Are dabbling ducks major players or merely noise in freshwater ecosystems? A European perspective, with references to population limitation and density dependence

JOHAN ELMBERG

Aquatic Biology and Chemistry, Kristianstad University, SE-291 88 Kristianstad, Sweden.
E-mail: Johan.Elmberg@hkr.se

Abstract

Waterfowl ecologists consider ducks important players in patterns and processes of freshwater ecosystems. Limnologists and fish biologists, on the other hand, historically have "a bottom-up" view of the same systems, often regarding waterbirds as "background noise" compared to other biotic influences. Evidence for and against these largely opposing views is reviewed, focussing on European dabbling duck studies. In oligo- and mesotrophic wetlands at low breeding density, their role is likely to be overshadowed by biotic interactions between fish, invertebrates and plants. Conversely, many other freshwater systems may be affected by dabbling ducks in various ways, acting as dispersers of invertebrates and plants, as predators, and as eutrophicators. It is concluded that dabbling ducks affect freshwater systems more profoundly than has hitherto been acknowledged. In their turn, freshwater ecosystems affect the ducks' population ecology. In a less comprehensive treatment, the evidence for the major paradigms addressing population limitation in dabbling ducks is discussed briefly from a European perspective. It is concluded that top-down (predation) as well as bottom-up (food limitation) processes may both affect population size, but evidence for either is correlative, necessitating more experimental studies based on explicit predictions from pattern-oriented studies. In a discussion of the prospects for adopting a more adaptive management approach for European dabbling ducks, it is argued that a lack of information about annual variation in recruitment and harvest rates are major obstacles to understanding population change and for adopting a more adaptive management. A compilation of European studies about density dependence in Mallard *Anas platyrhynchos* indicates that population regulation may be a common phenomenon in this species, with possible important ramifications for research as well as management programmes.

Key words: adaptive management, density dependence, population limitation, regulation.

From a European perspective there are several reasons why duck species and populations are of human interest and concern. First, there are some 9,000,000 duck hunters in the European Union, more than inhabitants in some member states. Secondly, millions of birdwatchers and other people enjoy watching wetland birds as a popular pastime. Widespread birds enjoyed by many naturally require management, which has resulted in hundreds of thousands of landowners becoming aware of ducks and other waterbirds. With so many people concerned, politicians and administrators also need to be interested in these birds. Finally, ducks are potential hosts and dispersers of pathogens that cross taxonomic barriers and infect humans, making them a natural focus for research in the fields of virology, veterinary medicine and the transmission of infectious diseases.

Does such widespread interest mean that ducks are well-studied? The answer is definitely "yes"; search strings including the word "duck" produces thousands of hits in electronic scientific literature database searches. Searching on Mallard *Anas platyrhynchos* produces three times as many hits as either Blackbird *Turdus merula* or Roe Deer *Capreolus capreolus*, both of which are well-studied (1,786, 663 and 584 hits, respectively, in the Biological Sciences data base on 20 March 2009; http://csaweb108v.csa.com/). This confirms that the duck research community works with well-studied organisms, and that it has a responsibility to synthesise, generalise and disseminate results. Ducks are in many ways model organisms, and those researching these species have better opportunities than most to draw broad conclusions from their work and to extrapolate their findings. Such syntheses and overviews help to describe emerging patterns and stimulate further research, thus complementing traditional exhaustive but more retrospective reviews.

This overview paper considers three connected topics at the heart of dabbling duck ecology, as seen from a European perspective: 1) whether they are major players or merely noise (that is, rather peripheral compared to other ecological processes) in freshwater systems, 2) population limitation, and 3) adaptive management opportunities for the species. While the first part of the paper reviews evidence in the published literature of how dabbling ducks may affect their environment, the second two points are addressed by a more general discussion of how these birds, in return, are affected by their environment, and how this may be used for management purposes.

Major players or merely noise?

