AQUATIC CONSERVATION: MARINE AND FRESHWATER ECOSYSTEMS

Aquatic Conserv: Mar. Freshw. Ecosyst. (in press)

Published online in Wiley InterScience (www.interscience.wiley.com). DOI: 10.1002/aqc.718

Invasion of artificial ponds in Doñana Natural Park, southwest Spain, by an exotic estuarine copepod

DAGMAR FRISCH*, HÉCTOR RODRÍGUEZ-PÉREZ and ANDY J. GREEN

Department of Conservation Biology, Doñana Biological Station, Avda. Maria Luisa s/n, E-41013 Sevilla, Spain

ABSTRACT

1. During a study of five artificial brackish ponds situated in Doñana Natural Park and the Guadalquivir delta between July 2001 and June 2002, a total of six copepod species (two calanoids, three cyclopoids and one harpacticoid) were recorded. All of them are typical of brackish or estuarine habitats.
2. The estuarine calanoid copepod *Acartia tonsa* (originally from North America) was present in all the ponds studied. This exotic species has been found previously in European estuaries, but has not previously been recorded from artificial wetlands.
3. Both the relative and absolute abundance of the species varied significantly among months and ponds. *A. tonsa* was most abundant during autumn and spring, while *Calanipeda aquae-dulcis* was most abundant in summer. This seasonal pattern of the copepod community composition was different from that reported in studies from other European estuaries or wetlands.
4. The invasion by and dominance of *A. tonsa* in the area of Doñana Natural Park has important implications for the conservation of the diverse native zooplankton fauna in the natural marshes of the adjacent Doñana National Park, which includes endemic species.

KEY WORDS: salt marsh; coastal wetland; *Acartia tonsa*; *Calanipeda aquae-dulcis*; estuarine copepods; Doñana Natural Park

INTRODUCTION

Estuaries are transition zones between marine and freshwater habitats with fluctuating salinity ranges. They are inhabited by a mixture of marine, estuarine and freshwater zooplankton fauna associated with the salinity gradient (e.g. Baldó *et al.*, 2001; Vincent *et al.*, 2002; Vieira *et al.*, 2003; Tackx *et al.*, 2004). Coastal salt marshes are often inhabited in large numbers by estuarine fauna (Quintana *et al.*, 1998), which may colonize these habitats via hydrological connections, e.g. channels and rivulets between the estuary and the coastal wetlands.

*Correspondence to: D. Frisch, Department of Conservation Biology, Doñana Biological Station, Avda. Maria Luisa s/n, E-41013 Sevilla, Spain. E-mail: dfrisch@sistern.net

Received 10 July 2004
Accepted 9 April 2005

A tolerance for salinities ranging from marine to freshwater conditions is typical for estuarine organisms and has enabled many exotic species to invade continental freshwater habitats, e.g. the amphipod *Gammarus tigrinus*, the zebra mussel *Dreissena polymorpha*, or the copepod *Eurytemora affinis* (Lee and Bell, 1999). Once established in new habitats, exotic species can have deleterious consequences on the native fauna and flora, leading to shifts in the dominance structure of planktonic communities (Lehman and Cáceres, 1993; Hoffmeyer, 2004) and the extinction of native species (Ruiz *et al*., 1999).

The increase in commercial shipping has made estuaries and connected habitats especially vulnerable to invasion by exotic species. Shipping activities account for 22% of introduced species in estuaries and marine habitats in the Ponto-Caspian region (Grigorovich *et al*., 2002). Many invertebrates, including copepods, have been found in ballast water in various parts of Europe (Leppäkoski *et al*., 2002). Various crustaceans have been introduced to the Guadalquivir estuary, south-west Spain, in the ballast water of ships visiting the port of Sevilla (Cuesta *et al*., 1996). The Veta la Palma wetland complex in Doñana Natural Park is flooded artificially by water pumped from the Guadalquivir estuary, making the occurrence of invasive planktonic species very likely.

In this paper we present the first study of zooplankton in Doñana Natural Park, focusing on the copepod community in Veta la Palma. As a component of the zooplankton, copepods are important food for juvenile fish, macroinvertebrates and filter-feeding waterbirds (Hurlbert *et al*., 1986; Euliss *et al*., 1997; Cardona *et al*., 2001). The main aim of the present study was to determine the species composition of the zooplankton community and its spatial and temporal fluctuation in the Veta la Palma wetlands with specific emphasis on the presence of introduced species. We consider the implications of our findings for the conservation of Doñana, which contains some of Europe's most important wetlands.

METHODS

Study area and pond description

Veta la Palma (36° 57′ N, 6° 14′ W) is a private estate situated within the Doñana Natural Park and adjacent to the Doñana National Park (Figure 1) at a distance of approximately 23 kilometres from the coast. The National Park contains 30 000 ha of natural, temporary marshes and is considered as one of the most important wetlands in Europe, especially because of its overwhelming importance for waterbirds. Over a million waterbirds use the area for wintering or on migration to and from Africa (Martí and del Moral, 2002). It is also of great importance for breeding waterbirds (Martí and del Moral, 2003). The National Park is declared a UNESCO World Heritage Site, a Biosphere Reserve, a Ramsar site and a Special Protection Area under the European Union Birds Directive. The Natural Park (including Veta la Palma) has a lower level of protection and lacks international protection status, despite the fact that Veta la Palma easily meets those Ramsar criteria for wetlands of international importance based on waterfowl (http://www.ramsar.org/key_guidelines_index.htm).

