

# Effects of sediment organic matter on mortality, growth and development of the polychaetes *Capitella teleta* and *Capitella* sp. (Annelida: Capitellidae) in laboratory conditions

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**Summary:** The endobenthic deposit-feeder polychaetes of the *Capitella capitata* species complex have a strong relation with organically enriched sediments (OES). The effect of non-organically enriched sediments (NOES, 0.09% of organic content) and OES (6.26% of organic content) on mortality, growth and development of juveniles and adults of *Capitella teleta* (cultured for more than 40 years) and *Capitella* sp. from Alfacs Bay, Tarragona, Spain (acclimatized for one month) were analysed in laboratory conditions. Juveniles and adults were exposed (all individuals separately in different dishes) to the two treatments, periodically observed and measured until death. NOES considerably impaired survival, growth rates and development of juveniles and adults of both species, which showed highly variable negative growth rates under OES. Juvenile and adult *C. teleta* showed an improved maturity under OES, even producing two protandrous and one protogynous individuals, whereas no *Capitella* sp. reached maturity during the experiment.

**Keywords:** Polychaeta; sibling species; organic-enriched sediment; food limitation; juveniles, adults; Long Island; Alfacs Bay; deposit feeders.

**Efectos de la materia orgánica del sedimento en la mortalidad, crecimiento y desarrollo de los poliquetos *Capitella teleta* y *Capitella* sp. (Annelida: Capitellidae) en condiciones de laboratorio**

**Resumen:** Los poliquetos endobentónicos consumidores de depósito pertenecientes al complejo de especies de *Capitella capitata* tienen una fuerte relación con sedimentos enriquecidos orgánicamente (SEO). En condiciones de laboratorio, se analizó el efecto de sedimentos no enriquecidos orgánicamente (SNEO, 0,09% de materia orgánica) y SEO (6,26% de materia orgánica) en la mortalidad, crecimiento y desarrollo de juveniles y adultos de *Capitella teleta* (cultivada por más de 40 años) y *Capitella* sp. de la bahía dels Alfacs, Tarragona, España (aclimatada durante un mes). Juveniles y adultos fueron expuestos a los dos tratamientos (todos los individuos separados en cajas individuales) y fueron observados y medidos periódicamente hasta la muerte. SNEO produjo un deterioro considerable en la supervivencia, tasas de crecimiento y desarrollo de juveniles y adultos de ambas especies, los cuales mostraron tasas de crecimiento negativas muy variables en SEO. Los juveniles y adultos de *C. teleta* en SEO mostraron una madurez mejorada, incluso produciendo dos individuos protándricos y un proterogino, mientras que ningún individuo de *Capitella* sp. alcanzó la madurez durante el experimento.

**Palabras clave:** Polychaeta; especies hermanas; sedimento orgánicamente enriquecido; limitación de alimento; juveniles; adultos; Long Island; bahía dels Alfacs; consumidores de depósito.

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## INTRODUCTION

The endobenthic deposit-feeder polychaetes belonging to the *Capitella capitata* (Fabricius, 1780) species complex have been reported worldwide in polluted and organically enriched marine and estuarine sediments, often being referred to as bioindicators (e.g. Pearson and Rosenberg 1978, Méndez et al. 1997, 2000). The *Capitella capitata* complex consists of at least 50 sibling species, with about 13 being described from laboratory cultures (Grassle and Grassle 1976, Blake 2009). The non-interbreeding, morphologically similar cryptic species of this complex are distinguishable mainly by protein variation and ecophysiological, developmental and reproductive features (Wu et al. 1991, Linke-Gamenick et al. 2000a, Adkins and Schulze 2011). However, only a few have been described in detail (Méndez 2016).

The genus *Capitella* mostly includes opportunistic r-selected species able to produce either free-swimming planktotrophic or benthic lecithotrophic larvae (Grassle and Grassle 1974, Méndez 2002, Adkins and Schulze 2011) and showing a wide geographical and interspecific variety of reproductive strategies (Méndez et al. 2000). The latter include planktotrophy, lecithotrophy and direct development, as well as hermaphroditism and poecilogony, which give rise to differences in size and duration of the life stages, number of brooded embryos, and ciliation patterns in metatrochophore larvae (Méndez et al. 2000, 2019, Méndez 2016).

