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RESEARCH ARTICLE

Factors affecting monthly variation in population density of the capitellid polychaete *Heteromastus filiformis* in a hyperhaline Mediterranean coastal lagoon

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Abstract

1 - The aim of the study was to elucidate the population ecology of opportunistic species in the Mediterranean coastal lagoon environment by investigating the monthly variation in population density of the capitellid polychaete *Heteromastus filiformis* and the potential environmental factors affecting it in an eu- to hyperhaline (Homa lagoon, Eastern Aegean Sea).

2 - Monthly samplings were conducted from January 2006 to January 2007.

3 - A Principal Component Analysis (PCA) was conducted using the values of several abiotic variables of the water and sediments. A randomization procedure based on eigenvalues showed the presence of only one significant axis; according to the bootstrapped eigenvector method, salinity and dissolved oxygen were found to load significan**tly on the first axis, having negative and positive weights, respectively.

4 - Salinity, which exceeded 40 psu all year round except for February-March, peaked in July-September (59-61.5 psu), while dissolved oxygen concentrations were lowest from July to October (2.3-3.9 mg l^{-1}).

5 - Population density of H. filiformis was low (21-58 individuals m^{-2}) through most of the year; however, a recruitment was detected in spring (290 ind.m^{-2}) followed by a significant decrease in density in summer.

6 - Density was significantly correlated with the first PCA component (positive correlation) and with salinity (negative correlation), particularly indicating that (a) relatively lower salinities (<50 psu) in early spring may favor reproductive activity and subsequent recruitment, while higher salinities (>50 psu) during summer may have negative effects on population density, and (b) salinity effects during summer may have been increased by other simultaneously effective environmental conditions (low oxygen concentrations).

7 - Our results indicate that opportunistic species experience extreme environmental conditions, particularly high salinities, during summer in eu- to hyperhaline Mediterranean coastal lagoons, which restrain them to develop highly abundant populations.

Keywords: marine invertebrate, opportunistic species, population density, population structure, salinity, sediments, lagoon, Aegean Sea.

Introduction

Coastal lagoons are shallow coastal water bodies, separated from the sea by a barrier, connected at least intermittently to the sea by one or more restricted inlets and usually oriented parallelly to the coast (Kjerfve, 1994). Depending on their geomorphological and hydrological status, coastal lagoons may be characterized by sharp daily and seasonal variations in physico-chemical parameters (e.g. in salinity, which may range from completely fresh to hypersaline) (Kjerfve, 1994). These sharp variations in physico-chemical parameters cause changes in the distribution patterns of organisms and in the structure of their communities (Koutsoubas *et al.*, 2000). Although lagoonal biota may suffer natural disturbance, coastal lagoons are often highly productive and ideal systems for aquaculture projects (Kjerfve, 1994). However, these shallow environments are frequently impacted by anthropogenic inputs and human activities (Kjerfve, 1994). Several coastal lagoons experience severe degradation caused by the organic enrichment owed to increased anthropogenic wastes poured in their basins (Lardicci *et al.*, 2001a).

In Mediterranean coastal lagoons the macrozoobenthos is represented mainly by three species groups, namely: (a) a group of typically euryhaline brackish-water species which are characteristic of lagoon zones, (b) a group of marine species which prefer low hydrodynamic environments and, (c) a group of opportunistic species, i.e. of short-lived, shallow-dwelling, surface deposit-feeding species, primarily annelids, which tolerate organic enrichment and are abundant in this kind of environments (Lardicci *et al.*, 1997). The structure and dynamics of the macrozoobenthic community and the associated environmental factors have been investigated in several Mediterranean coastal lagoons, some of them suffering from long summer dystrophic crises or extreme salinities (e.g. Lardicci *et al.*, 1997; Koutsoubas *et al.*, 2000; Mistri, 2002; Kevrekidis, 2004). In addition, ecological aspects of some typically lagoonal macroinvertebrates have been also studied in some Mediterranean coastal lagoons (e.g. Kevrekidis, 2005a; Kevrekidis & Wilke, 2005; Casagranda *et al.*, 2006; Kevrekidis *et al.*, 2009a, 2009b). On the other hand, little attention has been paid on the population dynamics of opportunistic species in the Mediterranean coastal lagoons (e.g. Kevrekidis, 2005b), despite they frequently dominate the macrobenthic fauna. A better understanding of this subject can provide an insight in the structure and functioning of the coastal lagoon ecosystems and could contribute to the enhancement of predictive models for sustainable management of coastal lagoons.

