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Top-predator effects of jellyfish *Odessia maeotica* in Mediterranean salt marshes

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ABSTRACT: Jellyfish can act as planktonic top predators, and their effects may cause drastic changes in the plankton structure of marine and freshwater systems. However, the top predator effects may not necessarily be the same in species-poor habitats as they are in species-rich habitats. The present study analyses the effects of the small lacunae jellyfish *Odessia maeotica* in a species-poor habitat, Mediterranean salt marshes in the wetlands of Empordà (NE Iberian Peninsula). A field experiment was carried out in March 2008 to assess the direct and indirect effects of *O. maeotica* on plankton composition. Our results show that the presence of *O. maeotica* changed the plankton composition through top-down effects. Changes were strong in zooplankton, because *O. maeotica* can suppress almost the entire trophic level of large zooplankton (>50 µm). Weak indirect effects on phytoplankton composition were observed as well. When *O. maeotica* was present, changes in the relative abundance of the phytoplankton species were found, but there was no net increase in phytoplankton biomass. Our results suggest that these weak indirect effects may be the result of trophic cascade effects coupled with the oligotrophic conditions of these salt marshes. Thus, trophic cascade effects lead to an increase in ciliate biomass, and these ciliates would feed on small algae (jellyfish–copepods–ciliates–small algae), while oligotrophic conditions would prevent increases in algal biomass.

KEY WORDS: Jellyfish · *Odessia maeotica* · Top-down · Bottom-up · Brackish waters · Trophic cascade · Food web

INTRODUCTION

Jellyfish are widespread in both marine and limnic systems (e.g. Dumont 1994), and can act as planktonic top predators, causing direct and indirect changes in lower trophic levels, through cascading effects (Oguz et al. 2001, Pitt et al. 2007). Predation is the main direct effect on zooplankton (e.g. Larson 1987, Stibor & Tokle 2003, Smith & Alexander 2008), since jellyfish can feed on copepods (e.g. Dodson & Cooper 1983, Purcell et al. 1999, Costello & Colin 2002), cladocerans (Davis 1955, Dodson & Cooper 1983, Purcell 2003) and fish eggs (e.g. Purcell 1985, Dumont 1994). Indirect effects may also appear, such as changes in the plankton structure of lower trophic levels due to cascade effects (Olsson et al. 1992, Granéli & Turner 2002, Stibor et al. 2004). In this regard, some studies have pointed out an increase of phytoplankton in the presence of jellyfish (Lindahl & Hernroth 1983, Jankowski & Ratte 2001).

The effects of a top predator are variable and depend on the complexity of the aquatic community (Polis & Strong 1996, Stibor et al. 2004). Most studies on the trophic role of jellyfish are carried out in marine or freshwater systems where medusae act as top predators affecting the zooplankton (e.g. Larson 1987, Baird & Ulanowicz 1989, Stibor & Tokle 2003) and phytoplankton populations (e.g. Huntley & Hobson 1978, Riisgård 1998). However, the jellyfish's role as a top predator in simpler communities may be different, since, as pointed out by Strong (1992), the effects of a top predator in species-poor habitats would be expected to be different than in species-rich habitats.

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The large fluctuations in the salinity of brackish water systems (e.g. Barnes 1989) mean that only well-adapted species can successfully inhabit such environments (Bamber et al. 1992, Boix et al. 2008). As a consequence, brackish waters are especially interesting systems because top predators can be studied in a species-poor habitat.

Daan (1986) and Purcell & Nemazie (1992) suggest negligible effects of jellyfish controlling the plankton population in brackish systems. However, the small jellyfish *Odessia maeotica* (Ostroumoff, 1896) can dominate the plankton community in Mediterranean salt marshes in situations of confinement (low water turnover), reducing the plankton species diversity and the copepod populations to only a few isolated harpacticoids (Quintana et al. 1998a). Therefore, the top-predator behaviour of small jellyfish in brackish systems still needs to be clarified.

Despite the potential importance of jellyfish in the food web structure, there are relatively few experimental studies dealing with their effects on plankton communities. This could be due to some intrinsic difficulties that exist when studying these organisms (e.g. unpredictable occurrences, tank size effects; Toonen & Chia 1993, Boero et al. 2008). Nevertheless, many of these experimental difficulties are reduced when working with small-sized medusae, which make small jellyfish especially suitable for experimental approaches. In this sense, recent experimental studies carried out with *Craspedacusta sowerbii*, a small freshwater jellyfish species (mean bell diameter: <20 mm), have successfully demonstrated its effect (both direct and indirect) on a plankton community (Jankowski 2004, Jankowski et al. 2005).

In the present study, we carried out a short-term field experiment using tanks in a Mediterranean brackish lagoon with the aim to finding out if *Odessia maeotica* acts as a top predator, exhibiting direct and indirect control on plankton communities. We compared plankton structures in the presence of jellyfish with those in their absence. Because brackish habitats have simple communities, we would expect the top predator to exert a strong effect. In order to establish the strength of the effect, we simulated the strongest possible effects of *O. maeotica* by removing plankton organisms >50 µm (mainly zooplankton taxa), since small jellyfish, such as *O. maeotica* (e.g. *Craspedacusta sowerbyi*), feed on organisms >50 µm (e.g. Dodson & Cooper 1983, Dumont 1994, Spadinger & Maier 1999). The hypotheses to be tested were that *O. maeotica* (1) cause a strong direct effect on zooplankton by removing most of the plankton >50 µm and (2) cause indirect cascading effects on lower trophic levels, including small zooplankters, phytoplankton and bacteria, as a consequence of the depletion of the large zooplankters.

MATERIALS AND METHODS

Study site and *Odessia maeotica*. The study was carried out in the wetlands of Empordà (NE Iberian Peninsula), a series of Mediterranean shallow coastal lagoons, free from tidal influence, whose hydrological regime is determined by the occurrence of floods caused by meteorological disturbances in autumn and winter, and the process of desiccation during summer (Quintana 2002). In these coastal lagoons, the small jellyfish *O. maeotica* (mean bell diameter: 8 mm) has been captured in high densities in periods of confinement and under oligotrophic conditions (March to June) (Quintana et al. 1998a). This jellyfish is a Hydrozoa of the Moerisiidae family which exhibits alternation of generations: sessile polyps (asexual generation) and medusae (reproductive generation).

Stomach content. Prior to the experiment, the potential prey of *Odessia maeotica* were identified in the stomach contents of individuals captured in March 2007 in the same salt marsh in which the experiment was performed. Twenty-five *O. maeotica* individuals were captured using a net with a mesh size of 1.2 mm. Immediately, they were fixed with 4% formaldehyde solution and stored. *O. maeotica* stomachs were processed, identifying and counting the prey items found in each stomach using a stereomicroscope.

Experimental design. Our experiment to study the effects of *Odessia maeotica* on plankton was carried out in the field in March 2008, when the presence of potential prey for *O. maeotica* was detected. The lagoon was 60 cm deep and oligotrophic (2.08 µM dissolved inorganic nitrogen and 1.35 µM soluble reactive phosphorous) and was characterised by a conductivity of 53.30 mS cm^{-1}. The dissolved oxygen at the start of the experiment was 70%.

Five samples of 8 l of water were collected from the lagoon and processed to provide information on the 'initial conditions' of the plankton structure. Fifteen hermetically closed transparent PVC tanks (8 l capacity) were used in the experiment. Five of them were filled with 8 l of lagoon water without *Odessia maeotica* (hereafter 'control'). Another 5 tanks were filled with lagoon water, and 15 *O. maeotica* individuals were added to each tank (hereafter '*Odessia* treatment'). This density of *O. maeotica* was similar to the maximum densities of medusae observed in these lagoons (Quintana et al. 1998a). The last 5 tanks were filled with lagoon water previously filtered through 50 µm mesh (hereafter 'filtered treatment') in order to simulate the strongest possible jellyfish effect, i.e. total suppression of the large plankton trophic level.

