Influence of gut morphology on passive transport of freshwater bryozoans by waterfowl in Doñana (southwestern Spain)

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Abstract: Waterbirds have been proposed as important vectors for the passive dispersal of those aquatic invertebrates and plants that lack a capacity for active dispersal between isolated water bodies. We analysed the frequency of internal transport of bryozoan propagules (statoblasts) by waterbirds in Doñana, Spain, by examining their presence in the intestines and ceca of dead birds and analysing the role of different aspects of gut characteristics in explaining variation in the presence/absence and abundance of statoblasts. Of the 228 samples examined, 7.9% presented intact statoblasts of *Plumatella fungosa* (Pallas, 1768), *Plumatella emarginata* Allman, 1844, and two unidentified *Plumatella* species. For a given bird species, individuals with heavier gizzards and shorter ceca had a lower incidence and abundance of statoblasts in the lower gut. Grit mass and intestine length were unrelated to the presence or abundance of statoblasts. Our results suggest that waterbirds frequently transport bryozoans on a local scale, with lighter gizzards and longer ceca favouring such transport. Lighter gizzards are likely to destroy fewer propagules before they reach the lower gut. Species and individuals with longer ceca are particularly good candidates for long-distance dispersal of bryozoans, given the longer passage time of propagules that enter the ceca.

Résumé : On croit que la sauvagine joue un rôle important comme vecteur de la dispersion passive entre les plans d'eau isolés des invertébrés et des plantes aquatiques qui ne possèdent pas de capacité de dispersion active. Nous avons analysé la fréquence du transport interne de propagules (statoblastes) de bryozoaires par la sauvagine à Doñana en cherchant leur présence dans l'intestin et les caecums d'oiseaux morts et en voyant comment les divers aspects des caractéristiques du tube digestif peuvent expliquer la variation de la présence/absence et de l'abondance des statoblastes. Des 228 échantillons analysés, 7,9 % contenaient des statoblastes intacts de *Plumatella fungosa* (Pallas, 1768), de *Plumatella emarginata* Allman, 1844 et de deux autres espèces non identifiées de *Plumatella*. Chez une même espèce d'oiseaux, les individus à fort gésier et à caecums courts présentent une incidence et une abondance moindres de statoblastes dans leur tube digestif inférieur. La masse de gravillons et la longueur de l'intestin n'influent pas sur la présence ou l'abondance de statoblastes. Nos résultats indiquent que les oiseaux aquatiques transportent souvent des bryozoaires à l'échelle locale, particulièrement ceux qui ont un gésier léger et des caecums longs, des caractères qui favorisent le transport. Les gésiers plus légers sont moins susceptibles de détruire les propagules avant qu'ils n'atteignent le tube digestif inférieur. Les individus et les espèces à caecums plus allongés sont des bons candidats pour le transport de longue distance des bryozoaires, parce que le temps de passage des propagules qui pénètrent dans les caecums est plus long.

[Traduit par la Rédaction]

Introduction

Freshwater bryozoans (Phylactolaemata) are common, sessile, colonial invertebrates; highly cosmopolitan species are distributed over most of the globe (Wood 2001). Sexual reproduction results in the production of short-lived larvae that generally settle and metamorphose near the mother colony (Mukai 1982). Reproduction is also achieved asexually by producing small (<1 mm) dormant buds (statoblasts). Statoblasts enable the recovery of populations after unfa-

vourable winter conditions (Okamura and Hatton-Ellis 1995), and their small size and capacity to resist desiccation, freezing, and ingestion by birds (Brown 1933; Charalambidou et al. 2003) make them good candidates for transport by migratory waterfowl both internally and externally (adhered to the plumage).

Recent genetic evidence for low levels of gene flow suggests that the bryozoan populations in different water catchments across Europe are not isolated and that dispersal of statoblasts occurs along waterbird flyways (Freeland et al.

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Table 1. Summary of gut and grit characteristics (mean ± SE; sample size in parentheses) for the species studied.

