

DISTRIBUTION AND ECOLOGY OF THE GENUS OPHRYOTROCHA (POLYCHAETA: DORVILLEIDAE) IN ITALIAN HARBORS AND LAGOONS

R Simonini

► To cite this version:

R Simonini. DISTRIBUTION AND ECOLOGY OF THE GENUS OPHRYOTROCHA (POLYCHAETA: DORVILLEIDAE) IN ITALIAN HARBORS AND LAGOONS. Vie et Milieu / Life & Environment, 2002, pp.59-65. hal-03198733

HAL Id: hal-03198733 https://hal.sorbonne-universite.fr/hal-03198733v1

Submitted on 15 Apr 2021 $\,$

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

DISTRIBUTION AND ECOLOGY OF THE GENUS OPHRYOTROCHA (POLYCHAETA: DORVILLEIDAE) IN ITALIAN HARBORS AND LAGOONS

R. SIMONINI

Dipartimento di Biologia Animale, Università degli Studi di Modena e Reggio Emilia, Via Campi 213/D, 41100 Modena, Italy simonini.roberto@unimo.it

OPHRYOTROCHA DISTRIBUTION ECOLOGY HARBORS BRACKISH ENVIRONMENTS

> OPHRYOTROCHA RÉPARTITION ECOLOGIE PORTS LAGUNES

ber 2001 to investigate the distribution of the genus *Ophryotrocha* in Italian harbors and lagoons. In the localities examined to date, six species belonging to the genus *Ophryotrocha* have been found. In particular, *O. japonica* has been recorded for the first time along European and Mediterranean coastlines. There are considerable differences in the spatial and temporal distribution of these species. The species most commonly found were *O. labronica* and *O. japonica*. *O. puerilis* seems to be confined to the Ligurian and Tyrrhenian coastlines, while *O. hartmanni, O. macrovifera* and *O. robusta* are less widespread than the other species. *O. labronica* and *O. japonica* colonize brackish lagoons as well as harbor environments. Its wide distribution and some features of its biological cycle suggest that *O. japonica* may have been introduced as a result of maritime traffic and/or aquaculture. The consequences of seasonality on population dynamic and the links between environmental instability and life history features in some *Ophryotrocha* species are discussed.

ABSTRACT - A series of field studies were conducted from March 1999 to Octo-

RÉSUMÉ – L'échantillonnage du genre *Ophryotrocha* a été poursuivi de mars 1999 à octobre 2001 afin d'étudier sa distribution dans les ports et les lagunes d'Italie. Six espèces de ce genre ont été examinées à ce jour. *O. japonica* est signalée pour la première fois le long des côtes européennes et méditerranéennes. Des différences considérables existent dans la distribution spatiale et temporelle de chaque espèce. Les espèces les plus communes sont *O. labronica* et *O. japonica*. *O. puerilis* se limite aux côtes ligures et tyrrhéniennes. *O. hartmanni, O. macrovifera* et *O. robusta* sont moins largement réparties que les espèces précédentes. *O. japonica* et *O. labronica* colonisent aussi bien les ports que les lagunes. La large distribution et quelques caractéristiques du cycle biologique font penser que *O. japonica* a été introduite par les transports maritimes ou par l'aquaculture. Les conséquences de la saisonnalité sur la dynamique des populations et les relations entre l'instabilité du milieu et les caractéristiques des traits de vie des espèces de Ophryotrocha sont discutées.

INTRODUCTION

The genus *Ophryotrocha* (Dorvilleidae: Eunicida: Polychaeta) was established in the 19th century for the species *Ophryotrocha puerilis* Claparède and Mecznikow, 1869, collected on the bottom of the tanks of the Naples aquarium. Since then, about 50 species of *Ophryotrocha* have been reported, all less than 20 mm in length. One exception, *O. geryonicola* Esmark, 1878, lives in the branchial chambers of some species of crabs and can reach 140 mm (Wesenberg-Lund 1938, Mori & Belloni 1985, Pleijel & Eide 1996). The species belonging to this genus live in very diverse environments, from the inter-tidal zones to the ocean bottoms (Parenti 1961, Hilbig & Blake 1991, Eibye-Jacobsen & Kristensen 1994).