The science of limnology has traditionally taken the bottom-up view of wetland ecosystems, that basic conditions of productivity have an overriding effect on ecosystem state. Partly as a reflection of this, classic and contemporary limnology textbooks neglect waterfowl or treat them peripherally (*e.g.* Wetzel 2001; Kalff 2002). For decades, fish were treated in the same way, but their important role in freshwater systems – as top predators and planktivores – is now widely recognised. Waterbirds continue to be overlooked in modern freshwater ecology textbooks (*e.g.* Brönmark

& Hansson 2005; Lampert & Sommer 2007), despite the 25 years that have passed since Hurlbert & Chang (1983) coined the term "ornitholimnology" and gave striking examples of how waterbirds may act as "major players" in wetland ecosystems.

Since then it has been demonstrated that waterbirds, like fish, may influence the structure of freshwater systems and alter their state. For example, piscivorous birds can affect the behaviour and recruitment of fish (Wood 1987; Piersma *et al.* 1988; Winfield 1990; Feltham 1995; Allouche & Gaudin 2001), flamingos, coot, geese and swans may alter vegetation and turbidity of lakes (Comín *et al.* 1997; Bird *et al.* 2000; Marklund *et al.* 2002; Rodríguez-Pérez & Green 2006), and ducks and geese can contribute to eutrophication of wetlands (Moss & Leah 1982; Marion *et al.* 1994; Olson *et al.* 2005). Among other important contributions, the "Working Group on Aquatic Birds" under the auspices of *Societas Internationalis Limnologiae* has launched five international symposia devoted to limnology and aquatic birds (*e.g.* Kerekes 1994), which clearly show that waterbirds can be major players in freshwater ecosystems. However, studies of dabbling ducks (*Anas* sp.) have long remained scarce in this context, and they have not been reviewed before, especially from a European perspective.

Europe has seven widespread species of dabbling duck: Wigeon *Anas penelope*, Gadwall *A. strepera*, Teal *A. crecca*, Mallard, Shoveler *A. clypeata*, Pintail *A. acuta*, and Garganey *A. querquedula,* most of which are long- to medium-distance migrants utilising different environments in two or more biomes during their annual cycle (*e.g.*, Delany & Scott 2006). Accordingly, there is no straightforward answer as to whether they are major players or mere noise in freshwater ecosystems, because this necessitates consideration of the different parts of their annual cycle. Scientific literature database searches confirm that the breeding season is well studied compared to the spring and autumn migratory periods (Table 1). These papers form the backbone for the broad picture that follows about the role of dabbling ducks in freshwater systems, starting with the winter season.

Many European dabbling ducks winter on more or less seasonal Mediterranean wetlands, many situated close to intensive agricultural areas. Several species show pronounced behavioural diel patterns in winter to take advantage of this spatial habitat configuration; ducks roost and rest more extensively during the day, and then commute to nocturnal foraging sites (Tamisier & Dehorter 1999). In the absence of a comprehensive literature review of diets, seeds seem to predominate in the winter diet of most European dabbling duck species (Cramp & Simmons 1977). Wintering duck densities are frequently very high (compared to those on breeding grounds), at daytime roosts as well as at nocturnal foraging sites. Recent studies demonstrate that commuting ducks frequently transport seeds and "help invertebrate eggs to fly" between wetlands (Green *et al.* 2002; Figuerola & Green 2002; Green & Figuerola 2005), making them main players in these systems in the sense that they potentially affect dispersal, colonisation and species composition patterns of plants and invertebrates (Soons *et al.* 2008). It also

Table 1. The number of scientific papers published on two common species of dabbling duck studied at different times of year. Data from the Biological Sciences database (http://csaweb108v.csa.com/), 20 March 2009.