The tanks were placed in the lagoon and fixed to the sediment by strings and tent pegs, and incubated for 72 h under the natural conditions of temperature (14°C

at initial time of the experiment) and light at a depth of 10 to 15 cm. Finally, 5 additional samples of 8 l from the same lagoon (hereafter 'lagoon') were taken directly after incubation. After the 72 h incubation, all individuals of *Odessia maeotica* were found to be alive. They were then sorted and fixed with 4% formaldehyde. Their biomass was estimated by measuring biovolume and converting it to dry weight (Malley et al. 1989) to check that predation pressure in all replica experiments was similar (ranging from 7.48 to 7.92 mg C l^{-1}).

Zooplankton was obtained from the retained material by filtering the 8 l of water through a 50 µm mesh and was immediately fixed with 4% formaldehyde solution. Taxonomic identification and counting of individuals were carried out using a stereomicroscope and an inverted microscope. Biomass was estimated using the equations of Malley et al. (1989) for Polychaeta larva and calanoids and cyclopoids (nauplii, copepodites and adults); of Dumont et al. (1975) for harpacticoid nauplii, copepodites and adults; and of Telesh et al. (1998) for rotifers.

Microplankton and large nanoplankton between 5 and 50 µm in size were obtained by filtering 125 ml of water through a 50 µm mesh and were then fixed in the field with Lugol's iodine and stored under dark conditions until analysis. Taxonomic identification and cell-counting were performed using an inverted microscope (Utermöhl 1958). Biovolumes were calculated from measurements of the linear dimensions of cells under the inverted microscope, using appropriate geometric formulae (Ruttner-Kolisko 1977, Hillebrand et al. 1999). Ciliate biovolume was estimated by approximation of the body shape to geometric shapes. Biomass was estimated using the equations of Menden-Deuer & Lessard (2000) for diatoms and chlorophytes and of Putt & Stoecker (1989) for ciliates.

Bacterioplankton and autotrophic pico- and nanoplankton samples were obtained by filtration through a 50 µm mesh and were then fixed with 1% paraformaldehyde and 0.05% glutaraldehyde (final concentration), immediately deep frozen in liquid nitrogen and stored at –20°C. Their abundance and biovolume were obtained using a flow cytometer (FACScalibur from Becton and Dickinson) with laser emission at 488 nm (for method details see López-Flores et al. 2006). The bacterioplankton biovolume was calculated using the equation described in Gasol & Del Giorgio (2000). Autotrophic pico- and nanoplankton biovolumes were calculated from measurements of linear dimensions of cells by means of cytometry through a calibration curve as described elsewhere (Olson et al. 1989, Rodríguez et al. 2002, López-Flores et al. 2006). Biomass was estimated using the equations of Lee & Fuhrman (1987) for bacterioplankton and of Verity et al. (1992) for picoplankton and nanoplankton.

To differentiate heterotrophic from autotrophic pico- and nanoplankton, DAPI (4′-6-diamidino-2-phenylindole) fixation was used (Porter & Feig 1980). The samples were mixed by inversion and left to stain for 10 min with the fluorochrome DAPI (final concentration of 0.5 µg ml^{-1}). Then, they were carefully filtered through a 0.2 µm polycarbonate filter (Millipore, Isopore membrane filters), and the filters were mounted on a glass slide and examined by epifluorescence microscopy with a UV excitation filter block and 1000× oil immersion. At least 300 individuals were enumerated per sample (Liu et al. 2005). By visualizing the DAPI-stained nuclei (blue) and the chlorophyll *a* (chl *a*) autofluorescence (red) it was possible to locate and differentiate heterotrophic from autotrophic pico- and nanoplankton. Heterotrophic pico- and nanoplankton biovolumes were calculated from the measurements of the linear dimensions of cells taken under epifluorescence microscopy, using appropriate geometric formulae. Biomass was estimated using the equations of Verity et al. (1992).

Some experiments have provided evidence that indirect effects are better explained if size discrimination of lower trophic levels is performed (Stibor et al. 2004). Therefore, to study the direct and indirect effects of *Odessia maeotica*, 3 planktonic organism data sets were used: (1) data of mesozooplankton and microzooplankton >50 µm (hereafter 'large plankton'), (2) data of pico-, nano- and microplankton <50 µm (hereafter 'small plankton') and (3) data of both groups (hereafter 'small + large plankton').

Comparisons between treatments and fractions allowed us to test the hypotheses listed below, as well as those regarding the direct effects (on large zooplankton) and indirect effects (on lower trophic levels; small plankton) of jellyfish presence in brackish environments:

Test 1 (tank effects): Hypothesis — The enclosure of water in a hermetically closed tank does not cause any effect on plankton composition. Lagoon samples versus control samples in final conditions were compared using the small + large plankton data set.

Test 2 (time effects): Hypothesis — No changes in plankton assemblages are expected between initial and final conditions, because our experiment covers a short time period (72 h). Initial conditions versus control samples were compared using the small + large plankton data set.

Test 3 (Odessia direct effects): Hypothesis — The presence of *O. maeotica* causes strong significant changes in large zooplankton organisms. Control samples versus *Odessia* treatment samples were compared using the large plankton data set.

Test 4 (strongest Odessia effects): Hypothesis — *O. maeotica* acts as a top predator in a species-poor habitat causing an effect similar to the total suppression of

the large zooplankton. *Odessia* treatment versus filtered treatment samples were compared using small plankton data set.

Test 5 (Odessia indirect effects): Hypothesis — The presence of *O. maeotica* causes changes in lower trophic levels by indirect cascading effects. Control samples versus *Odessia* treatment samples were compared using small plankton data sets.

Data analysis. All tests were performed using a multivariate approach (considering plankton structure) to check the effects of *Odessia maeotica* on the plankton community. Then, a univariate approach (taking into account 5 community parameters) was used to check if jellyfish affects these parameters. In both approaches, the biomass of *O. maeotica* added in the course of the experiment was not considered.

The multivariate approach was based on a correspondence analysis (CA), coupled with between-group analyses (Dolédec & Chessel 1989). The between-group analyses allowed us to obtain the centroid of each group (i.e. each treatment) and to test the differences among these groups. Differences among groups were checked using the Monte-Carlo permutation test (999 unrestricted permutations under the reduced model). The null hypothesis of this test stated that the relative proportion in biomass of plankton taxa did not differ among groups (initial conditions, lagoon, control, *Odessia* and filtered treatments). This procedure was used to check the significance of the (1) general effects (using the small + large plankton data set), (2) direct effects (using the large plankton data set) and (3) indirect effects (using the small plankton data set).

Additionally, 5 post hoc tests were carried out according to the 5 hypotheses previously described. Two of these post hoc tests were performed using the small + large plankton data set and tested the differences between lagoon and control treatment samples (tank effects) and between initial conditions and control treatment samples (time effects). Another post hoc test was carried out with the large plankton data set and tested the differences between control and *Odessia* treatment samples (*Odessia* direct effects). The last ones were carried out with the small plankton data set and tested the differences between *Odessia* and filtered treatment samples (strongest *Odessia* effects) and between control and *Odessia* treatment samples (*Odessia* indirect effects). The significance between the groups compared in each post hoc test was assessed using Monte-Carlo permutation tests (999 unrestricted permutations under the reduced model). All multivariate analyses were performed with ade4 package (Dray & Dufour 2007) written in R language.

