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Life history and temporal distribution of *Orchestia* sp. cf. *cavimana* (Amphipoda, Talitridae) on a lake shore in central Italy

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A B S T R A C T

The life history of the amphipod *Orchestia* sp. cf. *cavimana* (Heller, 1865) was studied throughout the course of a year with monthly samplings and the use of pitfall traps along the shores of Lake Albano in central Italy. The data thus obtained showed two peaks in abundance (the first in June and the second in October) and a minimum capture frequency in February. Egg-bearing females were recorded in spring and late summer, whilst recruitment occurred from spring to autumn, with maximum in June and October. The data collected also indicated the presence of a positive correlation between the abundance of talitrids and both temperature and sediment moisture. Morphological analysis enabled the identification of four different cohorts (with a lifespan of the species of approximately 12–15 months) all four of which remained distinguishable throughout the course of the year. It, moreover, enabled sex determination in individuals of 5 or more millimetres. The subsequent distribution indicated that, when significant, the sex ratio was female biased and that maximum size was greater in males. In particular, maximum sizes were recorded in spring for both males and females and were of 17.5 and 13.0 mm, respectively. Furthermore, the total body length recorded for egg-bearing females was positively correlated with the number of eggs in their brood pouch.

Introduction

Life cycles are of fundamental importance in the understanding of life dynamics, growth, recruitment and reproduction. Their knowledge is likewise essential in the optimization of both the study and the sampling of a species. Objects of the present study are amphipods: organisms at the base of different food chains, which are considered to be important bio-indicators of coastal environments. Even though several studies have been published regarding those of marine sandy shores throughout the world (Italy: Fanini et al. 2008; Mediterranean Basin: Ugolini et al. 2008; Iceland: Ingólfsson et al. 2007; Brazil: Cardoso 2002), environments which are strongly colonized by these semi-terrestrial crustaceans, little is known on the talitrids of river banks and lake shores (Hendrickx et al. 1998).

Orchestia cavimana (Heller, 1865) is a talitrid amphipod that inhabits the debris and the stones of hard substrates along the river banks and lake shores of the Mediterranean (type locality: Cyprus), the Black Sea, northern Europe and the Atlantic coast of North Africa (Lincoln 1979). It has recently been found in new locations both of the northeastern Baltic Sea (1999) and of northwestern Estonia (2002) (where the species is considered invasive; Herkül et al. 2006). Furthermore, in 2000 (Akbulut and Sezgin 2000), it was also reported for the very first time on a Turkish coast. *O. cavimana* has been widely studied embryologically (Ungerer and Wolff 2005; Wolff and Scholtz 2002, 2006, 2008), and in particular, it has been adopted in different studies undertaken to clarify the position of the Tetraconata (Ungerer and Scholtz 2008). These studies have resulted in the formulation of the "Tetraconata hypothesis", which supports the existence of a close relationship between crustaceans and hexapods. As reported in Libertini et al. (2008) "the populations from Lake Garda (Italy) and other North European sites, previously reported as *Orchestia cavimana* (Heller, 1865), are under systematic review and will be ascribed to a new species (*Orchestia garbinii* sp.n.) genetically close to the typical *O. cavimana*" (Ketmaier and De Matthaeis in press). In light of Ketmaier and De Matthaeis' (in press) study that indicates that on the basis of both allozymes and mtDNA, the presence of a profound phylogeographic hiatus between the Cypriot/Ukrainian and the European populations and in compliance with the standards of zoological nomenclature, the name *O. cavimana* should be exclusively adopted to designate the Cypriot and Ukrainian populations. The present study therefore refers to the population of central Italy discussed as *O.* sp. cf. *cavimana*.

Given on one side the strong embryological interest in this species and on the other its phylogenetic significance, a database centered on ecological aspects could be extremely informative. Furthermore, this is required especially considering the almost

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complete absence of such studies (Akbulut and Sezgin 2000; Herkül et al. 2006), and that of the few present, none take into account Italian populations. The present study therefore wishes to investigate the parameters that characterize this species' life cycle, such as the abundance, the number of yearly cohorts, the reproductive period, the sex ratio, the fertility, the recruitment and the relation between brood size and female total body length. The study also wishes to identify any differences in population structure with respect to supralittoral talitrids of marine coasts. A one-year study was therefore conducted on the life history and distribution of the talitrid *O.* sp. cf. *cavimana* on the beach of Lake Albano in central Italy.

Materials and methods

Study site

O. sp. cf. *cavimana* was sampled once a month, from October 2007 to September 2008, in four selected sites along the shores of Lake Albano in central Italy (Fig. 1). The four sites were chosen on the basis of location, and in particular because they were all only moderately affected by tourism and fishing. The main sampling location (Site A) is a sand-pebble shore 80 m long and 15 m wide (41°45′37.60″N, 12°39′53.50″E). Sampling location B is near an ex-effluent of the lake and is characterized by pebbles and boulders larger than 15 cm. In site C, the shore is almost absent and exclusively present near indentations of the cliffside. However, safety reasons and in particular the presence of unstable rocks, which began to fall from the cliffside after the beginning of the winter rains, obliged the substitution of this site with a safer one with similar characteristics named site D.

