

OPINION

# Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies

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## SUMMARY

1. Inland wetlands constitute ecological islands of aquatic habitat often isolated by huge areas of non-suitable terrestrial habitats. Although most aquatic organisms lack the capacity to disperse by themselves to neighbouring catchments, many species present widespread distributions consistent with frequent dispersal by migratory waterbirds.
2. A literature review indicates that bird-mediated passive transport of propagules of aquatic invertebrates and plants is a frequent process in the field, at least at a local scale. Both endozoochory (internal transport) and ectozoochory (external transport) are important processes.
3. The characteristics of the dispersed and the disperser species that facilitate such transport remain largely uninvestigated, but a small propagule size tends to favour dispersal by both internal and external transport.
4. We review the information currently available on the processes of waterbird-mediated dispersal, establishing the limits of current knowledge and highlighting problems with research methods used in previous studies. We also identify studies required in the future to further our understanding of the role of such dispersal in aquatic ecology.

*Keywords:* dispersal capacity, seed dispersal, egg dispersal, habitat colonisation, community composition

## Introduction

Continental wetlands usually consist of isolated units of temporary or permanently flooded areas in a 'sea' of habitat not suitable for aquatic organisms. Many aquatic plants and invertebrates lack the mobility necessary to travel directly from one catchment to another, to colonise new areas and to disperse to neighbouring water bodies in different catchments. Despite this apparent isolation of freshwater habitats, many aquatic plant and invertebrate species have widespread distributions (Good, 1953; Raven, 1963; Sculthorpe, 1967; Brown & Gibson, 1983; WCMC, 1998), spanning several continents in some cases. Although

some recent genetic studies have demonstrated that some 'species' are in fact morphologically similar complexes of sibling species (Hebert & Wilson, 1994), others have identified widely distributed species (Hebert & Finston, 1996). However, there are also numerous aquatic organisms with very restricted distributions (Frey, 1987; Stemberger, 1995). One major reason for such differences is that widespread species have a greater capacity to disperse and can thereby colonise new areas and maintain gene flow between different areas (Bohonak, 1999; Clobert *et al.*, 2001).

Passive dispersal capacity is a key trait explaining patterns of distribution and community composition of non-mobile organisms (Jenkins & Buikema, 1998). For example, Primack & Miao (1992) showed that limited dispersal capacity can restrict the distribution of many terrestrial species of plants. Similarly, despite the high potential for seed dispersal by water

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currents, the same occurs in *Zostera marina*, a marine macrophyte, 80% of seedlings were found less than 5 m away from the mother plant (Orth, Luckenbach & Moore, 1994). Dispersal capacity is also of vital importance in determining responses to climatic changes (Davis, 1989; Graham, Turner & Dale, 1990).

Although there is much information available about animal-mediated dispersal in terrestrial ecosystems (see reviews in Sorensen, 1986; Traveset, 1998), relatively little is known about the processes affecting long-distance dispersal between aquatic habitats, where waterbirds presumably are an important vector.

Many waterbirds undertake long migratory journeys from their breeding areas at extreme latitudes towards more temperate areas during the winter (del Hoyo, Elliott & Sargatal, 1992). Waterbirds have long been considered a major disperser of aquatic organisms, transporting plant and invertebrate propagules in their guts (endozoochory or internal dispersal) or attached to their bodies (ectozoochory or external dispersal) (Darwin, 1859; Ridley, 1930). However, most evidence for such dispersal by waterbirds is anecdotal and detailed quantitative investigations on the patterns of such transport are very scarce (see our review below). Recent indirect evidence supporting the role of long-distance dispersal by waterbirds comes from studies of the genetic population structure of different aquatic species. Most of these studies have concluded that geographical distance is usually unrelated to the genetic distance between populations (Hebert & Finston, 1996; Hollingsworth, Preston & Gornall, 1996; Vanoverbeke & DeMeester, 1997; Mader, van Vierssen & Schwenk, 1998; Freeland, Noble & Okamura, 2000). One exception is a study of the fennel pondweed *Potamogeton pectinatus* in Europe (Mader *et al.*, 1998). However, in this case the association between genetic and geographic distances was only significant for ponds not visited by swans during migration (considered the main potential disperser of *P. pectinatus* in the study area). The genetic distribution of *Daphnia laevis* reflects the major waterfowl (ducks, geese and swans) flyways in North America, with higher similarity between populations in a North-South than an East-West direction (Taylor, Finston & Hebert, 1998). Similarly, the genetic distribution of the bryozoan *Cristatella mucedo* in northern Europe follows the major waterfowl flyway in this region (Freeland *et al.*, 2000). However, the lack of association between genetic and geographic distances