The community parameters used in the univariate approach included species diversity, size diversity, species richness, total biomass and average body size. Species diversity was measured using the Shannon-Wiener index (Pielou 1969) and calculated using biomass abundance. Size diversity and average body size were calculated using the Kernel estimation (Quintana et al. 2008). Finally, species richness and total biomass were also calculated. These 5 community parameters were calculated considering the 3 organism data sets (large plankton, small plankton and small + large plankton) for control, *Odessia* and filtered treatments. Analyses of variance (ANOVA) and Welch statistics (when the assumption of variance homogeneity was violated) were used to test for significant differences among treatments for the 5 community parameters calculated. When a significant result was obtained in the ANOVA, the Tukey post hoc multiple comparison test was applied to identify which treatments were significantly different. All ANOVA were performed using SPSS 15.

Relationship between *Odessia maeotica* and plankton structure in natural conditions. Available data on *O. maeotica* and plankton abundances from a previous study (Quintana et al. 1998a) carried out from February to June (1989 to 1991) in the same salt marshes allowed us to find out whether, under natural conditions, increases in *O. maeotica* densities could be related to decreases of plankton abundances. Correlations between *O. maeotica* biomass and zooplankton biomass or chl *a* as a surrogate for the biomass of primary producers were calculated by means of the Pearson correlation coefficient.

RESULTS

Stomach content

The stomach content analysis showed that the diet of *Odessia maeotica* was mainly composed of large zooplankton organisms (Table 1). Calanoid copepods at all stages of their developmental were the most abundant prey found in the stomach content of *O. maeotica*. Although less represented, harpacticoids and rotifers were also part of the *O. maeotica* diet.

Effects on plankton structure

Twenty-three taxa present in the small + large plankton data set of all treatments were included in the CA (Fig. 1A). The first 2 axes of the CA explained 78.57% of the total variance: the first axis explained 61.73% and the second axis explained 16.84%. The first axis separated samples with real and simulated effects of our *Odessia maeotica* experiment (including *Odessia* and filtered treatments) from those without

Table 1. *Odessia meotica*. Stomach analyses of 25 individual jellyfish caught in open waters in March 2007 in the same area where the experiments were carried out during March 2008. No. of prey per stomach and preysize values are means (SD)

Prey type	No. of stomachs	No. of prey per stomach	Prey size (µm)
Adult *Calanipeda aquaedulcis*	11	2.45 (1.62)	1140 (280)
Copepodite *Calanipeda aquaedulcis*	11	3.19 (2.29)	560 (140)
Nauplius *Calanipeda aquaedulcis*	10	3.90 (2.87)	210 (70)
Copepodite harpacticoid	1	1	280
Brachionus sp.	2	1.5 (0.5)	110 (20)
Testudinella sp.	1	1	200
No prey	8	–	–

O. maeotica experimental effects (initial conditions, lagoon and control) (Fig. 1B). In these latter treatments, the community was characterised by a higher biomass of calanoids and euglenophytes, while in treatments with *O. maeotica* effects the community was characterised by higher biomass of smaller plankton taxa (i.e. ciliates, picoflagellates and bacterioplankton) (see Appendix 1). The second axis separates samples where *O. maeotica* was actually present (lagoon and *Odessia* treatment) from samples without *O. maeotica* (initial conditions, control and filtered treatments) (Fig. 1B). When *O. maeotica* was present, a higher biomass of ciliates, rotifers and chlorophytes characterised the plankton community, while when *O. maeotica* was absent, a higher biomass of harpacticoid copepods, autotrophic picoplankton, diatoms and cryptophytes characterised the plankton community.

When the large plankton data sets were analysed, the first 2 axes of the CA explained 79.54 % of the total variability observed (Fig. 2A). The first axis explained 47.02 % and separated samples of simulated *Odessia maeotica* effects (filtered treatment) from the rest of the treatments (initial conditions, lagoon, control and *Odessia* treatment) (Fig. 2B). The second axis explained 32.52 % and separated samples with *O. maeotica* effects (*Odessia* and filtered treatment) from samples without *O. maeotica* experimental effects (initial conditions, lagoon and control). The gradients observed on both axes could be related to differences in zooplankton body sizes. The *Odessia* treatment was characterised as having only the smallest zooplankton taxa (rotifers and nauplii of harpacticoids). Similarly, filtered treatment samples were characterised by the presence of small zooplankton, although some larger organisms were also present (nauplii and copepodites of cyclopoids and adult harpacticoids). On the other hand, initial conditions,

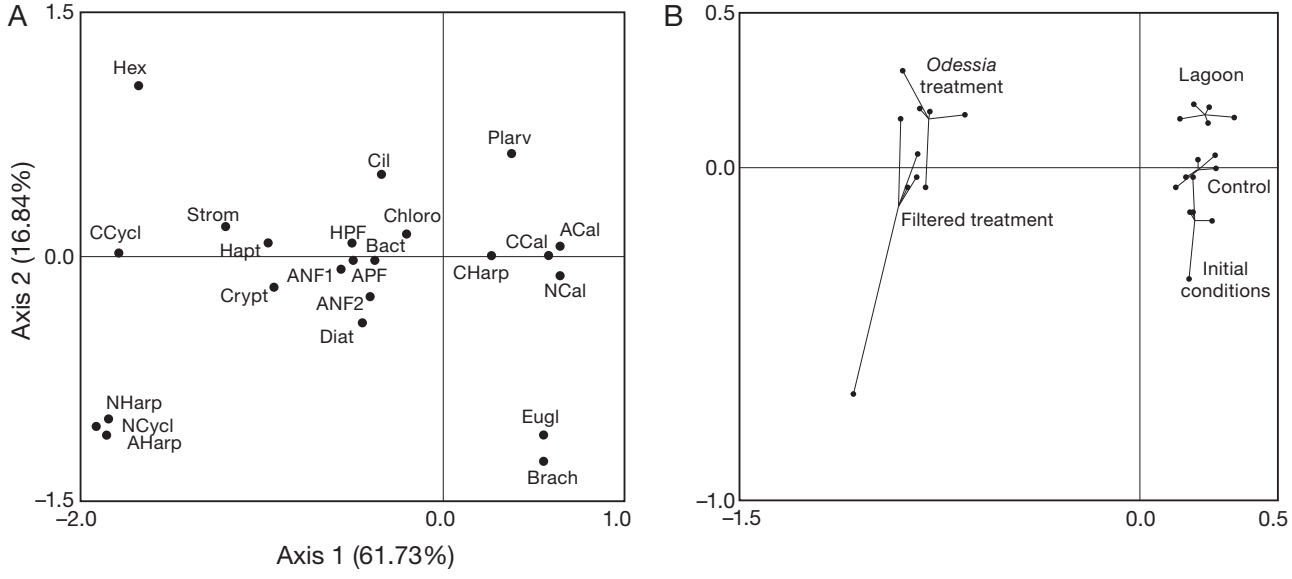

Fig. 1. Correspondence analysis for plankton taxa: ordination of (A) the 23 taxa and (B) the 25 samples analysed. APF: autotrophic picoflagellates; ANF1: autotrophic nanoflagellates 1; ANF2: autotrophic nanoflagellates 2; ACal: adult calanoid (*Eurytemora velox*); AHarp: adult harpacticoid (*Mesochra* sp.); Bact: bacterioplankton; Brach: *Brachionus* sp.; Cil: ciliate; Chloro: chlorophytes; CCal: copepodite calanoid; CCycl: copepodite cyclopoid; CHarp: copepodite harpacticoid; Crypt: cryptophytes; Diat: diatoms (*Amphora* sp., *Navicula* sp., *Nitzschia* sp.); Eugl: euglenophytes; Hapt: haptophytes; Hex: *Hexartra* sp.; HPF: heterotrophic picoflagellates; NCal: nauplii calanoid; NCycl: nauplii cyclopoid; NHarp: nauplii harpacticoid; Plarv: Polychaeta larvae; Strom: *Strombidium* sp.

