J. Limnol., 63(Suppl. 1): 75-84, 2004

Use of ephippial morphology to assess richness of anomopods: potentials and pitfalls

Jochen VANDEKERKHOVE*, Steven DECLERCK, Maarten VANHOVE, Luc BRENDONCK, Erik JEPPESEN[1,2)], José Maria CONDE PORCUNA[3)] and Luc DE MEESTER

Laboratory of Aquatic Ecology (Katholieke Universiteit Leuven), Ch. de Bériotstraat 32, 3000 Leuven, Belgium
[1)]Department of Freshwater Ecology (The National Environmental Research Institute), Vejlsøvej 25, P.O. Box 314, DK-8600 Silkeborg, Denmark
[2)]Department of Plant Ecology, University of Aarhus, Nordlandsvej 68, DK-8240 Risskov, Denmark
[3)]Instituto del Agua (Universidad de Granada), Ramón y Cajal 4 (edif. Fray Luis de Granada) E-18071 Granada, Spain
*e-mail corresponding author: Jochen.Vandekerkhove@bio.kuleuven.ac.be

ABSTRACT

Zooplankton species richness is typically assessed through analysis of active community samples. These samples ought to be collected at many different locations in the lake and at multiple occasions throughout the year so as to cover the spatial and temporal heterogeneity in active community structure. A number of studies have shown that high numbers of species can be retrieved with a limited effort through hatching of dormant eggs isolated from lake sediments. However, dormant eggs of different species differ in their propensities to hatch, resulting in biased assessments of species composition, abundance and richness. In this paper, we explore the potentials and pitfalls of a third method to assess cladoceran species richness. For twenty European lakes, we identified the number of ephippium morphotypes in sediment samples taken on a single occasion. The morphotype richness was well correlated with species richness as assessed through hatching of dormant forms and through analysis of active community samples covering a six month period. However, not all species had a species-specific ephippial morphotype, consequently resulting in an underestimation of true species richness.

Key words: hatching, resting eggs, species richness, Cladocera, dormancy, ephippia

1. INTRODUCTION

Traditionally, zooplankton species richness is assessed through analysis of active community samples (AC samples; e.g. Fryer 1985; Armengol & Miracle 1999; Dodson 2000; Jeppesen *et al*. 2000). Using this approach, assessment of the number of species present over multiple seasons and years (i.e. total richness) requires elaborate sampling campaigns because of the high spatial and temporal variability in zooplankton community composition (Arnott *et al*. 1998; De Meester *et al*. 1999; Grover 1999; Burks *et al*. 2002). The number of sampling occasions can be reduced by identifying hatchlings isolated from lake sediment samples, as suggested by Jeppesen *et al*. (2003) and Brendonck & De Meester (2003). These authors suggest that seasonal and, to a limited extent, year-to-year variation observed in active communities is integrated in the dormant egg bank or as remains of other body parts like carapaces, headshields etc. This integration might result from a combination of processes, like sediment focussing, bioturbation (Kearns *et al*. 1996) and wind-borne resuspension events (Douglas & Rippey 2002). Vandekerkhove *et al*. (2004 a, submitted) indeed found an increasing taxonomical similarity between cladoceran assemblages hatched from single date sediment samples with assemblages in AC samples covering an increasing period of time (1 day to 5 years). Their results suggest that superficial sediment layers do contain a mixture of eggs deposited during different seasons and years.

Although the number of species hatched from sediment samples is typically higher than the number of species caught with snap-shot sampling the active community (May 1986, Havel *et al*. 2000; Crispim & Watanabe 2001; Duggan *et al*. 2002; Vandekerkhove *et al*. 2004 b, submitted), the resulting species lists are in both cases most likely incomplete and biased. Species lists acquired through hatching of dormant eggs are biased due to the fact that some populations seldom or never form resting eggs (Jeppesen *et al*. 2003) and to the variation among taxa in their response to specific hatching stimuli (Schwartz & Hebert 1987; Carvalho & Wolf 1989; Cáceres 1998). The latter source of bias can be partly ruled out by incubating the eggs under a wide range of hatching conditions (Vandekerkhove *et al*., in preparation), but this is time consuming and labor-intensive. An alternative approach is offered by direct identification of the dormant eggs. The latter approach is, however, hampered by the lack of knowledge of dormant egg morphology in the smaller zooplankton, such as the cladocerans. Another though more time consuming approach is to identify other body parts of zooplankton stored in the surface sediment (Frey 1986).