Sampling and data analysis

Pitfall traps were adopted in order to collect spontaneously active talitrids on the substrate surface (Chelazzi et al. 2005; Pavesi et al. 2009). In site A, the pitfall traps were arranged following a "T" disposition along two continuous transects (the first perpendicular and the second parallel to the shoreline) and distanced, respectively, 3 and 20 m so as to cover the extremes (the length and width) of the beach. Altogether 10 traps were set in site A (5 in length and 5 in width) whereas the limited space availability enabled the positioning of exclusively one in each of the other sites. Due to the above-mentioned safety reasons, the trap in site C was adopted exclusively until February 2008 and it was then replaced, until the end of sampling, by a trap in site D. The traps were partially filled with loam in order to keep the animals alive and they were then left on the shore all night. On the following morning the individuals were collected and fixed in 70% alcohol. In all sites temperature and penetrability were recorded at each trap. Temperatures were measured with a Hg thermometer at 3:00 p.m. and at a depth of 10 cm, whereas penetrability was calculated as the portion, in centimetres, of a metallic probe penetrating the substrate when dropped vertically from a height of 1 m.

Sediment moisture, conductivity and pH were measured in the laboratory. Moisture was calculated as the difference between the weight of a wet sediment sample and its dry weight after 48 h storage at 60 °C. Conductivity and pH were determined after the addition of distilled water (5:1), a 30 min agitation and then filtration. Amphipods were sexed and divided into four demographic categories: males, females (subdivided into: females with and without oostegites, ovigerous females and females bearing embryos), juveniles and embryos. Sexes, in adults, were distinguished by the presence, in males, of genital papillae. All individuals that did not present any secondary sexually dimorphic features were considered juveniles. Each individual was measured to the nearest millimetre under a stereomicroscope. In particular, total body length was measured from the base of the first antenna to the base of the telson. The individuals were then grouped, on the basis of the body length thus obtained, into 0.5 mm size classes. The minimum lengths recorded for both female and male adults, was of 5 mm whereas the total length of juveniles was less than 5 mm and of embryos less than 2 mm. The breeding status,