The burrowing polychaete *Heteromastus filiformis* (Claparède, 1864) (Capitellidae), which is regarded as a highly opportunistic species (Pearson & Rosenberg, 1978), has been frequently found in Mediterranean coastal lagoons (e.g. Arvanitidis *et al.*, 1999; Koutsoubas *et al.*, 2000; Lardicci *et al.*, 2001b; Mistri, 2002; Reizopoulou & Nicolaidou, 2007). It displays an extended geographic distribution in the northern and southern hemispheres and a wide bathymetric range, appearing from intertidal to deep-sea environments (Hartmann-Schröder, 1996). *H. filiformis* is a selective motile deposit-feeder (Fauchald & Jumars, 1979) and it is tolerant to hypoxic and temporary anoxic sediments (Oeschger & Vismann, 1994). Due to its high densities, *H. filiformis* can play an important role in sediments reworking (Neira & Höpner, 1993; Gillet & Gorman, 2002; Quintana *et al.*, 2007). In brackish water habitats, this polychaete has been mainly found from meso- to euhaline conditions (e.g. Watling, 1975; Read, 1984; Gouvis *et al.*, 1998; Ysebaert *et al.*, 2005; Maggiore & Keppel, 2007; Lourido *et al.*, 2008). In spite of its wide geographic distribution and its significant role in various coastal ecosystems, little is known on several aspects of *H. filiformis* biology and ecology. In particular, as regards to its population ecology, information is mainly available from polyhaline and poly- to euhaline estuarine environments (Shaffer, 1983; Gillet & Gorman, 2002), while, to our knowledge, the population dynamics of this capitellid polychaete and the associated environmental variables in the poikilohaline Mediterranean coastal lagoons have not been investigated.

The present study aims: (1) to describe the monthly variation in population density of *H. filiformis* in a eu- to hyperhaline Mediterranean coastal lagoon (Homa lagoon, Eastern Aegean Sea) and (2) to identify the key environmental variables affecting its population. The monthly variation in population structure of *H. filiformis* is additionally described. Provided that (a) in the Mediterranean brackish habitats macrobenthic fauna usually experiences extreme environmental conditions (e.g. high temperature and salinity, low oxygen concentration) during summer (e.g. Koutsoubas *et al.*, 2000) and (b) *H. filiformis* is a marine species which tolerate hypoxic and temporary anoxic sediments (Oeschger & Vismann, 1994) and has been frequently found in brackish coastal habitats in salinities mainly in the meso- to euhaline range (e.g. Watling, 1975; Read, 1984; Gouvis *et al.*, 1998; Ysebaert *et al.*, 2005; Maggiore & Keppel, 2007; Lourido *et al.*, 2008), we predict that population density of this capitellid polychaete in the study area will be affected negatively to a significant extent by extreme summer conditions, particularly by high salinities.

Materials and Methods

Study area

Gediz Delta is an extensive coastal wetland in Izmir Bay, Eastern Aegean Sea, consisting of salt and freshwater marshes, large saltpans and four lagoons (WWF, 2000) and protected by the Ramsar Convention and the Bern Convention (Tapan, 2003). Homa lagoon, occupying an area of about 1500 ha and having a depth varying between 0.5 and 1 m, communicates with the sea mainly through two openings (Fig. 1). A total of 18 polychaete species have been recorded in this lagoon, among which *H. filiformis*, by Ergen *et al.* (2002). Fishing of economically important species (*Mugil cephalus, Liza ramada, L. saliens, L. aurata, Sparus aurata, Anguilla anguilla, Dicentrarchus labrax, Solea solea*) is the main exploitation pattern occurring in the lagoon (İlkyaz *et al.*, 2006).

Sampling and laboratory techniques

Monthly samples were collected during January 2006 to January 2007 (except for December 2006) at station B3 (26º29’52’’N-38º19’17’’E) (Fig. 1). Each time, 12 random sampling units were taken with a modified van Veen grab (Larimore, 1970); the grab covered a surface of 400 cm2 (20 x 20 cm) and penetrated to a depth of 20 cm. The samples were sieved immediately through a 0.5 mm screen. Sediment samples were taken with a small corer for both particle size analysis and organic matter concentration. Depth and temperature, salinity, dissolved O^2 and pH of the water near the bottom, as well as temperature of the sediments at a depth of 1 cm were also measured. Sediment analysis and organic matter concentration measurement were made according to the methods described by Hakanson & Jansson (1983) and Hach (1988) respectively.