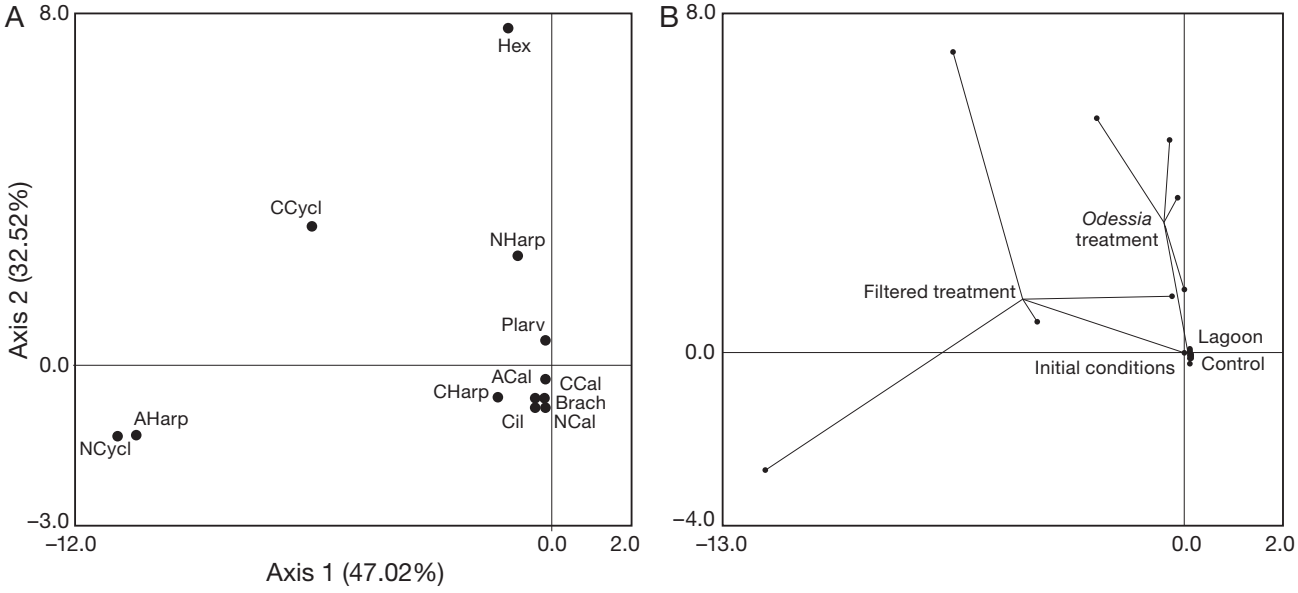

Fig. 2. Correspondence analysis for large plankton (>50 µm): ordination of (A) the 12 taxa and (B) the 25 samples analysed. ACal: adult calanoid (*Eurytemora velox*); AHarp: adult harpacticoid (*Mesochra* sp.); Brach: *Brachionus* sp.; Cil: ciliate; CCal: copepodite calanoid; CCycl: copepodite cyclopoid; CHarp: copepodite harpacticoid; Hex: *Hexartra* sp.; NCal: nauplii calanoide; NCycl: nauplii cyclopoid; NHarp: nauplii harpacticoide; Plarv: Polychaeta larvae

lagoon and control were characterised by a high biomass of large zooplankton (copepodites and adult of calanoids) (Appendix 1).

Taking only the small plankton data set into account, the first 2 axes of the CA explained 82.44% of the total variability observed (Fig. 3A). The first axis explained 59.63% and separated initial condition samples from those of final conditions (i.e. taken after 72 h: lagoon, control, *Odessia* and filtered treatments) (Fig. 3B). The small plankton from initial condition samples was characterised by a higher biomass of only autotrophic organisms (euglenophytes, diatoms and autotrophic picoflagellates), while the one from the final conditions had a higher biomass of other organisms such as bacterioplankton, auto- and heterotrophic picoflagellates and ciliates (Appendix 1).

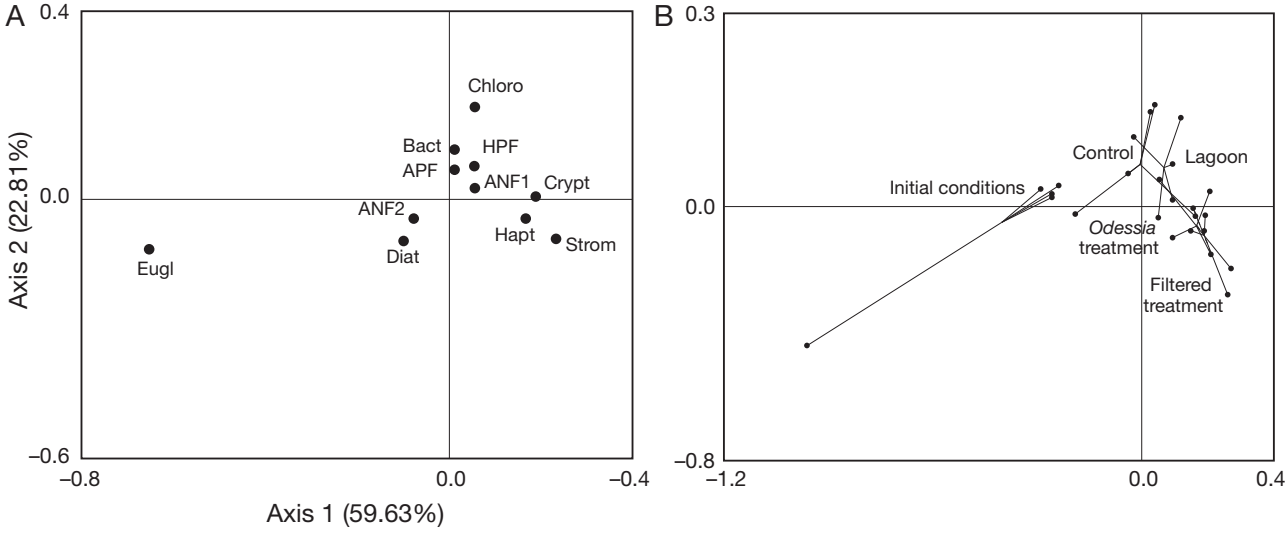

Fig. 3. Correspondence analysis for plankton small plankton (<50 µm): ordination of (A) the 11 taxa and (B) the 25 samples analysed. APF: autotrophic picoflagellates; ANF1: autotrophic nanoflagellates 1; ANF2: autotrophic nanoflagellates 2; Bact: bacterioplankton; Strom: *Strombidium* sp.; Chloro: chlorophytes; Crypt: cryptophytes; Diat: diatoms (*Amphora* sp., *Navicula* sp., *Nitzschia* sp.); Eugl: euglenophytes; Hapt: haptophytes; HPF: heterotrophic picoflagellates

The second axis explained 22.81% of total variance and separated samples with *Odessia maeotica* experimental effects (*Odessia* and filtered treatments) from samples without *O. maeotica* experimental effects (lagoon and control) (Fig. 3B). The small fraction of the plankton community without *O. maeotica* effects was characterised by higher biomass of bacterioplankton, auto- and heterotrophic picoplankton and autotrophic nano- and microplankton, while the small fraction of the plankton community with *O. maeotica* experimental effects was characterised by higher biomass of ciliates and haptophytes.