The species most widely studied are those like O. puerilis, O. diadema Åkesson, 1976, and O. labronica La Greca and Bacci, 1962. They live in the fouling community of harbors. Their behavioural and reproductive characteristics and the ease with which they can be reared in the laboratory make them valid model organisms both for ecological and life-history studies and for researches into sex determination, sexual evolution and the ethological aspects of reproduction and mating (Zunarelli 1962, Åkesson 1973, 1975, 1976, 1982, 1984, Åkesson & Costlow 1978, Rolando 1982, Kegel & Pfannenstiel 1983 a, b, Sella 1985, 1988, 1990, 1991, Berglund 1986, 1990, 1991, Grothe & Pfannenstiel 1986, Premoli & Sella 1995, Premoli et al. 1996, Gambi et al. 1997, Prevedelli & Zunarelli Vandini 1998, Cassai & Prevedelli 1999, Sella & Ramella 1999, Paavo et al. 2000, Prevedelli & Simonini 2001, Dahlgren et al 2001).

The checklist of the polychaetes reported for Italy shows five species belonging to the genus *Ophryotrocha* (Castelli *et al.* 1995). In addition to the deep-water species *O. geryonicola*, found on the Ligurian seabeds in association with the crab *Geryon longipes* there have been reports of *O. hartmanni* Huth, 1933, *O. labronica*, *O. macrovifera* nomen nudum (Åkesson 1973, 1975) and *O. puerilis* (see Mori & Belloni 1985, Castelli *et al.* 1995).

This paper integrates the previous information on the distribution and ecology of the genus *Ophryotrocha* in Italy with the data obtained from a series of field studies conducted in various Italian harbors and lagoons between March 1999 and October 2001.

MATERIALS AND METHODS

Samples of fouling material were taken by scraping the wharves of harbors and lagoons with a sharp-edged net with a handle. Samples were collected at nine locations (the harbors of Genoa, La Spezia, Leghorn, Rimini and Ravenna; the lagoons of Orbetello, Venice and Mar Piccolo of Taranto) over a two- year period for a total of 24 surveys (Fig. 1), of which nine were conducted in the harbor of Ravenna. In the laboratory, the samples were transferred to small aquaria kept at 20-24°C. After a few hours, conditions at the bottom of the aquaria become anoxic, causing many of the animals to climb up the walls to reach the surface. With the aid of a lamp, the Ophryotrocha can be identified through the aquarium walls on account of their dark jaws, prior to being removed with a pipette. A laboratory culture was established for each species found at each locality, given that, in many cases, identification of the actual species of Ophryotrocha can only be achieved with live animals; not only do many of the morphological characteristics crucial to classification emerge more clearly in alive than in preserved specimens, but there are some sibling species that can only be recognised through the study of their biological cycle and reproductive characteristics and/or by comparing and crossing them with standard strains that have been previously classified. The identity of most species has been checked on live material by B. Åkesson, who maintains "the Ophryotrocha gene bank", cultures of 18 species, in his laboratory in Göteborg. The Ophryotrocha from polluted coastal areas adapted readily to the laboratory conditions (24°C; 12 h light/ dark photoperiod; salinity, 30-32 psu; diet, frozen spinach). More details about laboratory rearing are reported in Prevedelli & Zunarelli Vandini (1998).

Some specimens were narcotised with MgCl², observed under a stereomicroscope (Zeiss Stemi 2000-C) and photographed *in vivo* with a digital camera (Polaroid

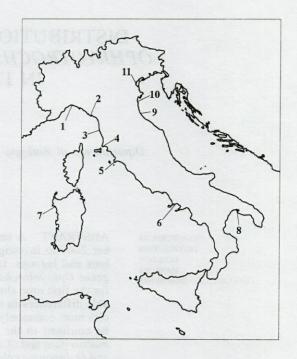


Fig. 1. – Localities in which one or more species of *Ophryotrocha* were found (data from present study and previous investigation). 1) Genoa harbor; 2) La Spezia harbor; 3) Leghorn harbor; 4) Piombino harbor; 5) Orbetello lagoon; 6) Gulf of Naples; 7) Alghero harbor; 8) Mar Piccolo of Taranto; 9) Rimini harbor; 10) Ravenna harbor; 11) Venice lagoon.

DMC-Ie). Selected references relating to the description and distribution in Italy of all the *Ophryotrocha* hitherto reported along the Italian coastline are given, as well as a brief description of each species found during the 1999-2001 surveys.