Search string	Number of papers
(Mallard OR Teal) AND winter	136
(Mallard OR Teal) AND spring	104
(Mallard OR Teal) AND (summer OR breeding OR moult)	404
(Mallard OR Teal) AND (fall OR autumn)	92

seems probable that dabbling ducks can alter vegetation composition by physical wear and tear while foraging, at least where they occur at high densities for prolonged periods (*cf.* Marklund *et al.* 2002). Two other possible effects of intensive winter utilisation by dabbling ducks – food depletion and eutrophication – remain little studied and thus poorly understood. Data from the Camargue, south France, suggest that food there is not depleted in winter (Tamisier & Dehorter 1999), whereas other French studies indicate the opposite (Guillemain *et al.* 2000; Legagneux 2007). However, the possibly differential temporal utilisation patterns of food items of different profitability (where profitability is a balance of energy content in relation to feeding technique and handling time) remain to be addressed.

The present literature search (Table 1) as well as a topically wider review (Arzel *et al.* 2006) show that little is known about the extent to which dabbling ducks have an effect on their spring staging sites, specifically on their plant and animal communities. However, spring migration is rapid in most dabbling duck species, with birds rarely staying for protracted periods at any locality, at least not during the first two-thirds of the northbound journey (Arzel & Elmberg 2004). It is a fair but largely untested assumption that spring staging dabbling ducks are confined to feed on whatever food remains from the previous season. This is true for seeds as well as allegedly crucial protein-rich invertebrates, the annual activity period of which has often not started when ducks stage in spring and when they return to the breeding areas (Arzel & Elmberg 2004).

Many of Europe's dabbling ducks breed on oligo- to mesotrophic wetlands in the boreal zone, in generally low densities. Many lakes have one or two pairs of breeding dabbling duck, compared to tens of thousands of fish, among which Perch *Perca fluviatilis*, Roach *Rutilus rutilus*, and Pike *Esox lucius* are the most widespread and common species (*e.g.* Öhman *et al.* 2006). Such lakes will hold on average *c.* 6 kg of duck for *c.* 10 weeks, whilst a ton or more of fish is present throughout the year. In terms of classical systems ecology and food webs, ducks are naturally "mere noise" in such a scenario, and there are no indications that dabbling ducks play key roles in these systems, neither as predators nor as prey, although their role as dispersers of invertebrate eggs and plant propagules remains unstudied and may be significant (*cf.* Brochet *et al.* in press). The latter is perhaps more significant in biotic interactions and trophic webs of moulting wetlands, which are generally more productive and where ducks often occur at higher densities.

Autumn migration of European dabbling ducks is much slower and gradual than spring migration (Fransson & Pettersson 2001; Wernham *et al.* 2002). Post breeding, fall migration is the season of greatest duck abundance, when most adopt a granivorous diet. Breeding lakes, moulting lakes, and other wetlands in the boreal zone are deserted by all species (except Mallard) by August or September (Elmberg 1985), long before seed depletion is likely to occur, and while aquatic invertebrates are still abundant and active. South-bound dabblers instead congregate on more eutrophic wetlands, one-third or mid-trip down the flyway. Slower migration, higher numbers and higher densities of dabblers suggest that they may be "major players" in food chains and for biotic interactions at this time of year, but firm evidence remains scarce. Most aquatic plants at higher latitudes shed their seeds in late summer, so autumn migration is also a period during which significant dispersal of plant propagules by dabbling ducks is likely (*cf.* Charalambidou & Santamaria 2005), especially a southward spread of boreal and temperate species. More unequivocally demonstrated, however, is the significant role dabbling ducks have in fall as vectors of infections, as immuno-naïve juveniles move southwest and congregate in increasing numbers along the route (*e.g.* Wallensten *et al.* 2007).