Veta la Palma contains 37 ponds (total 3125 ha), which are used for extensive fish culture and were created between 1990 and 1993 (Figure 1). These ponds are shallow (average depth 30 cm) and connected to deeper canals used to transport water to and from the Guadalquivir estuary. This site is used for culturing estuarine fish such as European seabass, *Dicentrarchus labrax*, flathead mullet, *Mugil cephalus*, and gilthead seabream, *Sparus auratus*, as well as Atlantic ditch shrimp, *Palaemonetes varians*. Submerged vegetation is dominated by wigeongrass, *Ruppia maritima* (which forms extensive beds between April and July). The shores and islands are covered with saltmarsh vegetation, especially *Arthrocnemum macrostachyum* and *Suaeda* spp. Some patches of *Phragmites australis* and *Scirpus maritimus* and the alien *Spartina densiflora* occur on the shoreline.

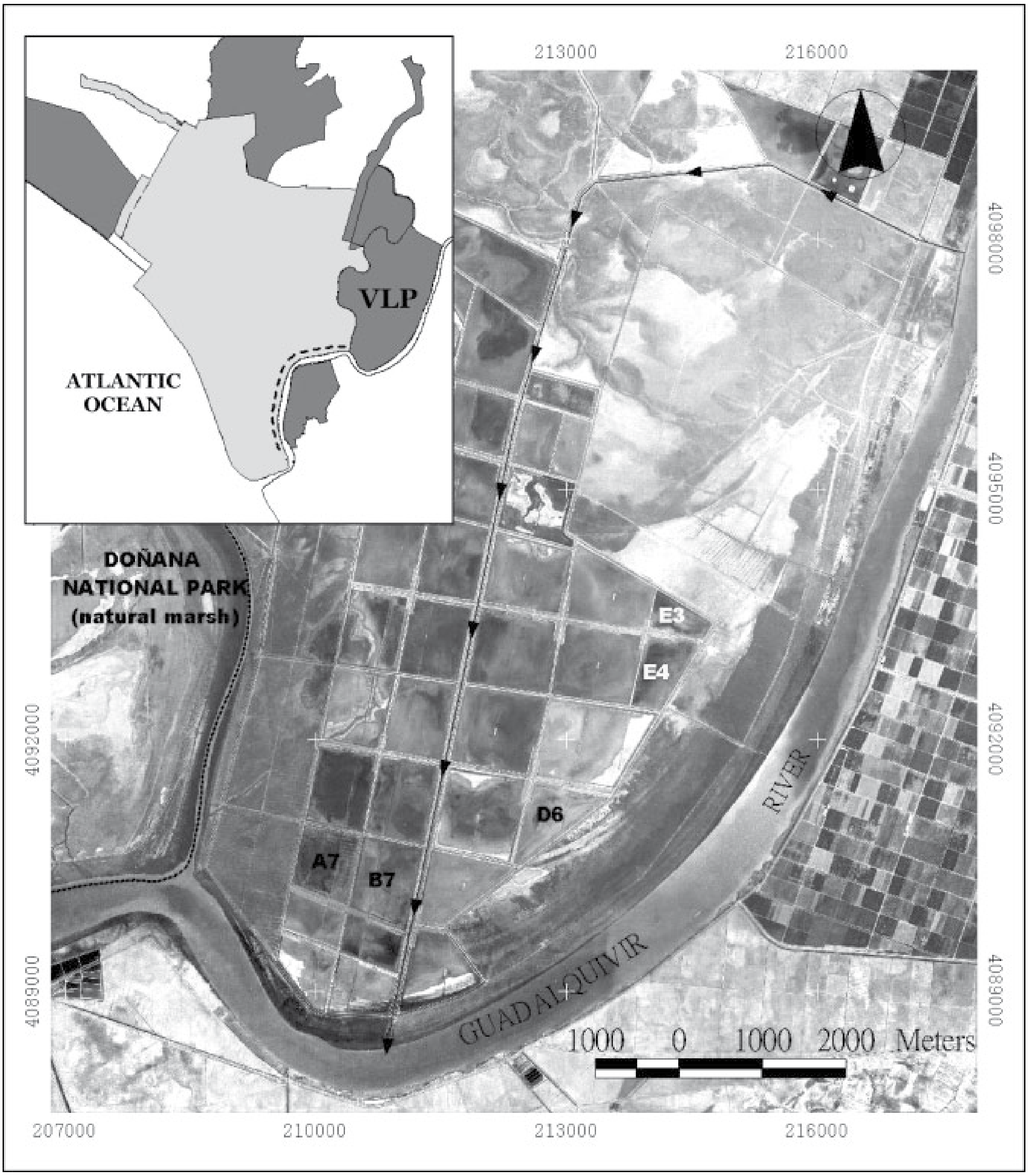

Figure 1. Map of the study area (Veta la Palma, Doñana Natural Park). Ponds sampled for the present study are labelled as A7, B7, D6, E3 and E4. The black line with arrows denotes the direction of the main channel, the dotted line represents the border between Doñana National Park and Doñana Natural Park. Source: Digital Orthophoto of Andalucia (1998–1999), UTM projection, European Datum 1950 Spain and Portugal, Zone 30, scale 1:60.000. The insert shows a map of the areas of Doñana National Park (light grey) and Doñana Natural Park (dark grey). The position of the dyke constructed to isolate the marshes of the National Park from the estuary is shown on the inserted map with a dotted line along the Guadalquivir River