RESULTS AND DISCUSSION

The distribution of the genus *Ophryotrocha* along the Italian coastline, including bibliographic data, is shown in Fig. 1. The presence of each species in each of the examined localities is reported in Table I.

It appears that, in the harbor and brackish-water environments examined to date in Italy, there are six species belonging to the genus *Ophryotrocha*. The sampling carried out in this study discovered the presence of *O. puerilis*, *O. macrovifera* and *O. labronica*. A species morphologically very similar to *O. labronica* but with a few different features was also found and identified by Professor Bertil Åkesson of the University of Göteborg (Sweden) as *Ophryotrocha japonica* nomen nudum (Pleijel and Eide, 1996) (Fig. 2A-E). Table I. List and distribution of *Ophryotrocha* species along the Italian coastline. 1) Genoa harbor; 2) La Spezia harbor; 3) Leghorn harbor; 4) Piombino harbor; 5) Orbetello lagoon; 6) Gulf of Naples; 7) Alghero harbor; 8) Mar Piccolo of Taranto; 9) Rimini harbor; 10) Ravenna harbor; 11) Venice lagoon (species not present: -; species present, historical data only: 0; present study only: •; both: *).

Species	Location										
	1	2	3	4	5	6	7	8	9	10	11
O. puerilis	*	-	0	-	-	0	•	-	-	-	-
O. labronica	*	•	*	0	•	0	-	•	•	•	*
O. macrovifera	0	-	-	-	-	-	-	-	-	-	•
O. japonica	-	•	•	-	•	-	-	•	-	•	•
O. hartmanni	-	-	0	0	-	-	-	-	-	-	-
O. robusta	0	-	-	-	-	-	-	-	•	-	-
Total species per site	4	2	4	2	2	2	1	2	1	2	3

Species found in this study

Ophryotrocha puerilis

This species was found only in the harbors of Genoa and Alghero. All the specimens belong to the Mediterranean sub-species Ophryotrocha p. puerilis. It is the largest species of Ophryotrocha found in this study (0.8-1.3 cm in length). The head is formed by a prostomium and metastomium, both clearly defined. The prostomium is characterised by a pair of dorsal antennae and ventral palps and two dorso-lateral eyes. The forceps of the adults are falciform. The parapodia present dorsal and ventral cirrii. O. puerilis is a protandrous hermaphrodite that lays its eggs (100-110 µm in diameter) in gelatinous masses with a soft, sticky surface (egg mass of other species reported here have membranous surfaces). It has 2n=8 chromosomes (Claparede & Mecznikow 1869, La Greca & Bacci 1962, Bortesi 1964, Åkesson 1973, 1975. 1984).

Previous studies reported its presence in the harbors of Genoa, Leghorn and Naples (La Greca & Bacci 1962, Bortesi 1964, Castelli *et al.* 1995; Premoli & Sella 1995, Åkesson pers comm, Sella pers comm).

Ophryotrocha labronica

O. labronica was collected in both harbor and brackish environments. It was found in Genoa, La Spezia, Leghorn, Orbetello, Taranto, Rimini, Ravenna and Venice. All the populations are inter-fertile and belong to the cosmopolitan sub-species Ophryotrocha l. labronica. The adults (4 mm in length) exhibit a triangular prostomium with a transverse strand of pigments that connects the two eyes, two very short antennae and no palps. The prostomium and metastomium are largely joined (Fig. 2D, E). The right branch of the forceps shows a double apical tooth. O. labronica was originally described as a protandrous hermaphroditic species, even though numerous gonochoric populations were subsequently reported. The females lay rigid, tubular masses of eggs (120 µm in diameter) and care for the brood (La Greca & Bacci 1962, Akesson 1970 1972 a, b, 1973, 1975, 1984, Lanfranco & Rolando 1981). This species heads the "labronica group" belonging to the genus *Ophryotrocha* and consisting of some sibling gonochoric species, most of them with 2n=6 chromosomes except for *O. robusta* nomen nudum (Åkesson, 1973b) and *O. rubra* nome nudum (Pleijel & Eide 1996) that have 2n=10 chromosomes (Åkesson 1972 a, b, 1973, 1975, 1984).

