Great cormorants reveal overlooked secondary dispersal of plants and invertebrates by piscivorous waterbirds

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Abstract

In wetland ecosystems, birds and fish are important dispersal vectors for plants and invertebrates, but the consequences of their interactions as vectors are unknown. Darwin suggested that piscivorous birds carry out secondary dispersal of seeds and invertebrates via predation on fish. We tested this hypothesis in the great cormorant (*Phalacrocorax carbo* L.). Cormorants regurgitate pellets daily, which we collected at seven European locations and examined for intact propagules. One-third of pellets contained at least one intact plant seed, with seeds from 16 families covering a broad range of freshwater, marine and terrestrial habitats. Of 21 plant species, only two have an endozoochory dispersal syndrome, compared to five for water and eight for unassisted dispersal syndromes. One-fifth of the pellets contained at least one intact propagule of aquatic invertebrates from seven taxa. Secondary dispersal by piscivorous birds may be vital to maintain connectivity in meta-populations and between river catchments, and in the movement of plants and invertebrates in response to climate change. Secondary dispersal pathways associated with complex food webs must be studied in detail if we are to understand species movements in a changing world.

Keywords: Great cormorant *Phalacrocorax carbo*, fish, piscivory, endozoochory, seed dispersal, wetland

1. Introduction

Dispersal is crucial for the persistence of species inhabiting aquatic habitats because these are often discontinuous in space and time [1]. Many aquatic species disperse as seeds or diapausing stages by vectors such as water, wind, fish, waterbirds or mammals [2]. Successive transportation by multiple vectors (secondary dispersal) can extend dispersal routes, increasing connectivity for plants and invertebrates [3]. Although waterbirds and fish are both major vectors [4,5], the possibility of secondary dispersal by their interactions has been little explored [6].

After daytime fishing, piscivorous birds such as cormorants, mergansers, pelicans and herons commonly roost close to water at night and regurgitate indigestible prey remains as pellets. The potential of this bird-fish interaction for secondary dispersal previously led Darwin [7] and Mellors [8] to experimentally feed fish containing seeds or invertebrates to piscivorous birds, later retrieving viable propagules in excreta. There are anecdotal observations of endozoochory by piscivorous birds in the field, i.e. one Australian pelican *Pelecanus conspicillatus* dropping contained seeds and invertebrate eggs, and two great cormorant *Phalacrocorax carbo* stomachs contained *Carex* seeds [9,10]. This supports potential dispersal by piscivorous birds, but quantitative evidence is lacking [6].

The aim of this study was to quantify the importance of secondary dispersal of plants and invertebrates by piscivorous birds. Specifically, we considered (1) the taxonomic and ecological diversity of propagules egested by piscivores, (2) the relationship between ingested fish species and propagules retrieved, (3) the frequency and generality of this dispersal mechanism across localities. We studied these questions in seven colonies of great cormorants.

2. Methods

(a) Study species

The great cormorant is a widespread colonial waterbird with an expanding population of 120000 individuals in Northwestern Europe and a global population of several million [11]. Great cormorants are piscivorous and forage during daytime in coastal areas, estuaries, lakes and rivers [12]. Important freshwater prey species include Cyprinidae (e.g. common roach *Rutilus rutilis,* common carp *Cyprinus carpio)* and Percidae (e.g. European perch *Perca fluviatilis*) [e.g. 13]. Indigestible prey remains are regurgitated daily in one pellet of 5 to 10 g dry mass [13].

(b) Field sampling and examination

Pellets were collected below roosting trees or on shores at seven locations in Denmark, Sweden and The Netherlands (figure S1, electronic supplementary information table S1). Pellets were individually stored in zip bags at -20°C (n=61), at 7°C (n=31) or were lost in the post for several weeks (n=20). Pellets were weighed and examined in the laboratory for plant diaspores (hereafter "seeds"), intact invertebrates (including diapausing stages), and fish remains. To exclude propagules that potentially attached to the exterior of pellets after egestion, we only included propagules completely covered in mucus (figure S1).