The scattered information currently available suggest that for the plethora of cladoceran groups, the variation in dormant egg morphology among species is quite limited. A noteworthy exception to this overall pattern is offered by Anomopoda, a highly diverse group, both morphologically and taxonomically. Anomopods enclose their dormant eggs in a protective envelope, called an ephippium. The most comprehensive published overview of ephippium morphology is included in the identification key for central European cladoceran species by Flößner (2000). Illustrations of ephippia are provided for about one third of the 114 species covered by this work. Bastiansen *et al*. (in preparation) did a vast literature survey and found drawings or pictures of the ephippia for a total of 101 species. These species covered almost half of the central European cladoceran fauna (47 of 114 sp.; Flößner 2000), but still only about a quarter of the known cladocerans.

In this paper, we assess the morphological richness of ephippia in sediments of 20 European lakes. Morphological richness (MORPH) is correlated to taxonomical richness, as assessed through analysis of AC samples and through hatching of dormant eggs (HATCH). Ephippia were incubated individually and hatchlings were reared and identified to species level to determine whether morphological characterisation of ephippia allows identifications at species level.

2. MATERIALS AND METHODS

The study lakes covered four European countries: Denmark (4 lakes), The Netherlands (2 lakes), Belgium (10 lakes) and Spain (4 lakes). Active communities were sampled monthly during the growing season (May-October) of 2000 or 2001, both in the littoral and the pelagic zone. For each lake, one pooled sample was created covering spatial and temporal variation. A more detailed account of active community sampling and processing is given at the website of the Bioman project (url: http://www.kuleuven.ac.be/bio/eco/bioman/).

Sediment samples were collected in between two growing seasons in 2001 at five randomly chosen locations each in the littoral and in the pelagic. After a pre-incubation period in the dark of at least six months in the refrigerator (temperature: 4 °C), a pooled sample was created for every lake covering the spatial variation in the dormant egg bank. Dormant eggs were isolated from sub-samples by the Onbé-Marcus method (Onbé 1978; Marcus 1990; Vandekerkhove *et al*. 2004, accepted) and randomly allocated to two treatments. One set of ephippia was used for direct morphological analysis. Additional sub-samples were processed for each lake until at least 35 ephippia were obtained or until there were no more ephippia. Pictures were taken of all ephippia retrieved from a given sub-sample. These ephippia were next individually incubated in 50 ml recipients at 15 °C and long day/short night conditions (16 h light per day, Vandekerkhove *et al*. 2004, in preparation). Hatchlings were transferred within 24 hours to 50-ml vessels with filtered pond water and fed with *Scenedesmus* (100,000 cells ml^{-1}). They were grown until they could be identified using Flößner (2000). In a second treatment, the taxonomic richness in the dormant egg bank was assessed in a more standardised way, where batches of isolated ephippia were incubated in 2-l aquaria, and subsequently identified to species level (Vandekerkhove *et al*. 2004, submitted b).

