exhibit patchy distribution on a global scale.

*O. macrovifera* is rare in the investigated area and in the Mediterranean, where it was previously reported only from the harbour of Kyrenia (Cyprus, Levantine Sea). Yet, *O. macrovifera* could be regarded as an anphi-Atlantic species, because it was also found in the Eastern and Western Atlantic.

The subspecies *O. l. labronica* was very common in the Mediterranean and in the Lusitanian province. The only reports outside these areas are isolated populations living in the gulf of Aqaba (Israel, Northern Red Sea) and in the Sydney harbour (Australia). Other reports of *O. labronica* from the North Pacific referred to the subspecies *O. l. pacifica*.

*O. adherens* is a cosmopolitan species: in the Mediterranean, besides the southern Sicily, it was only found in Cyprus (Levantine Sea); other reports of *O. adherens* came from the Canary and Hawaii Islands.

*Ophryotrocha japonica* and *O. diadema* were originally reported from the Pacific coasts. Today, the former is also common and widespread in the Mediterranean, the latter is known only from Southern Sicily (present study) and Los Angeles harbour, California.

#### Main hypothesis proposed to explain the patchy distribution of *Ophryotrocha* species

Several hypotheses were proposed to justify the worldwide, patchy distribution of some species and sub-species of *Ophryotrocha*: isolated populations could be remnants of a wider continuous distribution, the result of anthropogenic dispersion by means of sea traffic, and, not least,

the by-product of an heterogeneous sampling effort in different biogeographic areas (Paavo *et al.* 2000, Simonini 2002, Åkesson & Paxton 2005).

Remnant populations are not uncommon in temperate seas: for example, several boreal Atlantic species living in the North Adriatic are considered to be ice-ages remnants, especially from the Würm glacial period (Bianchi 2007). In the case of *O. l. labronica*, in accordance with Åkesson & Paxton (2005) the isolated populations of Sydney harbour, which are perfectly interfertile with the Mediterranean ones, may be a remnant of an earlier wider distribution, which also included the Indo-Pacific realm. This hypothesis arose from the assumption that *Ophryotrocha* species may be evolving at a very slow rate, as suggested by the high morphological similarity of the *O. labronica* sibling species (Åkesson & Paxton 2005) and the discovery of fossil *Ophryotrocha* sp. jaws from the Cretaceous that were indistinguishable from modern forms (Eriksson & Lindström 2000, Åkesson & Paxton 2005). If the remnant hypothesis is correct, *O. labronica* should be considered a “true” cosmopolitan species. A worldwide distribution was reported for a number of polychaetes [e.g. *Capitella*, ssp. (Grassle 1984), *Stygocapitella subterranea* (Schmidt & Westheide 2000), *Scoloplos armiger* (Bleidorn *et al.* 2006)], but genetic studies have revealed that only few species are truly cosmopolitan (e.g. *Hesionides arenaria*, Schmidt & Westheide 2000, *Ctenodrilus serratus*, Westheide *et al.* 2003).

The cosmopolitan distribution of a number of polychaetes was the result of human introductions (e.g. *Sabellapallanzanii*, Patti & Gambi 2001, *Proscoplos cygnochaetus*, Meyer *et al.* 2008). Ports represent the main gate for the introduction of non-indigenous species (NIS) in