Fish remains and propagules were identified and examined for damage under a microscope (keys in table S2). Fish length was estimated using species-specific regressions for sagittal otolith width [14]. For plant taxa, Ellenberg habitat indicator values for moisture ('Feuchtigkeit'; F) [15,16] and dispersal syndromes [17] were identified.

We attempted to hatch or germinate propagules from 51 unfrozen pellets. Individual seeds were placed on 1% agar with a 14h light (22±2ºC) to dark (18±2ºC) schedule, and monitored daily during two months. Invertebrate propagules were placed at 25°C in Tissue-Culture-plates with 1 ml deionized water in the shade (total darkness for sponge gemmules).

(c) Statistical analyses

Non-random co-occurrence patterns among particular fish species and propagules were analysed in a network analysis in R [18]. For every pairwise combination of species in the pellets we calculated Spearman rank correlations (ρ) to analyse possible associations of their presences. All pairwise combinations formed a co-occurrence matrix for all pellet contents, which we visualized for correlations with $\rho>0.3$ and $p<0.05$ as edges (connections) between nodes (species) using the plot.network() function in package statnet [19]. Node size is proportional to the number of pellets containing that species, and edge width is proportional to ρ . The R code including more details is available in the electronic supplementary material.

3. Results

Forty-eight of 112 pellets (43%) contained at least one intact plant or invertebrate propagule [20]. Broken propagules were found in a further eight pellets. Thirty-seven pellets (33%) contained ≥ one intact seed, and 22 pellets (20%) ≥ one intact invertebrate propagule. Seeds were found at six of seven locations, and invertebrate propagules at two locations (table 1). Mean±SD pellet dry mass was 7.65±6.96 g (range 1.59–49.23 g, n=83).

Seventy-three intact diaspores were recovered from 16 families of angiosperms plus Charophyceae. Among intact seeds, we identified 21 taxa to species-level and three to family level (table 1). Three plant families (Adoxaceae, Fabaceae, Polygonaceae) and the *Potamogeton*-genus were represented only by broken seeds. *Actinidia deliciosa* (Kiwi fruit) is alien to Europe, although common in gardens. Five of the 21 species are characteristic of wet or submerged habitats, five of moist to wet habitats and ten of dry to moist habitats. Dispersal syndromes varied, with only two species assigned to endozoochory compared to five for hydrochory and eight for barochory (unassisted, table 1). Three of 54 unfrozen seeds (5.6%) germinated: one *Chenopodium glaucum,* one *Schoenoplectus tabernaemontani* and one *Atriplex patula.*

We found 256 intact invertebrate propagules, including 186 gemmules of the sponge *Ephydatia fluviatilis* from one pellet. Seven different invertebrate taxa were found (from four families), a lower diversity than of plants ($X^2=74.9$, $df=1$, $P<0.001$). One *Plumatella casmiana* statoblast was found in a Dutch pellet (probably alien for Europe, T. Wood pers. comm. 2017), and one *Plumatella repens* statoblast hatched.

Fish remains were found in 104 pellets, with a mean±SD of 1.5±1.2 fish taxa (range 0-4) and 10.9±12.8 individuals per pellet (range 0-51), of a mean length of 7.7±3.7 cm (range 3.2-41.3). Common taxa were European perch*,* Eurasian ruffe *Gymnocephalus cernuus* and common roach (table S3). Fish lengths varied between species and locations (table S4).

Fish, plant and invertebrate contents of pellets were partly interrelated (table S5). Pellets with more fish held a higher diversity of invertebrates, and pellets with more invertebrate taxa held significantly more plant taxa. Fish species associated with multiple propagule species were Zander *Sander lucioperca* and bullhead *Myoxocephalus scorpius*; five additional fish species were associated directly with one propagule species (figure 1, table S6).