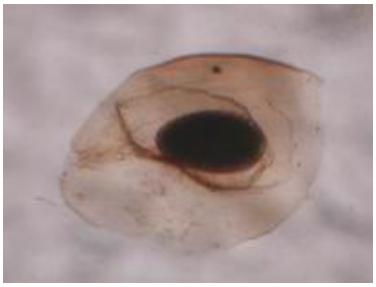
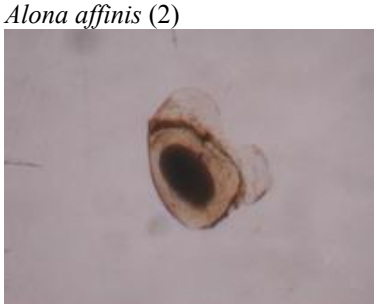
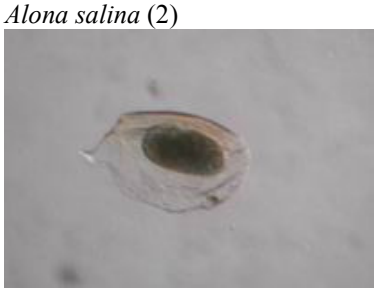
Ephippia were assigned to morphotypes based on their size, gross morphology and special features that were readily visible on digital pictures, like number, orientation and position of the eggs, position of spines and shape of the dorsal ridge. For lakes yielding at least 35 ephippia for morphological analysis, 35 hatchlings in the hatching experiments using dormant egg bank samples and 35 individuals in the AC samples, morphological and taxonomical richness was determined after rarefaction to 35 individuals (Primer 5.5.2; Clarke & Warwick, 1994), and compared among MORPH, HATCH and AC. Identifications were done by experienced limnologists.

3. RESULTS

A total of 698 ephippia was assigned to 21 different morphotypes (Tab. 1). The number of Anomopod morphotypes per lake significantly to marginally significantly correlated with the number of anomopod species yielded in hatchling assemblages and in AC samples, respectively (Fig. 1; MORPH – HATCH: $r = 0.65$, $P < 0.045$ and MORPH – AC: $r = 0.60$, $P < 0.067$). The number of anomopod species found in the hatchling assemblages was very well correlated with the number of anomopod species found in the AC samples (Fig. 1; AC – HATCH: $r = 0.78$, $P < 0.009$).

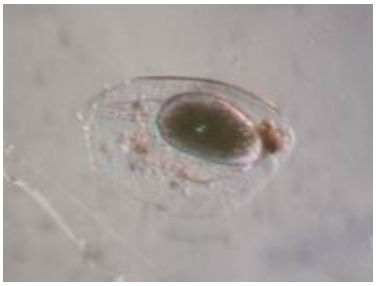
Of all isolated ephippia some contained one egg (Tab. 1; MT01 – MT09 + MT13 – MT18 + MT21), two eggs (MT10 – MT12 + MT20) or four eggs (MT19), of which about one third hatched. Morphotypes MT19 to MT21 yielded no hatchlings. Ephippia assigned to morphotype MT19 contained more than two eggs, typical for ephippia of primitive chydorids (e.g. *Eurycercus* sp.) and of macrothricids (e.g., *Ophryoxus* and *Lathonura* sp.; Fryer 1996). The MT19 ephippium, however, was found in a Danish lake where no such taxa occur in the hatchling assemblages (Vandekerkhove *et al*. 2004, submitted b) and in the active community (Declerck *et al*. 2004, in preparation). The MT20 morphotype could not unambiguously be assigned to a particular species. The current information on ephippium morphology suggests that no species in the AC samples nor in the hatchling assemblages of the lakes where the MT20 morphotype was collected, produces ephippia similar to the MT20 morphotype. The MT20 morphotype is highly similar to *Ilyocryptus* ephippia (K. Jensen, pers. comm.). Possibly, the ephippium was produced by an *Ilyocryptus* species (K. Jensen, pers. comm.).

Tab. 1. List of morphotypes detected in the present study. A picture is shown of the ephippium of each species hatched from a given morphotype. If no hatchlings were obtained, an unidentified ephippium assigned to the morphotype is provided. The name of the species and its number of hatchlings are written under each picture. ID: morphotype code (number of ephippia assigned to this morphotype is given in parenthesis). Characteristics: potential number of eggs per ephippium, size (maximum width parallel to dorsal ridge) and other morphological characteristics used in the present study to identify morphotypes.