Bird species	Ceca length (cm)	Intestine length (cm)	Grit mass (g)	Gizzard mass (g)
Anas clypeata L., 1758	10.1±1.4 (24)	224.6±34.9 (24)	0.733±0.439 (23)	8.39±2.64 (20)
Anas crecca L., 1758	8.1±2.3 (3)	97.2±18.3 (3)	0.573±0.348 (3)	7.85±1.47 (2)
Anas platyrhynchos L., 1758	11.9±2.1 (52)	131.8±24.3 (52)	0.991±1.287 (39)	22.48±7.35 (47)
Anas strepera L., 1758	15.0±3.2 (14)	132.8±17.2 (14)	0.744±0.636 (14)	15.26±3.29 (5)
Anser anser (L., 1758)	23.2±3.2 (28)	224.2±28.2 (28)	20.070±10.020 (28)	194.42±67.48 (21)
Aythya ferina (L., 1758)	10.2±2.6 (6)	111.9±15.7 (6)	1.434±1.264 (7)	16.51±6.00 (7)
Fulica atra L., 1758	14.2±3.3 (69)	109.6±20.0 (69)	2.439±3.689 (67)	26.09±11.07 (65)
Gallinula chloropus (L., 1758)	9.2±3.3 (5)	67.6±20.1 (5)	2.402±2.020 (5)	11.72±5.25 (5)
Netta rufina (Pallas, 1773)	11.8±2.6 (7)	115.4±13.7 (7)	2.201±1.159 (7)	24.13±6.04 (7)
Porphyrio porphyrio (L., 1758)	8.0±1.5 (15)	75.4±13.5 (15)	4.804±3.964 (9)	21.85±11.43 (13)

Note: *Porphyrio porphyrio* and *Gallinula chloropus* are sedentary species; the other eight are migrants.

2000). However, little information is available on the frequency of transport of statoblasts by waterbirds in the field (Figuerola and Green 2002*a*). Recently, Figuerola et al. (2003) documented the presence of intact *Plumatella* sp. statoblasts in 3 of 401 fecal samples from migratory waterfowl in Doñana (southwestern Spain). In the same locality, no statoblasts were found adhered to the feathers or feet of 47 birds examined (Figuerola and Green 2002*b*), although anecdotal observations elsewhere indicate that *Cristatella mucedo* Cuvier, 1798 statoblasts (equipped with hooks, unlike *Plumatella* sp. statoblasts) adhere to waterfowl feathers (Bilton et al. 2001) and *Plumatella* sp. statoblasts can stick amongst mud to the feet of ducks (de Guerne 1888).

In this paper, we examine the presence of statoblasts in the lower gut of a range of waterbird species in Doñana. The gut morphology of a given waterfowl species varies greatly with diet, reproductive status, and other variables, and such variation can have major implications for passive dispersal of invertebrates and plants (Charalambidou and Santamaría 2002). We assess the effects of intraspecific variation in gut morphology and grit mass on the probability of transporting statoblasts internally and thus of dispersing bryozoans.

Materials and methods

Carcasses of 10 species of waterbirds (Table 1) were obtained from several sources. Carcasses included illegally shot birds confiscated by police and those found at recovery centers after a toxic spill in the Doñana area (Grimalt et al. 1999) or during an epidemic of unknown causes. Birds used in these analyses were collected during four time periods: 12 July 1997 to 2 February 1998, 26 June 1998 to 30 March 1999, 19 June 1999 to 14 February 2000, and on 27 October 2000. Birds were dissected, and the digestive tract from the gizzard below was removed and frozen until further analysis. At a later date, the samples were defrosted and the length of each extended intestine (excluding ceca) was measured to the nearest 0.5 cm before the intestines were emptied and their contents conserved in 70% alcohol. The two ceca were separated, their lengths measured to the nearest 0.5 cm, and the contents conserved in separate tubes in 70% alcohol. The average length of the two ceca was used in the statistical analyses. Hereinafter "intestines" refers to that part of the intestine excluding the ceca and "guts" refers to the intestines and ceca combined. Contents of intestines and ceca were

sieved using a 0.04-mm sieve and examined with a dissecting microscope. Intact statoblasts or fragments were counted and stored in absolute alcohol. The gizzard was weighed (wet mass, g) after removing its grit and food contents and drying excess water with tissue paper. The grit was separated from food material by decantation and then dried and weighed. Sample sizes varied slightly between different measurements because gizzards had been removed from some birds before we obtained them. The statoblasts present in the gizzards were not included in our analyses, as most were likely to be destroyed before passing into the intestines. However, once propagules reach the intestines intact, they are likely to survive until defecation (Charalambidou and Santamaría 2002).