in aquatic organisms does not constitute direct evidence supporting bird-mediated dispersal, but rather indicates that populations are not at equilibrium, or that colonisation events are independent of geographic distance. This may be because dispersal is more frequent in the direction of bird migration or between major stopover areas, but alternatively may be because loss of alleles as a result of drift is not balanced by their replacement by gene flow between populations in a region (McCauley, 1993).

In this paper we review the research conducted to date on waterbird-mediated dispersal of aquatic organisms, highlighting the series of processes involved and assessing the likely frequency of such dispersal in the field. We concentrate on quantitative and semiquantitative studies rather than anecdotal observations. We identify pitfalls and limitations of existing studies and methodologies and highlight some of the key questions that remain unanswered in this field. Finally, we identify some priorities for future research on the processes involved in the dispersal of aquatic organisms by birds. In this review, we do not deal with the question of how well a propagule is likely to compete to establish itself in an aquatic community once it has been dispersed by a waterbird (e.g. questions such as whether that propagule will be well adapted to the new environment, whether it can compete with conspecifics already present, or whether the arrival of a new genotype would be detectable given the size of existing seed or propagule banks in the wetland).

### **Internal transport step 1: do waterbirds consume propagules?**

To facilitate internal dispersal, waterbirds first need to ingest propagules of aquatic organisms. Such ingestion may be voluntary when the propagules themselves constitute the foraging resource exploited by the animals, or involuntary when propagules are ingested with leaves, invertebrates or other preferred food items. The relative frequency of dispersal may be higher following involuntary digestion, as seed-eating birds can destroy most seeds ingested, whereas ingestion of seeds by consumers of leaves or insects may have less impact on their viability. Thus, in a given bird community, some species may be legitimate seed dispersers and others seed predators (Jordano, 1992; Traveset, 1998).

Diet studies of migratory waterfowl (Anatidae) have shown that they consume large quantities of propagules of aquatic organisms from a wide variety of species. This is especially the case for duck species (see, e.g. Cramp & Simmons, 1977; Thomas, 1982; Batt *et al.*, 1992). The filter-feeding method typically used by ducks is relatively unselective, and they typically ingest various classes of food items at a given time. It is thus difficult *a priori* to assess whether seeds and other propagules are ingested voluntarily or not.

Coots (*Fulica* sp.), flamingoes (*Phoenicopterus* sp.) and other groups of waterbirds also consume important quantities of seeds and other propagules (e.g. Cramp & Simmons, 1977). Waders (Charadriidae and Scolopacidae) are a particularly interesting group because of their long-distance migrations and capacity for long-distance dispersal. Many species consume invertebrates that may contain resting eggs (Cramp & Simmons, 1983), and some species often ingest seeds of saltmarsh plants (Pérez-Hurtado, Goss-Custard & Garcia, 1997).

Diet studies of waterbirds generally have an aut-ecological perspective focussing on the nutritional or habitat requirements of the waterbird species and, while giving information about the ingestion of propagules, they do not consider whether or not such propagules survive digestion. Most studies are carried out on oesophagus or gizzard contents, but even diet studies via faecal analyses do not consider how many propagules survive ingestion intact (e.g. Pérez-Hurtado *et al.*, 1997; Green & Selva 2000).

### Internal transport step 2: can propagules survive digestion by waterbirds?

Various experiments on the survival of invertebrate and plant propagules after digestion by waterbirds have been carried out by feeding a large number of propagules to captive-reared ducks or waders (Table 1). Droppings were generally collected for a variable number of hours after consumption of the seeds (usually 24 h or less, but Proctor, 1968, included droppings collected at least 10 days after the feeding of the propagules), and the intact propagules were then cultured in the laboratory to assess their viability. These experiments have shown that a range of seeds, oospores, phytoplankton spores and crustacean eggs can survive digestion (see Table 1). For most of the species tested, some propagules survived digestion,

except for phytoplankton where, amongst seven algae species tested, only the spores of one diatom germinated after digestion (Atkinson, 1970, 1971).