Nevertheless, the life cycle of the different species follows a similar pattern. With faecal materials, substrate and potential food, females construct brood tubes that are open at both ends to allow oxygenation. The fertilized eggs are brooded until the trochophore stage (Reish 1980). In species with planktotrophic development they are then directly hatched (then progressing to the metatrochophore stage in the water column), whereas in lecithotrophic species they stay inside the tube until they reach the metatrochophore stage (George 1984). The juvenile stage can be reached inside the tube (direct development) or in the sediment after settling of metatrochophores. Juveniles are already vermiform, with a complete segmentation, a clear distinction between thorax and abdomen and a chaetal arrangement consisting of capillaries in the first three segments and hooded hooks in the subsequent ones (Méndez 1995). Juveniles are first transparent, and then become pink and red because of haemoglobin production until they become immature adults (Méndez 2002, 2006); a change from intense red to greyish red indicates that specimens are becoming old (Méndez 2006). Adult males bear genital spines between chaetigers 8 and 9 (Reish 1980). Immature females bear paired, yellowish, sac-like ovaries suspended by mesenteries in the ventral coelomic cavity throughout the mid-body segments (Bellan et al. 1972, Eckelbarger and Grassle 1983), which become visibly white when mature (Méndez 2002, 2006, Méndez and Barata 2015).

Field and laboratory studies have demonstrated that growth depends strongly on environmental food

availability (Forbes and Lopez 1990, Qian and Chia 1992, Linton and Taghun 2000, among others) and quality (Qian and Chia 1991, Hu et al. 2003, Ramskov and Forbes 2008). The presence of high amounts of food accelerated growth and offspring production in a species of *Capitella* and increased fecundity (because their generation time became shorter), while limiting food-induced growth delays (thus increasing generation time), and egg size became food-quality mediated (Qian and Chia 1992). Such a key role of organic matter in the physiology of the species of *Capitella* allows us to focus our study on determining the effects of two different organic content conditions on mortality, growth and development of two populations of *Capitella* in laboratory conditions.

## MATERIALS AND METHODS

### Test organisms

*Capitella teleta* was first identified as *Capitella* sp. I (Grassle and Grassle 1976) and later designated as *C. teleta* (Blake et al. 2009). It is a hermaphroditic species with lecithotrophic development originally found in organically polluted sediments in Setauket Harbour (Long Island, New York, USA) and then successfully cultured in the Department of Life Sciences and Chemistry of the Roskilde University, Denmark (DLSCRU) for many generations over more than 40 years (Ramskov et al. 2009). This species has been considered the most opportunistic among the *Capitella* complex because of its rapid growth rate and numerical dominance in organically enriched areas (Grassle and Grassle 1974, Tsutsumi 1987, Forbes et al. 1994). It is thus the subject of much ecological and experimental research worldwide (Méndez et al. 2000). The specimens analysed in this study came from DLSCRU.

*Capitella* sp. has not been morphologically described in a formal way. It was collected at the Trabucador Beach (40°63'N 0°79'E, Alfacs Bay, Tarragona, Spain) in October 2012, at about 30 cm depth on sandy sediments with 0.5±0.04% of organic matter (OM) content. OM was always estimated as loss by ignition (Dean 1974) and expressed as average ±standard error based on three measurements. The sediment was sieved through a 0.5 mm mesh and the retained worms were sorted with forceps. The accompanying fauna was mainly composed of amphipods, isopods and gastropods, together with polychaetes of the families Capitellidae, Spionidae, Phyllodocidae, Maldanidae and Sabellidae.

### Cultures

All specimens were cultured in plastic aquaria (20×12×17 cm) containing 200 g (dry weight) of clean sediment from Vallcarca Beach (41°14'N 1°52'E, Sitges, Barcelona, Spain), previously washed with freshwater (to kill fauna), dried (60°C) and sieved to keep the <250 µm fraction (OM=0.089±0.007%). Each stock culture contained 1.5 L of aerated and filtered (<30 µm) seawater with 31 ppm for *C. teleta* (Ramskov

et al. (2009) and 34 ppm for *Capitella* sp. (native water salinity) and was maintained at 20°C in the dark. Once in the aquaria, the worms were fed weekly with 0.5 g of artificial food (Méndez et al. 2013, Méndez and Barata 2015, Méndez 2016) consisting of a mixture of equal parts of commercial fish food (Wardley\*), baby cereal (Milupa) and dried spinach (Forbes et al. 1996, Ramskov and Forbes 2008), dried, ground and sieved to less than 250 µm. The worms were acclimatized for six (*C. teleta*) and one (*Capitella* sp.) months prior to the start of the experiments (OM=6.536±0.060%). The experiments were performed at the Department of Environmental Chemistry of the Institute of Environmental Assessment and Water Research (IDAEA) of the Spanish National Research Council (CSIC).