Research highlighted in this review demonstrates that dabbling ducks deserve more attention from limnology and aquatic ecology in general, including their textbooks. The question of whether dabbling ducks are major players or noise in freshwater ecosystems may seem scientifically imprecise, but it is definitely heuristic rather than rhetorical. Integrating duck ecology more with limnology would stimulate further work into the role of ducks as dispersers of seeds, plant parts, and invertebrate eggs, throughout flyways and the annual cycle. In addition, future research should determine whether dabblers have cascading effects in their own food webs, at least under conditions where they occur in large numbers for a longer time, notably at moulting, fall staging and wintering sites. Finally, their role as pathogen vectors is a new and developing field of research. Avian influenza is merely one of several examples where dabbling ducks may be "major players", both within aquatic ecosystems and as a link between these and terrestrial ones (Olsen *et al.* 2006).

What limits European populations of dabbling ducks?

Having acknowledged that dabbling ducks may affect their environment more profoundly than has generally been thought, it is fair to revisit briefly the question of how the environment in turn affects dabbling ducks. Population limitation is a long-established field of avian research, but also one with many inherent methodological problems (Newton 1998). As harvested game, linking the issue of basic population limitation amongst ducks to those of long-term population fluctuations, and consideration of whether hunting mortality is additive or compensatory to natural mortality, are central to their study (Williams *et al.* 2001; Baldassarre & Bolen 2006). The number of annual citations in this research area has risen from a mere dozen in the early 1990s to > 150 in 2008 (hits in Science Citation Index/ISI web of knowledge 20 March 2009; search string: "population limitation AND (dabbling duck OR Mallard OR Teal OR Wigeon OR Pintail OR Gadwall OR Shoveler OR Garganey)"). A review of these citations reveals three major paradigms relating to population limitation in dabbling ducks: 1) top-down control by non-human predators, 2) bottom-up control by food limitation, and 3) neither, where the populations are kept far below carrying capacity by winter weather, disease and hunting. Without attempting a comprehensive review, which would involve addressing extensive North American literature on the subject, the evidence for and against these paradigms is presented below from a European perspective.

Descriptive and experimental studies show that predation on nesting adults, eggs and ducklings is significant and may affect population trajectories (Martin 1988; Sargeant & Raveling 1992; Opermanis 2001; Opermanis *et al.* 2001). Experimental work based on simulated Mallard nests demonstrates density-dependent nest survival, implying that predation may not only limit but also regulate breeding success (Gunnarsson & Elmberg 2008; Elmberg *et al.* 2009). Impacts of nest predation appear to vary among biomes, with landscape configuration, as well as with nesting phenology (Gunnarsson & Elmberg 2008; Elmberg *et al.* 2009). Variation in overall survival of natural nests is likely to be huge in Europe, just as it is in North America. The role of predatory fish, notably pike, for breeding success in terms of duckling predation and patterns of wetland use is also uncertain (Solman 1945; Elmberg *et al.*, unpubl. data). Experimental studies addressing patterns of lake use and breeding success in relation to occurrence of predatory fish are underway (Dessborn *et al.* unpubl. data). Predation on ducks in autumn and winter remains much less studied, but modelling of ringing recovery data indicates that it amounts to less than hunting mortality (Gunnarssson *et al.* 2008). In summary, there is evidence that top-down control by natural predators may limit breeding success, but the temporal and spatial importance of this process outside the breeding season remains insufficiently understood.

What is the evidence for bottom-up control of dabbling duck populations by food limitation? Dozens of studies describe abundance patterns of invertebrates and seeds, the main foods of dabbling ducks, but since these birds are opportunistic feeders, food availability has not generally been related to subsequent diet selection or profitability. A third type of food, fresh green plant material, is consumed in significant amounts by Wigeon and Gadwall, and periodically by other dabblers (Cramp & Simmons 1977). Arzel *et al.* (2009) found that Teal left the wintering grounds before invertebrates started to become more abundant, and that spring staging sites were used and left before the vernal increase in invertebrate numbers there. Studies of dabbling duck diet and food availability upon arrival at the breeding grounds are lacking. Observations from northern Sweden and sub-arctic Norway indicate very low invertebrate abundance at these sites at this time (Arzel & Elmberg, unpubl. data), but that flooded meadows and littoral areas offer seeds left from the preceding year (*cf.* Grelsson & Nilsson 1991). Patterns of spring food abundance – as well as subsequent selection – need to be studied further, especially as dabblers are generally thought to be mainly carnivorous at this time in preparation for breeding (notably egg formation).