Some of these studies compared the survival of different species after digestion to investigate which propagule characteristics favour internal transport by birds. These studies have produced contradictory results. De Vlaming & Proctor (1968) tested the resistance of seeds of 23 wetland plant species to digestion by mallard *Anas platyrhynchos* and killdeer *Charadrius vociferus*. They concluded that resistance to digestion is higher for small seeds with hard covers and is also affected by the characteristics of the disperser species (gizzard structure and retention time of seeds in the gut were proposed as the most important characteristics). In a similar study with mallard, Holt (1999) concluded that resistance to digestion was unrelated to size and lignin content in seeds of eight wetland plant species. However, she reported that the proportion of non-destroyed seeds germinating after ingestion by birds was positively associated with the size and lignin content of the seeds.

The study of the propagule characteristics that facilitate survival after digestion is important in order to understand the factors that affect the colonisation and dispersal capacities of different aquatic organisms. However, various problems limit the usefulness of the experimental set-ups used so far to address this topic. First, the numbers of birds used in these studies were very low (Table 1) and sometimes not stated by the authors, making it hard to interpret the results obtained given the high intraspecific variability in the structure and size of the digestive organs of waterbirds (Kehoe, Ankney & Alisauskas, 1988). Secondly, various factors can affect the structure of digestive organs of captive waterbirds, including time in captivity (Clench & Mathias, 1995) and diet (Al-Dabbagh, Jiad & Waheed, 1987). This makes results difficult to compare between studies. Although we can be confident of results obtained by feeding different seed types simultaneously to the same individual bird, the percentage of seeds surviving digestion reported in different studies are not directly comparable, as differences in seed viability between studies could be because of either the characteristics of the seeds or the characteristics of the birds used in the experiment (even when either dispersed or disperser organisms belong to the same species).

**Table 1** Summary of experiments carried out to test the viability of propagules after digestion by waterbirds. The number of individual birds used in the experiments is reported in brackets

Propagule species	Disperser species	Summary of main results	Reference
Eggs of two gastropods	<i>Anas platyrhynchos</i> (5) <i>Charadrius vociferus</i> (10)	A small proportion of the eggs of two species of gastropoda remained viable after digestion	Malone (1965b)
<i>Artemia</i> (Crustacea)	<i>Anas platyrhynchos</i> (5–20)	Some survived passage, eggs entering in the ceca are retained for much longer than expected from intestine length	Malone (1965a)
<i>Artemia</i>	<i>Tadorna tadorna</i> (2)	Hatching efficiency of cysts was unchanged by passage through <i>Ph. Ruber</i> , and reduced by <i>T. tadorna</i>	MacDonald (1980)
Twelve genera of crustaceans	<i>Phoenicopterus ruber</i> (2)	Some species hatched after digestion, others did not	Proctor (1964)
<i>Artemia</i> , other invertebrates, algae and <i>Chara</i> (Characeae)	<i>Anas platyrhynchos</i> (34)	Survived digestion by <i>Ch.vociferus</i> better than by <i>A. platyrhynchos</i>	Proctor <i>et al.</i> , (1967)
<i>Artemia</i> and other invertebrates, algae and <i>Chara</i>	<i>Anas platyrhynchos</i>	All survived digestion	Proctor & Malone (1965)
<i>Nitella</i> (Characeae)	Duck (1)	Some germinated after digestion	Imahori (1954)
<i>Riella americana</i> (Riellaceae)	<i>Anas platyrhynchos</i> (3)	Germination and development 'similar' to undigested spores	Proctor (1961)
Six species of <i>Chara</i>	<i>Anas platyrhynchos</i> (3)	Some germinated after digestion	Proctor (1962)
<i>Asterionella</i> (Diatomea)	<i>Anas platyrhynchos</i> (4)	None germinated after digestion	Atkinson (1970)
Five diatomea, one Cyanophyta	<i>Anas platyrhynchos</i> (4)	Only one diatomea species germinated after digestion	Atkinson (1971)
<i>Potamogeton nutans</i> (Potamogetonaceae)	<i>Anas platyrhynchos</i>	60% germinated after digestion	Guppy (1906)
<i>Scirpus paludosus</i> (Cyperaceae)	<i>Anas platyrhynchos</i> (1)	Some germinated after digestion	Low (1937)
Seeds of 23 wetland plant species	<i>Charadrius vociferus</i> (≥5)* <i>Anas platyrhynchos</i> (≥4)*	Small seeds and those with a hard cover have higher resistance to digestion. Retention time longer in <i>Ch. vociferus</i> than in <i>A. platyrhynchos</i>	De Vlaming & Proctor (1968)
Seeds of eight wetland plants species	<i>Anas platyrhynchos</i> (4–16)	Large seeds and those with a hard cover germinate better after digestion, no effects of these variables on resistance to digestion	Holt (1999)
<i>Najas marina</i> (Najadaceae)	<i>Anas platyrhynchos</i> (4)	Thirty per cent survived digestion, more than 30% germinated	Agami & Waisel (1986)
Seeds of 13 plant species	Twelve species of birds (2–5)	Retention times longer in waders than in ducks (up to 10 days)	Proctor (1968)
Seed of five plant species	Three species of ducks (5)	Viable seeds recovered for four of the seed species	Powers <i>et al.</i> (1978)