O. labronica was previously found in Genoa, Leghorn, Piombino, Naples and Venice (La Greca & Bacci 1962, Robotti 1979, Lanfranco & Rolando 1981, Rolando 1981, 1984, Cognetti 1982, Rolando & Giorda 1982, Castelli *et al.* 1995, Premoli & Sella 1995, Premoli *et al.* 1996, Prevedelli & Zunarelli, Vandini 1998, Åkesson pers comm, Sella, pers comm).

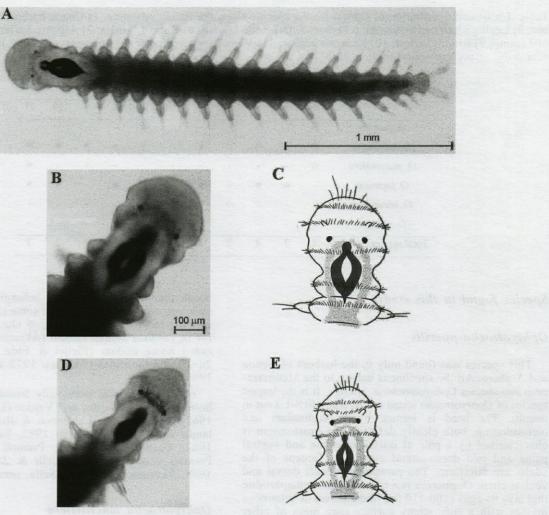
Ophryotrocha macrovifera

This species was found only in the fouling communities of the wharves in the Venice lagoon. It is a gonochoric species with 2n=6 chromosomes belonging to the "labronica group". It is distinguishable from *O. labronica* on account both of its larger eggs (170-180 µm in diameter) and, above all, of outcomes of its crossing with standard strains. It seems that there is considerable variability in the egg sizes of the different populations: the specimens collected in Venice lay eggs with a diameter of only 150 µm (Akesson 1973b, 1984, Plejel & Eide 1996). Levinton (1983) reported egg diameters of 134 µm and 146 µm for two Florida populations.

The Italian checklist of polychaetes reports its presence along the central-northern Adriatic coast. It has also been reported in the harbor of Genoa (Castelli *et al.* 1995, Åkesson pers comm).

Ophryotrocha japonica

This species has been recorded for the first time along European and Mediterranean coastlines. It was collected in La Spezia, Leghorn, Orbetello, Taranto, Rimini, Ravenna and Chioggia. Population density was high in all the above localities. It has been previously reported only from some harbor environments along the Asiatic and American coastlines of the Pacific Ocean. The populations collected in this study are inter-fertile both be-



Altarian (1999) and at hite 1995 and margin 1973 & b. 1975, 1975

Fig. 2. – Ophryotrocha japonica and O. labronica. A, adult of O. japonica. B, C, head of O. japonica. D, E, head of O. labronica.

tween themselves and with the Pacific specimens (Åkesson pers comm). Like that of O. labronica, the head of O. japonica displays two short antennae and no palps, and the right branch of the forceps has a double apical tooth. The diploid chromosome number is 2n=6 chromosomes. O. japonica also has some peculiar features: the adults are frequently more than 5 mm in length and, in particular, have a roundish, enlarged head lacking the transverse strand of pigments between the two eyes that characterises O. labronica and O. macrovifera (Fig. 2A-C). O. japonica lays eggs (130-140 µm in diameter) in rigid, tubular or "spoon-shaped" masses. Both males and females share parental care of the developing embryos. One week after egg laying, at 24°C, the larvae of O. japonica hatch from the egg clusters with 2-3 setigers. O. macrovifera larvae hatch with 1-2 setigers; the larvae of other species reported in this study hatch without setigers.

Species of Ophryotrocha reported for Italy but not found in this study

Previous studies had reported the presence of two species not found in the present study.

Ophryotrocha hartmanni was found only in Leghorn and Piombino harbors (Parenti 1961, 1962, Åkesson 1973, Cognetti 1982, Castelli *et al.* 1995).

Ophryotrocha robusta was found in different surveys in the harbor of Genoa (Åkesson 1973b, 1984, Rolando 1982, 1984, Sella pers comm).