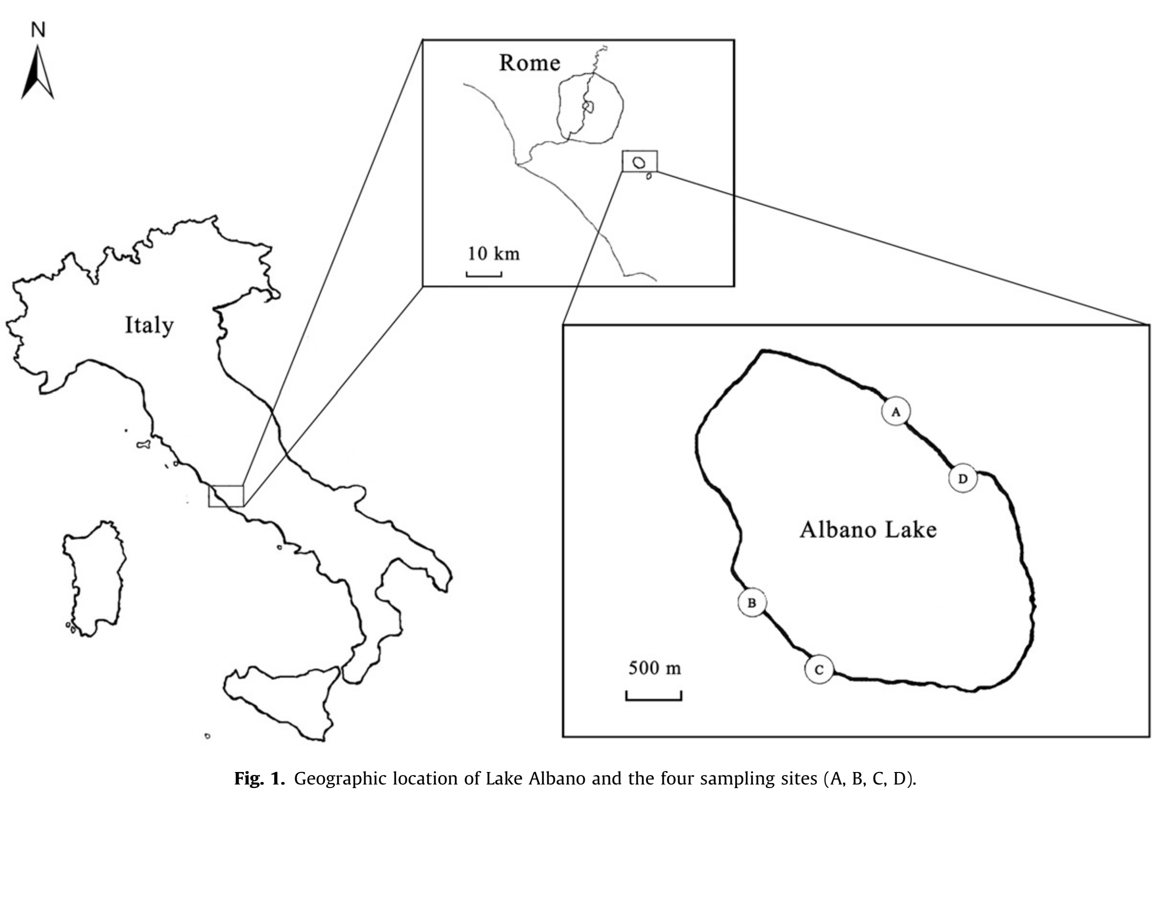

Fig. 1. Geographic location of Lake Albano and the four sampling sites (A, B, C, D).

recruitment, sex ratio and proportion of each population category were recorded. The chi-squared test (χ^2) was used to determine differences in occurrence of males and females. Linear regression between (1) on one side, the total length of females and the number of eggs they carried and (2) on the other, amphipod categories and environmental parameters, was analysed with STATISTICA 6.0 software. Cohorts were identified by size frequency analysis using the Bhattacharya (1967) method implemented in FISAT 1.1.3 software (FAO-ICLARM Stock Assessment Tools 2000–2004; Gayanilo and Pauly 1997).

Results

The values recorded for the environmental factors investigated during the whole sampling period are shown in Table 1. Temperature varied from 4 °C in February 2008 to 26.5 °C in August 2008. Sediment moisture ranged from 12.7% in September 2007 to 18.38% in June 2008. Sediment penetrability showed a minimum value in December 2007 (12.33 mm) and a maximum in June 2008 (22.27 mm). pH varied from 7.85 in October 2007 to 8.7 in May 2008. Conductivity ranged from 216.66 μS in December 2007 to 489.3 μS in September 2007. Linear regression indicated the presence of a positive relation between temperature and both overall number of individuals and abundance of each demographic category (with the exception of females, Table 2). It similarly indicated the existence of a positive relation between sediment moisture and both overall abundance of individuals and that of juveniles. Due to their scarcity, embryos were not considered in the statistical analyses.

O. sp. cf. *cavimana* was found, throughout the year, under pebbles and boulders at every sampling site. Overall, the individuals captured were 4663. Females were the most represented (43.81%; n=2043) followed by juveniles (33.78%; n=1575) and males (20.93%; n=976); embryos (1.48%; n=69), instead, showed a much lower capture frequency. The temporal abundance of *O.* sp. cf. *cavimana* was calculated as the total percentage value in each sampling (Fig. 2). The maximum capture frequencies were found in June 2008 (32.89%; n=1534) and in October 2007 (31.03%; n=1447) whereas, the lowest ones occurred in winter and, in particular, in November 2007 (0.77%; n=36) and in February 2008 (0.06%; n=3). In Table 3, we listed the number of individuals sampled at sites A, B, C and D so as to assess where and when the species was present along the shores of Lake Albano. Although the data thus obtained does not seem to delineate a specific pattern, it does indicate the species reached

Table 1
Temporal distribution of environmental parameters investigated in the area of Albano Lake in all sites throughout the study period.

Months 2007–2008	Minimum–Maximum (Mean) temperature (°C)	Sediment moisture (%)	Penetrability (mm)	pH	Conductivity (μS)
October	17–19 (18)	16.56	14.92	7.85	489.30
November	8–11 (9)	13.66	14.16	8.36	231.50
December	6–9.5 (8)	15.13	12.33	8.22	216.66
January	5.5–10.5 (8.5)	14.74	14.30	8.47	218.82
February	4–7.5 (5.5)	15.70	13.12	8.67	199.10
March	10–16 (13)	18.33	15.17	8.70	229.50
April	15–18 (17)	17.84	15.00	8.64	285.83
May	19–25 (22.5)	16.83	15.50	8.70	455.60
June	22–26 (24.5)	18.38	22.27	8.65	246.16
July	20–25.5 (23.5)	13.57	17.27	8.55	337.26
August	20.5–26.5 (24.5)	14.26	17.84	8.50	384.50
September	14–17 (15)	12.70	14.55	8.46	362.52

Table 2
Linear regression between *O.* prope *cavimana* abundance and environmental parameters in Albano Lake (2007/2008).