Hypothesis testing

Test 1: 'tank effects'

A tank effect was detected on the plankton structure, because we obtained significant differences between the lagoon treatment and the control samples (Monte-Carlo permutation test; $p < 0.01$). This could be explained by the presence of small *Odessia maeotica* detected in the lagoon samples. In fact, lagoon samples were located in a similar position to *Odessia* treatment samples (both were positive values on Axis 2 when considering the small + large plankton data set; Fig. 1B). In contrast, no tank effect was detected for any community parameters (Table 2).

Test 2: 'time effects'

As in Test 1, time effects on plankton structure were detected, since a significant difference was found between the initial conditions and control samples (Monte-Carlo permutation test; $p = 0.02$). On the other hand, no time effects were detected for any community parameters (Table 2).

Test 3: '*Odessia* direct effects'

The between-group analyses performed with the large plankton data set revealed significant differences between the control and the *Odessia* treatment (Monte-Carlo permutation test; $p = 0.01$). In the control samples, there was a higher biomass of large organisms (mainly calanoids) than in the *Odessia* treatment samples (Fig. 2A). Direct effects of *Odessia maeotica* were also detected in community parameters (Table 2). Total planktonic biomass ($F_{1,7} = 282.65$, $p < 0.01$) and average body size ($F_{1,7} = 14.64$, $p = 0.01$) were significantly lower in the samples from the *Odessia* treatment than in the control ones (Table 3).

Test 4: 'strongest *Odessia* effects'

No significant differences were found in the small plankton data set (Monte-Carlo permutation test; $p = 0.78$) between the *Odessia* and filtered treatments. Similarly, no significant differences were found between the *Odessia* and filtered treatments for any community parameter (Table 2). These results showed that *Odessia maeotica* exerts the strongest possible effect on the plankton community, since we did not find any significant differences between the *Odessia* treatment samples and the samples in which all organisms >50 µm had been artificially removed.

Table 2. Results of ANOVA for the different tests — Test 1: tank effects; Test 2: time effects; Test 3: *Odessia* direct effects; Test 4: strongest *Odessia* effects; Test 5: *Odessia* indirect effects. Samples and data sets used for each test are also indicated. µ: size diversity; *H*: species diversity; *S*: species richness; TB: total biomass (µg ml^{-1}); BS: average body size (µg ml^{-1}); (*W*): Welch test; **p ≤ 0.01 (after Bonferroni correction)

Test	Parameter	df_1	df_2	*F*	p
Test 1:	µ	1	4.61	0.68	0.45(*W*)
Lagoon vs. control	*H*	1	8	3.97	0.08
(data set: small + large plankton)	*S*	1	8	18.75	0.03
	TB	1	8	1.85	0.21
	Log BS	1	8	3.69	0.91
Test 2:	µ	1	8	0.46	0.52
Initial conditions vs. control	*H*	1	8	4.51	0.06
(data set: small + large plankton)	*S*	1	8	0.93	0.37
	TB	1	8	2.93	0.13
	Log BS	1	8	0.19	0.68
Test 3:	µ	1	3.01	1.11	0.37(*W*)
Odessia treatment vs. control	*H*	1	3.05	0.02	0.89(*W*)
(data set: large plankton)	*S*	1	7	2.78	0.14
	Log TB	1	7	282.65	<0.01**
	BS	1	7	14.64	0.01**
Test 4:	µ	1	8	0.01	0.96
Odessia treatment vs. filtered	*H*	1	8	0.13	0.73
treatment	*S*	1	8	2.31	0.17
(data set: small + large plankton)	TB	1	8	4.51	0.07
	BS	1	8	0.62	0.45
Test 5:	µ	1	8	0.27	0.62
Odessia treatment vs. control	*H*	1	8	1.25	0.29
(data set: small plankton)	*S*	1	8	0.06	0.82
	TB	1	8	2.25	0.17
	BS	1	8	0.03	0.86

Table 3. Mean (SD) values of community parameters of plankton for initial conditions, lagoon, control, *Odessia* treatment and filtered treatment, taking into account plankton taxa. μ: size diversity; *H*: species diversity; *S*: species richness; TB: total biomass (μg ml^{-1}); BS: average body size (μg ml^{-1}). Parameters with the same superscript letter (^{a}, ^{b}, or ^{c}) do not differ significantly among treatments ($p < 0.05$, Tukey post hoc tests)

Data set	Parameters	Initial conditions	Lagoon	Control treatment	*Odessia* treatment	Filtered
Small + large plankton	μ	0.91 (1.34)^{a}	1.42 (0.37)^{a}	1.44 (1.10)^{a}	1.80 (0.54)^{a}	1.78 (0.35)^{a}
	H	1.23 (0.15)^{a}	1.27 (0.22)^{a}	1.05 (0.11)^{a}	1.36 (0.12)^{a}	1.34 (0.11)^{a}
	S	12.20 (1.30)^{a}	15.20 (0.84)^{a}	13.20 (1.92)^{a}	11.80 (1.64)^{a}	13.60 (2.07)^{a}
	TB	147.27 (38.86)^{a}	204.00 (84.85)^{a}	190.33 (40.72)^{a}	24.27 (4.57)^{a}	19.04 (3.06)^{a}
	BS	$1.39 \cdot 10^{-6}$ ($2.45 \cdot 10^{-6}$)^{a}	$2.20 \cdot 10^{-7}$ ($4.63 \cdot 10^{-8}$)^{a}	$3.82 \cdot 10^{-7}$ ($1.69 \cdot 10^{-7}$)^{a}	$8.88 \cdot 10^{-7}$ ($1.22 \cdot 10^{-6}$)^{a}	$4.41 \cdot 10^{-7}$ ($3.25 \cdot 10^{-7}$)^{a}
Large plankton	μ	2.46 (0.18)^{a}	2.58 (0.17)^{a}	2.29 (0.09)^{a}	1.59 (0.31)^{a}	1.27 (0.01)^{a}
	H	0.79 (0.09)^{a}	1.02 (0.12)^{a}	0.75 (0.04)^{a}	0.62 (0.48)^{a}	0.79 (0.52)^{a}
	S	4.6 (0.89)^{a}	6.8 (0.45)^{a}	5.00 (1.22)^{a}	3.40 (1.14)^{a}	4.80 (1.30)^{a}
	TB	125.46 (35.40)^{a}	192.16 (84.14)^{a}	175.20 (40.54)^{a}	3.95 (6.05)^{b}	0.38 (0.54)^{b}
	BS	0.60 (0.12)^{a}	0.47 (0.17)^{a}	0.88 (0.09)^{a}	0.32 (0.31)^{b}	0.01 (0.01)^{c}
Small plankton	μ	1.46 (2.02)^{a}	1.18 (1.32)^{a}	1.03 (2.14)^{a}	0.28 (2.38)^{a}	1.30 (1.46)^{a}
	H	0.93 (0.03)^{a}	1.10 (0.03)^{a}	1.15 (0.06)^{a}	1.20 (0.08)^{a}	1.27 (0.03)^{a}
	S	7.60 (0.55)^{a}	8.40 (0.54)^{a}	8.00 (1.87)^{a}	8.40 (0.89)^{a}	8.80 (0.84)^{a}
	TB	21.81 (6.24)^{a}	11.84 (3.39)^{a}	15.14 (6.91)^{a}	20.32 (3.46)^{a}	18.67 (3.44)^{a}
	BS	$3.00 \cdot 10^{-6}$ ($6.65 \cdot 10^{-6}$)^{a}	$3.13 \cdot 10^{-6}$ ($1.77 \cdot 10^{-7}$)^{a}	$1.72 \cdot 10^{-6}$ ($3.47 \cdot 10^{-6}$)^{a}	$1.42 \cdot 10^{-6}$ ($1.19 \cdot 10^{-6}$)^{a}	$4.41 \cdot 10^{-6}$ ($6.18 \cdot 10^{-6}$)^{a}

Test 5: '*Odessia* indirect effects'

The between-group analyses performed only with the small plankton data set showed significant differences between the control and the *Odessia* treatment samples (Monte-Carlo permutation test; $p = 0.03$). In the control samples there was a higher biomass of bacterioplankton, pico- and nanoplankton, while in the *Odessia* treatment samples there was a higher biomass of ciliates and haptophytes (Fig. 3A). However, significant differences were not detected for any community parameter (Table 2). Therefore, our results showed significant but weak indirect effect of *Odessia maeotica* presence in lower trophic levels, since it was only detected at the community structure level.