Intact statoblasts collected from each gut were observed using a dissection microscope in an attempt to sort them to species level. Taxonomic resolution of many statoblasts requires observation of the fine structure of the chitinous statoblast valves; thus, scanning electron microscopy (SEM) was subsequently conducted on representatives of apparently different statoblasts to obtain information on the range of species present. For SEM, statoblasts representative of each putative species were cleaned with detergent in an ultrasonic cleaning bath for 3 min, washed in distilled water, dehydrated in graded acetones over 2 h, and air-dried. Dried statoblasts were mounted on aluminium stubs, sputter-coated with gold, and oven-dried for 10 min at 60 °C. They were examined with a JEOL JSM-T300 scanning electron microscope.

All statoblasts found were from the genus *Plumatella*. The statoblasts from different species were pooled for statistical analysis because they were not all identified to the species level. Furthermore, because their gross morphology was similar (Fig. 1), we did not expect that survival of gut passage would vary among the bryozoan species found in our study.

Statistical analyses

The presence/absence and abundance (excluding counts of zero) of bryozoan statoblasts in lower guts were analysed separately using general linear modelling (McCullagh and Nelder 1989). For presence/absence data, the dependent variable was modelled using a binomial error distribution and logit link. Data on statoblast abundance were analysed using a gamma error distribution and an inverse link, be-

Fig. 1. SEM image of a *Plumatella fungosa* statoblast.

40 µm
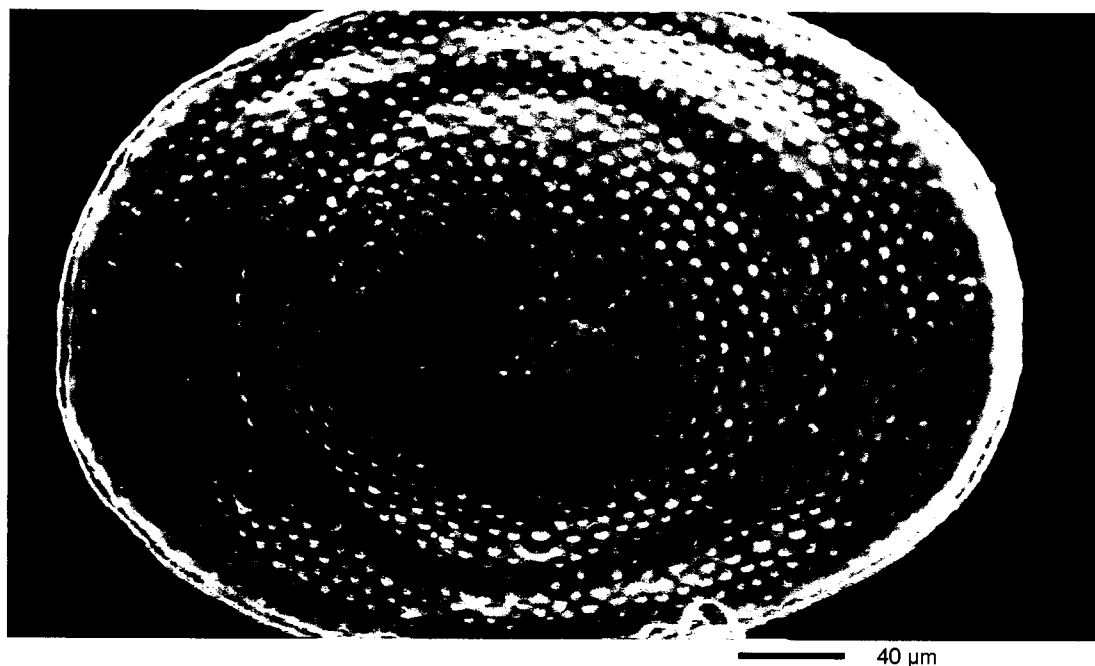
Table 2. Number of waterbirds sampled (*n*), number of individuals with intact and (or) fragmented bryozoan statoblasts in the ceca, intestines, or both, and range for the number of intact statoblasts reported in the lower gut.