### Experimental sediments

Sediments from Vallcarca Beach were used to prepare two experimental conditions: (1) non-organically enriched sediments (NOES), washed with freshwater, dried (60°C), sieved to less than 250 µm (OM=0.089±0.007%); and (2) organically enriched sediments (OES), a mixture of 100 g (dry weight) of clean, dry (60°C) and <250 µm sieved sediment with 0.5 g of artificial food (OM=6.264±0.052%, similar to the acclimatizing sediments). No more artificial food was added to the OES to avoid fungi and bacteria development, as occurred in previous experiments (pers. obs.) or a decrease in oxygen concentrations. Experimental sediments were stored dry until used. Sediments and seawater (<30 µm filtered, 31 ppm for *C. teleta* and 34 ppm for *Capitella* sp.) were replaced weekly.

### Experimental design

Twelve pale or transparent juveniles with a length of 1.9 to 6.5 mm (*C. teleta*) and 3.7 to 10.6 mm (*Capitella* sp.) bearing eyes and lacking sexual structures were selected, placed individually in 2 cm diameter plastic dishes containing 0.3 g (dry weight) of rehydrated experimental sediments and 3 mL of filtered seawater and kept at 20°C in the dark. Each dish contained one juvenile to record data at individual level. Measurements and qualitative observations (mortality, haemoglobin production and development of reproductive structures) were taken until all worms died, every 6 to 8 days for *C. teleta*, and every 3 to 4 days (days 1–51) and 6 to 8 days (day 58 until death) for *Capitella* sp.

Adult worms with haemoglobin (7.6–9.3 mm for *C. teleta*; 6.5–13.8 mm for *Capitella* sp.) were selected and placed individually in 3.5 cm diameter plastic dishes containing 0.5 g (dry weight) of rehydrated experimental sediment and 7 mL of filtered seawater and kept at 20°C in the dark until all worms died. Mature specimens were identified by the genital spines (males) and the yellow (immature) or white (mature) ovaries (females) (Méndez and Barata 2015). Three males and three females of *C. teleta* and six immature females with yellow ovaries of *Capitella* sp. (males were absent) were selected and observed individually. Measurements, mortality and development of reproductive

structures were recorded for each worm until death, every 4 to 7 days for *C. teleta*, and every 3 to 4 days (days 1–41) and 6 to 7 days (day 48 until death) for *Capitella* sp.

Juveniles and adults were photographed each census day for body volume (V) determination, as  $V = \pi A^2/4L$ , where  $A$  is the area and  $L$  the length (Forbes et al. 1994). When possible, three photographs of each worm were taken to estimate an average V. Photographs were taken with a camera (Nikon Digital Sight DS-R1) connected to a dissecting microscope (Nikon SMZ1500, mod. CDS230). Body length and area were measured using the NIS-Elements AR 3.0. S16 software (Nikon Laboratory imaging, 1991-2008). Both juveniles and adults were observed and measured one day after being placed in their respective treatments (experimental and census day 1) to avoid handling stress (i.e. animals jerking and curling), which could hinder the photographic process and thus cause mistakes in V estimates.

### Calculations

Juvenile and adult mortality (as percentages) for NOES and OES was calculated as the number of living individuals in each census day divided by the number

Table 1. – Relationships between census days depicted in mortality graphs (Fig. 2) and body volume (Fig. 3) graphs and real days (Days).

<i>Capitella teleta</i>		<i>Capitella</i> sp.			
Census days	Days	Census days	Days	Census days	Days
1	1	1	1	24	114
2	7	2	4	25	121
3	14	3	8	26	129
4	21	4	11	27	136
5	28	5	15	28	143
6	35	6	18	29	150
7	42	7	22	30	157
8	49	8	25	31	164
9	57	9	29	32	171
10	64	10	33	33	185
		11	36	34	191
		12	40	35	202
		13	43	36	209
		14	47	37	227
		15	51	38	234
		16	58	39	240
		17	65	40	247
		18	71	41	254
		19	78	42	256
		20	85	43	265
		21	92	44	272
		22	99	45	279
		23	107	46	287

Table 2. – Size as mean body volume  $\pm$  standard deviation (range), number of individuals (N) and maximum days when measurements could be performed of juveniles and adults of the two species of *Capitella* under NOES and OES.