\*Indicates that different types of propagules were tested in different individual birds.

There are also statistical problems with those studies that take each seed as the unit for analyses without accounting for the effects of individual ducks (the case for all studies cited in Table 1). This leads to pseudoreplication, as the resistance and viability of seeds digested by the same duck cannot be considered statistically independent observations. This can be solved by including a random factor controlling for individual-related effects on seed digestion and viability in the analyses (see Bennington & Thayne, 1994, for more information on random factors).

It is also difficult to compare different studies because the methods used to feed propagules to experimental birds differ widely between and within studies (force-feeding, mixed with leaves, grain or inside gelatinous pills, see, e.g. Proctor & Malone, 1965). The type of food ingested with the propagules can strongly influence the rate of passage through the digestive tract (Malone, 1965a). Furthermore, the conditions optimal for germination differ between propagule species. As Proctor (1964) recognised for crustacean eggs, the apparent differences in viability of different propagule species after digestion may merely reflect interspecific differences in requirements for germination or hatching. This problem can be solved by the use of control (undigested) propagules to determine the suitability of the germination procedures used (see, e.g. Agami & Waisel, 1986), and by making statistical comparisons of germination rates of digested and undigested propagules. To date, few studies have included such analyses, and none have separated the effects of digestion on the speed of propagule germination from its effects on long-term viability (see Traveset, 1998, for a review of this problem in studies of terrestrial organisms). For example, Agami & Waisel (1986) found that digestion by mallards accelerated germination of holly leaved naiad *Najas marina* seeds, but did not assess its effects on long-term viability.

There is evidence that waterbird species can differ widely in their potential for internal dispersal (see De Vlaming & Proctor, 1968), but the variables explaining such differences remain uninvestigated. Gizzard structure (as suggested by Proctor, Malone & De Vlaming, 1967), the nature of grit in the gizzard (Mateo, Guitart & Green, 2000) and intestine and caeca length (see Malone, 1965a) are variables that seem likely to influence survival of propagules and their retention time (see below) and that should be

considered in future studies. Fibrous diets in mallards lead to heavier gizzards (Miller, 1975; Kehoe *et al.*, 1988) more likely to crush propagules, and gizzards become heavier in periods of the annual cycle when waterbird diets are more plant-based (see review in Piersma, Koolhaas & Dekinga, 1993). Herbivorous and omnivorous waterbirds have heavier gizzards than carnivorous species (Kehoe & Ankney, 1985; Barnes & Thomas, 1987), and such differences are likely to influence the proportion of propagules passing undigested through the birds. The ingestion of *Artemia* eggs with grit (sand) reduced their survival of digestion (MacDonald, 1980).