The Veta la Palma wetlands are a major part of the Doñana ecosystem and often hold the majority of waterbirds present in Doñana when the temporary marshes in the National Park are dry. Recent studies of waterbird ecology have focused on the Veta la Palma wetlands (e.g. Figuerola *et al*., 2003; Green and

Sánchez, 2003; Figuerola and Green, 2004). Salinity varies from 7 g L^{-1} during winter to near 15 g L^{-1} in August and September, while pH ranged from 9.3 to 10.3 during the study period. The macroinvertebrate community is low in diversity and contains a mixture of groups typical of marine (e.g. the polychaete *Hediste diversicolor*) and continental aquatic (e.g. the corixid *Sigara stagnalis*) habitats. During the present study, copepods were the dominant crustaceans recorded amongst the zooplankton (excluding ostracods and *P. varians* shrimps) and no cladocerans were recorded. In other samples from the study area, small numbers of two cladoceran species have been recorded: *Daphnia magna* and *Moina brachiata* (personal observation).

Mean monthly air temperature during the study period was between 11.8°C in February 2002 and 23.5°C in July 2001. Since data on water temperature were not available and the ponds are very shallow, air temperature was used as a surrogate of water temperature. Mean precipitation is 562 mm yr^{-1} with a range of 158–1062 (Castroviejo, 1993).

Veta la Palma ponds are dried and reflooded in a rotating cycle to allow fish to grow prior to harvest. We selected five ponds, which varied in the length of time for which they had been flooded (pond age) at the beginning of the sample period in April 2001. Two of them (A7 and B7) had been flooded less than 6 months and two (E3 and E4) for more than 18 months. D6 had an intermediate flooding time.

Sampling methods

Samples were collected in April, July and October 2001, and February and June 2002. Four replicate samples were taken from each pond. Zooplankton was sampled by placing a PVC tube of 20 cm diameter through the water column down to the sediment. The water was stirred inside the pipe and taken out with a jug from the sediments upwards. By using this method, the water column was constantly mixed during the sampling procedure, ensuring complete sampling of the water column and extraction of all the water present in the pipe. Water samples were filtered through a 250-μm sieve. The depth of the water column was measured to allow us to calculate the volume filtered. Water depth at sampling points varied between 9 and 37 cm. Each sample was preserved with formalin and stored.

Qualitative and quantitative analysis of copepods

For the faunal analysis, copepods were sexed and staged at species level according to Brylinski (1981), Einsle (1993) and Dussart (1967, 1969). Both adult and juvenile copepods of all copepod species were counted, using a Sedgewick-Rafter chamber under a light microscope (magnification × 100). To quantify the number of individuals, the complete sample was counted, with the exception of two samples, which contained more than 2000 individuals. These two samples were concentrated to 20 mL and three subsamples of 1 mL each were counted. Throughout this paper, we present results for adult copepods.

Statistical analysis

In order to analyse variation in the composition of the copepod community, we calculated the relative abundance of *A. tonsa* adults as a percentage of all copepod adults present. Arcsine-transformed percentages were used as the dependent variable in a 2-way ANOVA. The main predictors were site (a fixed factor of five levels corresponding to different ponds) and month of sampling (a fixed factor of five levels). We also analysed absolute abundance of *A. tonsa* in the same manner as described above (2-way ANOVA, main effects of site and month). Fisher LSD *post hoc* tests were used to establish significant differences between individual pairs of ponds or months. All statistical analyses were carried out with Statistica 6.0 (StatSoft, 2001).

RESULTS

Six copepod species were identified in the ponds of Veta la Palma. The Calanoida were represented by *A. tonsa* Dana 1848 and *Calanipeda aquae-dulcis* Kritschagin 1873, and the Cyclopoida by *Halicyclops magniceps* (Lilljeborg 1853), *Halicyclops neglectus* Kiefer 1935, and *Halicyclops rotundipes* Kiefer 1935. Harpacticoida were represented by *Cletocamptus* cf. *retrogressus* Shmankevich 1875.