	Volume (mm <sup>3</sup> )		N	Days
<i>Capitella teleta</i>				
Juveniles in NOES	0.11 $\pm$ 0.08	(0.06–0.29)	12	42
Juveniles in OES	0.47 $\pm$ 0.24	(0.04–0.78)	12	57
Adults in NOES	1.18 $\pm$ 0.60	(0.73–1.93)	6	33
Adults in OES	1.51 $\pm$ 0.55	(0.63–2.29)	6	33
<i>Capitella</i> sp.				
Juveniles in NOES	0.70 $\pm$ 0.31	(0.27–1.19)	12	51
Juveniles in OES	1.55 $\pm$ 0.61	(0.77–2.83)	12	164
Adults in NOES	-	-	6	0
Adults in OES	1.28 $\pm$ 0.51	(0.51–2.59)	6	217

Table 3. – Development of reproductive structures in juveniles and their initial and average ( $\pm$  standard deviation) body volumes. NO, not observed; Hb, haemoglobin, YO, yellow ovaries; WO, white ovaries; GS, genital spines; 1st app to 4th app, appearance of yellow ovaries.

Developmental structures	Experimental days	Initial volume range (mm <sup>3</sup> )	Mean volume (mm <sup>3</sup> )	N
<i>Capitella teleta</i> NOES				
Pink spots of Hb	7–42	0.03–0.16	0.1 $\pm$ 0.1	12
Red spots of Hb	NO	NO	NO	NO
YO	NO	NO	NO	NO
YO + GS	NO	NO	NO	NO
YO + WO	NO	NO	NO	NO
<i>Capitella teleta</i> OES				
Pink spots of Hb	1–7	0.84–0.28	0.14 $\pm$ 0.07	8
Red spots of Hb	1–57	0.48–0.85	0.64 $\pm$ 0.18	4
YO - 1st app	7–42	0.53–0.63	0.58 $\pm$ 0.05	3
YO - 2nd app	14–42	0.53	0.53	1
YO - 3rd app	21–42	0.75	0.75	1
YO - 4th app	42	0.57	0.57	1
Female + GS	14–48	0.99	0.99	1
WO	21–34	0.72–0.81	0.77 $\pm$ 0.06	2
<i>Capitella</i> sp. NOES				
Pink spots of Hb	4–58	0.68–1.69	1.15 $\pm$ 0.33	8
Red spots of Hb	NO	NO	NO	NO
YO	NO	NO	NO	NO
YO + GS	NO	NO	NO	NO
YO + WO	NO	NO	NO	NO
Old	NO	NO	NO	NO
<i>Capitella</i> sp. OES				
Pink spots of Hb	4–24	0.45–2.59	1.68 $\pm$ 0.68	8
Red spots of Hb	25–164	1.20–2.28	1.81 $\pm$ 0.56	3
YO	25–164	1.20–2.28	1.81 $\pm$ 0.56	3
YO + GS	NO	NO	NO	NO
YO + WO	NO	NO	NO	NO
Old	191–254	-	-	1

of dead individuals in the subsequent census day (taking into account the number of days for each period). Due to the high number of days that elapsed until the death of all the individuals of *Capitella* sp., the graphic representations of mortality and body volume results were built for the two species using census days (i.e. days when observations and measurements were made) instead of real days (Table 1). Size and development data (Tables 2-4) refer to real days (hereafter termed “days”).

Growth rates ( $\text{mm}^3 \text{ day}^{-1}$ ) were calculated for each worm as the difference in V between one day and the subsequent one, divided by the number of days between measurements. Global growth rates for each developmental stage and treatment were estimated as the mean for all analysed worms. Worms dying during the first and second days were not taken into account.

## RESULTS

### Worms

The stock cultures after the acclimation period contained juveniles, males, females and brooding females for *C. teleta* and a low number of specimens lacking males and brooding females for *Capitella* sp. The latter were characterized by having a conical (instead of dorsoventrally flattened) prostomium lacking eyespots, capillary chaetae from chaetiger 1 to 4–7, a ventral depression along the posterior abdominal region, and a pygidium that was a large, simple, rounded, dark lobe lacking anal cirri (Fig. 1).

### Mortality

Living juveniles of *C. teleta* were observed until days 42 (in NOES) and 57 (in OES), while adults always died on day 33 (Tables 1 and 2; Fig. 2A). Mortality in *Capitella* sp. was highly variable. Four juveniles died on day 1 in the two treatments. In NOES, seven juveniles (66.7%) died on day 33 (mean survivorship = 24 days), while the last juvenile died on day 58. Six juveniles (83.3%) in OES survived before day 43 (mean survivorship = 26 days), while the last two juveniles died on days 164 and 254, respectively. The six adults died on day 1 in NOES, while five adults (83.3%) in OES died before day 15 (mean survivorship = 8 days) and the last adult died on day 279 (Tables 1 and 2; Fig. 2B).