Bird species	*n*	Ceca	Intestines	Ceca and intestines	Range
Anas clypeata	24	1/1	1/1	1/1	27
Anas crecca	3	0/0	0/0	0/0	
Anas platyrhynchos	53	8/10	2/2	8/10	1–74
Anas strepera	14	0/1	0/0	0/1	
Anser anser	29	0/0	1/1	1/1	1
Aythya ferina	7	0/1	0/0	0/1	
Fulica atra	69	5/6	3/3	7/8	1–27
Gallinula chloropus	5	0/0	0/0	0/0	
Netta rufina	7	1/1	0/0	1/1	1
Porphyrio porphyrio	17	0/0	0/0	0/0	

Note: The number to the left of a slash refers to the number of samples with intact statoblasts, and the number to the right refers to the total number of samples with statoblasts (whether intact or fragmented).

cause the gamma distribution adjusted better to our count data than the poisson distribution, as shown by the over-dispersion observed in models fitted with the poisson distribution (see Crawley 1993). An initial model including all the independent variables (intestine length, ceca length, gizzard mass, grit mass) was adjusted to the data, and we selected the final regression model using backwards selection, retaining those variables significant at an alpha level of 0.10. For variables excluded from the final model, the tests presented in the paper correspond to the significance of the partial regression coefficients (with *F* tests) when the variable was added to the final reduced model.

The bird species from which each gut sample was obtained was included in the analysis as a random factor, since we were not interested in the differences between particular species but in how intraspecific morphological variation affects the probability of dispersal of bryozoans. Furthermore, there is great variation in gut morphology between members of a given species, and much overlap between the gut morphology of most of the species studied (Table 1). By controlling for bird species as a random factor, we tested the effect of intraspecific variation in gut morphology but not the effect of interspecific variation, which is confounded with other differences in distribution, habitat use, etc. All analyses were run with the macro GLIMMIX for SAS version 8.2 (SAS Institute Inc. 2000).

Results

Intact statoblasts were present in 18 (7.9%) of the 228 lower gut samples examined, and 23 (10.6%) contained intact and (or) identifiable fragments of statoblasts (Table 2). Statoblasts in 18 of the gut samples were examined for bryozoan identification. All statoblasts were floatoblasts of the genus *Plumatella*. Statoblasts of both *Plumatella fungosa* (Pallas, 1768) (Fig. 1) and *Plumatella emarginata* Allman,

1844 were identified, along with two apparently undescribed species (T. Wood, personal communication).

Presence/absence of statoblasts

For a given species, birds with heavier gizzards tended to have a lower incidence of statoblasts or their remains in their lower guts ($F_{[1,181]} = 3.62$, $P = 0.06$). Birds with longer ceca had a significantly higher incidence of statoblasts in their guts ($F_{[1,181]} = 8.12$, $P = 0.005$). Neither intestine length ($F_{[1,180]} = 0.28$, $P = 0.60$) nor grit mass ($F_{[1,166]} = 0.54$, $P = 0.46$) explained a significant amount of variance in the presence/absence of statoblasts. When we focussed only on the presence of intact statoblasts, ceca length was the only variable entering the model ($F_{[1,179]} = 4.98$, $P = 0.03$). None of gizzard mass ($F_{[1,179]} = 2.49$, $P = 0.12$), grit mass ($F_{[1,164]} = 0.19$, $P = 0.66$), or intestine length ($F_{[1,178]} = 0.22$, $P = 0.64$) improved the fit of the model.

Presence of statoblasts in the intestines (all intestine samples with statoblast fragments also contained intact statoblasts) was not significantly explained by any of the variables considered. None of intestine length ($F_{[1,225]} = 0.99$, $P = 0.32$), ceca length ($F_{[1,224]} = 0.07$, $P = 0.80$), gizzard mass ($F_{[1,196]} = 0.00$, $P = 0.97$), or grit mass ($F_{[1,206]} = 0.18$, $P = 0.68$) influenced the probability of finding statoblasts in the intestines.

However, the presence of statoblasts (intact or fragmented) in the ceca was negatively related to gizzard mass ($F_{[1,178]} = 6.61$, $P = 0.01$) and positively related to ceca length ($F_{[1,178]} = 14.12$, $P = 0.0002$). The presence of statoblasts in the intestines was positively related to the probability of finding statoblasts in the ceca ($F_{[1,178]} = 15.03$, $P = 0.0001$). However, neither intestine length ($F_{[1,177]} = 1.23$, $P = 0.27$) nor grit mass ($F_{[1,163]} = 0.00$, $P = 0.95$) improved the fit of the model containing the above three predictors. The results for the presence of intact statoblasts only indicated the same significant relationships with gizzard mass ($F_{[1,178]} = 5.20$, $P = 0.02$), ceca length ($F_{[1,178]} = 10.10$, $P = 0.002$), and presence of statoblasts in the intestine ($F_{[1,178]} = 15.98$, $P < 0.0001$), and similar nonsignificant relationships with grit mass ($F_{[1,163]} = 0.26$, $P = 0.61$) and intestine length ($F_{[1,177]} = 1.42$, $P = 0.23$).