Distribution of Ophryotrocha in Italy

In all the localities examined and in almost all the surveys carried out, one or more species of *Ophryotrocha* were found (Fig. 1, Table I). There are considerable differences in the distribution of each species. The species most commonly found is *O. labronica*, present in ten of the eleven localities considered. Surprisingly, *O. japonica* was found in eight of the nine localities sampled between 1999 and 2001, while *O. puerilis* seems to be confined to four harbors along the Ligurian and Tyrrhenian coastlines. The data obtained hitherto suggest that *O. hartmanni*, *O. macrovifera* and *O. robusta*, each reported in only one or two localities, are less widespread than the other species. Also, while *O.* puerilis, O. hartmanni and O. robusta were found only in harbor environments, O. labronica and O. japonica were found in brackish habitats as well. O. japonica is always found together with O. labronica.

Introduction of O. japonica into the Mediterranean Sea

Harbors and brackish waters are particularly exposed to the invasion of alloctonous species, which may be introduced mainly as a result of maritime traffic (ships' hulls, bilge waters and ballast) and aquaculture (Cognetti & Maltagliati 2000). Among the polychaetes, various alloctonous species such as the sabellid *Branchiomma luctuosus* and *Desdemona ornata*, the spirorbid *Spirorbis marioni* and *Pileolaria berkeleyana*, the spionid *Streblosoma hesslei* and the lumbrinerid *Lumbrineris inflata* have been reported in Italian harbors and lagoons (Giangrande *et al.* 1981, Zibrowius & Bianchi 1981, Lardicci & Castelli 1986).

O. japonica is morphologically a sibling species of O. labronica, a typical Mediterranean species, from which it differs markedly, however, on account of certain characteristics, such as maximum size, head pigmentation and some reproductive traits. It seems unlikely that O. japonica is a cosmopolitan species that escaped the attention of the previous investigators; all the species of Ophryotrocha previously reported along the Italian coastline were subjected to morphological and reproductive studies that would have enabled the two species to be identified quite easily (La Greca & Bacci 1962, Parenti 1962, Robotti 1979, Lanfranco & Rolando 1981, Rolando 1982, Premoli & Sella 1995, Prevedelli & Zunarelli Vandini 1998). The wide distribution of O. japonica in lagoons as well as in harbors, and certain features of its biological cycle, such as the relatively long period of development inside the egg mass, suggest that this species may have been introduced recently as a result of sea traffic and/or through the introduction of live animals for aquaculture such as seeds of mussels or fish.

Ecology of Ophryotrocha species

In theory, all the species of *Ophryotrocha* considered in this study reproduce all year round, but considerable seasonal differences have been observed in relation to population densities among *O. labronica*, *O. puerilis* and *O. japonica*. The population densities of each species also appear to vary along the seasons; *O. labronica*, for example, is particularly abundant in summer and at the beginning of autumn, but rare during winter. The samplings carried out in the harbor of Genoa between 1999 and 2001 confirm that *O. labronica* and *O. puerilis* are sympatric, but, while the former is more abundant during the warm season, the latter occurs more frequently during the winter and spring months (Premoli & Sella 1995, Zunarelli Vandini pers comm). Seasonal variations in their respective densities were also observed for the populations of *O. labronica* and *O. japonica* in Ravenna harbor: *O. japonica* is more abundant during the cold season, *O. labronica* in the summer months, while in the autumn they are evenly balanced.

It is possible that this tendency to vicariousness is due to some sort of inter-specific competition between the different Ophryotrocha species. On the other hand, numerous studies have shown that variations in temperature can affect the characteristics of the life history, influencing the population growth rates of some small polychaetes with a semi-continuous iteroparous reproductive strategy (Åkesson 1976, Levin & Creed 1986, Chu & Levin 1989, Åkesson & Costlow 1978, 1991). Temperature also influences the biological cycle, life history and demography of a population of O. labronica, originally from the harbor of Genoa (Prevedelli & Simonini 2001). It is therefore likely that most of the differences in the density and distribution among the species of Ophryotrocha is due to their different sensitivity to the seasonal variations in temperature, which could influence the recruitment of populations throughout the year and their capability to colonize and to maintain themselves in such unpredictable environments.