### Growth

Juveniles and adults of *C. teleta* were smaller in NOES than in OES (Table 2) and showed a general V reduction during the experiment (Table 1; Fig. 3A). Their growth rates were always negative, both for juveniles ( $N=12$ ,  $-0.012 \pm 0.012 \text{ mm}^3 \text{ day}^{-1}$  in NOES,  $0.0006 \pm 0.01 \text{ mm}^3 \text{ day}^{-1}$  in OES) and for adults ( $N=5$ ,  $-0.03 \pm 0.05 \text{ mm}^3 \text{ day}^{-1}$  in NOES and  $0.09 \pm 0.08 \text{ mm}^3 \text{ day}^{-1}$  in OES).

*Capitella* sp. also showed reductions in V at the end of the experiment. Juveniles in NOES were smaller (Table 2), and those in OES showed a general increase in the first part of the experiment and reached a maximal average V ( $2.83 \text{ mm}^3$ ) on day 58 (two individuals), which was higher than the maximal V of the only living adult in OES ( $1.82 \text{ mm}^3$  on day 51) (Table 1; Fig. 3B). Growth rates for juveniles were  $-0.03 \pm 0.011 \text{ mm}^3 \text{ day}^{-1}$  ( $N=8$ ) in NOES and  $-0.017 \pm 0.47 \text{ mm}^3 \text{ day}^{-1}$  ( $N=7$ ) in OES, and  $0.034 \pm 0.38 \text{ mm}^3 \text{ day}^{-1}$  for adults in OES ( $N=3$ , alive until day 15) ( $N=3$ ) and  $0.032 \pm 0.04 \text{ mm}^3 \text{ day}^{-1}$  ( $N=3$ , from day 1 to 217, when the last survivor could be measured because it was not damaged). The growth rate of this survivor from day 1 to 217 was negative ( $-0.002 \pm 0.10 \text{ mm}^3 \text{ day}^{-1}$ ,  $N=1$ ; 31 observations). Under OES, the sporadic peaks corresponded to the two juveniles and one adult that survived longer, thus causing a high standard deviation (Fig. 3).

### Development

The juveniles of *C. teleta* in NOES remained transparent with a few pinkish haemoglobin spots, without developing reproductive structures or producing tubes during the whole experiment (Table 3). In contrast, some specimens in OES reached the adult stage, becoming initially red (because of a high haemoglobin production) and then building a high number of tubes. Yellow ovaries appeared between days 7 and 42 and white ovaries between days 21 and 34 (two individuals). One female developed genital spines on day 14, indicating hermaphroditism, and remained like that until dead.

The eight living juveniles of *Capitella* sp. exposed to NOES had little haemoglobin and did not become adults during the experiment (Table 3). Only three specimens in OES produced high amounts of haemoglobin and developed yellow ovaries, but did not reach maturity. Only

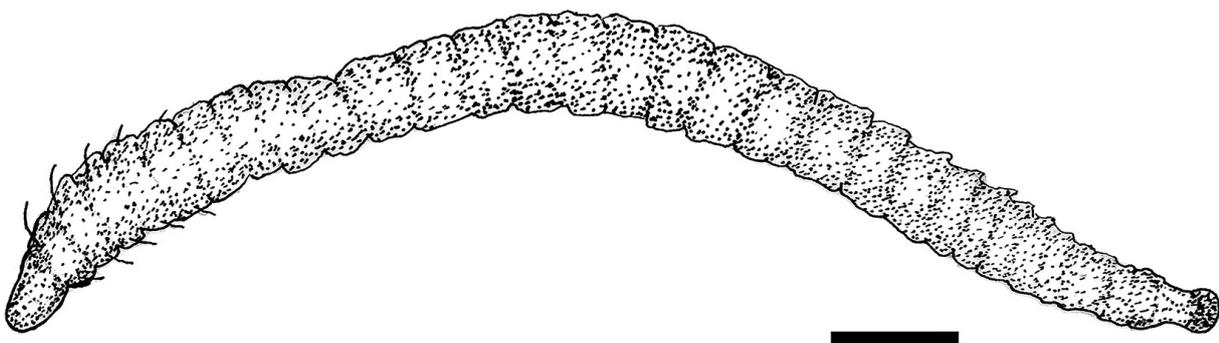


Fig. 1. – Immature female of *Capitella* sp. in lateral view (scale bar: 1 mm).