In the laboratory, the specimens of *Heteromastus filiformis* were separated from the remaining macrobenthos and were counted and measured; the length of the thorax (L12) was measured with the aid of an eye-piece micrometer under a stereomicroscope to the nearest 0.01 mm (see Gillet & Gorman, 2002).

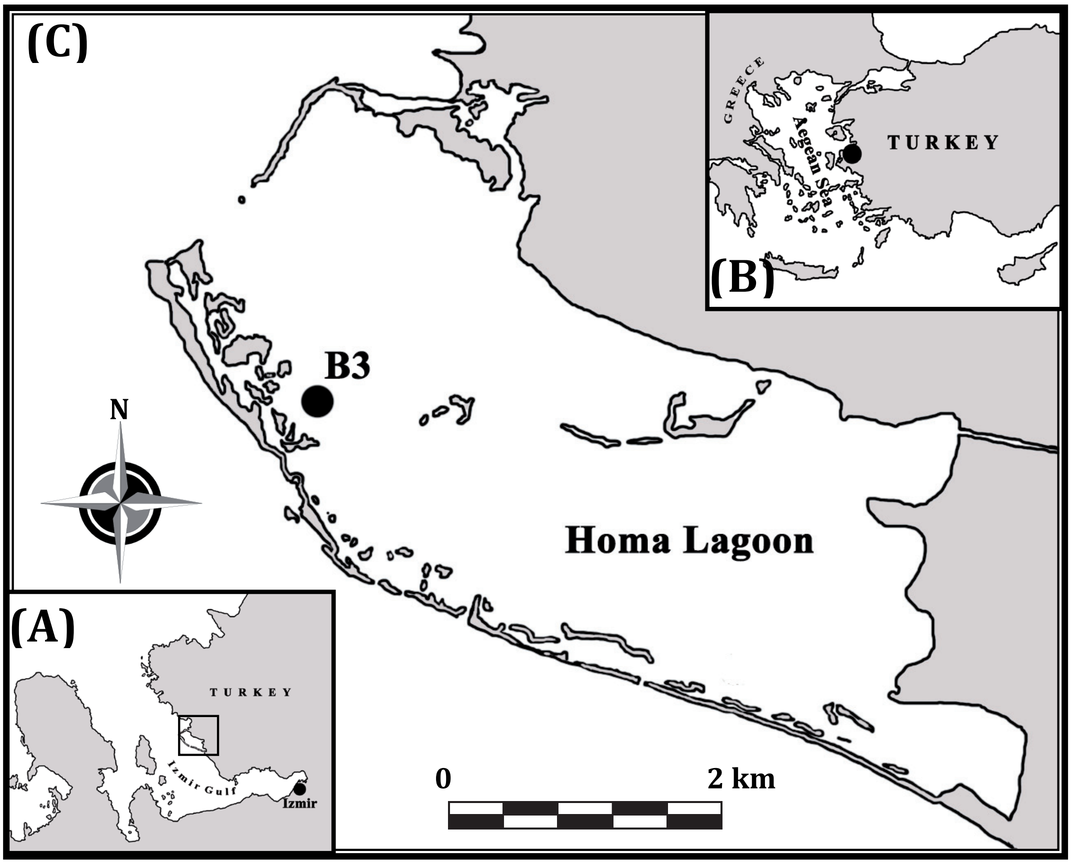

Figure 1. (A)-(B) Geographical location of the study site. (C) Map of Homa lagoon, indicating the sampling station.

Data analysis

A Principal Component Analysis (PCA) was conducted using the values of these abiotic variables for which there was a complete array of data. In the cases of intercorrelated variables, only one of the highly correlated variables was used. Variables were normalized and the PCA was performed using the PRIMER package developed at Plymouth Marine Laboratory, Plymouth, U.K. and functions of the program «R» (R Development Core Team, 2006). The number of principal components for which eigenvalues accounted for a significant amount of total variance was identified by use of an objective randomization procedure based on the eigenvalues (Peres-Neto *et al.*, 2005). The randomization protocol was conducted as follows: the values within variables in the data matrix were randomized and a PCA was conducted on the reshuffled data matrix. Then, this procedure was repeated a total of 999 times. The p-value for the each axis and the observed eigenvalue was estimated as: (number of random eigenvalues for axis k equal to or larger than the observed + 1) / 1000. The contribution of individual variables to significant principal components was assessed using the bootstrapped eigenvector method (Peres-Neto *et al.*, 2003). This method re-samples entire rows from the original data with replacement and computes ordinations for each bootstrapped sample. One thousand bootstrap samples were drawn and a PCA was performed on each of them. Variables with 95% confidence intervals around their loadings that did not incorporate zero were considered to contribute significantly to the relevant component. For the computations we used R code snippets provided by Pedro Peres-Neto.