Table 1. ANOVA of relative abundance (percentage of adults, arcsine-transformed) of *Acartia tonsa*, testing for the main effects of site and month and their interaction df = degrees of freedom MS = mean square

	df	MS	F	*p*
Site	4	12.61	117.26	<0.0001
Month	4	19.10	177.60	<0.0001
Site∗month	16	3.66	34.04	<0.0001
Error	72	0.11		

Table 2. ANOVA of absolute densities of adult *Acartia tonsa*, testing the main effects of site and month and their interaction

	df	MS	F	*p*
Site	4	1411.94	20.95	<0.0001
Month	4	1411.94	20.95	<0.0001
Site∗month	16	477.91	7.09	<0.0001
Error	72	67.41		

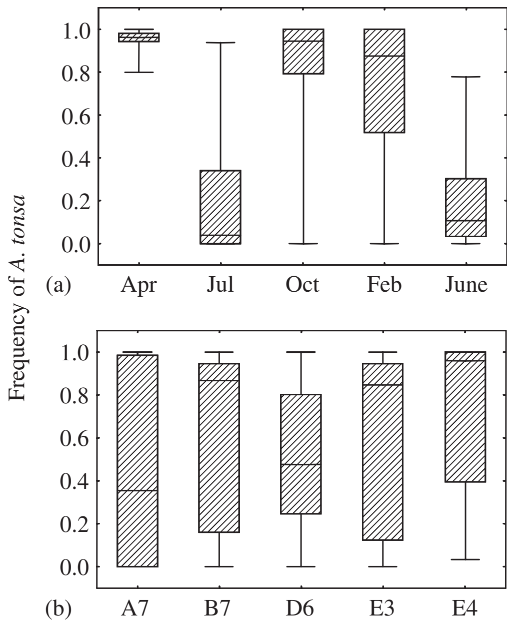

Figure 2. Relative abundance of adult *Acartia tonsa* in the Veta La Palma ponds. Graphs represent medians (line), and the 75th and 25th percentile (upper and lower part of the boxes, respectively). Error bars show maximum and minimum relative abundance. (a) Seasonal relative abundance of *A. tonsa* (includes data from all five ponds). (b) Pond-specific density in the five ponds studied (includes data from five sample dates)

The copepod assembly was dominated on all sample dates and at all ponds by the two calanoid copepods (Figure 3), which jointly reached maximum densities of 734.2 Ind L^{-1} in pond E4 on 5 June 2002. Maxima of *A. tonsa* and *C. aquae-dulcis* were 59.5 Ind L^{-1} (E4, 13 July 2001) and 709.9 Ind L^{-1} (E4, 5 June 2002) respectively. Cyclopoid and harpacticoid copepods generally only contributed very small numbers of individuals with usually less than 1 Ind L^{-1}. The maximum density of this group was 4.3 Ind L^{-1} on 6 June 2002 in pond D6. *A. tonsa*, *C. aquae-dulcis* and *H. magniceps* were recorded in all five ponds studied. *H. neglectus*, *H. rotundipes* and *C. retrogressus* were present in four, three and two ponds respectively.