Most information relating to the distribution of Ophryotrocha comes from localities in northern and central Italian coast. The differences in the geographical and temporal distribution of each species, and the new reports of O. japonica, indicate that the investigation should be extended to others Mediterranean harbors and brackish areas, not only to find new species but also to map the distribution of the hitherto reported species in greater detail. Yet, the analysis of the bibliographic data in conjunction with those emerging from the present surveys demonstrates that the genus Ophryotrocha is widespread in Italian harbors and polluted brackish waters. The species living in such anthropogenic stressed environments often adopt opportunistic strategies (Cognetti 1982, 1992). The estimated growth rates of O. labronica in the laboratory were equal to or greater than those of typically opportunistic species (Prevedelli & Simonini 2001). It is very probable that, in their natural environment, the species belonging to the genus Ophryotrocha also adopt an opportunistic strategy. Cognetti (1982, 1992) reported that, before 1975, in the harbor of Piombino, O. labronica and O. hartmanni colonised the most polluted zones characterised by high levels of metals and PCB, where other polychaete species, known as opportunistic, were

not present. After 1975, when environmental conditions improved, *O. hartmanni* disappeared and the population of *O. labronica* steadily declined. All the species of *Ophryotrocha* living in harbors and brackish habitats rapidly reach sexual maturity, have a relatively high fecundity, lay their eggs in tubular or gelatinous masses, exhibit parental care and develop directly. These features could enable them to tolerate the considerable variations induced in size and structure of their populations by the exposure to pollutants and by the environmental instability that characterise these habitats.

ACKNOWLEDGEMENTS – The author wish to thank D Prevedelli (Modena) for her support during these years. Many thanks to F Molinari, MA Todaro, M Mauri and AM Pagliai (Modena) and to G Sella (Turin) and B Åkesson (Göteborg) for their remarks and suggestions that greatly improved the manuscript. This work was supported by the Italian Ministero dell'Università e della Ricerca scientifica e tecnologica (MURST).

REFERENCES

- Åkesson B 1970. Sexual conditions in a population of the polychaete *Ophryotrocha labronica* La Greca and Bacci from Naples. *Ophelia* 7: 167-176.
- Åkesson B 1972a. Incipient reproductive isolation between geographic populations of *Ophryotrocha labronica* (Polychaeta: Dorvilleidae). *Zool Scr* 1: 207–210.
- Åkesson B 1972b. Sex determination in *Ophryotrocha labronica* (Polychaeta: Dorvilleidae). *In* Fifth European Marine Biology Symposium, B. Battaglia ed, Piccin, Padova: 163-172.
- Åkesson B 1973. Reproduction and larval morphology of five *Ophryotrocha* species (Polychaeta, Dorvilleidae). Zool Scr 2: 145-155.
- Åkesson B 1975. Reproduction in the genus Ophryotrocha (Polychaeta, Dorvilleidae). Pubbl Staz Zool Napoli 39 Suppl: 377-398.
- Åkesson B 1976. Temperature and life cycle in *Ophryotrocha labronica* (Polychaeta, Dorvilleidae). *Ophelia* 15: 37-47.
- Åkesson B 1982. A life table study on three genetic strains of *Ophryotrocha diadema* (Polychaeta: Dorvilleidae). *Int J Invert Repr Dev* 5: 59-69.
- Åkesson B 1984. Speciation in the genus *Ophryotrocha* (Polychaeta, Dorvilleidae). *In* Polychaeta Reproduction, A Fisher & HD Pfannenstiel eds, Fortschritte der Zoologie 29, Gustav Fisher Verlag, Stuttgart, New York: 299-316.
- Åkesson B, Costlow JD 1978. Effects of temperature and salinity on the life cycle of *Ophryotrocha diadema* (Polychaeta, Dorvilleidae). *Ophelia* 17: 215-229.
- Åkesson B, Costlow JD 1991. Effects of constant and cyclic temperatures at different salinity levels on survival and reproduction in *Dinophilus gyrociliatus* (Polychaeta: Dinophilide). *Bull Mar Sci* 48 (2): 485-499.
- Berglund A 1986. Sex change by a polychaete: effects of social and reproductive costs. *Ecology* 67: 837-845.