Spearman's rank correlation coefficient (ρ) was applied to explore significant correlations. The significance of the monthly variation in population density over the year was tested by Kruskal-Wallis's one-way analysis of variance. The significance of the differences in population density between two successive months was tested with Mann-Whitney U-test. Non parametric statistical tests were performed since the sample size was usually small, leading to statistics based on ranks rather than raw values (Zar, 1984). On the basis of the thoracic length (L12), individuals were grouped into size classes; a size class interval of 1 mm was adopted, following Gillet & Gorman (2002).

Results

Abiotic variables

The monthly variation in abiotic variables of the water and sediments throughout the sampling period at the study site is shown in Table 1. Depth fluctuated between 50 cm and 70 cm almost throughout the sampling period. Water temperature near the bottom showed the lowest value in January 2006 (3.4 °C) and the highest one in June (26.6 °C); sediment temperature showed a monthly variation highly correlated with water temperature ($\rho = 0.968$, n=12, $p < 0.001$). Salinity values exceeded almost throughout the annual cycle 40 psu (except for late winter-early spring); they gradually increased from March (33.1 psu) onwards, attained a value higher than 50 psu in June, peaked in July-August (61.5-61.6 psu) and, then, gradually decreased up to January 2007 (42 psu) (Table 1). Salinity was highly correlated with both water and sediment temperature ($\rho = 0.795$ and 0.816 respectively, n = 12, $p < 0.01$). Dissolved O^2 varied between 5.3 and 9.6 mg l^{-1} during the most of the sampling period but between 2.3 and 3.9 mg l^{-1} during July to October (Table 1), indicating sediment anoxic conditions. Values of pH ranged from 8.0 to 8.8 (Table 1).

The sediment was sandy mud. The percentage of silt-clay varied between 55 and 80 % during the most of the sampling period, while on the other hand the percentage of sand ranged between 15 and 45% (Table 1). The percentage of silt-clay was highly correlated (negative correlation) with that of sand ($\rho = -0.970$, n = 12, $p < 0.001$).The values of sediment organic matter varied from 1.75

Table 1 - Monthly values of the water and sediment variables at station B3 in Homa lagoon during January 2006 to January 2007.

		J'06	F	M	A	M	J	J	A	S	O	N	J'07
Water	**Depth (cm)**	55	65	50	40	50	50	75	80	70		70	55
	Temperature (ºC)	3.4	10.5	11.5	17.5	24.2	26.6	25.2	25.5	23.6	17.5	14.1	12.8
	Salinity (psu)	41.6	37.1	33.1	42.3	42.1	50.7	61.6	61.5	58.9	51.9	46.2	42
	Dissolved Oxygen (mg l^{-1})	5.3	6.7	6.8	5.8	5.9	6.3	2.3	3.7	3.9	3.6	9.6	5.7
	pH	8.8	8.8	8.3	8.5	8.5	8.5	8.2	8.0	8.4	8.4	8.4	8.3
Sediment	**Temperature (ºC)**	3.4	10.5	11.5	16	22.5	26	24	26	23	17.3	13	10
	Sand (%)	20	25	30	45	20	45	20	15	30	16	42	27
	Silt-clay (%)	80	75	70	55	78.9	54.9	80	85	70.0	84	48	73
	Organic matter (%)	2.42	2.73	2.18	1.75	2.6	3.09	3.42	4.86	1.94	2.54	2.8	4.1

to 2.8 % during the most of the sampling period and scored (3.09-4.86 %) in summer and January 2007 (Table 1), indicating that Homa lagoon was affected to some extent by organic enrichment.

A PCA was conducted using figures for salinity, dissolved O2, pH, silt-clay percentage and sediment organic matter. The randomization procedure based on eigenvalues showed the presence of only one significant axis ($p < 0.05$) that accounts for 54.9% of the variability in the original data. According to the bootstrapped eigenvector method, only salinity and dissolved oxygen were found to load significantly on the first axis ($p < 0.05$) having negative and positive weights respectively, while a nearly significant p-value was obtained for pH (Table 2).