	Total	Males	Females	Ovigerous females	Juveniles
Temperature	ß=0.35**	ß=0.436***	n.s.	ß=0.449*	ß=0.503***
Sediment Moisture	ß=0.29***	n.s.	n.s.	n.s.	ß=0.355*
Penetrability	n.s.	n.s.	n.s.	n.s.	n.s.
pH	n.s.	n.s.	n.s.	n.s.	n.s.
Conductivity	n.s.	n.s.	n.s.	n.s.	n.s.

Asterisks refer to significant P values. *$P<0.05$; **$P<0.005$; ***$P<0.001$.

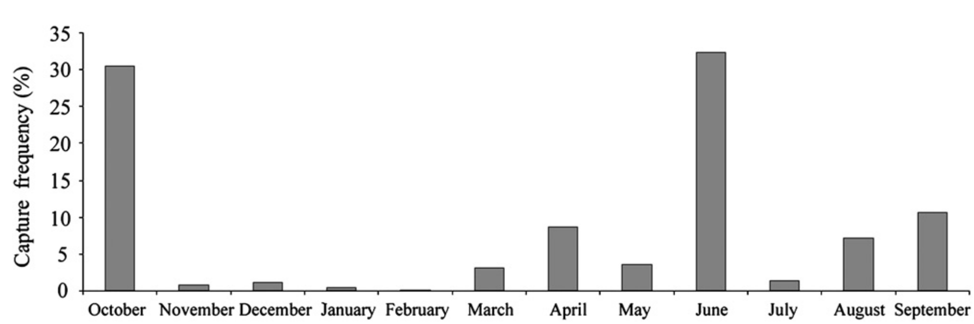

Fig. 2. Monthly capture frequency of *O.* sp. cf. *cavimana* on the shores of Lake Albano from October 2007 to September 2008. Data is relative to captures with pitfall traps; it is calculated as the percentage of the overall total annual captures from all pitfall traps.

maximum presence in October (A: $n=1345$; B: $n=93$; C: $n=9$) and in June (A: $n=1344$; B: $n=17$; D: $n=173$).

The monthly variation in frequency subdivided per size class (Fig. 3a) showed similar patterns for both males and females. Juveniles were always less frequent than adults except for in the months of June and September 2008. The highest juvenile capture frequencies were during these months and October 2007; embryos were instead found in June (1.14%, highest capture frequency), August and September.

The ratio between males and females, when significantly different from 1:1 was always female biased, with a minimum χ^2 in April (1.36, $\chi^2=8.36$ $p<0.01$) and a maximum one in November (5.4, $\chi^2=13.78$ $p<0.001$). It was, on the other hand, not significant in February (2, $\chi^2=0.00$ n.s.), May (0.92, $\chi^2=0.16$ n.s.) and July (1.32, $\chi^2=0.7$ n.s.). In Fig. 3b the proportion of each size class in females is provided. Egg-bearing females were found in two periods: April–May–June and August–September. Breeding peaked in June (5.29%) and was high in spring and low during summer. The temperature and sediment moisture recorded were highest during the first breeding period. Females with oostegites were sampled throughout the year with the sole exception of February whereas females bearing embryos were found in June, August and September. Linear regression indicated that the relation between the number of eggs per brood and female body length was always statistically significant (April: ß=0.43, $p<0.01$; May: ß=0.53, $p<0.05$; June: ß=0.36, $p<0.0001$; August: ß=0.87, $p<0.0001$). September, however, was not taken into account in the analysis due to the fact that sampling did not provide enough egg-bearing females for data analysis. The number of eggs in the brood chamber ranged from 5 to 20, whilst the total length of these females varied between 8 and 13 mm.

Total body length ranged from 5 to 13 mm in females, and from 5 to 17.5 mm in males. The population structure of *O.* sp. cf. *cavimana* is graphically represented by histograms based on length–frequency distribution (Fig. 4 a–n). However, the mean total length of the individuals sampled in February was not calculated for they were solely three. Graphical analysis of frequency distributions revealed four different cohorts, indicated with the letters A, B, C and D (Fig. 5). Cohort A included mature males and females. It appeared in October 2007 and disappeared in May 2008 (dotted lines indicate the probable presence of individuals of the cohort). Cohort B first appeared in October 2007 and had a lifespan of 12 months, persisting until September 2008. For four months it consisted mainly of immature males and females. The amphipods of this cohort grew rapidly during the spring and during the period we identified as the species' breeding period. Cohort C appeared in May and disappeared in September and consisted of juveniles born throughout the breeding period. Lastly, cohort D appeared in May and lasted until September, with mature individuals reproducing mainly in August. None of the cohorts constituted the entire population throughout the year.

Table 3
Number of individuals at sites B, C and D in Albano Lake.