marine environments (Occhipinti-Ambrogi 2007). It was estimated that in European coastal waters about 40 % of NIS were transported by ships (ballast water and hull ships) (Gollash 2006). An additional 16 % of NIS entered through the trade of living organisms (Gollash 2006) used for aquaculture or recreational/scientific aquaria, which are often located near harbour areas. The anthropogenic dispersion by means of ship traffic and aquaculture practices is considered the cause of the recent appearance in the Mediterranean of *O. japonica* and *O. diadema*. In fact, the Mediterranean strains of both species were interfertile with the Pacific ones (Simonini 2003, Åkesson pers comm, Sella pers comm). The high incidence of *O. japonica* in Italian harbours, together with the patterns of life history differentiation of populations from the North Adriatic, Ligurian and Ionian seas (Simonini & Prevedelli 2003) suggested that the current distribution of *O. japonica* could be the results of several independent introductions from different localities or at different times. On the other hand, the occurrence of a single population of *O. diadema* in southern Sicily suggests that this species could have been introduced in recent times. Anthropogenic dispersion from the Mediterranean was also proposed to explain the occurrence of the isolated Australian population of *O. labronica*, as an alternative to the “remnant” hypothesis (Åkesson & Paxton 2005). In fact, a number of native Mediterranean species living in port environments, such as the polychaete *Sabella spallanzanii* and the bivalve *Corbula gibba*, that were transported to the southern hemisphere by ship traffic, have successfully colonized Sydney harbour in recent years (Patti & Gambi 2001, AMBS 2002). Other considerations support the possibility of anthropogenic dispersion of *Ophryotrocha* species. Several cases of involuntary introductions of *Ophryotrocha* into aquaculture tanks and aquaria were observed (e.g. Day 1967, Fauchald & Jumars 1979, Åkesson & Paxton 2005). Moreover, they are of the right size

to live in the interstices of the fouling communities on the hulls of ships, and are considered to be hardy enough to survive in the ballast water (Bonnier 1893, Simonini 2002, Åkesson & Paxton 2005, Paxton & Åkesson 2007). Further examinations of ship fouling and sediment from ballast water tanks should confirm the possibility of anthropogenic dispersion for *Ophryotrocha* species.

The species belonging to the genus *Ophryotrocha* do not only live in fouling habitats. In the last 20 years, a surprisingly high number of *Ophryotrocha* species have been described from deep sea bottoms (Northwest Atlantic slope and rise: Hilbig & Blake 1991, North America seeps: Robinson *et al.* 2004, Levin *et al.* 2003). Some other species, such as *O. gracilis* Huth, 1933 and *O. bacci Parenti*, 1961, live in the interstices of littoral sediments. The simultaneous hermaphrodites *O. hartmanni* and *O. adherens* were known from both harbour fouling and marine incoherent bottoms subjected to high organic enrichment: *O. hartmanni* was locally very abundant in the proximity of Scottish aquaculture plants (Pereira *et al.* 2003, Hall-Spencer *et al.* 2006), while *O. adherens* was found in benthic communities living near a sewage outfall in the Hawaiian Islands (Paavo *et al.* 2000), and in the sediment below a tuna farm and a mussel aquaculture plant in the Mediterranean (Dal Zotto & Simonini pers observ). Both species were able to tolerate eutrophication and could reach very high densities at the source of organic pollution, but their abundance decreased rapidly at increasing distances (Paavo *et al.* 2000, Hall-Spencer *et al.* 2006) after cessation of organic input (Pereira *et al.* 2003). The sexual strategy of these species could favour the persistence of low density populations outside the organically polluted area. In fact, in habitat where the density is very low, simultaneous hermaphroditism is considered to be advantageous for small-sized interstitial species because it greatly increases the probability of finding a partner (Westheide 1984, Puurtinen & Kaitala

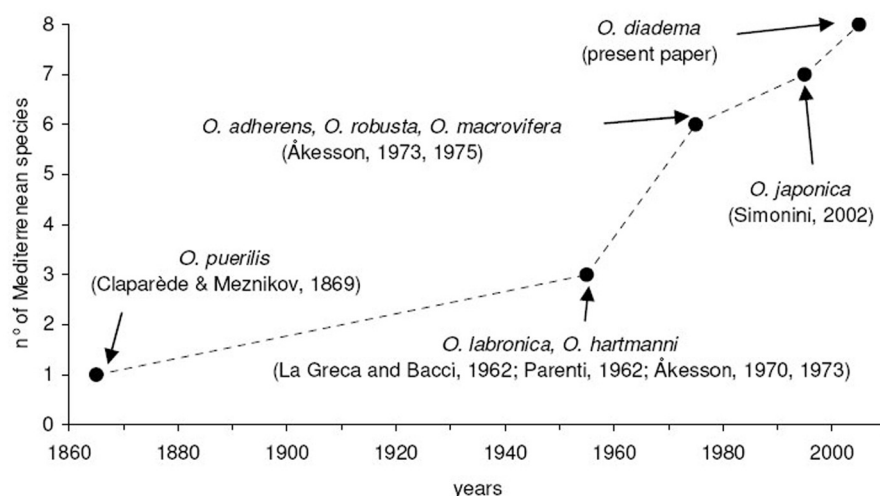


Fig. 4. – Temporal trend of the number of *Ophryotrocha* species, with the chronology of reports of each species in the Mediterranean Sea.