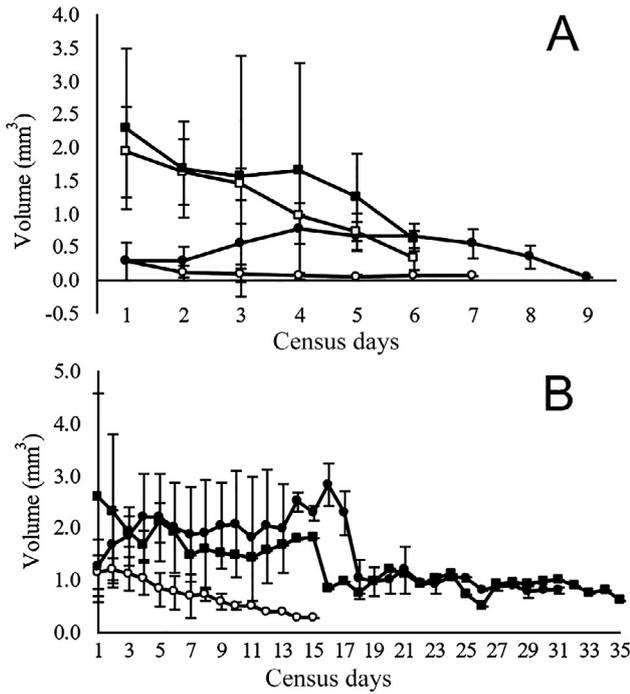


Fig. 2. – Time course of average body volume  $\pm$ sd. A, *Capitella teleta* (empty circles, juveniles in NOES; full circles, juveniles in OES; full triangles, adults in NOES and adults in OES). B, *Capitella* sp. (empty circles, juveniles in NOES; full circles, juveniles in OES; empty squares, adults in NOES; full squares, adults in OES).

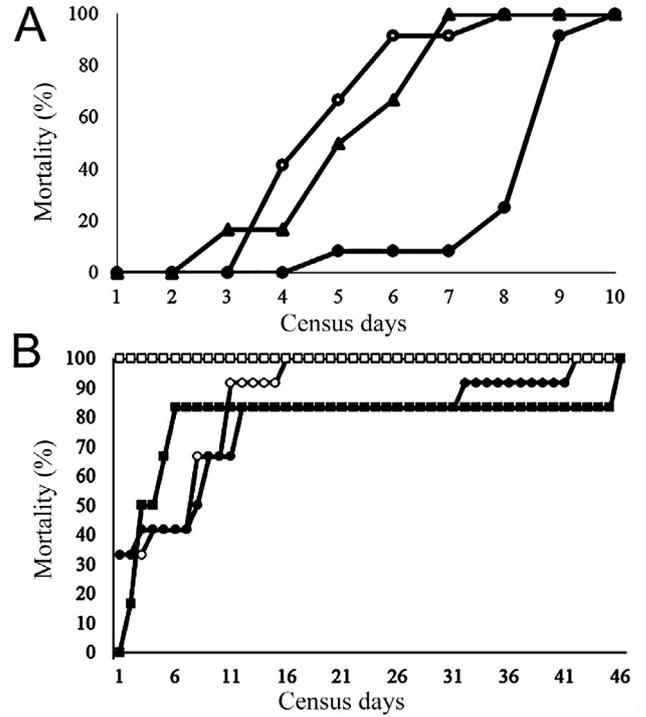


Fig. 3. – Time course of mortality (%). A, *Capitella teleta*; B, *Capitella* sp. (empty circles, juveniles in NOES; full circles, juveniles in OES; empty squares, adults in NOES; full squares, adults in OES).

Table 4. – Initial and final body volumes until death of adults, development of sexual structures (worm volumes between brackets) and days of appearance (GS, genital spines; YO, yellow ovaries; WO, white ovaries; \* no more pictures taken because the worm was broken).