Months 2007–2008	A	B	C	D
October	1345	93	9	–
November	36	0	0	–
December	46	8	0	–
January	17	2	1	–
February	3	0	0	–
March	119	0	–	24
April	402	1	–	2
May	171	1	–	0
June	1344	17	–	173
July	66	0	–	2
August	300	0	–	2
September	437	7	–	35

Discussion

The species was sampled in four selected sites along the shores of Lake Albano and was present, in site A (the one where the

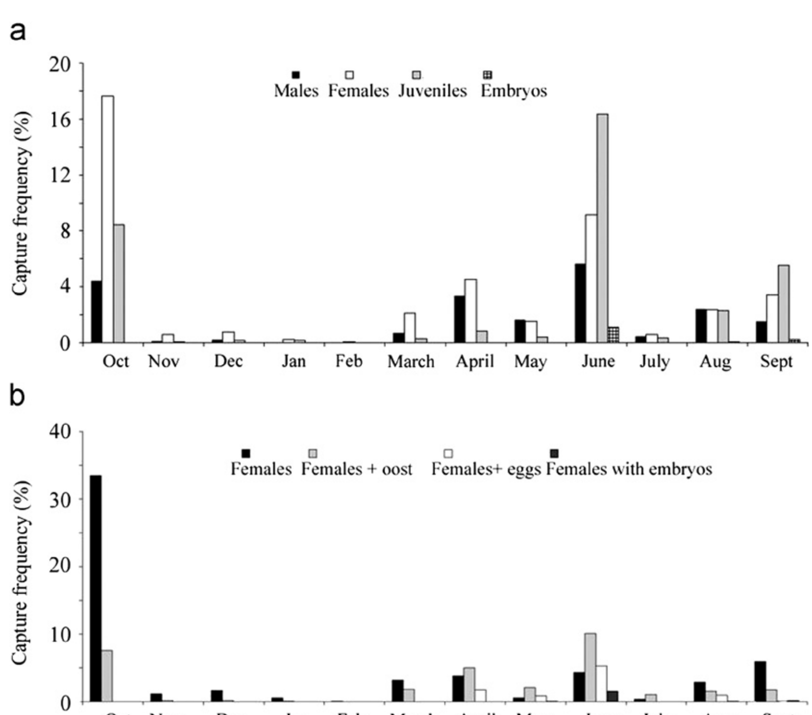

Fig. 3. (a) Monthly capture frequency of *O.* sp. cf. *cavimana* divided into size classes and (b) of females divided into four groups. Data regards captures with pitfall traps calculated as a percentage of the total annual captures in all traps during the period October 2007–September 2008.