Abundance of intact statoblasts

The abundance of statoblasts in the lower guts was negatively related to gizzard mass ($F_{[1,10]} = 5.70$, $P = 0.04$). A nearly significant negative correlation with intestine length was detected ($F_{[1,10]} = 4.03$, $P = 0.07$). Neither grit mass ($F_{[1,6]} = 2.02$, $P = 0.21$) nor ceca length ($F_{[1,9]} = 0.13$, $P = 0.73$) improved the fit of the model containing the above two predictors.

Abundance of statoblasts in the ceca was greater in birds with smaller gizzards ($F_{[1,11]} = 9.22$, $P = 0.01$) and longer ceca ($F_{[1,11]} = 5.67$, $P = 0.04$). However, neither grit mass ($F_{[1,7]} = 0.21$, $P = 0.66$) nor intestine length ($F_{[1,10]} = 3.00$, $P = 0.11$) improved the fit of the model. Abundance of statoblasts in the intestine was not significantly related to any of the variables analysed: gizzard mass ($F_{[1,10]} = 1.48$, $P = 0.25$), grit mass ($F_{[1,7]} = 2.43$, $P = 0.16$), ceca length ($F_{[1,11]} = 1.38$, $P = 0.26$), or intestine length ($F_{[1,11]} = 2.33$, $P = 0.15$).

Discussion

This study suggests that waterbirds have an important role in the passive transport of bryozoan propagules within and between wetlands. By examining the contents of the final part of the digestive tract, where little further digestion takes place, we found intact statoblasts (from four different *Plumatella* species) in 7.9% of the birds examined. Waterbirds are abundant in Doñana: winter counts of migratory Anatidae alone exceed 300 000 individuals (Martí and del Moral 2002). Thus, even this low percentage of birds transporting bryozoans suggests that several tens of thousands of birds are dispersing bryozoans on a daily basis within our study area. Although we have not tested the viability of these propagules, previous experiments have demonstrated that a small proportion of bryozoan statoblasts ingested by birds survive digestion and hatch into small colonies (Brown 1933; Charalambidou et al. 2003). The frequent presence of statoblasts recorded in the lower guts of waterbirds from Doñana contrasts with the lower frequency reported in droppings from the same area (0.7%, Figuerola et al. 2003), since some of the carcasses were collected at the same time and place as the droppings. This difference is probably due to the fact that the contents of a gut are excreted in a large number of droppings.

As well as the bryozoans observed in this study, ducks in Spain have been found to present statoblasts of *Plumatella repens* L., 1785, *C. mucedo*, and *Fredericella sultana* (Blumenbach, 1779) in their gizzards (Sánchez et al. 2000; Fuentes et al. 2004). Passive transport over short distances (e.g., as birds move between feeding and roosting sites) seems certain to occur on a regular basis, but are bryozoans undergoing long-distance dispersal via waterbirds? Most of the bird species studied are migrants that make long-distance movements from Doñana to Northern Europe or Africa (see Scott and Rose 1996). Charalambidou et al. (2003) demonstrated that statoblasts of *C. mucedo* were retained for up to 44 h inside duck guts, although most of the propagules were defecated in the first 4 h after ingestion. The longer retention times suggest the possibility of low-frequency transport between water bodies separated by hundreds of kilometres. However, transport of propagules may not result in effective gene flow if the transported propagules cannot become established owing to competition with a locally adapted and saturated population (De Meester et al. 2002).

We have shown that for a given bird species, certain morphological characteristics of individuals are associated with a high probability of presence and (or) higher abundance of statoblasts in their gut. Birds with smaller gizzards and longer ceca (Table 1) are likely to be good candidates for the transport of propagules, since these variables are associated with a high frequency and abundance of bryozoan statoblasts. Consequently, gizzard mass and ceca length could be considered characteristics associated with disperser quality (sensu Schupp 1993). The relevance of gizzard size at the interspecific level has recently been illustrated by a study of the community of waterbirds in Doñana dispersing seeds of *Ruppia maritima* L. Species with smaller gizzards dispersed a higher proportion of ingested seeds than species with larger gizzards, which digested a higher proportion of ingested seeds (Figuerola et al. 2002). In our study, the rele-

vance of gizzard size is probably due to a higher probability of detecting both intact propagules and their remains. Larger gizzards will destroy a higher fraction of ingested statoblasts, making it harder to detect their presence in the intestines. Diet is related to intra- and interspecific variation in gizzard size in ducks and waders (Kehoe et al. 1988; Piersma et al. 1993). Consequently, individuals or species feeding on softer prey seem more likely to disperse a large fraction of ingested propagules.