4. Discussion

This is the first quantitative field study of dispersal of plants and invertebrates by piscivorous birds. Great cormorants regurgitate pellets containing intact propagules previously ingested by fish prey. Pellets contained seeds of terrestrial, freshwater and marine plant species, indicating potential secondary dispersal for species with a range of habitat requirements. Terrestrial seeds are often blown or washed into the water and ingested (like aquatic seeds) by fish, followed by avian secondary dispersal. We confirmed the viability of seeds of three plant species and one bryozoan statoblast, and many of the other taxa we recorded are already known to survive passage through the guts of waterfowl [5]. Our first exploration of species interactions (figure 1) suggests secondary dispersal may connect aquatic and terrestrial environments, e.g. associations of Atlantic cod *Gadus morhua* with Brassicaceae and longspined bullhead *Taurulus bubalis* with Caryophyllaceae.

Among prerequisites for effective secondary dispersal are that (1) birds reach a new suitable location before egestion, and (2) propagules can establish in a suitable microhabitat. Both aspects depend on bird behaviour. Many cormorants roost in trees partially overhanging the water and partially above land, providing opportunities for both aquatic and terrestrial plants to reach suitable microhabitats. Cormorants may also provide germinating plants with nutrient-rich guano [21]. Great cormorants often travel up to 45 km between roosting and foraging locations, with occasional movements >200 km [22]. Tags inserted in fish have been retrieved >39 km from tagging locations [23], and >10 km in one of our study locations (Lake Roxen). Dispersal over several tens of kilometres is therefore possible throughout the annual cycle, and perhaps much further during migrations.

Our results raise key questions for future research, including (1) possible overlap of secondary dispersal with primary dispersal by other vectors, e.g. ducks. We found six plants in cormorant pellets not recorded from the diet of European dabbling ducks (table 1), and reported bird-mediated dispersal of freshwater sponges for the first time. Detailed comparisons between primary and secondary dispersal by different avian vectors are needed. (2) The importance of secondary dispersal relative to other vectors, and how its importance varies with colony size, over seasons and between individual birds. This study found considerable spatial and temporal variability in pellet content, which deserves more detailed investigations. (3) Germinability of unfrozen seeds was low compared with studies on omnivorous waterbirds; possibly because passing two digestive systems severely impacts viability. Future research should extract propagules quickly from piscivore excreta, and study effects of double gut passage on viability. (4) We found secondary dispersal of alien species (table 1), but further exploration is needed. (5) Associations among particular fish species, among propagule species and between fish and propagule species require more detailed inspections to unravel specific secondary dispersal pathways.

We conclude that piscivorous birds may be major dispersal vectors that require more scientific attention. Since most plants dispersed lack a fleshy fruit, they are assumed to rely on mechanisms with less potential for long-distance dispersal than endozoochory (table 1). Secondary dispersal by piscivorous birds may play an important role in maintaining connectivity in meta-populations and between river catchments, and in the movement of plants and invertebrates in response to climate change.

Ethics. All fieldwork was authorized by landowners.

Data accessibility. Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.fj669. R code for the network analysis is available in the electronic supplementary material.

Authors' contributions. C.H.A.v.L.: Collected pellets, analysed the data and wrote the article. A.L.-K.: Collected pellets, identified and germinated propagules. M.O.: Collected pellets and identified fish remains. A.J.G.: Conceptualized and designed the study, and cowrote the article. All authors contributed to writing the manuscript, approved the final version and are accountable for all content.

Competing interests. We have no competing interests.

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Tables

Table 1: Intact plant seeds and invertebrates from cormorant pellets. Ellenberg F classes 4–6 represent dry-to-moist, 7–9 moist-to-wet and 10–12 wet-or-submerged habitats [16]. Species are sorted by the number of recovered propagules, while indicating the number of pellets, viable propagules that germinated or hatched (per number tested), sampling locations (Ringkøbing Fjord (RK), Roxen Lake (RL), Havsstensfjord Vadholmen (HV), Björningarna (B), North Mittholmarna (NM), South Mittholmarna (SM), Fortmond (F)), and assigned dispersal syndromes [17]. Species indicated in bold are not known to be dispersed by European dabbling ducks [24]. *Actinidia deliciosa* is alien to Europe, and therefore has no Ellenberg F value.