Relationship between *Odessia maeotica* and plankton structure in natural conditions

A negative correlation was found in natural samples (data from 1989 to 1991; Quintana et al. 1998a) between *O. maeotica* biomass and total zooplankton biomass ($r = -0.61$, $p = 0.03$) and between *O. maeotica* biomass and chl *a* ($r = -0.80$, $p < 0.05$) (Fig. 4A,C). Because our experimental results indicate that the biomass of ciliates was higher when *O. maeotica* was present, we also tested the correlation between *O. maeotica* biomass and ciliate biomass. According to our results, in natural conditions, this relationship also exists, and a positive correlation ($r = 0.61$, $p = 0.05$) between ciliate biomass and *O. maeotica* biomass was obtained (Fig. 4B). However, some caution has to be taken when interpreting this significant result since it is influenced by the presence of one extreme point. No correlation was found between *O. maeotica* biomass and soluble reactive phosphorous ($r = -0.19$, $p = 0.56$) or between *O. maeotica* biomass and dissolved inorganic nitrogen ($r = 0.06$, $p = 0.86$) (Fig. 4D,E).

DISCUSSION

The direct effects of *Odessia maeotica* are mainly focused on large zooplankton through predation. The results of our experiments showed a decrease in zooplankton biomass and average body size in the presence of *O. maeotica*. These changes are related to a decrease in calanoid biomass. Calanoids were the dominant organisms in the experiment in the absence of the medusae, but were almost absent after 72 h of the *Odessia* treatment. The field data support this finding, since increases in *O. maeotica* were significantly related to decreases in zooplankton biomass. Moreover, stomach content analysis also supported the existence of a direct effect mediated by predation. Our results coincide with existing studies that also describe the predatory behaviour on zooplankton by other jellyfish species (e.g. Hansson et al. 2005, Pitt et al. 2008,

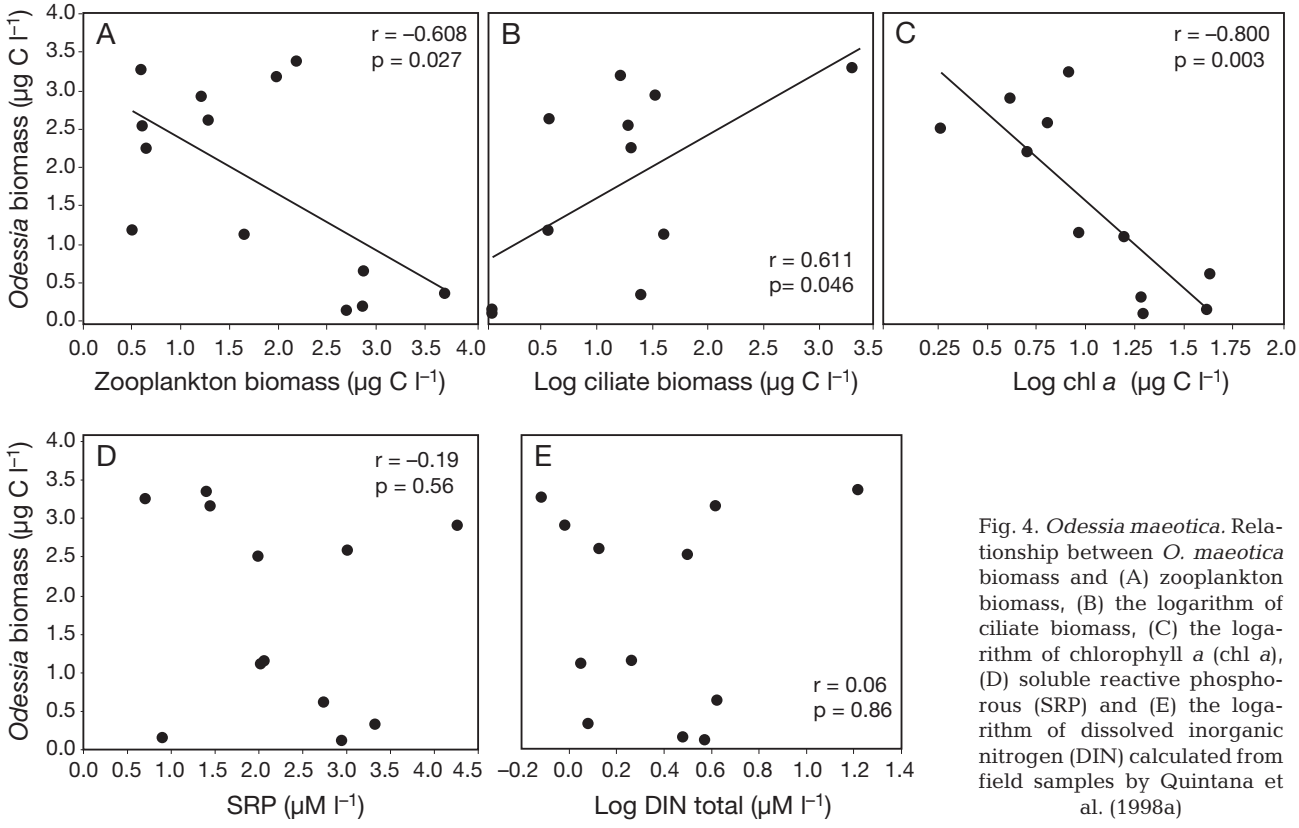

Fig. 4. *Odessia maeotica*. Relationship between *O. maeotica* biomass and (A) zooplankton biomass, (B) the logarithm of ciliate biomass, (C) the logarithm of chlorophyll *a* (chl *a*), (D) soluble reactive phosphorous (SRP) and (E) the logarithm of dissolved inorganic nitrogen (DIN) calculated from field samples by Quintana et al. (1998a)

Smith & Alexander 2008), confirming the top-predator role of *O. maeotica* in brackish ecosystems.

Although large jellyfish can control the plankton population through predation (Behrends & Schneider 1995), smaller jellyfish species may fail to control the plankton population if copepod growth rates are higher than jellyfish grazing rates on them (Daan 1986, Purcell 1992). Thus, Purcell et al. (1994) concluded that the control of the copepod population was the result of a combination of different factors such as predation, bottom-up effects and physical effects. Similarly, an experimental study performed with a freshwater jellyfish species (*Craspedacusta sowerbii*), also described a possible bottom-up effect due to nutrient supplies (Jankowski et al. 2005). Although, our experiments showed copepod reduction values (98% depletion after 72 h of incubation) similar to those observed by Jankowski et al. (2005) (approx. 70 to 80% depletion after 48 h of incubation), in our case the experiment was performed without the addition of nutrients. Moreover, in these brackish systems, *Odessia maeotica* populations appear in very specific conditions of high values of salinity (30.74 ± 11.29 mS cm^{-1}), low dissolved inorganic nitrogen (2.25 ± 1.05 µM) and a low nitrogen:phosphorus ratio (2.15 ± 3.16); and when these physical and chemical conditions change *O. maeotica* populations disappear (Quintana et al. 1998a,b). Thus, the absence of nutrient inputs and the low nutrient concentration, especially of dissolved inorganic nitrogen, would make it difficult to have a bottom-up effect.