 *Acroperus harpae* (24)	ID: MT01 (36) Characteristics: ➢ 1 egg ➢ 0.46 – 0.60 mm ➢ transparant ➢ narrowing sharply at posteroventral side
 *Alona affinis* (2)	ID: MT02 (3) Characteristics: ➢ 1 egg ➢ 0.52 – 0.58 mm ➢ transparent ➢ narrowing smoothly at posteroventral side
 *Alona rectangula* (5)	ID: MT03 (29) Characteristics: ➢ 1 egg ➢ 0.25 – 0.33 mm ➢ transparant ➢ caudally widening
 *Alona salina* (2)	ID: MT04 (21) Characteristics: ➢ 1 egg ➢ 0.33 – 0.41 mm ➢ dark coloured ➢ caudally widening
 *Bosmina longirostris* (15)	ID: MT05 (52) Characteristics: ➢ 1 egg ➢ 0.27 – 0.38 mm ➢ spine at lower side of caudal margin

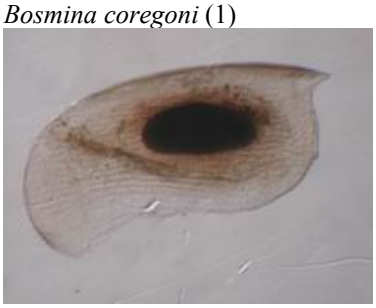
(continued)

Tab. 1. Continuation



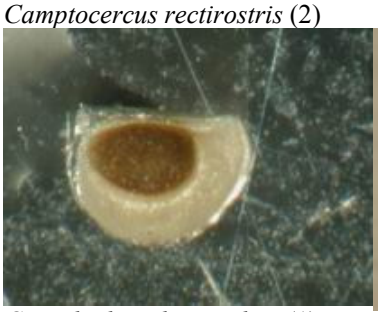
Bosmina coregoni (1)

ID: MT06 (1)
Characteristics:
- 1 egg
- 0.45 mm
- spine at upper side of caudal margin

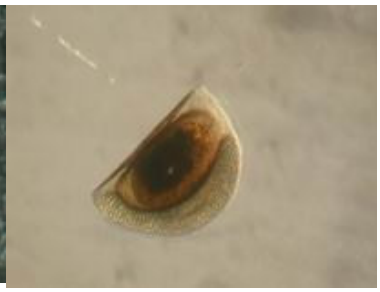


Camptocercus rectirostris (2)

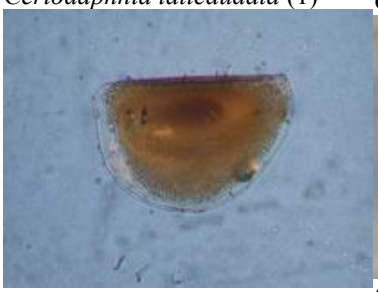
ID: MT07 (6)
Characteristics:
- 1 egg
- 0.66 – 0.93 mm
- height:width < 1:2



Ceriodaphnia laticaudata (1)



Ceriodaphnia pulchella (34)



Ceriodaphnia quadrangula (2)

Ceriodaphnia reticulata (6)

ID: MT08 (125)
Characteristics:
- 1 egg
- 0.30 – 0.47 mm
- egg in dorsal part
- often with floating cells
- symmetrical

Chydorus sphaericus (2)

ID: MT09 (7)
Characteristics:
- 1 egg
- 0.27 – 0.35 mm
- circular

(continued)

Tab. 1. Continuation

Daphnia magna (22)

D: MT10 (37)
Characteristics:
- 2 eggs
- 1.03 – 1.59 mm
- height:width < 1:1
- eggs more or less horizontal
- spine at anterior and posterior side

Daphnia galeata (23)

Daphnia pulex (11)