### Internal transport step 3: do propagules stay long enough in a waterbird to be dispersed over a long distance?

The maximum dispersal distance of a propagule by internal transport is limited by how long the propagule remains in the gut of a waterbird (retention time), and how far the bird is capable of flying during that period. There is little information about retention times of propagules in waterbirds, although studies of terrestrial birds suggest that retention time should be longer for smaller propagules (Levey & Grajal, 1991; Izhaki, Korine & Arad, 1995). Agami & Waisel (1986) reported retention times of 10–12 h for *N. marina* seeds in mallards, whilst Swanson & Bartonek (1970) found that some *Scirpus* seeds can be retained in the guts of blue-winged teal *Anas discors* for over 72 h, although their viability was not tested. Malone (1965a) investigated how foods consumed with the propagules influence retention time in Mallards. Retention time changed significantly with the food provided with eggs of the crustacean *Artemia salina*, with minimum and maximum retention time of viable eggs being twice as long when fed with corn (mean maximum retention of viable propagules of over 5 h) than when fed with a non-fibrous aquatic plant (*Elodea canadensis*).

Ducks fly at speeds of 60–78 km h<sup>-1</sup>, and waders at speeds of 48–60 km h<sup>-1</sup> (Welham, 1994). Green-winged teal *Anas crecca* have been known to migrate over 1200 km in less than 24 h (P. Clausen, pers. comm.). During migration, Pintail *A. acuta* often move about 1000 km between satellite locations at 72 h intervals (Miller *et al.*, 2000). Thus, it is clear that propagules can be dispersed long distances by

internal transport, although the frequency of such long-distance dispersal events remains unknown.

### External transport: can propagules adhere to waterbirds?

Experiments on the potential for external transport of propagules by adhesion to the feathers, bills or legs of waterbirds are even scarcer than for internal transport. A number of anecdotal observations of organisms adhering to plumage have been reported (Maguire, 1959; Maguire, 1963; Swanson, 1984). Although a number of experiments to determine the characteristics of seeds that facilitate transport by adhesion have been performed for terrestrial organisms (Sorensen, 1986; Kiviniemi & Telenius, 1998), experimental evidence for aquatic organisms is scarce. The earliest study was performed by Darwin (1859), who removed the leg of a dead waterbird and placed it in a tank with pond snails. The snails crawled onto the bird foot and many stayed there when he removed the foot from the water and waved it around to simulate flight. Many years later, Segerstråle (1954) established that the amphipod *Gammarus lacustris* can adhere to the plumage of ducks for up to 2 h, and *Cercopagis* (Cladocera) also fouled to the plumage of a dead trial duck (Makarewicz *et al.*, 2001). In freshwater environments, exposure to desiccation during transport is likely to limit the potential of many aquatic organisms to disperse by adhesion. As yet no study has addressed how desiccation affects the viability of different kinds of propagules. Many seeds and resting eggs are likely to be highly resistant to desiccation (e.g. Bilton *et al.*, 2001). However, Frisch (2001) showed that the larval resting stages of two cyclopoid copepod species die within 24 h, even at 100% relative humidity, suggesting that desiccation limits the distance of dispersal of the larvae by waterbirds. There is anecdotal evidence that smaller propagules and those with hook-like structures are more likely to be attached to waterbird plumage. Statoblasts of bryozoans that have hooks have often been observed on moulted duck feathers (Okamura & Hatton-Ellis, 1995), and Vivian-Smith & Stiles (1994) described the characteristics of the seeds found adhered to waterfowl. Seeds and resting eggs that float are obviously more likely to become attached to plumage. However, we are not aware of any experiments testing how different propagule morphologies

influence their potential to remain attached to waterbirds.

### With what frequency are propagules dispersed by waterbirds in the field?

The studies reviewed above show that waterbirds have the potential to transport propagules, but do not provide us with information about the frequency of waterbird-mediated dispersal in the field. Waterbirds are not only potentially important as agents of long-distance dispersal and of colonisation of new habitats, but also as agents of dispersal at a local scale. There are very few field studies of the frequency of transport (summarised in Table 2), but they are enough to show that waterbird-mediated transport occurs at a high frequency in the field both by internal and external transport, specially for plant seeds. For example, Powers, Noble & Chabreck (1978) reported 17 species of non-digested angiosperm seeds in the intestines of 51 hunted ducks, and Vivian-Smith & Stiles (1994) reported angiosperm seeds attached to the feathers and feet of 28 out of 36 brant geese *Branta bernicla* and ducks.