Developmental structures	Initial volume (mm <sup>3</sup> )	Final volume (mm <sup>3</sup> )	Death day	New sexual structures	
				Volume (mm <sup>3</sup> )	Appearance days
<i>Capitella teleta</i> NOES					
Male 1 with GS	2.26	2.26	11	-	-
Male 2 with GS	2.02	0.94	25	-	-
Male 3 with GS	1.86	0.37	33	-	-
Female 1 with YO	1.39	0.21	33	-	-
Female 2 with YO	0.97	1	33	-	-
Female 3 with WO	1.29	0.45	33	-	-
<i>Capitella teleta</i> OES					
Male 1 with GS	1.68	0.06	11	YO (0.06)	5
Male 2 with GS	2.34	0.81	20	-	-
Male 3 with GS	2.44	1.11	33	YO (0.48)	12
Female 1 with YO	1.06	0.54	33	WO (1.78)	5
Female 2 with YO	1.68	2.16	33	GS (0.96)	12
Female 3 with WO	4.53	0.72	33	-	-
<i>Capitella</i> sp. OES					
Female 1 with YO	1.69	* 0.62	279	-	-
Female 2 with YO	1.91	1.91	4	-	-
Female 3 with YO	3.43	3.74	7	-	-
Female 4 with YO	0.95	1.25	11	-	-
Female 5 with YO	1.28	2.38	15	-	-
Female 1 with YO	6.27	4.03	7	-	-

one individual survived for 254 days; it was greyish and moved slowly, indicating that it had become old. In both treatments, tube production was low.

None of the adults of *C. teleta* raised in NOES developed sexual structures (Table 4), while in OES, two males developed yellow ovaries at days 5 and 12, respectively, and a female developed genital spines at day 12, indicating hermaphroditism. Only one female developed white ovaries at day 5. None of the *Capitella* sp. immature females with yellow ovaries from OES reached maturity (Table 4).

## DISCUSSION

The two populations of *Capitella* studied here came from different localities and living conditions. *Capitella teleta*, an opportunistic species originally inhabiting very polluted environments (Blake et al. 2009), came from a laboratory culture held for more than 40 years (Ramskov et al. 2009). *Capitella* sp. came from natural population inhabiting a low organically enriched environment and was acclimatized to laboratory conditions for a brief period just before the experiments started. *Capitella teleta* showed females, males and hermaphrodites, while all *Capitella* sp. were females, hindering developmental comparisons. *Capitella teleta*, as described by Blake et al. (2009), was smaller than *Capitella* sp., a prostomium flattened dorsoventrally (conical in *Capitella* sp.), eyespots in adults (absent in *Capitella* sp.), capillary chaetae in chaetigers 1–7 (1–4/7 in *Capitella* sp.) and a pygidium with two rounded lobes and a narrow dorsal slit-like notch (with a large simple rounded and dark lobe in *Capitella* sp.).

*Capitella* sp. did not produce mature males and females or brooding females, and did not develop reproductive structures in laboratory conditions, which prevented both its formal description and proper comparisons with other morphologically described sibling species from close locations, such as *Capitella* sp. A from Les Cases d'Alcanar, Tarragona, a town less than 20 km from the Trabucador Beach (Méndez 2016) or *Capitella capitata* (Méndez 1995) and *Capitella* sp. B (Méndez 2002), both from Barcelona. Our *Capitella* sp. is probably the same species as that of a field population from disturbed sands (OM <1%) from the Trabucador Beach showing females with brooding tubes and males with modified chaetae, with continuous reproduction over one year studied by Martin and Grémare (1997). These authors used the width of the fourth thoracic setiger to infer biomass (instead of total body length), which prevented proper comparisons with our *Capitella* sp. However, compared with the populations from nearby (i.e. less than 3 km away) organically enriched muds, those in disturbed sands showed more stable and less productive populations, as well as much lower biomasses and densities (<0.4 vs. >15 g of dry weight m<sup>-2</sup> and <5000 vs 170000. ind m<sup>-2</sup>, respectively) and smaller individuals (0.2 µg dry weight ind<sup>-1</sup> vs. 0.5 µg dry weight ind<sup>-1</sup>) (Martin and Grémare 1997), which strongly supports not only the key role of OM in structuring the populations but also its influence in their responses at individual level.

During our experiments, the weekly replacement of sediments provided enough food for the two species to feed, as demonstrated during their acclimation and in previous stock cultures of *C. teleta* (Méndez et al. 2013) and *Capitella* sp. A (Méndez 2016). Also, the sediment in the original stock culture of *C. teleta* had enough food to feed all worms (OM=3.00±0.21%) (Ramskov et al. 2009), a similar value to that used in their experiments (maximum OM=3%) (Ramskov and Forbes 2008).