Food limitation on breeding lakes has been demonstrated experimentally for Mallard ducklings on oligo- and mesotrophic boreal wetlands (Sjöberg *et al.* 2000; Gunnarsson *et al.* 2004). These studies imply that low availability (or profitability) explains the landscape-level distribution pattern of "many empty lakes" evident throughout the boreal and sub-arctic breeding grounds of Teal, Mallard, and Wigeon. Food limitation on freshwater moulting and autumn staging sites has not been studied in Europe (Boertmann & Riget 2006 concerns a brackish system), although moult and autumn staging take place during the peak in annual dabbling duck abundance. Moulting and autumn staging sites are used for longer periods than spring staging sites; hence it seems more likely that dabblers may deplete food resources or at least affect their future abundance by their utilisation of these sites in late summer and early autumn. Finally at the wintering sites, there is no evidence to suggest that dabbling ducks are limited by food during winters with "normal" weather (Tamisier 1971; Tamisier & Dehorter 1999), although local food depletion and/or depletion of favoured foods are probably regular occurences (Guillemain & Fritz 2002). The issue is hard to tackle by descriptive methods, since much of winter foraging is nocturnal, with birds moving between sites trading off feeding opportunities and risks (*e.g.* predation and disturbance). Baiting and agricultural practices to manage ducks by providing more food further complicate the picture, both having become more popular in some wintering areas (Legagneux 2007).

In summary, food abundance does limit breeding success in some areas, and unverified patterns as well as theory suggests that this may also be true for some of the staging sites used shortly before arrival at breeding lakes (Arzel *et al.* 2006). Although there is no firm evidence that food is limiting dabbling ducks outside the breeding grounds, conditions on moulting and autumn staging sites need more attention, especially in relation to possible carry-over effects to the next season (*cf.* Guillemain *et al.* 2008). Moreover, during moult, autumn migration and winter, the complicated trade-offs between food abundance, food handling time, energy content of different food types, and predation risk, may, when studied in more detail and as interactions, produce new interpretations and insights (*cf.* Arzel *et al.* 2007). More study is also required of the taxonomic, temporal and spatial generality of the potential mis-match between prey abundance and timing of duck migration (*cf.* Arzel & Elmberg 2004; Arzel *et al.* 2009), the pattern whereby ducks tend to leave wintering and spring staging sites before energy- and protein-rich invertebrate prey increase in abundance. The unresolved issues about food limitation in dabbling ducks mentioned here are in great need of experimental approaches.

The third paradigm about population limitation in dabbling ducks similarly offers a mixture of clear results and uncertainties in need of further study. For example, it has long been known that extreme cold or prolonged winters may reduce waterfowl populations far below carrying capacity (Newton 1998), and that populations may need many years to recover from such events (Nilsson 2005). Effects of inclement weather on breeding success have not been documented spatially or temporally, although studies demonstrate effects on duckling survival (Koskimies & Lahti 1954; Krapu *et al.* 2000; Gunnarsson *et al.* 2006). However, there have been few cold winters with extensive ice coverage in the Baltic and surrounding countries in the last two decades, and thus little large-scale winter mortality. Rather, the lack of severe weather likely explains the positive population change for many European dabbling duck populations during this period. Despite outbreaks of avian influenza and other more local disease episodes, there have been no major die-offs of dabbling ducks in Europe in the last two decades. It should be noted, however, that almost nothing is known about sub-lethal effects of infections, which may have greater consequences for populations than the truly lethal ones. This is because significant population level effects may go undetected because milder infections have the potential to reduce survival or fecundity in a large number of individuals; sick ducks may be more closely implicated in population change than dead ones.