There are no studies to date that combine information on the quantities of propagules in faeces or attached externally to waterbirds with precise information on the movements of the birds; the distances over which the propagules were dispersed in these studies are thus open to conjecture.

### Priorities for future research

Our review of published studies demonstrates that many organisms can potentially be dispersed by waterbirds, and that these processes are likely to be frequent enough to have a major impact on metapopulation dynamics and gene flow in many aquatic organisms, at least at a local scale. The relative importance of different vectors (waterbirds and other animals; this study, Lowcock & Murphy, 1990; wind, Brendonck & Riddoch, 1999; rain, Jenkins & Underwood, 1998; and man, Reise, Gollasch & Wolff, 1999) for dispersal of different propagule types at different scales needs to be addressed.

Further research is required from a range of disciplines to advance our understanding of how bird-mediated dispersal can shape the structure of aquatic communities. There are various questions

**Table 2** Summary of studies analysing the potential frequency of dispersal by waterbirds in the field. The type of organisms dispersed, the prevalence of propagules (proportion of individuals or faecal samples carrying at least one intact propagule), and the number and species of disperser are listed

Propagule species	Prevalence of propagules	Disperser species	Reference
<b>Studies on internal transport</b>			
Four genera of Cladocera – Ostracoda	17%	18 ind. of ≥4 species of waterbirds	Proctor (1964)
Metazoans	0%	<i>Anas platyrhynchos</i>	Jenkins & Underwood (1998)
Two species of Amphipods	8%	12 ducks of 3 species	Daborn (1976)
<i>Clara zeylanica</i> and <i>Clara braunii</i> (Characeae)	34%	47 ind. of ≥ 7 species of waterbirds	Proctor (1962)
Seeds of 17 plant species	53%	51 ind. of 7 species of Anatidae	Powers <i>et al.</i> (1978)
<i>Potamogeton</i> sp. (Potamogetonaceae)	23%	13 <i>Anas platyrhynchos</i>	Guppy (1906)
Seeds of plants of ≥ 12 genera	38%	71 <i>Charadrius vociferus</i>	De Vlaming & Proctor (1968)
Seeds of plants of seven genera	46%	6 species of Anatidae	Holt (1999)
Fruits of five plants	79%	250 <i>Chloephaga picta</i> and <i>C. podiocephala</i>	Willson, Traveset & Sabag (1997)
Chlorophyte and Cyanophyta	present	96 ind. of 25 species of waterbirds	Proctor (1959)
Spores of <i>Riella</i> (Riellaceae)	present	waterbirds	Proctor (1961)
Algae	80%	20 ind. of 4 species of waterbirds	Atkinson (1972)
<b>Studies on external transport</b>			
Seeds ≥11 genera of wetland plants	78%	36 ind. of 4 species of Anatidae	Vivian-Smith & Stiles (1994)

relating both to the characteristics of the propagules that are dispersed (size, shape, hardness, resistance to desiccation) and to the characteristics of the disperser and their effects on the potential for dispersal.

A range of focussed experiments are needed to establish how the various characteristics of different propagules influence their potential to be transported internally (quantifying digestibility, retention time, etc.) or externally (quantifying time spent attached to plumage, resistance to desiccation, etc.). A number of different genetic methods to estimate the tails of the propagules' dispersal distance curves are under active development (Cain, Milligan & Strand, 2000), opening promising opportunities to test the relation between propagule characteristics and dispersal capacity, and to investigate the frequency of long-distance dispersal phenomena in the field.

Research is required on how the diet and structure of digestive organs of waterbirds affects the proportion of propagules surviving digestion, and their retention time. The retention time of propagules in the digestive system determines the range of distances potentially travelled by the propagules via internal transport (Proctor, 1968). However, retention time may also have profound effects on the viability of digested propagules; for example, the propagules retained longest may have lower survival. Although some authors have suggested that longer retention times are because of variability in the passage through the intestines and that these may have little effect on the viability of propagules (Clench & Mathias, 1992), others have stated that variation in retention times was because of variation in the time spent in the gizzard, which is likely to lead to a strong effect of retention time upon viability (Proctor *et al.*, 1967). Thus there is a need for detailed experiments on the effects of retention time upon future viability of propagules.