*Capitella teleta* and *Capitella* sp. showed physiological differences in our two treatments, which were reflected in different mortality, growth and development. The species of the *C. capitata* complex have high physiological and morphological variability, with even sibling offspring from a single female having different responses to identical environment conditions (Qian and Chia 1991). However, in general terms, juveniles and adults of *C. teleta* survived longer than those of *Capitella* sp., which agrees with previous observations leading *C. teleta* to be considered the most tolerant species among the *C. capitata* complex (Grassle and Grassle 1974, Tsutsumi 1987, Forbes et al. 1994). Its high tolerance to adverse conditions may explain its higher survivorship under NOES than under OES. Its generation time in cultures has been reported to vary, depending on food abundance and temperature, from 20 days (Tenore and Chesney 1985) to 30 to 40 days (Grassle 1984, Whitlatch and Zajac 1985, Tsutsumi et al. 1990), and can reach up to 147 days (Linke-Gamenick et al. 2000b), which agrees with the high juvenile and adult survivorship in our treatments.

*Capitella teleta* (like *Capitella* sp. I) may be found at low densities in organic-poor sediments, where they only produce small numbers of larvae (Grassle and Grassle 1974, 1976, Tsutsumi et al. 1990); this is in agreement with the scarcity of specimens in the studied field population of *Capitella* sp., with only 0.51% of OM. The high variability in mortality and growth of *Capitella* sp. could be attributed to a failure in acclimatizing to laboratory conditions, which may also explain why some worms survived long under NOES, where the organic content was similar to that of their natural habitat. However, the extremely high survivorship shown by two juveniles (164 and 254 days) and one adult (279 days) under OES suggests a higher longevity, comparable to *C. capitata* (one year lifespan; Warren 1976), *C. capitata* (nine months lifespan; Lardicci and Ceccherelli 1994), *Capitella* sp. L (one year lifespan; Gamenick and Giere 1994) and *Capitella* sp. Y, (six months on average, two years and a half of maximum survivorship; Méndez 2006).

Although juvenile and adult growth was highly variable and negative for both species, all juveniles showed higher shrinkage in NOES than in OES, as expected owing to relationships between growth and environmental food availability (Tenore 1977, Tsutsumi et al. 1990, Linton and Taghun 2000). Though food content in the experiments proved to be enough to feed adults, the higher size reduction of adults of *C. teleta* in OES could be attributed either to food quality

(Quian and Chia 1991, Hu et al. 2003) or to investing energy in developing sexual structures rather than growing (Ramskov and Forbes 2008).

Our observations confirm the importance of organic enrichment for development and reproduction in the species of the *Capitella* complex (Grémare et al. 1988, 1989, Marsh et al. 1990), with juveniles of *Capitella* sp. under NOES not reaching the adult stage, and no adults under NOES developing new sexual structures, while juveniles of *Capitella* sp. under OES reached the immature adult stage and juveniles and immature adults of *C. teleta* under OES reached maturity.

The presence of ovaries and genital spines in an individual of *C. teleta* under OES confirmed its hermaphroditism (Petraitis 1990, Blake et al. 2009, Ramskov et al. 2009). Most species of the *Capitella* complex appear to be only protandrous (having genital spines first and then also white ovaries), while protogyny (having ovaries first and then also genital spines) seems to be rarer (Grassle and Grassle 1977, Petraitis 1990, Ramskov et al. 2009). However, protogynous specimens appeared when the species was exposed to fluoxetine, a beneficial result as protogyny could be an excellent strategy for ensuring the population survivorship in natural conditions (Méndez et al. 2013, Méndez and Barata 2015). However, the fact that one immature female developed genital spines during our experiments suggests that other factors (e.g. type of sediment or artificial food) could also trigger protogyny.

The scarcity of mature males and females and brooding females in the field population of *Capitella* sp. prevented progeny production and made it impossible to follow the development of the species in the laboratory. Although some juveniles under OES showed yellow ovaries (immature stage), none of them developed white ovaries (mature stage). In some species of the complex, the period of storage of coelomic oocytes in females is minimal when there are mature males in the culture (Eckelbarger and Grassle 1983), which could explain the females' delay in or lack of maturity during our experiments. Knowing the life cycle of *Capitella* sp. could improve the design and interpretation of experiments testing environmental stress effects at individual and population levels, which would require further future laboratory studies.

Our results confirm the role of sediment organic content in the physiological responses of benthic detritivores, with juvenile and adult survival, growth and development of both *C. teleta* and *Capitella* sp. being impaired under NOES. Moreover, juveniles and adults of *C. teleta* under OES developed sexual structures, including two protandrous and one protogynous individuals. Finally, we suggest that the negative growth rates in worms under OES could be better attributed to food quality or to investing energy in developing sexual structures rather than in growing.

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