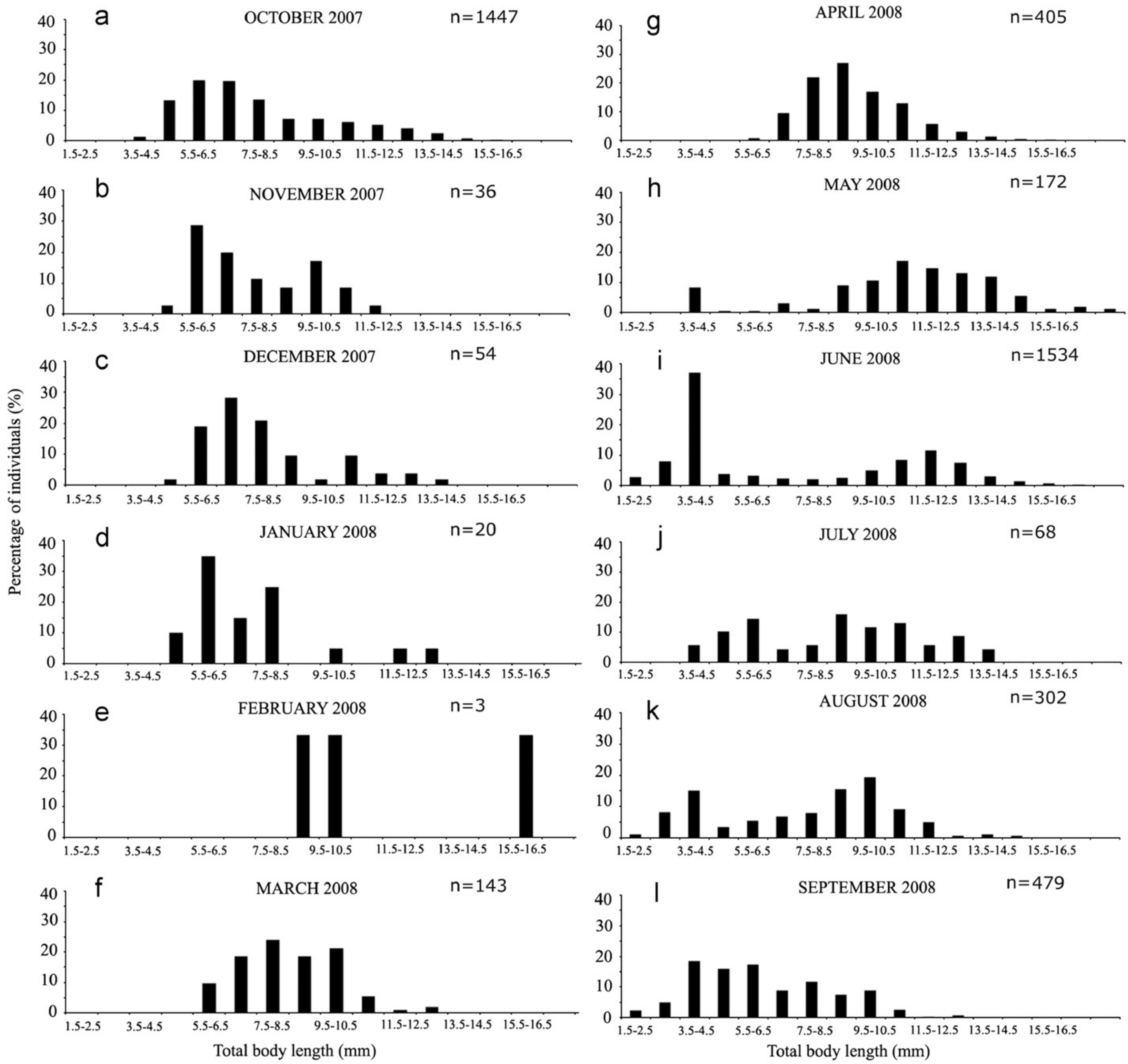

Fig. 4. Size frequency distribution of *O.* sp. cf. *cavimana* throughout the sampling period in Albano Lake (2007/2008).

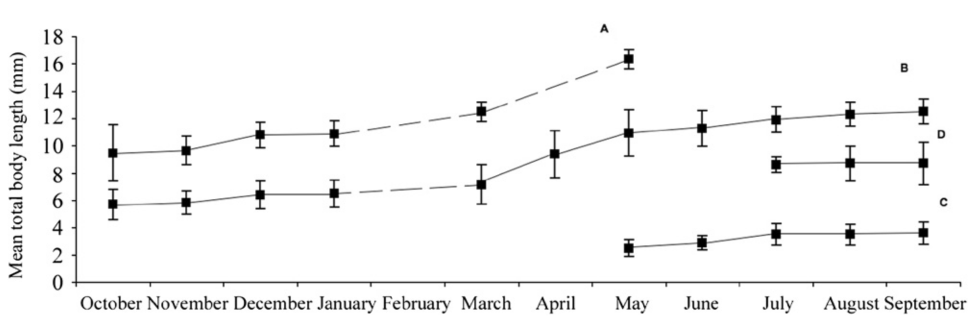

Fig. 5. Temporal development of the cohorts of *O.* sp. cf. *cavimana* within the sampling period October 2007–September 2008. Dots = mean body length; bar lines = standard deviation; dotted lines: missing individuals.

transect was placed), throughout the year. Even though the number of individuals collected in sites B, C and D was decidedly inferior, due to the limited space availability and the consequent presence of a single trap in each, the data nonetheless enabled the detection of trends similar to those observed in site A. Linear regression indicated the presence of a positive correlation between the abundance of individuals and both temperature and sediment moisture, thus indicating that these are hence important factors capable of influencing the presence and abundance of the species. Moreover, Herkül et al. (2006) found that the size structure of the population of *O. cavimana* in the Black Sea was principally related to humidity and wrack biomass.

The species was always present during the year, albeit less frequently in winter due to low temperatures; there was a minimum in February probably due to frost, which limited the nocturnal surface activity of the animals. This seems to be in accordance with the study undertaken by Scapini et al. (1992) of a population of *T. saltator* sampled on a central Italian beach, for they detected a decrease in activities as the temperature diminished. Yet, Herkül et al. (2006) noticed that the amphipod could survive extremely harsh winters and that the survival of *O.* sp. cf. *cavimana* does not seem to be affected by low temperatures.

In general, the temporal patterns detected for adults followed similar trends while the sex ratio, where significant, was always female biased. Females with oostegites were present throughout the year, while egg-bearing females were found in spring and late summer as a result of reproductive activities. A direct comparison of these two specific periods indicates that temperature and sediment moisture, both aspects which could plausibly influence reproduction, were higher in spring than they were in late summer. Similar relations have, in fact, already been observed and Morritt and Stevenson (1993) as well as Ingólfsson et al. (2007) have identified habitat temperature as the critical factor not only controlling reproduction but also shaping the breeding seasons in *O. gammarellus*. In *O.* sp. cf. *cavimana*, females with embryos were exclusively found in June, September and October. *O.* sp. cf. *cavimana* therefore shows a pattern analogous to the one observed in talitrids of marine coastal environments. Example of this is the fact that the reproductive period of *Talorchestia brito* is from February to September in Portugal and from March to November in Tunisia (Gonçalves et al. 2003) whereas, for *T. saltator*, it is from March to September in Portugal and from February to November in Tunisia (Marques et al. 2003).