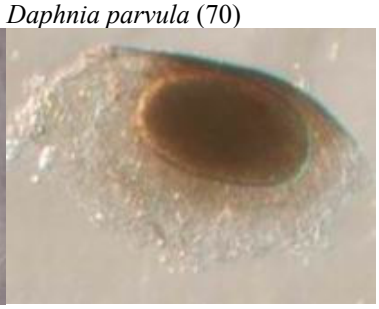
ID: MT11 (182)
Characteristics:
- 2 eggs
- 0.45 – 1.37 mm
- eggs vertical
- narrowing sharply at posteroventral side

Daphnia ambigua (15)

Daphnia parvula (70)

ID: MT12 (101)
Characteristics:
- 2 eggs
- 0.36 – 0.67 mm
- eggs vertical
- more or less symmetrical

Disparalona rostrata (1)



Rhynchotalona falcata (1)

ID: MT13 (12)
Characteristics:
- 1 egg
- 0.24 – 0.35 mm
- dorsal ridge concave
- egg in dorsal part

Graptoleberis testudinaria (2)

ID: MT14 (17)
Characteristics:
- 1 egg
- 0.33 – 0.40 mm
- transparent
- egg central in ephippium

(continued)

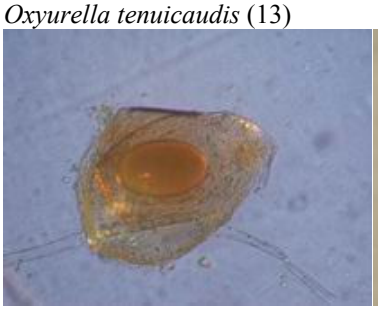
Tab. 1. Continuation

Leydigia acanthocercoides (2)

ID: MT15 (7)
Characteristics:
- 1 egg
- 0.37 – 0.56 mm
- opaque

Oxyurella tenuicaudis (13)

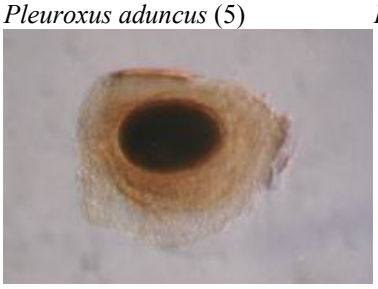
ID: MT16 (28)
Characteristics:
- 1 egg
- 0.37 – 0.51 mm
- egg in dorsal part



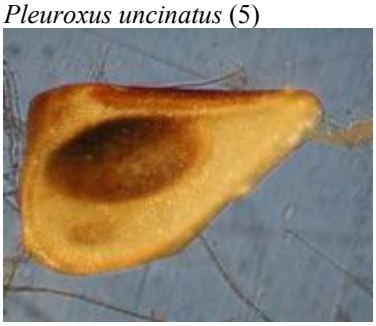
Pleuroxus aduncus (5)

Pleuroxus truncatus (1)

ID: MT17 (12)
Characteristics:
- 1 egg
- 0.36 – 0.51 mm
- height:width = 1:1



Pleuroxus uncinatus (5)



Simocephalus vetulus (3)

ID: MT18 (17)
Characteristics:
- 1 egg
- 0.66 – 0.89 mm
- narrowing sharply at posteroventral side

(continued)

Tab. 1. Continuation

 no hatchlings	ID: MT19 (1) Characteristics: ➢ > 2 eggs ➢ 1.54 mm ➢ height:width = 1:1
 no hatchlings	ID: MT20 (2) Characteristics: ➢ 2 eggs ➢ 0.22-0.36 mm ➢ height:width > 1:1
 no hatchlings	ID: MT21 (1) Characteristics: ➢ 1 egg ➢ 0.71 mm ➢ opaque

The MT21 ephippium contained a greenish egg, like the *Alona affinis* ephippia, but was larger and opaque. Possibly, the ephippium originated from *Alona quadrangularis*, a species very similar to *Alona affinis* that was observed in the corresponding active community.