Table 2 - Variable loadings on the first principal component and the associated probabilities (p) for the bootstrapped eigenvector

Variable	**Loading (PC1, 54.9%)**	***p***
Salinity	-0.489	0.025
Dissolved oxygen	0.492	0.020
pH	0.443	0.051
Silt-clay percentage	-0.387	0.057
Organic matter	-0.415	0.086

July, August, September and October samples showing negative scores on the first principal component were separated from the rest monthly samples, which almost all showed positive scores (Table 3).

Population structure

The smallest individual of *H. filiformis* collected throughout the annual cycle had a thoracic length (L12) of 2.5 mm, while the largest one a thoracic length of 11.5 mm. The population structure of *H. filiformis* during the months in which an adequate number of individuals was collected (during January to June 2006) is represented in Fig. 2 by histograms based on size frequency distributions. Recruitment was evident mainly in March, but in June as well, while a mass disappearance of large size individuals was observed mainly in May and June (Fig. 2). A spring cohort first appeared in early spring, while its major part disappeared in early summer, showing a life span of about 3-4 months (Fig. 2).

Table 3 - Row loadings on the first principal component.

Month	**Loading (PC1, 54.9%)**
Aug	-3.448
Jul	-2.473
Oct	-0.972
Sep	-0.602
Jan07	-0.500
May	0.472
Jun	0.632
Jan06	0.873
Mar	1.202
Feb	1.481
Apr	1.544
Nov	1.791

Population density

Population density of *H. filiformis* at the sampling site (annual mean ± SE: 87.0 ± 25.1 individuals m^{-2}) showed a significant monthly variation (Kruskal-Wallis one-way analysis of variance; $H = 55.57$, $df = 11$, $p < 0.001$); in particular, density values significantly