Weak indirect effects on small plankton and the microbial community were detected at the structure and composition levels. Nevertheless, our result did not show a significant increase of small autotrophic plankton biomass. Previous studies reported that the increase in total biomass of lower trophic levels (i.e. phytoplankton biomass) was due to evidence of an indirect effect of jellyfish (e.g. Jankowski & Ratte 2001). It could happen that the duration of our experiment was too short to show significant differences in total phytoplankton biomass. However, similar experiments, also performed with small jellyfish species, found differences in phytoplankton biomass after only 48 h (Jankowski et al. 2005), so 72 h should be sufficient time to obtain significant results. Therefore, the lack of an increase in the total phytoplankton biomass in our study may be related to (1) a trophic cascade effect and/or (2) the oligotrophic conditions in which *Odessia maeotica* occurs, which would not allow significant phytoplankton increases (López-Flores et al. 2006), even if phytoplankton grazers are suppressed. In our opinion, the most plausible explanation would be a combination of these 2 processes.

Regarding the trophic cascade effect, several studies have described changes in microplankton as being cascading trophic effects in the presence of jellyfish and their top-down effect through several trophic levels (e.g. Pitt et al. 2007). For example, Lindahl & Hernroth (1983), Jankowski & Ratte (2001) and Jankowski (2004) show that phytoplankton blooms can appear when grazing pressure by herbivorous zooplankton is reduced as a result of heavy predatory pressure by jellyfish. In our case, when *Odessia maeotica* was present, we found an increase of the ciliate *Strombidium* sp. and mixotrophic organisms (haptophytes and cryptophytes) and a decrease of autotrophic organisms (autotrophic picoflagellates, diatoms, chlorophytes and euglenophytes) and bacterioplankton. The increase of ciliates in the presence of jellyfish could be explained by an indirect effect, since jellyfish would prey on calanoids, which, in turn, prey on heterotrophic plankton (Brucet et al. 2008). Consequently, if calanoids are removed, small heterotrophic organisms, such as ciliates, may increase in density. Moreover, ciliates can feed on bacterioplankton (e.g. Kisand & Zingel 2000) and autotrophic organisms of pico- and nanoplankton (e.g. Christaki et al. 1999). Therefore, an increase of ciliates due to cascading trophic effects could also indicate high grazing pressure on the phytoplankton and bacterioplankton community, and, therefore, no increases in the biomass of these planktonic organisms would be detected.

On the other hand, nutrient concentration via bottom-up effects could alter the effects of trophic cascades (e.g. Danielsdottir et al. 2007). For example, in marine systems with low nutrient inputs, Sommer et al. (2002) and Stibor et al. (2004) described a trophic cascade effect similar to the one reported in our study (predator–copepods–ciliates–small algae), but this sequence changed when there was higher nutrient availability, with the final part ending with an increase in large algae. Stibor et al. (2004) related these differences to (1) low nutrient concentrations, which frequently exclude larger algae; and (2) the size-mediated predatory effect of ciliates, which is higher on small algae than it is on larger algae. As a consequence, they conclude that a positive effect of top predators over algal biomass is observed only in mesocosms with enhanced nutrient loading, whereas there are decreases in mesocosms receiving zero nutrient loadings. In fact, our experimental and field results agree with those by Stibor et al. (2004), in which a negative effect on phytoplankton was observed.

Summarizing, *Odessia maeotica* acts as top predator exerting top-down control on zooplankton and over the rest of the plankton community through a trophic cascade effect. When *O. maeotica* is present, the entire plankton community changes: through direct effects large zooplankton decrease and through indirect effects ciliates increase and autotrophic organisms decrease. Moreover, in contrast with previous studies in which the changes observed in planktonic communities with the presence of jellyfish species are explained by a combination of top-down and bottom-up controls (e.g. Jankowski et al. 2005), in our case, the observed direct and indirect effects may be due mainly to a top-down effect, since *O. maeotica* appears only under oligotrophic conditions, without any external nutrient input. Bottom-up effects could also appear due to excretion, mucus production and decomposition of jellyfish in oligotrophic environments (Pitt et al. 2009). Nevertheless our results suggest a strong top-down effect of the jellyfish without any interaction with nutrient supplies. In fact, Mediterranean brackish marshes are characterised by pulses of nutrient inputs coinciding with sudden flooding due to sea storms or intense rainfall. After these pulses, the water remains confined, with no other water inputs, leading to a decrease in water level and an increase in salinity due to evaporation (Quintana et al. 1998b, Quintana 2002). In such environments, physical factors such as flooding intensity determine pulse events and, in turn, nutrient loadings during pulses. Our results suggest that these 2 environmental situations (pulse and confinement) correspond to a change in the successional process associated with a change in the food web control mechanism. Thus, the pulse situation implies an allogenic succession when the food web is bottom-up controlled, whereas the confinement situation implies an autogenic succession when the food web is top-down controlled (situations of *O. maeotica* dominance). Abrupt shifts in the food web control mechanisms according to different environmental situations have been reported previously in brackish ecosystems (e.g. Petersen et al. 2008). Moreover, the existence of allogenic succession after a resource pulse and the posterior substitution by an autogenic process has been considered a general pattern in other aquatic ecosystems, such as freshwater temporary ponds (e.g. Lake et al. 1989, Boix et al. 2004).

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Appendix 1. Mean (SE) values of size, initial densities and biomass of all organism types found in different treatments. APF: autotrophic picoflagellates; ANF1: autotrophic nanoflagellates 1; ANF2: autotrophic nanoflagellates 2; HPF: heterotrophic picoflagellates. SP: small plankton; LP: large plankton