An alternative explanation for our results is that within a given species, individuals with smaller gizzards consume more statoblasts. Although little information is available on the relevance of bryozoans in waterfowl diet, the patchy distribution of bryozoans in the field (Okamura and Hatton-Ellis 1995) and the dependence of waterbirds on other more abundant resources (e.g., macrophytes, on which bryozoans grow, and a wide range of invertebrates; Green et al. 2002) make this explanation unlikely. We are aware of only one study of waterfowl diet in which bryozoans were found to be an important food item (Taylor 1978). We suspect that the *Plumatella* sp. statoblasts in our samples were ingested incidentally when waterfowl were feeding on plants or other invertebrates, or drinking. In a year-round study at El Hondo, Spain, *Plumatella* sp. statoblasts were found on the surface at wetland margins at a density of 98 m^{-2}, and were also abundant in sediments (C. Fuentes and A.J. Green, unpublished data). On the other hand, it is clear that differences in ecology between waterbird species should translate into differences in the ingestion rate of statoblasts (Green et al. 2002), and it is for this reason that we have confined our analyses to intraspecific patterns.

We have also found ceca length to be correlated with the presence and abundance of propagules at an intraspecific level. The functions of intestinal ceca are not clearly understood (see review in Clench and Matthias 1995), but it appears that a certain degree of fermentation takes place there and that solid particles are attacked by bacteria and fungi (McNab 1973). Although it has been demonstrated that birds can partially empty the ceca, cecal contents can be retained for longer periods than intestinal contents (Clench and Mathias 1992), and thus propagules are likely to accumulate there. Malone (1965) and Proctor et al. (1967) demonstrated that brine shrimp (*Artemia* sp.) eggs retained in the ceca took two to three times longer to come out in feces than eggs that bypassed the ceca. Thus, propagules retained in the ceca may be particularly prone to long-distance dispersal. Again, an alternative explanation for the greater presence of statoblasts in longer ceca could be that for a given species, individual birds with longer ceca consume more statoblasts. This seems unlikely, since species with longer ceca are predominantly herbivorous (Barnes and Thomas 1987; Clench and Mathias 1995), although statoblasts may be consumed incidentally during feeding on aquatic macrophytes. However, current knowledge of digestive function in birds suggests that our results are due to the higher destruction of statoblasts by birds with heavier gizzards and the higher probability of retention in longer intestinal ceca.

Although we found no significant partial effect of grit mass in our analyses, this may be because grit mass was correlated with gizzard mass ($F_{[1,167]} = 199.14$, $P < 0.0001$). Larger gizzards tend to hold more grit, which is likely to in-

crease the probability that propagules will be destroyed by crushing. Adding grit to the ingesta decreases the proportion of *Artemia* sp. eggs that survive gut passage (Charalambidou and Santamaría 2002).

In summary, our results suggest that for a given waterbird species, the individuals that play the most significant role in dispersing bryozoans will be those birds with smaller gizzards and longer ceca. Further research is required to establish whether this is the case for dispersal of propagules of other aquatic invertebrates and of plants, and how bird gut morphology affects propagule retention time and viability. Waterbirds show great plasticity in the size and functioning of their guts. This plasticity is not fully understood but is known to be related to diet, reproductive status, gender, or preparation for migratory movements (see Piersma and Lindström 1997; Charalambidou and Santamaría 2002 for reviews). Such plasticity has important implications for the role of waterbirds in dispersing other aquatic organisms. Dispersal mediated by waterbirds can help explain the rapid expansion of some exotic species. For example, *Pectinatella magnifica* (Leidy, 1851) was first cited in France in summer 1994 and rapidly expanded its distribution to a great part of France, from Vosges to the meridional area of the Rhone Valley (Rodriguez and Vergon 2002). This and other similar cases of range expansion of aquatic invertebrates provide exciting opportunities to test the relevance of bird-mediated dispersal and other possible mechanisms (e.g., watercourses, wind, and man) in explaining the distribution and dispersal of aquatic organisms.

Acknowledgements

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