Impacts of hunting on duck population size have to be considered within the third paradigm of population limitation, but these are difficult to quantify despite the research effort to date. European Union (EU) annual bag records for some species (notably Mallard and Teal) are remarkably high compared to estimated overall population size (Hirschfeld & Heyd 2005; Delany & Scott 2006), which may be a reason for concern. On the other hand, the pre-harvest size of European dabbling duck populations is unknown (see below about monitoring needs), and might be larger than thought. Further, recent studies indicate that density dependence may be a frequent and widespread process in dabbling duck demography (Table 2; Viljugrein *et al.* 2005), hence providing the case for hunting mortality being compensatory to some extent (*cf.* Pöysä *et al.* 2004).

In conclusion, there are elements supporting all three paradigms about population limitation in European dabbling ducks. The least equivocal evidence concerns predation and food limitation on nemoral and boreal wetlands, the only systems in which combined descriptive-experimental pattern-process studies have

Table 2. Evidence that density-dependent processes affect breeding Mallards have been found in all experimental studies carried out in Europe. The pattern from descriptive European studies (below) based on time series data (all except Andrén 1991) is less consistent.

Study type	Dependent variable	Evidence	Spatial scale	Biome	Nutrient status	Source
Experimental	Nest survival	Yes	Lake	Boreal	Meso-/oligotrophic	Elmberg *et al.* 2009
Experimental	Nest survival	Yes	Lake	Boreo-nemoral	Oligotrophic	Gunnarsson & Elmberg 2008
Experimental	Nest survival	Yes	Lake	Nemoral	Eutrophic	Gunnarsson & Elmberg 2008
Experimental	Nest survival	Yes	Lake	Mediterranean	Eutrophic	Elmberg *et al.* 2009
Experimental	Broods per nesting pair	Yes	Lake	Nemoral	Eutrophic	Elmberg *et al.* 2005
Experimental	Duckling survival	Yes	Lake	Boreal	Oligotrophic	Gunnarsson *et al.* 2006
Experimental	Duckling survival	Yes	Lake	Nemoral	Eutrophic	Elmberg *et al.* 2005
Descriptive	Nest survival	No	Lake (island)	Nemoral	Eutrophic	Andrén 1991
Descriptive	Nest survival	Yes	Lake	Nemoral	Eutrophic	Hill 1984
Descriptive	Broods per nesting pair	No	Lake	Boreal	Mesotrophic	Pöysä 2001
Descriptive	Broods per nesting pair	No	Lake	Boreal	Eutrophic	Pöysä 2001
Descriptive	Broods per nesting pair	No	Landscape	Boreal	Meso-/eutrophic	Pöysä 2001
Descriptive	Broods per nesting pair	No	Watershed	Boreal	Meso-/oligotrophic	Elmberg *et al.* 2003
Descriptive	Broods per nesting pair	Yes	Lake	Boreo-nemoral	Eutrophic	Elmberg 2003
Descriptive	Duckling survival	Yes	Lake	Nemoral	Eutrophic	Hill 1984
Descriptive	Duckling survival	Yes	Lake	Boreo-nemoral	Eutrophic	Elmberg 2003
Descriptive	Duckling survival	No	Watershed	Boreal	Meso-/oligotrophic	Elmberg *et al.* 2003
Descriptive	Fledglings per female	Yes	National	Boreal	Not defined	Gunnarsson *et al.* 2008
Descriptive	Overwinter survival	Yes	Lake	Nemoral	Eutrophic	Hill 1984

been carried out in a consistent fashion. It is reasonable to hypothesise that food availability outside the breeding season may also limit populations, especially when the possible intricate trade-offs between foraging profitability and predation risk are incorporated, although a major caveat remains the historical context of population limitation. Most wetlands in central and southern Europe have already been lost due to drainage for agriculture and urbanisation, and it therefore seems likely that present-day populations of dabbling ducks are much smaller than they were only a few centuries ago. Ultimately, habitat availability sets the outermost limit on overall carrying capacity and hence population size.