Although 3 of 21 morphotypes refused to hatch, 26 species were identified from the remaining morphotypes (Tab. 1). This implies that several species share similar morphotypes. We found no clear-cut criteria to discriminate between ephippia of different *Pleuroxus* species (*P. aduncus, P. truncatus* and *P. uncinatus*), different *Ceriodaphnia* species (*C. laticaudata*, *C. pulchella*, *C. quadrangula* and *C. reticulata*) and between ephippia of *Daphnia ambigua* and *D. parvula*, *D. galeata* and *D. pulex*, and *Disparalona rostrata* and *Rhynchotalona falcata*.

4. DISCUSSION

Our results suggest that estimates of Anomopod species richness can be obtained using ephippial morphology, as such avoiding labour intensive sampling programmes or hatching of ephippia. For most lakes identification of the number of ephippium morphotypes in the sediment yielded a richness measure correlated with species richness as determined in hatching experiments and through standard sampling of the active community. Morphological richness was, however, better correlated with the species richness of the hatchling assemblages than with that in the AC samples. This suggests that a longer time lapse is integrated by the surface (3 cm) egg bank samples than by the AC samples, even though they were taken during six consecutive months.

The compilation of species lists through hatching of dormant eggs or through analysis of AC samples is hampered by species specific propensities to emerge (Herzig 1985) and the difficulty to cover the total heterogeneity in active communities, respectively (Arnott *et al*. 1998). In sediments of two out of twenty lakes, we discovered ephippia originating from species that were neither observed in the AC samples nor in the hatchling assemblage. The MORPH approach, however, also has some shortcomings, that are partly unrelated to those of the hatching approach. The latter is suggested by the highly significant HATCH-AC correlation, that contrasts with the low correlation between MORPH and HATCH. Morphologically very similar ephippia sometimes gave birth to multiple species. This was commonly observed in species similar in size and shape, like

Ceriodaphnia laticaudata, *C. pulchella*, *C. reticulata* and *C. quadrangula*.

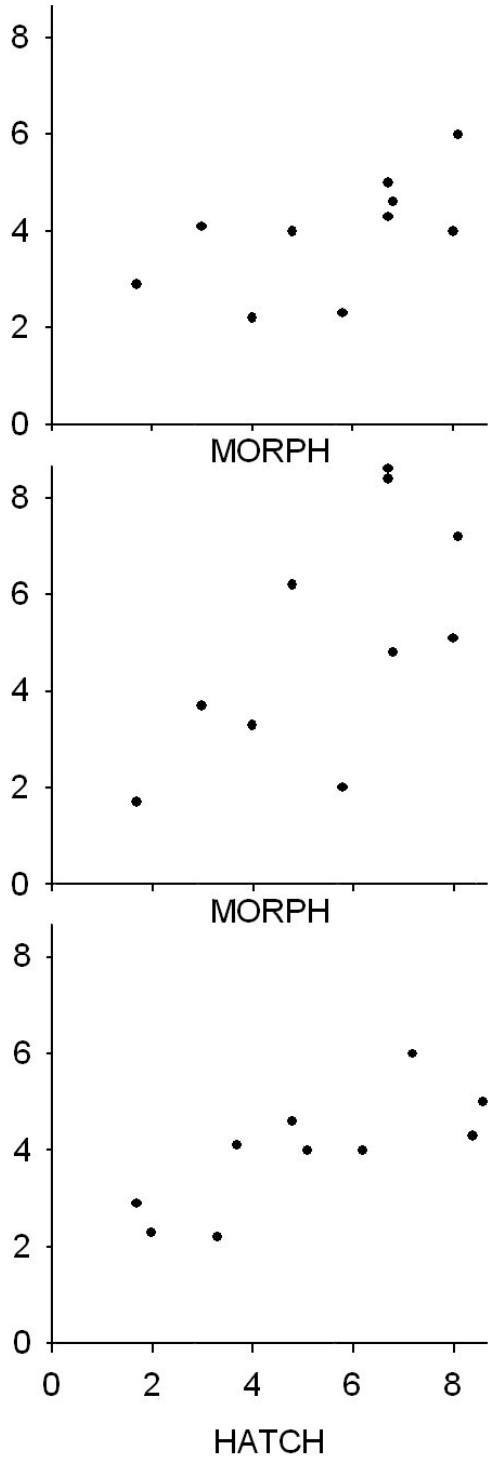


Fig. 1. Relationships between morphological richness of Anomopod ephippia (MORPH), species richness in corresponding active community samples (AC) and species richness in corresponding hatchling assemblages (HATCH) of 10 European lakes. Richness was assessed after rarefaction to 35 specimens, thereby excluding lakes for which less than 35 hatchlings or ephippia were observed.