- Berglund A 1990. Sequential hermaphroditism and the size advantage hypothesis: an experimental test. *Anim Behav* 39: 426-433.
- Berglund A 1991. To change or not to change sex: a comparison between two *Ophryotrocha* species (Polychaeta). *Evol Ecol* 5: 128-135.
- Bortesi O 1964. Differenziamento citosessuale in ceppi mascolinizzanti e femminilizzati di *O. puerilis puerilis. Boll Zool* 31 (2): 1103-1109.
- Cassai C, Prevedelli D 1999. Fecundity and reproductive effort in *Ophryotrocha labronica* (Polychaeta: Dorvilleidae). *Mar Biol* 133: 489-494.
- Castelli A, Abbiati M, Badalamenti F, Bianchi CN, Cantone G, Gambi MC, Giangrande A, Gravina MF, Lanera P, Lardicci C, Somaschini A, Sordino P 1995. Annelida Polychaeta, Pogonophora, Echiura, Sipuncula. In A Minelli, S Ruffo, La Posta eds, Checklist delle specie della fauna italiana, 19. Calderini, Bologna.
- Chu JW, Levin LA 1989. Photoperiod and temperature regulation of growth and reproduction in *Streblospio benedicti* (Polychaeta: Spionidae). *Inv Repr Dev* 15: 131-142.
- Claparède E, Mecznikow E 1869. Beiträge zur Erkenntnis der entwicklungsgeschichte der Chaetopoden. Z wiss Zool 16: 163-205.
- Cognetti G 1982. Adaptive strategy of brackish-water fauna in pure and polluted waters. *Mar Poll Bull* 13 (7): 247-250.
- Cognetti G 1992. Colonization of stressed coastal environments. *Mar Poll Bull* 24 (1): 12-14.
- Cognetti G, Maltagliati F 2000. Biodiversity and adaptive mechanism in brackish water fauna. *Mar Poll Bull* 40 (1): 7-14.
- Dahlgren TG, Åkesson B, Schander C, Halanych KM, Sundberg P 2001. Molecular phylogeny of the model annelid *Ophryotrocha*. *Biol Bull* 201 (2): 193-203.
- Eibye-Jacobsen D, Kristensen RM 1994. A new genus and species of Dorvilleidae (Annelida, Polychaeta) from Bermuda, with a phylogenetic analysis of Dorvilleidea, Iphitimidae and Dinophilidae. *Zool Scr* 23: 107-131.
- Gambi MC, Ramella L, Sella G, Protto P, Aldieri R 1997. Variation size in benthic polychaetes: systematic and ecological relationships. *J Mar Biol Ass UK* 77: 1045-1057.
- Giangrande A, Gambi MC, Fresi E 1981. Two species of Polychaetes new to the Mediterranean fauna. *Boll Zool* 48: 311-317.
- Grothe C, Pfannenstiel HD 1986. Cytophysiological study of neurosecretory of pheromonal influences on sexual development in *Ophryotrocha puerilis* (Polychaeta, Dorvilleidae). *Int J Invert Repr Dev* 10: 227-229.
- Hilbig B, Blake AJ 1991. Dorvilleidae (Annelida: Polychaeta) from the U.S. Atlantic slope and rise. Description of two new genera and 14 new species, with a generic revision of *Ophryotrocha*. *Zool Scr* 20: 147-183.
- Kegel B, Pfannenstiel HD 1983a. Evaluation of the pair-culture effect in *Ophryotrocha puerilis* (Polychaeta, Dorvilleidae). I. Pair-culture effect and the sex ratio. *Helg wiss Meer* 36: 205-213.
- Kegel B, Pfannenstiel HD 1983b. Evaluation of the pair-culture effect in Ophryotrocha puerilis (Poly-

chaeta, Dorvilleidae). II. Conditions for the moult of the upper jaw. *Helg wiss Meer* 36: 215-222.