The shortest gravid female was 5 mm long and carried 5 eggs in the brood pouch; the longest was instead 13 mm and had 20 eggs. There therefore seems to be no difference from marine coastal talitrids, which may, in fact, carry up to 17 (*O. gammarellus*; Dias and Sprung 2004) or 19 eggs (*Macarorchestia remyi*; Pavesi and De Matthaeis 2009). In *O.* sp. cf. *cavimana*, as well as in the above-mentioned talitrids, a positive relation has always been detected between female total body length and the relative number of eggs per brood: the longer the female, the more eggs she can carry.

In *O.* sp. cf. *cavimana*, total body length varied from 5 to 13 mm for females and from 5 to 17.5 mm in males, sizes which are greater than the ones reported in the literature. In their study Akbulut and Sezgin (2000) had, in fact, reported maximum total body lengths of 11 mm for the males sampled in the Black Sea. Ruffo (1993), on the other hand, found total body lengths of approximately 11 mm for both males and females at Cyprus whereas Herkül et al. (2006) found that males had a significantly greater mean length than females.

In this study we followed two generations throughout the year (cohorts D and A+B+C): the first with mature stages in winter and maximum reproductive activity in summer; the second with immature stages in winter, rapid growth and highest reproductive activity in spring. Individuals generated a new cohort in spring (May) and summer (July), with slow growth in winter and rapid growth in March, probably in relation to the higher temperatures. Increase in density in spring, summer and early autumn is a natural consequence of recruitment. Furthermore, the general decline observed in late autumn is possibly consequence of higher mortality rates in older individuals after the conclusion of the breeding season (Gonçalves et al. 2003). Overall, the lifespan observed in the current study is of approximately 12–15 months. Since Dias and Sprung (2004) found a lifespan of 8–12 months for a population of *O. gammarellus* in Portugal, and Marques et al. (2003) noted one of 6–9 months in central Italy for *T. saltator*, *O.* sp. cf. *cavimana* seems to, indeed, have a longer lifespan than coastal talitrids. However, much variation certainly exists for, at non-thermal sites in Iceland, Ingólfsson et al. (2007) reported that *O. gammarellus* required almost 2 years to reach sexual maturity.

Finally, our data demonstrates that the life cycle of a talitrid species living along a lake beach does reflect those of confamiliar species from marine coastal environments, indicating they adopt analogous strategies of habitat exploitment. Temporal distribution, reproductive activity and recruitment in fact show similar trends. Although temperature and sediment moisture are the environmental factors that most influence the species in both sea and lake shores, the microhabitat – restricting it to small beaches or indentations along the coasts – does not allow *O.* sp. cf. *cavimana* to move widely along the beaches. Whereas dispersal opportunities are provided to marine coastal talitrids by floating wracks and wood, *O.* sp. cf. *cavimana* presumably relies more on migratory birds, as many were often observed along the shores of Lake Albano.

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References

Akbulut, M., Sezgin, M., 2000. *Orchestia cavimana* Heller, 1865 (Amphipoda, Talitridae) in the Turkish Black Sea fauna. Turk. J. Mar. Sci. 6, 241–244.

Bhattacharya, C.G., 1967. A simple method of resolution of a distribution into Gaussian components. Biometrics 23, 115–135.

Cardoso, R.S., 2002. Behavioural strategies and surface activity of the sandhopper *Pseudorchestoidea brasiliensis* (Amphipoda: Talitridae) on a Brazilian beach. Mar. Biol. 141, 167–173.

Chelazzi, L., De Matthaeis, E., Colombini, I., Fallaci, M., Bandini, V., Tozzi, C., 2005. Abundance, zonation and ecological indices of a coleopteran community from a sandy beach-dune ecosystem of the southern Adriatic coast, Italy. Vie Milieu 55 (2), 127–141.

Dias, N., Sprung, M., 2004. Population dynamics and production of the amphipod *Orchestia gammarellus* (Talitridae) in a Ria Formosa saltmarsh (southern Portugal). Crustaceana 76, 1123–1141.

Fanini, L., Marchetti, G.M., Scapini, F., Defeo, O., 2008. Effects of beach nourishment and groynes building on population and community descriptors of mobile arthropodofauna. Ecol. Indic. 9, 167–178.

Gayanilo Jr, F.C, Pauly, D., 1997. The FAO-ICLARM Stock Assessment Tools (FISAT) Reference Manual. FAO Computerized Information Series (Fisheries), No. 8. FAO, Rome, p. 262..

Gonçalves, S.C., Marques, J.C., Pardal, M.A., Bouslama, M.F., El Gtari, M., Charfi-Cheikhrouha, F., 2003. Comparison of the biology, dynamics, and secondary production of *Talorchestia brito* (Amphipoda, Talitridae) in Atlantic (Portugal) and Mediterranean (Tunisia) populations. Estuarine Coast. Shelf Sci. 58, 901–916.