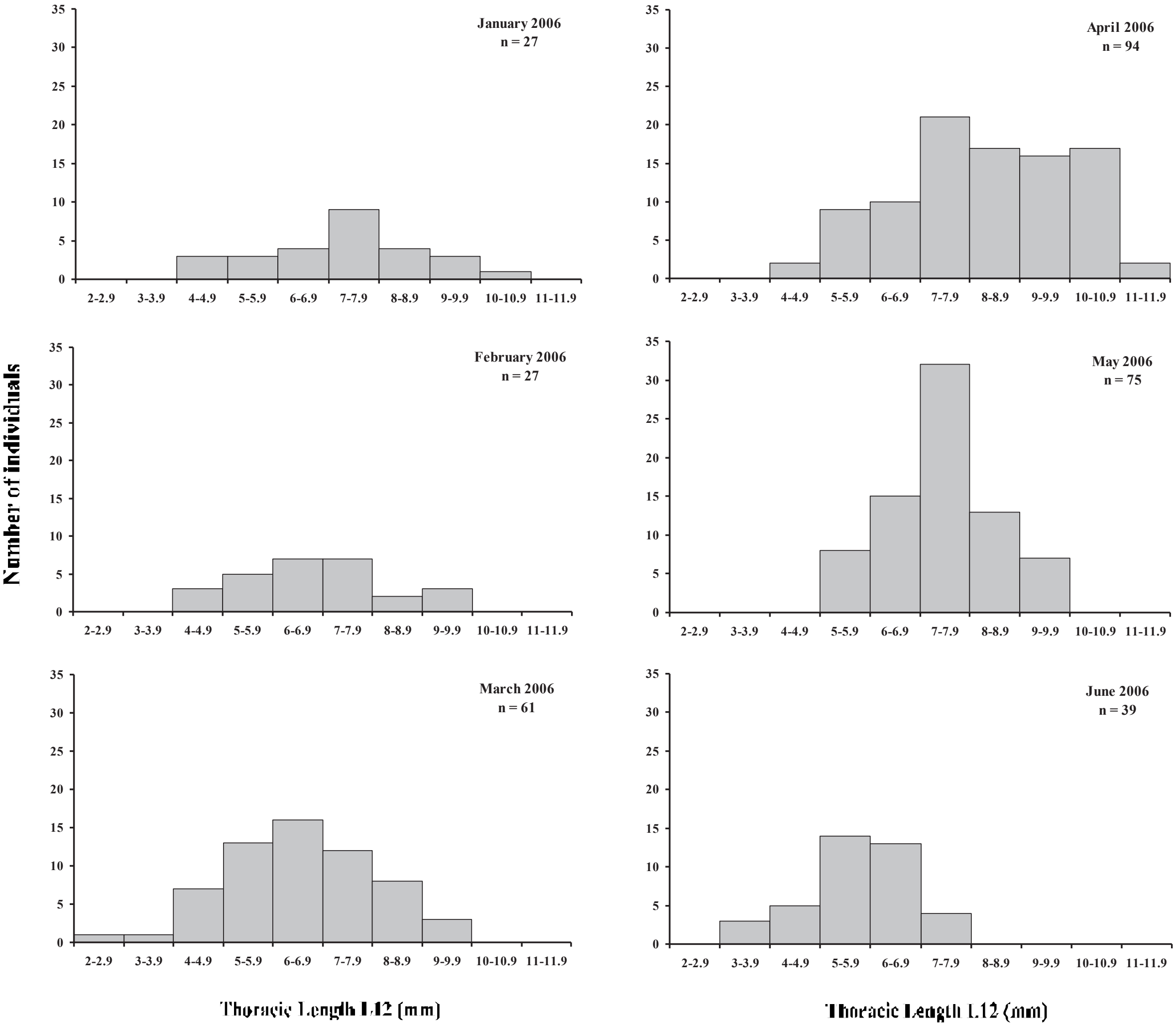

Figure 2. Population structure of *Heteromastus filiformis* during January to June 2006 at station B3 in Homa lagoon.

increased in March (mean: 147.9 ind. m-2) and in April (mean: 289.6 ind. m-2) and significantly decreased in July (mean: 37.5 ind. m-2) (Mann-Whitney U-test, $p < 0.05$, $p < 0.01$ and $p < 0.05$ respectively) while did not significantly varied between two successive sampling dates during the rest of the sampling period ($p > 0.05$) (Fig. 3). Population density was significantly correlated with salinity (negative correlation) (Table 4); the significant increase in population density during spring coincided with salinity values of 33-42 psu, while its decline during summer with a sharp increase in salinity values (from 42 to 62 psu) (Table 1, Fig. 3). Population density was also significantly correlated with the first component of the PCA (positive correlation) (Table 4); the comparatively low density values during the period from mid summer to mid autumn coincided with the highest salinity values (52-62 psu) and the lowest dissolved oxygen concentrations (2.3-3.9 mg l-*1*) (Tables 1-3, Fig. 3).

Discussion

Heteromastus filiformis observed all year round in the eu- to hyperhaline Homa lagoon is a common species in marine habitats, which according to Febvre (1968) also occurs in coastal lagoons. The occurrence of this

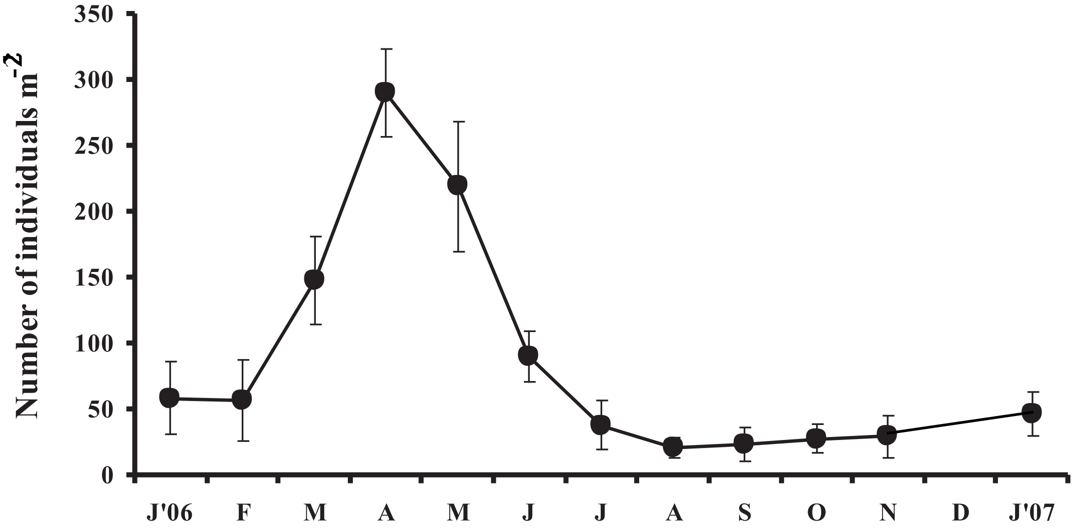

Figure 3. Monthly variation in population density (mean ± standard error) of *Heteromastus filiformis* at station B3 in Homa lagoon.

capitellid polychaete throughout the annual cycle in the study area could be mainly linked with the fact that Homa lagoon was affected to some extent by organic enrichment, since the distribution of *H. filiformis* has been associated with organic enrichment in several studies (e.g. Pearson & Rosenberg, 1978; Carvalho *et al.*, 2005).