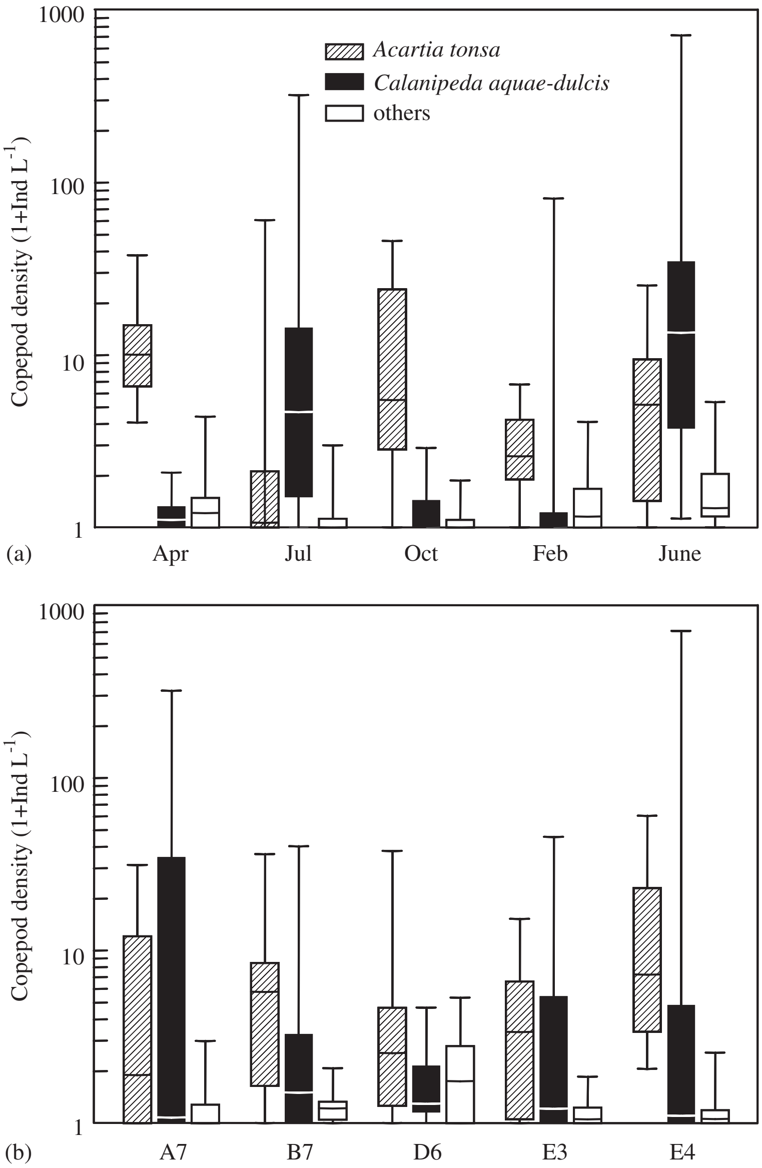

Figure 3. Density of adult copepods in the Veta La Palma ponds. *Acartia tonsa* and *Calanipeda aquae-dulcis* are shown separately. 'Others' is the sum of three cyclopoids *Halicyclops neglectus*, *Halicyclops rotundipes* and *Halicyclops magniceps* and the harpacticoid *Cletocamptus retrogressus*. Graphs represent medians (line), and the 75th and 25th percentile (upper and lower part of the boxes, respectively). To permit logarithmic scaling of the *y*-axis, 1 was added to all densities. Error bars show maximum and minimum densities. (a) Seasonal density of copepods pooled for five ponds. (b) Pond-specific density in the five ponds pooled for five months

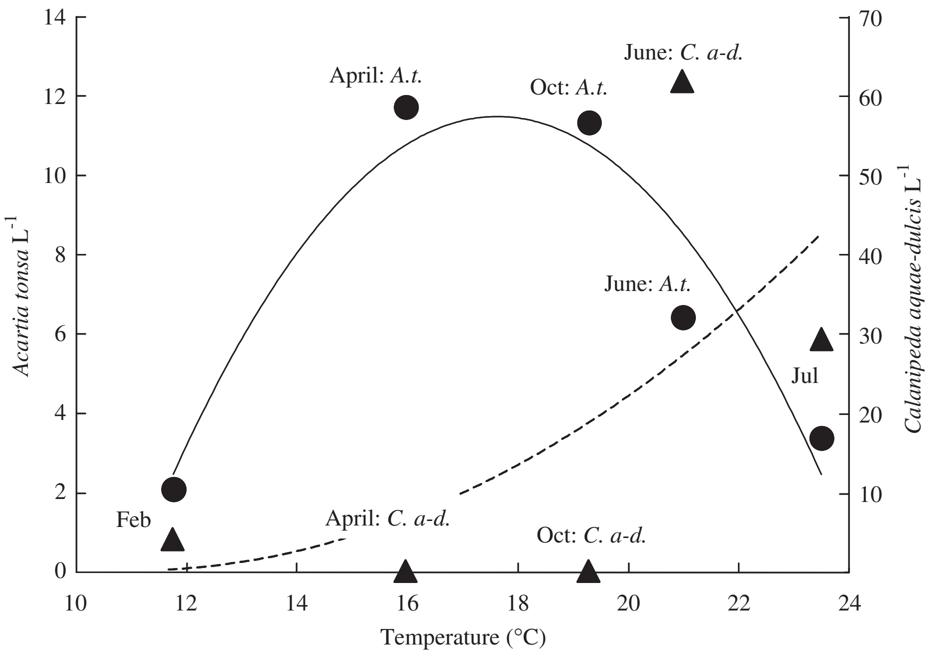

Figure 4. Average adult densities of five *Acartia tonsa* and *Calanipeda aquae-dulcis* populations (circles and triangles, respectively) in Veta la Palma in relation to mean monthly air temperature during the study period. The data points were fitted with the polynomial equations $y = -69.74 + 9.22 * x - 0.26 * x^2$ (unbroken line, *A. tonsa*) and $y = 33.86 - 6.03 * x + 0.27 * x^2$ (dotted line, *C. aquae-dulcis*)

A. tonsa was present in all sample months in each pond. However, there were major seasonal fluctuations of the copepod community, with absolute and relative abundance of *A. tonsa* differing significantly between months (Tables 1 and 2). In the cooler seasons, the copepod community was dominated by *A. tonsa*, whereas in the summer months (June, July) the dominant species was *C. aquae-dulcis* (Figures 2(a) and 3(a)). The relative abundance (Figure 2(a)) of *A. tonsa* was significantly lower in June and July than in any of the other months ($p < 0.0001$, Fisher LSD *post hoc* tests). The plot of absolute abundance against air temperature (Figure 4) illustrates highest abundance of *A. tonsa* at temperatures between 14 and 20°C, while abundance was lower when temperatures were higher or lower. This relation with temperature is reflected in the effect of month on absolute abundance of *A. tonsa*, which in April and October was significantly higher than in July and February (Fisher LSD post hoc tests, $p < 0.005$).

In addition to seasonal variation, there was also a spatial effect on community composition and on population size of *A. tonsa*. Both relative and absolute abundance of this species differed significantly among the five ponds studied (Tables 1 and 2). In three ponds (B7, E3 and E4) the median proportion of *A. tonsa* was much higher, lying between 0.85 and 0.96 (Figure 2(b)). However, *post hoc* tests showed that the differences between ponds were only significant for all pairs that included pond E4, in which both relative ($0.04 > p < 0.001$) and absolute ($0.02 > p < 0.001$) abundance of *A. tonsa* were highest.