Category	Species	Family	Ellenberg F	Dispersal syndrome	# intact propagules	# pellets	# germinated or hatched / attempted	sampling locations
Plant	Unknown	Charophyceae			15	5	0/15	RK, F
Plant	*Urtica dioica*	Urticaceae	6	epizoochory	11	6	0/9	RL, F
Plant	***Schoenoplectus tabernaemontani***	Cyperaceae	10	barochory	8	6	1/7	RK, RL
Plant	*Betula pendula*	Betulaceae	5	anemochory	5	5	-	RL, HV, B
Plant	*Suaeda maritima*	Amaranthaceae	8	hydrochory	5	5	0/4	B, F
Plant	*Atriplex patula*	Amaranthaceae	5	epizoochory	3	3	1/3	RK
Plant	***Limosella aquatica***	Scrophulariaceae	8	barochory	3	2	0/3	F
Plant	*Zannichellia palustris*	Potamogetonaceae	12	hydrochory	3	1	0/3	F
Plant	*Chenopodium glaucum*	Amaranthaceae	6	barochory	4	3	1/4	RK
Plant	*Potentilla anserina*	Rosaceae	5	barochory	2	1	0/2	F
Plant	***Actinidia deliciosa***	Actinidiaceae		endozoochory	1	1	0/1	F
Plant	*Alopecurus pratensis*	Poaceae	5	barochory	1	1	-	RL
Plant	*Carex nigra*	Cyperaceae	8	hydrochory	1	1	0/1	F
Plant	***Cochlearia officinalis***	Brassicaceae	6	barochory	1	1	-	SM
Plant	*Eleocharis uniglumis*	Cyperaceae	9	epizoochory	1	1	0/1	RK
Plant	*Plantago major*	Plantaginaceae	5	barochory	1	1	0/1	F
Plant	*Rubus fruticosus*	Rosaceae	6	endozoochory	1	1	0/1	F
Plant	*Ruppia cirrhosa*	Ruppiaceae	12	hydrochory	1	1	-	NM, SM
Plant	***Sagina apetala***	Caryophyllaceae	4	anemochory	1	1	-	B
Plant	***Salix triandra***	Salicaceae	8	anemochory	1	1	0/1	F
Plant	*Veronica beccabunga*	Plantaginaceae	10	barochory	1	1	0/1	F
Plant	*Zostera marina*	Zosteraceae	12	hydrochory	1	1	-	B
Plant	unknown	Apiaceae			1	1	0/1	RK
Plant	unknown	Poaceae			1	1	-	RL
Invertebrate	*Ephydatia fluviatilis*	Spongillidae			186	1	0/186	F
Invertebrate	*Daphnia pulex agg.* (Group)	Daphniidae			24	7	0/23	RL, F
Invertebrate	*Cristatella mucedo*	Cristatellidae			19	14	0/11	RL, F
Invertebrate	*Plumatella repens*	Plumatellidae			12	6	1/11	RL,F
Invertebrate	*Plumatella fungosa*	Plumatellidae			10	4	0/10	F
Invertebrate	*Plumatella emarginata*	Plumatellidae			3	3	0/3	F
Invertebrate	*Plumatella casmiana*	Plumatellidae			1	1	0/1	F