2002, Prevedelli *et al.* 2006). The *Ophryotrocha* species living in the interstices of muddy or sandy bottoms may be transported from the open sea into enclosed coastal environments (and vice versa) as a consequence of stochastic dispersal events (waves, currents, storms etc.), which are considered to be very important in the meiofauna dispersion (Hagerman & Rieger 1981, Palmer 1988, Schmidt & Westheide 2000). In this case, the distribution of most *Ophryotrocha* species may be wider than what is recognized today, and their broad and patchy distribution patterns could be explained by both non-stochastic ("anthropogenic introduction" and "remnant" hypotheses) and stochastic mechanisms.

The discontinuous distribution of widespread species may simply be due to a lack of observations. This effect cannot be easily quantified, but it should be inversely related to the sampling effort and the size of the investigated area. If this is the case, the analysis of the chronology of the reports of each *Ophryotrocha* species in the Mediterranean could give some indications (Fig. 4). The *Ophryotrocha* genus was established in the late 19<sup>th</sup> century for the species *O. puerilis*, which was described from specimens collected from Naples, in the Tyrrhenian Sea (Claparède & Mecznikow 1869). Several authors suspected that the original description of the species was based on a mixed population of *O. puerilis* and *O. labronica* (Åkesson & Paxton 2007 and references therein). The latter was formally described almost a century later by La Greca & Bacci (1962) from Leghorn (Ligurian Sea). In the same period, Åkesson (1970) found several populations of *O. labronica* in the Naples area, and Parenti (1962) identified *O. hartmanni* in the Piombino harbour, on the border between the Ligurian and Tyrrhenian Seas. Thereafter, the number *Ophryotrocha* species increased as a result of Åkesson's surveys throughout the Mediterranean, which led to the recognition of a number of populations of *O. puerilis*, *O. hartmanni* and *O. labronica*, and the identification of strains belonging to *O. adherens*, *O. macrovifera* and *O. robusta* (Åkesson 1973, 1984). Now, within the framework of Simonini (2002) and the present surveys, one or more strains of all the previously-known species and two new species of *Ophryotrocha* for the Mediterranean polychaetofauna have been found: *O. japonica* was reported for the first time in 1999 from the Ligurian and North Adriatic harbours (Simonini 2002); *O. diadema* was found in 2006, when surveys were extended to the southern biogeographic sectors (present paper). This trend a) suggests that "sampling effort", both in terms of number of sampling localities and spatial extension, plays a primary role in determining the number and the distribution of *Ophryotrocha* species; b) resembles the increasing trends of NIS recorded during the last decades in European coastal water (Gollash 2006 Fig. 1, 2), supporting the hypothesis that *O. japonica* and *O. diadema* may be true NIS for the Mediterranean.

The scant and patchy information outside the Mediter-

anean, together with the possibility of stochastic and non-stochastic passive dispersion, complicate the reconstruction of the biogeography of *Ophryotrocha* species on a global scale. Perhaps, it would be important to examine a fine meshed network of localities from different widely separated biogeographic provinces or realms, as has been done for the investigated area. It would be also advisable to couple the traditional approach based on crossing experiments with more recent molecular techniques, in order to find out whether the genetic patterns of *Ophryotrocha* species match the historical relationships among the geographical regions that these species now inhabit.

The increasing number of *Ophryotrocha* species found in the last 50 years suggests that additional new populations or species (non indigenous or undescribed) may occur in the Mediterranean. Nevertheless, the present knowledge on the distribution and occurrence of *Ophryotrocha* species in the Mediterranean could be used as a basis for further investigation in the nearby biogeographic provinces.

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