DISCUSSION

The copepod fauna of the Veta la Palma wetlands is exclusively represented by species typical of brackish or estuarine waters. Species of the cyclopoid genus *Halicyclops* are frequently found in coastal marine habitats and estuaries or in brackish inland habitats (Dussart, 1969; Heip, 1975; Rocha *et al.*, 1998). Likewise, the harpacticoid *C. retrogressus* is typical of salt marshes and is common in salt lake and salt work communities in Spain and other parts of the Mediterranean region (Dussart, 1967; Alonso, 1990; Williams, 1998).

C. aquae-dulcis has been recorded in European estuaries (Vieira *et al*., 2003) and Mediterranean salt marshes (Quintana *et al*., 1998; Turki and El Abed, 1999; Brucet, 2003). It was found to have moved from marine habitats into freshwater reservoirs in the Ponto-Caspian region (Grigorovich *et al*., 2002).

This is the first record of *A. tonsa* in European ponds or marshes to date. *A. tonsa* originated from coastal waters of North and South America where it mainly occurs in estuaries and shallow nearshore marine habitats (Mallin, 1991; Caudill and Bucklin, 2004). This species was first recorded in Europe in the early twentieth century (Remy, 1927) and has since invaded estuaries and coastal marine waters throughout Europe (Brylinski, 1981; Cervetto *et al*., 1999; Vincent *et al*., 2002; Castro-Longoria, 2003; Pastorinho *et al*., 2003; Vieira *et al*., 2003; Tackx *et al*., 2004). The closest locality where *A. tonsa* was previously reported is the Tagus estuary (Sobral, 1985), about 350 km away on the western coast of Portugal. *A. tonsa* has been present in the Guadalquivir estuary at least since 1998 (J.A. Cuesta and P. Drake, pers. comm.). It is very possible that the invasion of the Guadalquivir estuary preceded 1998, as *A. tonsa* was already present in samples collected in Veta la Palma in 1994 (J.A. Cuesta, unpublished data). The Veta la Palma ponds are directly fed by water from the Guadalquivir estuary, which is certain to be the mode of invasion for *A. tonsa* in this site.

The overall dominance of calanoid copepods over cyclopoids and harpacticoids in the zooplankton of the Veta la Palma ponds is similar to the situation in brackish ponds in El Hondo in south-east Spain (Armengol-Diaz *et al*., 2002). However, the copepod species diversity at Veta la Palma is low, and cladocerans were missing in the ponds studied, possibly related to the impact of the *A. tonsa* invasion. If *A. tonsa* was absent from this site, it is inevitable that other filter-feeding zooplankton, e.g. cladocerans, would take its place, especially between October and April. The zooplankton community of the Veta la Palma wetlands is dominated by *A. tonsa* in the cooler season. The seasonal pattern of *A. tonsa* with its main abundance between October and April parallels findings in other south European estuaries (Pastorinho *et al*., 2003; Vieira *et al*., 2003). However, the seasonal pattern displayed by *C. aquae-dulcis* in the Veta la Palma study ponds appears to be unusual. Here, *C. aquae-dulcis* dominated the copepod community in the summer months when average monthly air temperatures were above 22°C, but had low abundance or was absent from the ponds during the colder months. It has been described as eurytherm, tolerating temperatures between 3 and 30°C (Dussart, 1969; Einsle, 1993), but usually with a preference for cooler temperatures. In El Hondo, south-west Spain, this species was present mainly during the winter months (Armengol-Diaz *et al*., 2002). Its main reproductive period has been reported as March and April (Dussart, 1969). At Veta la Palma, *C. aquae-dulcis* appears to have a different phenology, probably owing to the invasion by *A. tonsa*, and to have a competitive advantage over *A. tonsa* only during the summer months.

With respect to spatial distribution, there were differences in the relative and absolute abundance of *A. tonsa*. Since measurements of physicochemical variables are not available for the ponds studied, it is difficult to relate pond specific environmental conditions to community composition. However, as the ponds are managed for commercial culturing of fish, an effort is made by the pond management to create similar conditions, constantly exchanging water between the ponds by active pumping. Differences in water chemistry are therefore unlikely to have caused differences in species composition. Likewise, pond age did not seem important, since ponds of the same age (e.g. E3 and E4) differed in copepod composition. Stochastic factors appear to produce important differences in the structure of zooplankton communities between ponds (Jenkins and Buikema, 1998) and our results may have been related to differences between ponds in fish stocks and waterfowl use.

The exotic species *A. tonsa* has successfully invaded the Veta la Palma wetlands in Doñana Natural Park, evidently via the estuary. The dominance of this exotic species in Veta La Palma and its mode of invasion raises concern for the native copepod fauna in the brackish marshes in the southern part of the National Park. These natural marshes support a species-rich copepod community including copepods endemic to this area (Furest and Toja, 1981; Fahd *et al*., 2000). Although these marshes originally had an extensive hydrological connectivity with the river estuary, they are now isolated by a dyke constructed in 1984 (Figure 1), which has had the effect of increasing the volume of water that can be stored in the natural marshes during the winter. Under a restoration plan designed to restore the hydrology of the system, there is now a proposal to remove this dyke (Saura *et al*., 2001). This would lead to regular flooding of the southern part of the marshes from the estuary, providing *A. tonsa* with a clear invasion route into the marshes. Although most of the natural marshes have lower salinities than the Veta la Palma ponds, a future invasion by *A. tonsa* into other areas of Doñana is possible as it is able to survive salinities down to 1 psu (Cervetto *et al*., 1999). We suggest that research on the invasion biology of *A. tonsa* and of its effects on the native copepod community is urgently required before a final decision is made to remove the dyke.