Figures

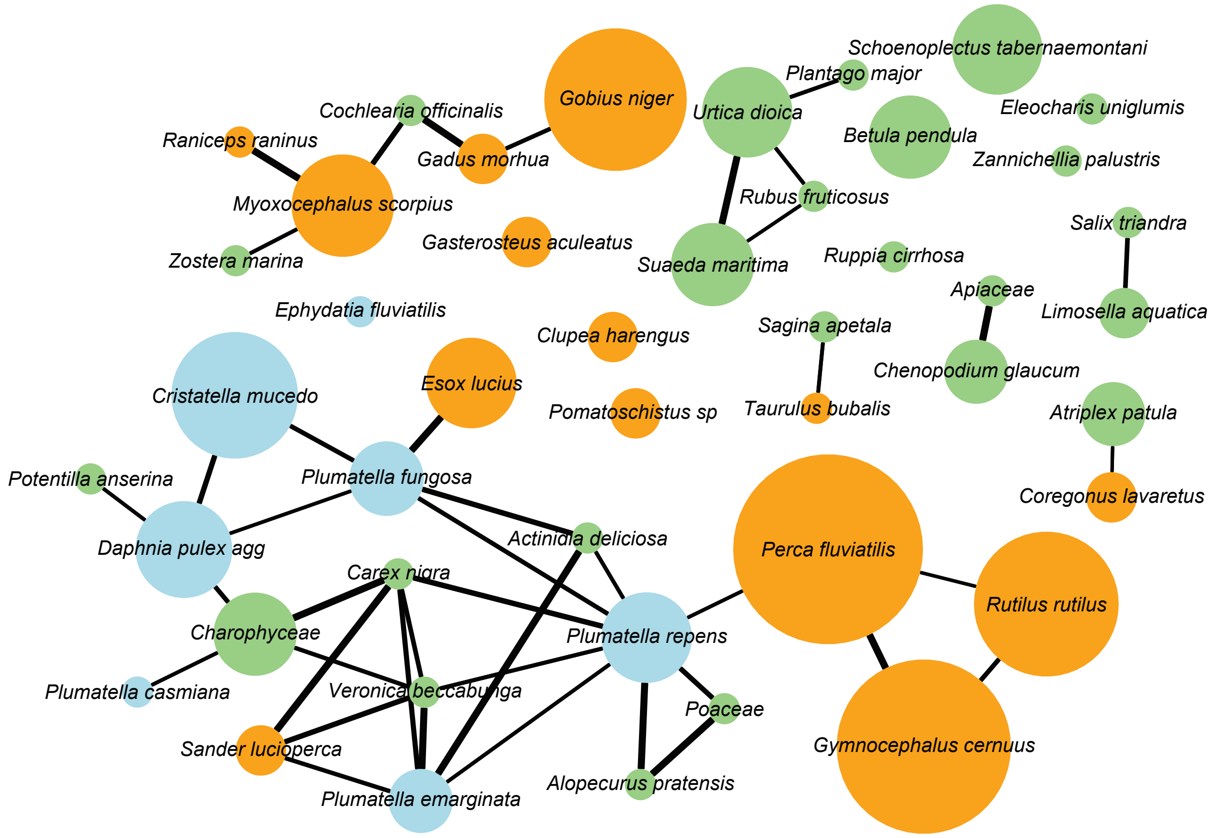

Figure 1: Network visualization of pellet contents depicting fish (orange), plant (green) and invertebrate (blue) species in nodes whose size depicts their abundance on a log-scale. Connecting lines depict correlations among species; line width scales to ρ. Unconnected species have no significant associations.

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Electronic Supplementary Material

Tables

Table S1: Sampling details for regurgitated pellets of great cormorants.