Heteromastus filiformis has been also previously found having comparable densities to those in Homa lagoon in some other Mediterranean coastal lagoons which are generally characterized by organic enrichment and poly- to euhaline waters (Gouvis *et al.*, 1998; Lardicci *et al.*, 2001b; Mistri *et al.*, 2001; Mistri, 2002; Salas *et al.*, 2005; see Table 5). For instance, this capitellid polychaete was dominant in zones of Mar Menor lagoon, SE Spain with high levels of sediment organic matter (5.1-7.7 %) coming from the primary production and the biological cycle of the macrophyte meadows (Salas *et al.*, 2005).

In general, this cosmopolitan species has been found in a wide variety of sediment types, but primarily in muddy sands, and from the intertidal zone to 1000 m depth (Hartman & Fauchald, 1971). It is frequently dominant in intertidal and shallow subtidal sediments, commonly reaching densities of

Table 4 - Spearman's rank correlation coefficient (ρ) values between density of *Heteromastus filiformis* and (a) the first PCA component and (b) abiotic variables at station B3; n=12; *: $p < 0.05$; NS: not significant.

	Variable	ρ	
PCA	**Component I**	0.587	*
Water	**Temperature**	-0.207	NS
	Salinity	-0.629	*
	Dissolved O_2	0.503	NS
	pH	0.494	NS
Sediment	**Temperature**	-0.294	NS
	Sand percentage	0.449	NS
	Silt-clay percentage	-0.403	NS
	Organic matter	-0.406	NS

Table 5 - Comparison of literature data on population density of various populations of *Heteromastus filiformis* in Mediterranean coastal lagoons (where S: salinity; WT: water temperature; dO2: dissolved oxygen; T: sediment textural class; Om: sediment organic matter).

Geographical area	**S** (psu)	**WT** (°C)	**dO$_2$** mg l^{-1}	**T**	**Om** (%)	**Density** (ind. m^{-2})	**Authors**
Orbetello lagoon, Thyrrenian Sea	33-42	6-27	3.7-10.3		6-14	26-285	Lardicci *et al.*, 2001b
Sacca di Goro, N. Adriatic Sea	22-35	6.8-28.5	1.4-14.5	mud	15.1	0.5	Mistri *et al.*, 2001
Valli di Comacchio, N. Adriatic Sea	17.3-35.3	4-26	5-9.9	mud		19.5-285.1	Mistri, 2002
Laki lagoon, N. Aegean Sea	31	24		mud	1.14	20	Gouvis *et al.*, 1998
Homa lagoon, E. Aegean Sea, St. B$_3$	33.1-61.5	3.4-26.6	2.3-9.6	sandy mud	1.8-4.9	21-290	present study

several hundreds and sometimes of several thousands of individuals m^{-2} (e.g. Cadèe, 1979; Shaffer, 1983; Dekker, 1989; Gillet & Gorman, 2002, and literature cited herein). The densities of this capitellid polychaete increase in moderately enriched conditions derived from human activities (Dauer & Conner, 1980; Dekker, 1989).

The length of the thorax L12 (12 chaetigers) of *H. filiformis* individuals in Homa lagoon was similar to that this species showed in the polyhaline zone of the Loire estuary, France (Gillet & Gorman, 2002), indicating that the body size of these populations was not affected by the existing differences in environmental conditions (e.g. salinity values). Callier *et al.* (2008) observed that the body size of *H. filiformis* increases with increasing sediment organic matter. Adults of *H. filiformis* are up to 15 cm in length and about 1 mm in diameter and extending 5-30 cm into the sediment and probably feed selectively on the clay-silt fraction in a head-down position (see Shaffer, 1983, and Holte, 1998, and literature cited herein).

The finding that recruitment of *H. filiformis* in the study area mainly occurred in early-mid spring implies that spawning may have mainly taken place in late winter-early spring. Rasmussen (1956) (according to Muus, 1967) found that the eggs of this capitellid polychaete are deposited in spherical gelatinous masses of 8 mm diameter containing several hundreds of eggs as well as that the larvae hatch after 2-3 days and after a pelagic life of 3-4 weeks adopt a benthic habit with 12-13 segments. Our results also suggest that spring cohort of *H. filiformis* in Homa lagoon displayed short longevity and accelerated maturity. These life history traits along with high fecundity are the predicted r-selected attributes of species living in the unpredictable brackish habitats (Southwood, 1988).