ACKNOWLEDGEMENTS

Fieldwork was funded by the Consejería de Medio Ambiente, Junta de Andalucía. DF was supported by the European Community — Access to Research Infrastructure action of the Improving Human Potential Programme in Doñana Biological Station. Pesquerías Isla Mayor SA allowed us to work in 'Veta la Palma'. HRP had a PhD grant from the CSIC-I3P programme funded by the European Union Social Fund. Esther Garcia and José Antonio Perea helped us to collect samples in the field and David Aragones helped to make the map. John Baxter and an anonymous referee are thanked for their constructive criticism on the manuscript.

REFERENCES

Alonso M. 1990. Anostraca, Cladocera and Copepoda of Spanish saline lakes. *Hydrobiologia* **197**: 221–231.

Armengol-Díaz X, Rodrigo MA, Oltra R. 2002. Caracterización del zooplancton de la zona sur del Parque Natural del Hondo (Alicante). *Ecología* **16**: 243–257.

Baldó F, Taracido LJ, Arias AM, Drake P. 2001. Distribution and life history of the mysid *Rhopalophthalmus mediterraneus* in the Guadalquivir estuary (SW Spain). *Journal of Crustacean Biology* **21**: 961–972.

Brucet S. 2003. Zooplankton structure and dynamics in Mediterranean marshes (Empordà Wetlands): a size-based approach. PhD thesis, Universidad de Girona, Spain.

Brylinski J-M. 1981. Report on the presence of *Acartia tonsa* Dana (Copepoda) in the harbour of Dunkirk (France) and its geographical distribution in Europe. *Journal of Plankton Research* **3**: 255–260.

Cardona L, Royo P, Torras X. 2001. Effects of leaping grey mullet *Liza saliens* (Osteichthyes, Mugilidae) in the macrophyte beds of oligohaline Mediterranean coastal lagoons. *Hydrobiologia* **462**: 233–240.

Castro-Longoria E. 2003. Egg production and hatching success of four *Acartia* species under different temperature and salinity regimes. *Journal of Crustacean Biology* **23**: 289–299.

Castroviejo J. 1993. Mapa del Parque Nacional de Doñana. Consejo Superior de Investigaciones Científicas y Agencia de Medio Ambiente de la Junta de Andalucía, Madrid.

Caudill CC, Bucklin A. 2004. Molecular phylogeography and evolutionary history of the estuarine copepod, *Acartia tonsa*, on the Northwest Atlantic coast. *Hydrobiologia* **511**: 91–102.

Cervetto G, Gaudy R, Pagano M. 1999. Influence of salinity on the distribution of *Acartia tonsa* (Copepoda, Calanoida). *Journal of Experimental Marine Biology and Ecology* **239**: 33–45.

Cuesta JA, Serrano L, Bravo MR, Toja J. 1996. Four new crustaceans in the Guadalquivir River estuary (SW Spain), including an introduced species. *Limnética* **12**: 41–45.

Dussart B. 1967. *Les Copépodes des Eaux Continentales d'Europe Occidentale*. Vol. I: *Calanoïdes et Harpacticoïdes*. N. Boubee: Paris.

Dussart B. 1969. *Les Copépodes des Eaux Continentales d'Europe Occidentale*. Vol. II: *Cyclopoïdes et Biologie*. N. Boubée: Paris.

Einsle U. 1993. *Crustacea*: *Copepoda*: *Calanoida und Cyclopoida*. Gustav Fischer Verlag: Stuttgart.

Euliss NH, Jarvis RL, Gilmer DS. 1997. Relationship between waterfowl nutrition and condition on agricultural drainwater ponds in the tulare basin, California: waterfowl body composition. *Wetlands* **17**: 106–115.

Fahd K, Serrano L, Toja J. 2000. Crustacean and rotifer composition of temporary ponds in the Donana National Park (SE Spain) during floods. *Hydrobiologia* **436**: 41–49.

Figuerola J, Green AJ. 2004. Effects of seed ingestion and herbivory by waterfowl on seedling establishment: a field experiment with wigeongrass *Ruppia maritima* in Doñana, south-west Spain. *Plant Ecology* **173**: 33–38.

Figuerola J, Green AJ, Santamaria L. 2003. Passive internal transport of aquatic organisms by waterfowl in Doñana, south-west Spain. *Global Ecology and Biogeography* **12**: 427–436.

Furest A, Toja J. 1981. Ecosistemas acuáticos del Parque Nacional de Doñana: distribución del zooplancton. In *Primer Simposio sobre el Agua en Andalucía*, Grupo de Trabajo de Hidrogeologia de la Universidad de Granada, Granada, Spain; 151–167.

Green AJ, Sánchez MI. 2003. Spatial and temporal variation in the diet of Marbled Teal *Marmaronetta angustirostris* in the Western Mediterranean. *Bird Study* **50**: 153–160.