Country	Location	Latitude	Longitude	Date	n	Treatment
Denmark	Ringkobing Fjord (RK)	55°59'13.7 N	8°16'54.6 E	12 Nov 2014	20	Unknown conditions
Sweden	Roxen Lake (RL)	58°30'00.0 N	15°40'00.0 E	15 Jun 2015	31	Frozen
	Havsstensfjord Vadholmen (HV)	58°19'45.9 N	11°45'37.7 E	5 July 2014	10	Frozen
	Björningarna (B)	58°15'46.2 N	11°49'14.7 E	16 Sept 2014	10	Frozen
	North Mittholmarna (NM)	57°57'59.3 N	11°43'44.2 E	26 Jun 2014	5	Frozen
	South Mittholmarna (SM)	57°57'50.5 N	11°43'44.8 E	26 Jun 2014	5	Frozen
The Netherlands	Fortmond (F)	52°21'28.2 N	6°05'46.3 E	9 Sept 2016	31	Stored at 7 ºC

Table S2: Keys used for species identification.

Taxon	Reference
Plant seeds	Cappers et al. (2012) and Bojnanský et al. (2007)
Cladoceran ephippia	Benzie (2005)
Sponge gemmules	Penney (1986)
Bryozoan statoblasts	Wood & Okamura (2005)
Fish	Kullander et al. (2012) and Leopold et al. (2001)

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Table S3: Fish prey taxa retrieved from pellets of great cormorants, including clearly identifiable prey remains, less confident identifications and unidentified fish prey. Data provided for each species are the number of pellets in which it was retrieved (Pellets), the total number of fish (Total), and number of fish per sampling location (abbreviated, see table S1). The number of fish was quantified conservatively by counting the most numerous left or right otoliths (i.e. one fish for every two otoliths).

Family	Species	Pellets	Total	Denmark (RK)	The Netherlands (F)	Sweden (B)	Sweden (HV)	Sweden (NM)	Sweden (SM)	Sweden (RL)
Unequivocal identifications										
Percidae	*Perca fluviatilis*	57	741	4	546					191
Percidae	*Gymnocephalus cernuus*	41	274	4	18					252
Cyprinidae	*Rutilus rutilus*	22	62		1					61
Gobiidae	*Gobius niger*	20	101		22	37	28	12	2	
Cottidae	*Myoxocephalus scorpius*	8	24			1	15	2	6	
Esocidae	*Esox lucius*	6	6		4					2
Percidae	*Sander lucioperca*	2	5		5					
Gadidae	*Gadus morhua*	2	3				2		1	
Clupeidae	*Clupea harengus*	2	2		1	1				
Gobiidae	*Pomatoschistus sp.*	2	2				1	1		
Salmonidae	*Coregonus lavaretus*	2	2	2						
Cottidae	*Taurulus bubalis*	1	2			2				
Gadidae	*Raniceps raninus*	1	1			1				
Gasteroidae	*Gasterosteus aculeatus*	2	2	2						
Uncertain identifications										
Gobiidae	*Neogobius melanostomus*	5	6		2	3	1			
Percidae	*Perca fluviatilis*	2	32		32					
Lotidae	*Lota lota*	2	2							2
Gobiidae	*Gobio gobio*	1	1		1					
Solenidae	*Solea solea*	1	1			1				
Percidae	*Gymnocephalus cernuus*	2	3	3						
Unidentified			727	68	149	300	40	72	30	68

Table S4: Size of retrieved fish for different countries, calculated using widths of intact otoliths (one otolith per individual fish). The number of otoliths (N), minimum, mean and maximum fish lengths (cm) are indicated for each species.

Country	Species	N	Minimum	Mean	Maximum
Denmark	*Gymnocephalus cernuus*	4	8.8	11.1	12.9
	Perca fluviatilis	2	20.5	20.7	20.9
	Coregonus lavaretus	2	21.7	23.5	25.3
Netherlands	*Perca fluviatilis*	546	3.2	5.8	12.5
	Gobius niger	22	3.3	5.3	7.8
	Gymnocephalus cernuus	18	4.1	6.0	12.6
	Sander lucioperca	5	5.0	7.4	10.8
	Esox lucius	2	15.3	28.3	41.3
	Rutilus rutilus	1	11.6	11.6	11.6
	Clupea harengus	1	12.0	12.0	12.0
Sweden	*Gymnocephalus cernuus*	252	4.2	7.3	13.8
	Perca fluviatilis	187	5.5	10.1	24.2
	Gobius niger	79	4.5	7.7	13.8
	Rutilus rutilus	50	6.9	15.2	22.4
	Myoxocephalus scorpius	23	7.5	12.6	18.0
	Gadus morhua	3	13.7	23.9	31.3
	Esox lucius	2	32.3	33.9	35.6
	Clupea harengus	1	9.2	9.2	9.2