Some species of passerine birds seem to initiate a period of fasting prior to the start of a migratory flight (Fransson, 1998). Piersma & Gill (1998) also reported a reduction in the size of the digestive organs of knots *Calidris canutus* during migration (see also Piersma & Lindström, 1997). If birds empty their digestive tracts prior to migration, this could reduce the potential for long-distance dispersal during migration. However, it seems unlikely that birds can completely empty their digestive organs, including the long caeca characteristic of waterfowl (Clench & Mathias, 1992, 1995).

Furthermore, evidence from terrestrial plants suggests that even low-frequency, long-distance dispersal events can have profound effects on patterns of colonisation and distribution (Cain, Damman & Muir, 1998), especially on the expected speed of range expansion (Higgins & Richardson, 1999).

No information is so far available on the characteristics of propagule shadows (microscale patterns in the dispersal movements of propagules via birds) in aquatic environments, or on the characteristics of the locations where propagules are redistributed by waterbirds in relation to the germination and growth requirements of the organisms. So far it is unknown if dispersal by waterbirds is directional, towards good (or bad) places for the growth of the organisms, or random (see Wenny & Levey, 1998, for an example of directional dispersal by bellbirds).

Satellite tracking is providing much new data on the long- and short-distance movements of waterbirds, although research to date has so far focussed on large swan and goose species that are likely to be less important for dispersal of aquatic organisms than smaller and more abundant ducks and waders (but see Miller *et al.*, 2000). The recoveries of ducks a couple of days after marking can also provide interesting information on the potential range of dispersal provided by waterfowl. Existing data are sufficient to show that long-distance movements by migratory waterbirds are not entirely confined to autumn and spring migration. Many waterfowl species undergo long-distance movements to moulting sites after breeding has been completed (Alerstam, 1990). After arriving at wintering sites, waterfowl and other waterbirds often undergo further mid-winter movements, e.g. related to spells of harsh weather (Ridgill & Fox, 1990) or to changes in water level in response to heavy rainfall (Simmons, Barnard & Jamieson, 1998). There generally appears to be a constant 'turnover' of individual waterbirds on wintering areas, and the only detailed study we are aware of found that the majority of green-winged teals *A. crecca* wintering in the Camargue stayed in the study area for less than 10 days (Pradel *et al.*, 1997).

Many waterbird species breeding at non-extreme latitudes are not strictly migratory but rather nomadic, making long-distance movements at any time of the year in response to spatial fluctuations in wetland availability (del Hoyo *et al.*, 1992; Kingsford & Porter, 1993). The frequent daily movements of all waterbirds

from foraging to resting areas at any time of the year and the exploratory movements of juveniles can potentially result in the dispersal of plant or invertebrate species or genotypes over larger distances, through successive short-distance dispersal steps. Such bird movements at a local scale tend to occur without any particular direction (as opposed to the directionality of migration), and can be very frequent during the periods of maximum propagule productivity (Wilkinson, 1997).

Much more information is required before we can understand the relative importance of the capacity for bird-mediated dispersal in structuring the composition of aquatic invertebrate and plant communities in comparison to other forces operating at a local scale, such as interspecific competition (MacIsaac & Gilbert, 1991) or resource constraints (Lampert, 1985). Likewise, much more information is needed before we can understand the role of bird-mediated dispersal in determining gene flow between populations of a given aquatic invertebrate or plant species, in comparison with other forces such as intraspecific competition, local adaptation and priority effects (see Husband & Barrett, 1996; Jenkins & Buikema, 1998). The main conclusion of our review is that the available information demonstrates that transport of aquatic organisms by waterbirds is frequent in the field, but that almost no information is available on which features of the disperser and dispersed organisms affect such processes, and how these influence the frequency of dispersal. Fortunately, dispersal processes are frequent enough at a local scale to facilitate further direct research of such processes in the field. To advance our knowledge of patterns of bird-mediated dispersal in aquatic environments, we recommend an approach combining quantitative analyses of the frequency of transport in the field at a local scale with experiments to test specific hypotheses on the effects of different parameters on dispersal capacity. Great care must be taken in field studies of natural dispersal vectors to separate their role from that of human vectors, which have greatly accelerated dispersal of some taxa (Reise *et al.*, 1999; Bilton *et al.*, 2001).

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