Grigorovich IA, MacIsaac HJ, Shadrin NV, Mills EL. 2002. Patterns and mechanisms of aquatic invertebrate introductions in the Ponto-Caspian region. *Canadian Journal of Fisheries and Aquatic Sciences* **59**: 1189–1208.

Heip C. 1975. Hibernation in the copepod *Halicyclops magniceps* (Lilljeborg, 1853). *Crustaceana* **28**: 311–313.

Hoffmeyer MS. 2004. Decadal change in zooplankton seasonal succession in the Bahía Blanca estuary, Argentina, following introduction of two zooplankton species. *Journal of Plankton Research* **26**: 181–189.

Hurlbert SH, Loayza W, Moreno T. 1986. Fish–flamingo–plankton interactions in the Peruvian Andes. *Limnology and Oceanography* **31**: 457–468.

Jenkins DG, Buikema AL. 1998. Do similar communities develop in similar sites? A test with zooplankton structure and function. *Ecological Monographs* **68**: 421–443.

Lee CE, Bell MA. 1999. Causes and consequences of recent freshwater invasions by saltwater organisms. *Trends in Ecology and Evolution* **14**: 284–288.

Lehman JT, Cáceres CE. 1993. Food-web responses to species invasion by a predatory invertebrate: *Bythotrephes* in Lake Michigan. *Limnology and Oceanography* **38**: 879–891.

Leppäkoski E, Gollasch S, Olenin S (eds). 2002. *Invasive Aquatic Species of Europe — Distribution, Impacts and Management*. Kluwer: Dordrecht.

Mallin MA. 1991. Zooplankton abundance and community structure in a mesohaline North-Carolina estuary. *Estuaries* **14**: 481–488.

Martí R, del Moral JC (eds). 2002. La invernada de aves acuáticas en España. Dirección General de la Naturaleza-SEO/BirdLife, Organismo Autónomo Parques Nacionales, Ministerio de Medio Ambiente: Madrid.

Martí R, del Moral JC (eds). 2003. *Atlas de las Aves Reproductoras de España*. Dirección General de Conservación de la Naturaleza y Sociedad Española de Ornitología: Madrid.

Pastorinho R, Vieira L, Ré P, Pereira M, Bacelar-Nicolau P, Morgado F, Marques JC, Azeiteiro U. 2003. Distribution, production, histology and histochemistry in *Acartia tonsa* (Copepoda: Calanoida) as means for life history determination in a temperate estuary (Mondego estuary, Portugal). *Acta Oecologica* **24**: 259–273.

Quintana XD, Comín FA, Moreno-Amich R. 1998. Nutrient and plankton dynamics in a Mediterranean salt marsh dominated by incidents of flooding. Part 2: Response of zooplankton community to disturbances. *Journal of Plankton Research* **20**: 2109–2127.

Remy P. 1927. Note sur un copépode de l'eau de saumâtre du canal de Caen á la mer, *Acartia tonsa*, Dana. *Annales de Biologie Lacustre* **15**: 169–186.

Rocha CEF, Iliffe TM, Reid JW, Suárez-Maorales E. 1998. A new species of *Halicyclops* (Copepoda, Cyclopoida, Cyclopidae) from Cenotes of the Yucatan peninsula, Mexico, with an identification key for the species of the genus from the Caribbean region and adjacent areas. *Sarsia* **83**: 387–399.

Ruiz GM, Fofonoff P, Hines AH, Grosholz ED. 1999. Non-indigenous species as stressors in estuarine and marine communities: assessing invasion impacts and interactions. *Limnology and Oceanography* **44**: 950–972.

Saura J, Bayán B, Casas J, Ruiz de Larramendi A, Urdiales C. 2001. Documento marco para el desarrollo del proyecto Doñana 2005. Ministerio de Medio Ambiente: Madrid.

Sobral P. 1985. Distribuçao de *Acartia tonsa* Dana no estuario do Tejo e sua relaçao com *Acartia claus* Giesbrecht. *Boletim do Instituto Nacional de Investigaçao das Pescas*, *Lisboa* **13**, 61–75.

StatSoft, Inc. 2001. Statistica (data analysis software system), version 6. www.statsoft.com.

Tackx MLM, De Pauw N, Van Mieghem R, Azémar F, Hannouti A, Van Damme S, Fiers F, Daro N, Meire P. 2004. Zooplankton in the Schelde estuary, Belgium and The Netherlands. Spatial and temporal patterns. *Journal of Plankton Research* **26**: 133–141.

Turki S, El Abed A. 1999. Nouvelles informations sur les copépodes calanoides et cyclopoides des eaux continentales tunisiennes. *Crustaceana* **72**: 157–169.

Vieira L, Azeiteiro U, Ré P, Pastorinho R, Marques JC, Morgado F. 2003. Zooplankton distribution in a temperate estuary (Mondego estuary southern arm: Western Portugal). *Acta Oecologica* **24**: 163–173.

Vincent D, Luczac C, Sautour B. 2002. Effects of a brief climatic event on zooplankton community structure and distribution in Arcachon Bay (France). *Journal of the Marine Biological Association of the United Kingdom* **82**: 21–30.

Williams WD. 1998. Salinity as a determinant of the structure of biological communities in salt lakes. *Hydrobiologia* **381**: 191–201.