Our observations along with the available information from other studies reveal that the life history of *H. filiformis* is quite variable. For instance, Shaffer (1983) reported that adults of this capitellid polychaete in the poly- to euhaline intertidal zone of North Inlet Estuary, Georgetown, USA were sexually mature through the winter and spawned in early spring, probably at the end of their second year. Buchanan & Warwick (1974) also reported that *H. filiformis* spawns sometime between January and April at the end of its second year in the mud of the Northumberland coast, England. Gillet & Gorman (2002) after having reviewed the available information noted that the reproductive period and the recruitment period of this capitellid polychaete occurred in spring in several European coastal locations from the Mediterranean Sea to the North Atlantic Ocean and the North Sea. However, these authors found that recruitment of *H. filiformis* in the polyhaline zone of the Loire estuary, France, occurred both in spring and in autumn. Gillet & Gorman (2002) also observed that the life time for a cohort was six to nine months depending on the recruitment period and the annual variations. *Heteromastus filiformis* is most probably able to modify its life cycle depending on environmental conditions, a fact that in all characterizes the opportunistic polychaetes (e.g Grassle & Grassle, 1974; Méndez *et al.*, 1997).

Our results indicate that the monthly variation in population density of *H. filiformis* in Homa lagoon was significantly related to that in salinity values. The observation that population density significantly increased during early and mid spring following the recruitment of the spring cohort suggests that salinities lower than 40 psu may favor the reproductive activity and/or the recruits survival. On the other hand, the fact that the significant decline in population density during summer coincided with a sharp increase in salinity values suggests that high salinities (> 50 psu) may negatively affect to a significant extent the magnitude of reproductive activity and the survival of this polychaete. *H. filiformis* has been frequently found in brackish coastal habitats in salinities mainly in the meso- to euhaline range (e.g. Watling, 1975; Read, 1984; Gouvis *et al.*, 1998; Ysebaert *et al.*, 2005; Maggiore & Keppel, 2007; Lourido *et al.*, 2008), indicating that it is a euryhaline marine species tolerating to some extent mainly low salinities. High cellular osmotic tolerance, which is widespread among euryhaline invertebrates and/or high capacity for osmoregulation are important prerequisites for euryhalinity (Kinne, 1971).

Our results, also, suggest that salinity effects on *H. filiformis* population during summer may have been increased by other simultaneously effective environmental conditions, mainly by low oxygen concentrations, despite this polychaete is considered as a tolerant species to hypoxic and temporary anoxic sediments (Oeschger & Vismann, 1994). On the other hand, the monthly variation in the organic enrichment possibly was not large enough to significantly affect that in population density of *H. filiformis*.

Seasonal patterns of numerical density being characterized by a peak in spring or by two peaks in spring and in autumn have been previously reported for other populations of *H. filiformis* (Shaffer, 1983; Gillet & Gorman, 2002, and literature cited herein). In general, macroinvertebrate abundance in northern habitats usually increases during the warmest period of the year following the increase in their reproductive activity (e.g. Zajac & Whitlatch, 1982). In the Mediterranean brackish habitats, the breeding season widens, but macroinvertebrate usually experiences extreme environmental conditions (e.g. high temperature and salinity, low oxygen concentration) and predation pressure during summer, resulting in a decline in density; as a consequence, seasonal patterns of macroinvertebrate abundance with a peak in winter or spring and sometimes a second peak in autumn and patterns with a peak in abundance in autumn have been observed (Kevrekidis, 2004, and literature cited herein).

In conclusion, our results mainly show that population density of *H. filiformis* significantly increased in spring following the spring cohort recruitment and significantly decreased in summer probably due to negative effects of extreme environmental conditions, mainly of high salinities on the magnitude of reproductive activity and survival, thus substantially supporting our initial hypothesis. Our results suggest that opportunistic species experience extreme conditions, particularly high salinities, during summer in Mediterranean eu- to hyperhaline coastal lagoons, which restrain them to develop highly abundant populations. Further studies should concentrate in more detail on multiple factors potentially affecting population ecology of *H. filiformis* as well as of other opportunistic species inhabiting the sharply fluctuating coastal lagoon environment.

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