Table S5: Correlation matrix for pellet contents, indicating Spearman´s rank correlation ρ. Asterisks indicate the corresponding *p*-values: *** <0.05, ** <0.01, *** <0.001**.

	Fish individuals	Fish species	Plant species	Invertebrate species	Plant diaspores
Fish species	**0.68***				
Plant species	0.04	-0.10			
Invertebrate species	**0.28**	**0.24***	**0.27***		
Plant diaspores	0.03	-0.11	**0.99***	**0.27**	
Invertebrate propagules	**0.28**	**0.24***	**0.26**	**0.99***	**0.26**

Table S6: Co-occurrences of fish and propagule taxa in pellets, indicated as the percentage of all pellets containing a particular fish taxon that also contained a particular propagule taxon. The number of pellets in which both taxa co-occurred is indicated in brackets and determines the colour intensity of cells for clarity.

	Clupea harengus	*Coregonus lavaretus*	*Esox lucius*	*Gadus morhua*	*Gasterosteus aculeatus*	*Gobius niger*	*Gymnocephalus cernuus*	*Myoxocephalus scorpius*	*Perca fluviatilis*	*Pomatoschistus sp*	*Raniceps raninus*	*Rutilus rutilus*	*Sander lucioperca*	*Taurulus bubalis*
Plants														
Actinidia deliciosa							3% (1)		2% (1)					
Alopecurus pratensis							3% (1)		2% (1)			5% (1)		
Apiaceae														
Atriplex patula		50% (1)												
Betula pendula						5% (1)	3% (1)		2% (1)			5% (1)		
Carex nigra							3% (1)		2% (1)				50% (1)	
Charophyceae						5% (1)	5% (2)		5% (3)				50% (1)	
Chenopodium glaucum														
Cochlearia officinalis				50% (1)		5% (1)		13% (1)						
Eleocharis uniglumis														
Limosella aquatica						5% (1)	3% (1)		4% (2)					
Plantago major						5% (1)	3% (1)		2% (1)					
Poaceae							3% (1)		2% (1)			5% (1)		
Potentilla anserina									2% (1)					
Rubus fruticosus						5% (1)			2% (1)					
Ruppia cirrhosa														
Sagina apetala						5% (1)								100% (1)
Salix triandra						5% (1)			2% (1)					
Schoenoplectus tabernaemontani							5% (2)		2% (1)			5% (1)		
Suaeda maritima			17% (1			15% (3)	3% (1)		5% (3)					
Urtica dioica						15% (3)	8% (3)		9% (5)			5% (1)	50% (1)	
Veronica beccabunga							3% (1)		2% (1)				50% (1)	
Zannichellia palustris							3% (1)		2% (1)					
Zostera marina						5% (1)		13% (1)						
Invertebrates														
Cristatella mucedo			17% (1			15% (3)	25% (10)		21% (12)			24% (5)	50% (1)	
Daphnia pulex agg			17% (1			10% (2)	8% (3)		11% (6)			5% (1)		
Ephydatia fluviatilis									2% (1)					
Plumatella casmiana									2% (1)					
Plumatella emarginata						5% (1)	5% (2)		5% (3)				50% (1)	
Plumatella fungosa			33% (2			5% (1)	5% (2)		7% (4)					
Plumatella repens			17% (1				10% (4)		11% (6)			5% (1)	50% (1)	

Figures

Figure S1: Regurgitated pellet from a great cormorant in Sweden (Picture: Maria Ovegård).