Hendrickx, F., Maelfait, J.P., Steeno, R., 1998. Arthropod populations occurring on the banks of the tidal part of the river Scheldt: distribution patterns and threats. Biol. Jb. Dodonaea 65, 152–153.

Herkül, K., Kotta, J., Kotta, I., 2006. Distribution and population characteristics of the alien talitrid amphipod *Orchestia cavimana* in relation to environmental conditions in the Northeastern Baltic. Sea Helgol. Mar. Res. 60, 121–126.

Ingólfsson, A., Ólafsson, Ó.P., Morritt, D., 2007. Reproduction and life-cycle of the beachflea (*Orchestia gammarellus* (Pallata) (Crustacea: Amphipoda) at thermal and non-thermal sites in the intertidal of Iceland: how important is temperature? Mar. Biol. 150, 1333–1343.

Ketmaier, V., De Matthaeis, E., in press. Allozyme and mtDNA reveal the occurrence of two divergent lineages in *Orchestia cavimana* (Talitridae). J. Crustacean Biol. 30(2).

Libertini, A., Trisolini, R., Rampin, M., 2008. Chromosome number, karyotype morphology, heterochromatin distribution and nuclear DNA content of some talitroidean amphipods (Crustacea: Gammaridea). Eur. J. Entomol. 105, 53–58.

Lincoln, R.J., 1979. British Marine Amphipoda: Gammaridea. British Museum (Natural History), London.

Marques, J.C., Gonçalves, S.C., Pardal, M.A., Chelazzi, L., Colombini, I., Fallaci, M., Bouslama, M.F., El Gtari, M., Charfi-Cheikhrouha, F., Scapini, F., 2003. Comparison of *Talitrus saltator* (Amphipoda, Talitridae) biology, dynamics, and secondary production in Atlantic (Portugal) and Mediterranean (Italy and Tunisia) populations. Estuarine Coast. Shelf Sci 58S, 127–148.

Morritt, D., Stevenson, T.D.I., 1993. Factors influencing breeding initiation in the beachflea *Orchestia gammarellus* (Pallas) (Crustacea: Amphipoda). J. Exp. Mar. Biol. Ecol. 165, 191–208.

Pavesi, L., Chelazzi, L., Iannilli, V., Lucchesi, B., Renzi, A., De Matthaeis, E., 2009. Abundance, temporal distribution and zonation patterns of talitrids on two Apulian sandy beaches (Southern Italy). Vie Milieu 59 (1), 7–20.

Pavesi, L., De Matthaeis, E., 2009. Life history of the amphipod *Macarorchestia remyi* (Schellenberg, 1950) on a Tyrrhenian sandy beach, Italy. Hydrobiol 635, 171–180.

Ruffo, S., 1993. The Amphipoda of the Mediterranean. Part 3. Gammaridea (Melphidippidae to Talitridae), Ingolfiellidea, Caprellidea. In: Bellan-Santini, D., Karaman, G., Krapp-Schickel, G., Ledoyer, M., Ruffo, S. (Eds.), Mémoires de l'Institut océanographique, Monaco, 13, 365–576. Mém. Inst. Océanogr. Monaco 13:xxi-xxv+577–814.

Scapini, F., Chelazzi, L., Colombini, I., Fallaci, M., 1992. Surface activity, zonation and migration of *Talitrus saltator* on a Mediterrean beach. Mar. Biol. 112, 573–581.

Ugolini, A., Ungherese, G., Somigli, S., Galanti, G., Baroni, D., Borghini, F., Cipriani, N., Nebbiai, M., Passaponti, M., Focardi., S., 2008. The amphipod *Talitrus saltator* as a bioindicator of human trampling on sandy beaches. Mar. Environ. Res. 65, 349–357.

Ungerer, P., Wolff, C., 2005. External morphology of limb development in the amphipod *Orchestia cavimana* (Crustacea, Malacostraca, Peracarida). Zoomorphology 124, 89–99.

Ungerer, P., Scholtz, G., 2008. Filling the gap between identified neuroblasts and neurons in crustaceans adds new support for Tetraconata. Proc. R. Soc. B 275, 369–376.

Wolff, C., Scholtz, G., 2002. Cell lineage, axis formation, and the origin of germ layers in the amphipod crustacean *Orchestia cavimana*. Dev. Biol. 250, 44–58.

Wolff, C., Scholtz, G., 2006. Cell lineage analysis of the mandibular segment of the amphipod *Orchestia cavimana* reveals that the crustacean paragnaths are sternal outgrowths and not limbs. Front. Zool.. 3, 19.

Wolff, C., Scholtz, G., 2008. The clonal composition of biramous and uniramous arthropod limbs. Proc. R. Soc. B 275, 1023–1028.