Adaptive management and prevalence of density dependence

Acknowledging that the historical loss of wetland habitat has reduced the potential carrying capacity of wetlands for Europe's dabbling duck populations, the question remains as to what decides their population changes now and in the near future. Adaptive management is an influential concept for addressing the issue of long-term sustainable harvest levels in the light of uncertainties related to management and biology (Johnson *et al.* 1993; Nichols 2000). Essentially, adaptive management rests on the idea that the harvest level is adjusted at regular intervals in accordance with estimates of recruitment and previous bag size for a particular species or a population. Many aspects of waterfowl management in North America in recent decades are of this type.

Management of European ducks could benefit from using a similar approach, but our continent comprises more than 40 nations and more languages still. In these countries there are also very different cultures and attitudes towards waterfowl, wetlands and hunting, and, most importantly, a rich flora of national hunting legislations. In essence, this is true for the EU too, although some initiatives to coordinate monitoring efforts and legislation have been taken. Yet waterfowl is one shared resource for the EU and Europe alike, and as ducks do not recognise our borders they also become one shared responsibility. Wetland reduction is still an issue locally, and there is increasing concern as to how climate change may affect duck populations through habitat change, pathogen load and phenological mis-matches with their food resources (Drever & Clark 2007). Consequently, conservation as well as hunting interests have much to gain from a more coherent all-European duck management policy.

The need for, aims of and prospects of such a common policy have been outlined in a previous paper (Elmberg *et al.* 2006), and it is beyond the scope of the present contribution to elaborate on this. Nevertheless, in keeping with undisputed basics of population ecology, future initiatives to adopt a more adaptive management of European dabbling ducks need to be based on: 1) monitoring of breeding population size, 2) monitoring of breeding success *before* annual harvest, 3) collecting harvest data at regular intervals, 4) collecting harvest data with consistent methods at a population or flyway level, and 5) a deeper understanding of the prevalence of density-dependent processes.

None of 1)–4) are primary objectives of the present European monitoring and management strategies. Hence, adoption of any of these items would constitute a significant improvement compared to the present situation, even if the objective is not to accomplish a full programme of adaptive management. With respect to item 5), there is now enough data to argue that one of the basic biological premises for successful adaptive management is at hand; there is an emerging pattern that density-dependent processes are widespread and frequently occurring in a model species, the Mallard (Table 2). In the context of harvest strategies it would be of utmost importance to find out whether mortality patterns during late summer and early autumn, too, have density-dependent components.

Conclusions

The last 20 years of waterfowl research have brought about a dramatic increase in autecological knowledge; some species of goose and duck have emerged as genuine model species, bridging traditional disciplines. The causes of migratory behaviour have become integrated with ecophysiology and life history theory. Extensive ringing programmes have taken research of duck populations from basic mapping of migratory routes to the development of a year-round understanding of individual movements and changes in distribution. Yet, as players in freshwater ecosystems, dabbling ducks remain under-appreciated in limnology and in ecology in general. For example, it was not anticipated even 10 years ago that virologists, epidemiologists and infectious disease specialists would have an urgent requirement for a better understanding of the movements and effects of disease on duck populations. Not only can dabbling ducks be major players in processes in ecological time, as described in this review, but perhaps also as drivers of selective regimes and co-evolution in more long-term evolutionary processes.

Given the uncertainty about the future environment, a deeper understanding of the processes limiting and possibly regulating populations is required. There is a need for more flyway-level studies as well as for more baseline information from temporally and spatially under-studied aspects highlighted in the present review. Now and in the future, descriptive data need to be challenged critically by experimentation in order to confirm underlying causes of population change. To achieve conservation and sustainable harvesting objectives there is a great need to start monitoring breeding population size and annual production pre-harvest. Recurring and internationally coordinated compilations of harvest bags are also much called for.

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