- La Greca M, Bacci G 1962. Una nuova specie di *Ophryotrocha* delle coste tirreniche (Annelida, Polychaeta). *Boll Zool* 29: 13-24.
- Lanfranco M, Rolando A 1981. Sexual races and reproductive isolation in *Ophryotrocha labronica* La Greca and Bacci (Anellida, Polychaeta). *Boll Zool* 48: 291-294.
- Lardicci C, Castelli A 1986. Desdemona ornata Banse, 1957 (Polychaeta, Sabellidae, Fabricinae); new record in the Mediterranean Sea. Oebalia 13: 195-201.
- Levin LA, Creed EL 1986. Effect of temperature and food availability on reproductive responses of *Streblospio benedicti* (Polychaeta: Spionidae) with planktotrophic or lecithotrophic development. *Mar Biol* 92: 103-113.
- Levinton JS 1983. The latitudinal compensation hypothesis: growth data and a model of latitudinal growth differentiation based upon energy budgets. I. Interspecific comparison of *Ophryotrocha* (Polychaeta: Dorvilleidae). *Biol Bull* 165: 686-698.
- Mori M, Belloni S 1985. Distribution, abundance and infestation of *Ophryotrocha geryonicola* (Annelida: Dorvilleidae) in *Gerion longipes* (Crustacea: Decapoda: Geryonidae) of Ligurian bathial bottoms. *Oebalia* 11: 277-287.
- Paavo B, Bailey-Brock J, Åkesson B 2000. Morphology and life history of *Ophryotrocha adherens* sp. nov. (Polychaeta: Dorvilleidae). *Sarsia* 85: 251-264.
- Parenti U 1961. Ophryotrocha puerilis siberti, O. hartmanni e O. bacci nelle acque di Roscoff. Cah Biol Mar 2: 437-445.
- Parenti U 1962. Variabilità sessuale di una nuova sottospecie di *Ophryotrocha hartmanni* del Mediterraneo. *Lincei- Rend Sc fis mat nat* 33: 78-84.
- Pleijel F, Eide R 1996. The phylogeny of *Ophryotrocha* (Dorvilleidae: Eunicida: Polychaeta). J Nat Hist 30: 647-659.
- Premoli MC, Sella G 1995. Sex economy in benthic polychaetes. *Ethol Ecol Evolut* 7: 27-48.
- Premoli MC, Sella G, Berra P 1996. Heritable variation of sex ratio in a polychaete worm. *J Evol Biol* 9: 845-854.
- Prevedelli D, Zunarelli Vandini R 1998. Effect of diet on reproductive characteristics of Ophryotrocha labronica (Polychaeta: Dorvilleidae). Mar Biol 132: 163-170.

- Prevedelli D, Simonini R 2001. Effects of temperature on demography of *Ophryotrocha labronica* (Polychaeta, Dorvilleidae). *Vie Milieu* 51 (4): 173-180.
- Robotti C 1979. Electrophoresis of proteins in three populations of *Ophryotrocha labronica*. *Experientia* 35: 596-597.
- Rolando A 1981. Early courtship and sexual differentiation in *Ophryotrocha labronica* La Greca and Bacci (Polychaeta Dorvilleidae). *Mon Zool Ital* 15: 53-61.
- Rolando A 1982. Sexual condition in a population of *Ophryotrocha robusta* (Annelida, Polychaeta) from Genova. *Atti Soc tosc Sci nat (B)*, 89: 145-152.
- Rolando A 1984. The sex induction hypothesis and reproductive behaviour in four gonochoristic species of the genus *Ophryotrocha* (Annelida Polychaeta). *Mon Zool Ital* 18: 287-299.
- Rolando A, Giorda R 1982. Male intersexes in *Ophryo*trocha labronica La Greca and Bacci (Polychaeta Dorvilleidae). *Mon Zool Ital* 16: 67-73.
- Sella G 1985. Reciprocal egg trading and brood care in a hermaphroditic polychaete worm. *Anim Behav* 33: 938-944.
- Sella G 1988. Reciprocation, reproductive success and safeguards against cheating in a hermaphroditic polychaete worm *Ophryotrocha diadema* Akesson, 1976. *Biol Bull* 175: 212-217.
- Sella G 1990. Sex allocation in the simultaneous hermaphroditic polychaete worm Ophryotrocha diadema. Ecology 71: 27-32.
- Sella G 1991. Evolution of biparental care in the hermaphroditic polychaete worm *Ophryotrocha diadema. Evolution* 45: 63-68.
- Sella G, Ramella L 1999. Sexual conflict and mating system in the dorvilleid genus *Ophryotrocha* and the dinophilid genus *Dinophilus*. *Hydrobiologia* 402: 203-213.
- Wesenberg-Lund E 1938. Ophryotrocha geryonicola (Bidenkap) (=Eteonopsis geryonicola Bidenkap) refound and redescribed. Göteborgs K Vetensk- o VitterhSamh Hand Ser B 6: 1-14.
- Zibrowius H, Bianchi CN 1981. Spirorbis marioni and Pileolaria berkeleyana, Spirorbidae exotiques dans le port de la Méditerranée Nord-occidentale. Rapp Comm Int Mer Médit 27: 163-164.
- Zunarelli R 1962. Il differenziamento citosessuale di tre specie di *Ophryotrocha*. Boll Zoll 24 (2): 417-423.
 - Reçu le 28 novembre 2001; received November 28,2001 Accepté le 22 janvier 2002; accepted January 22,2002