	Data set	Size (µm)	Initial conditions		Lagoon		Control		*Odessia* treatment		Filtered treatment	
			Density (ind. ml^{-1})	Biomass (µg ml^{-1})	Density (ind. ml^{-1})	Biomass (µg ml^{-1})	Density (ind. ml^{-1})	Biomass (µg ml^{-1})	Density (ind. ml^{-1})	Biomass (µg ml^{-1})	Density (ind. ml^{-1})	Biomass (µg ml^{-1})
Bacterioplankton	SP	0.38 (0.10)	$8.78 \cdot 10^{6}$ ($5.80 \cdot 10^{6}$)	0.07 (0.04)	$1.24 \cdot 10^{7}$ ($6.09 \cdot 10^{6}$)	0.08 (0.04)	$1.43 \cdot 10^{7}$ ($1.17 \cdot 10^{7}$)	0.10 (0.08)	$1.28 \cdot 10^{7}$ ($8.68 \cdot 10^{6}$)	0.09 (0.06)	$1.29 \cdot 10^{7}$ ($6.92 \cdot 10^{6}$)	0.08 (0.05)
APF	SP	1.95 (0.12)	$3.09 \cdot 10^{6}$ ($8.92 \cdot 10^{5}$)	6.62 (1.98)	$3.67 \cdot 10^{6}$ ($5.98 \cdot 10^{5}$)	6.83 (2.14)	$3.72 \cdot 10^{6}$ ($7.66 \cdot 10^{5}$)	7.05 (2.43)	$6.03 \cdot 10^{6}$ ($1.88 \cdot 10^{6}$)	10.05 (2.54)	$4.77 \cdot 10^{6}$ ($1.25 \cdot 10^{6}$)	7.96 (1.57)
HPF	SP	2.01 (0.32)	$7.14 \cdot 10^{3}$ ($2.45 \cdot 10^{3}$)	0.01 ($2.75 \cdot 10^{-3}$)	$9.92 \cdot 10^{4}$ ($5.80 \cdot 10^{3}$)	0.01 (0.01)	$1.03 \cdot 10^{4}$ ($6.39 \cdot 10^{3}$)	0.01 (0.01)	$1.34 \cdot 10^{4}$ ($7.72 \cdot 10^{3}$)	0.01 (0.01)	$9.60 \cdot 10^{3}$ ($4.11 \cdot 10^{3}$)	0.01 ($4.57 \cdot 10^{-3}$)
ANF1	SP	3.76 (0.22)	$1.37 \cdot 10^{5}$ ($3.62 \cdot 10^{4}$)	1.72 (0.48)	$1.19 \cdot 10^{5}$ ($2.94 \cdot 10^{4}$)	1.81 (0.78)	$2.30 \cdot 10^{5}$ ($8.30 \cdot 10^{4}$)	2.93 (1.16)	$2.95 \cdot 10^{5}$ ($9.64 \cdot 10^{4}$)	3.75 (1.04)	$3.58 \cdot 10^{5}$ ($1.47 \cdot 10^{5}$)	4.42 (1.34)
ANF2	SP	4.15 (0.31)	$5.94 \cdot 10^{5}$ ($2.16 \cdot 10^{5}$)	13.12 (3.91)	$1.64 \cdot 10^{5}$ ($6.22 \cdot 10^{4}$)	2.72 (0.89)	$2.76 \cdot 10^{5}$ ($1.82 \cdot 10^{5}$)	4.71 (3.66)	$3.35 \cdot 10^{5}$ ($1.25 \cdot 10^{5}$)	5.47 (1.18)	$5.94 \cdot 10^{5}$ ($2.16 \cdot 10^{5}$)	5.23 (1.53)
Chlorophytes	SP	8.70 (1.78)	4.02 (8.98)	$1.30 \cdot 10^{-4}$ ($2.91 \cdot 10^{-4}$)	20.76 (34.77)	$4.12 \cdot 10^{-3}$ ($7.65 \cdot 10^{-3}$)	4.02 (8.98)	$2.10 \cdot 10^{-4}$ ($4.70 \cdot 10^{-4}$)	8.03 (17.96)	$1.40 \cdot 10^{-4}$ ($3.13 \cdot 10^{-4}$)	12.05 (17.96)	$2.18 \cdot 10^{-4}$ ($3.45 \cdot 10^{-4}$)
Haptophytes	SP	8.78 (2.59)	642.42 (107.17)	0.02 (0.01)	$4.42 \cdot 10^{3}$ ($1.95 \cdot 10^{3}$)	0.16 (0.09)	$5.79 \cdot 10^{3}$ ($1.98 \cdot 10^{3}$)	0.18 (0.05)	$1.11 \cdot 10^{4}$ ($7.67 \cdot 10^{3}$)	0.35 (0.22)	$1.18 \cdot 10^{4}$ ($1.67 \cdot 10^{3}$)	0.37 (0.06)
Cryptomonas	SP	23.85 (2.34)	0.00 (8.98)	0.00 ($4.82 \cdot 10^{-3}$)	0.00 (8.98)	0.00 ($3.30 \cdot 10^{-3}$)	4.02 (11.00)	$2.16 \cdot 10^{-3}$ ($3.20 \cdot 10^{-3}$)	4.02	$1.48 \cdot 10^{-3}$	8.03	$2.29 \cdot 10^{-3}$
Ciliates (*Strombidium* sp.)	SP	29.56 (13.65)	4.02 (8.98)	0.01 (0.02)	168.64 (126.64)	0.22 (0.16)	32.12 (30.44)	0.11 (0.16)	473.00 (301.00)	0.58 (0.28)	521.96 (261.37)	0.57 (0.35)
Euglenophytes	SP	55.32 (19.12)	48.18 (107.74)	0.21 (0.48)	0.00	0.00	4.02	0.03 (8.98)	0.00 (0.06)	0.00	4.02	0.00 (8.98)
Diatoms (*Amphora* sp., *Navicula* sp., *Nitzschia* sp.)	SP	76.18 (45.35)	248.94 (130.57)	0.02 (0.01)	176.67 (82.04)	0.02 (0.01)	28.11 (33.59)	$2.36 \cdot 10^{-3}$ ($2.48 \cdot 10^{-3}$)	76.29 (16.80)	0.01 (0.01)	256 (122.44)	0.02 (0.01)
Nauplius harpacticoid	LP	88.33 (16.22)	0.00	0.00	0.00	$7.9 \cdot 10^{-5}$ ($1.77 \cdot 10^{-4}$)	0.08 (0.11)	$2.8 \cdot 10^{-5}$ ($6.2 \cdot 10^{-5}$)	0.13 (0.22)	$2.32 \cdot 10^{-4}$ ($4.03 \cdot 10^{-4}$)	17.20 (21.51)	$3.89 \cdot 10^{-3}$ ($4.20 \cdot 10^{-3}$)
Nauplius cyclopoid	LP	114.28 (29.92)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18 (0.28)	$4.17 \cdot 10^{-3}$ ($6.44 \cdot 10^{-3}$)
Hexarthra sp.	LP	186.90 (44.41)	0.00	0.00	0.00	0.00	0.00	0.00	0.03 (0.06)	$2.72 \cdot 10^{-3}$ ($6.09 \cdot 10^{-3}$)	0.00	0.00
Brachionus sp.	LP	189.40 (45.34)	0.05 (0.11)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nauplius calanoid	LP	0.02 (83.43)	37.65 (12.93)	6.96 (3.29)	39.95 (10.06)	4.19 (1.21)	23.50 (1.24)	3.63 (0.45)	0.35 (0.65)	0.01 (0.02)	0.78 (0.27)	229.87 (0.01)
Polychaeta larvae	LP	270.78 (142.80)	0.45 (0.21)	0.11 (0.16)	1.90 (0.68)	0.54 (0.15)	0.45 (0.27)	0.06 (0.05)	0.10 (0.16)	0.06 (0.09)	0.00	0.00
Ciliates	LP	295.00 (85.21)	0.20 (0.21)	0.10 (0.13)	0.45 (0.21)	0.18 (0.10)	0.15 (0.22)	0.06 (0.10)	0.48 (0.42)	0.20 (0.16)	0.08 (0.11)	0.02 (0.02)
Copepodite harpacticoid	LP	323.00 (112.24)	0.00	0.00	0.15 (0.14)	0.01 (0.01)	0.00	0.05 (0.10)	0.00	0.00	0.03 (0.06)	0.01 (0.02)
Adult harpacticoid (*Mesochra* sp.)	LP	446.50 (99.76)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03 (0.06)	0.37 (0.35)
Copepodite cyclopoid	LP	537.80 (116.81)	0.00	0.00	0.00	0.00	0.00	0.00	0.03 (0.06)	0.04 (0.09)	0.03 (0.06)	0.04 (0.09)
Copepodite calanoid	LP	717.48 (215.18)	41.60 (9.89)	80.34 (31.78)	62.90 (28.54)	99.40 (46.99)	68.90 (15.81)	109.42 (33.51)	0.13 (0.22)	0.39 (0.81)	0.05 (0.07)	0.03 (0.04)
Adult calanoid (*Eurytemora velox*)	LP	1448.01 (99.67)	5.65 (3.38)	37.96 (14.87)	10.90 (5.23)	73.76 (34.97)	7.13 (4.31)	61.97 (12.73)	0.00	0.00	0.00	0.00