The active individuals of these species are identified using characters not related to the general habitus of the animal, like the number of anal teeth on the postabdomen or the number of head pores (Flößner 2000). These characters are absent in ephippia, whose morphology is predominantly determined by the shape and size of the active individual but might in some cases be obtained from analysis of other remains in the sediment. Next to size and shape, also the number, orientation and position of the eggs, the number and position of spines and the shape of the dorsal ridge can be used as diagnostic features for the identification of sediment-borne ephippia. More research is needed to identify more diagnostic characters and to assess to what extent these characters have ecological instead of taxonomic relevance (Billiones *et al*. 2004, submitted). Gerrisch and Cáceres (2002) noticed that the percentage of the surface area of *Daphnia pulicaria* ephippia that is darkly pigmented ranged from 0.5 to 95.5%. Most of this variability was attributable to clonal variation, while environmentally induced variation was relatively small. Pigmentation of ephippia thus appears to be an unreliable character for species identification. Also, the size and shape of the ephippium may vary substantially within species. For example, in our study the size of *Daphnia magna* ephippia ranged from 1.03 to 1.59 mm. A similar size range for *D. magna* ephippia was revealed by Boersma *et al*. (2000; 1.14 to 1.53 mm), who showed that ephippial size of the ephippium is highly determined by the size of the mother. Similar observations are available for many other *Daphnia* species (Jeppesen *et al*. 2002). Billiones *et al*. (2004, in preparation) found that the shape of *Daphnia* ephippia was associated wih habitat type and size.

Identification of dormant eggs to species level based on their morphology is also difficult for rotifers. Duggan *et al*. (2002) identified seven to nine morphotypes in the sediments of two New-Zealand lakes using size and gross morphology. After hatching, however, two to three times more species emerged from the sediments than were recognized through morphological analysis.

5. CONCLUSIONS

Our results show that morphological analysis of ephippia allows a rapid first estimation of cladoceran species richness in shallow lakes. Only one sampling occasion is required and samples can be processed fast and immediately after collection. However, the low number of available diagnostic characters and the high intra-specific morphological variability of ephippia and low differences in morphology among some species preclude development of a user friendly key allowing species level identification of all Anomopod ephippia. Species with morphologically similar ephippia might be identified in lake sediments through analysis of preserved exoskeleton components (Frey 1986). The latter approach requires only a small amount of sediment, but

is time consuming as it involves preparation of microscope slides and detailed morphological analysis. Analysis of exoskeleton remains might be the only way to acquire accurate estimates of cladoceran richness in warm water lakes. In these lakes, production of ephippia tends to be very low (Jeppesen *et al*. 2003), so that large quantities of lake sediments have to be processed to retrieve sufficient numbers of ephippia.

ACKNOWLEDGMENTS

We thank the people from the Univeristy of Granada (J.M. Medina-Sánchez, J.A. Delgado-Molina, F. Bullejos and J. López-Ramos) and technicians at NERI (particularly K. Jensen and J. Stougaard-Petersen) for their help during the sampling campaign. Driss Cheheb is acknowledged for his help with the identification of ephippia. This study was supported by the EU-funded project BIOMAN (Biomanipulation and Human Impact in Shallow Lakes, EVK2-CT-1999-00046) and by the Danish Natural Science Research Council (research project "Consequences of weather and climate changes for marine and freshwater ecosystems. Conceptual and operational forecasting of the aquatic environment" (CONWOY).

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