Duck-fish competition in boreal lakes - a review

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Ducks share the aquatic environment with invertebrate-eating fish. Thus, competitive interactions may take place. Fish have been introduced to many formerly fishless lakes, which has profoundly affected the competitive and predatory relations in these waters. In this paper we review recent findings on duck-fish competitive interactions in boreal lakes. On a general level, analyses based on presence/absence data of fish have indicated that ducks can be negatively affected by fish. More rigorous studies where fish density has been considered have corroborated the pattern emerging from presence/absence studies. For the Common Goldeneye (Bucephala clangula) and Eurasian Perch (Perca fluviatilis), the effect of competition has been tested experimentally. In general, it appears that diving ducks such as Common Goldeneye, which forage in open water, are the most affected by fish, Common Teal (Anas crecca) is intermediate, whereas Mallard (A. platyrhynchos), which forage among the shore vegetation, is little affected. Likelihood or the strength of competition between ducks and fish may also depend on habitat productivity and structure. Numbers of invertebrates are higher among vegetation where there are less fish preying on them. Duck-fish interactions are important to take into account when planning wetland creation and restoration for ducks. There is also an urgent need to mitigate the effects of fish introductions in wetlands.

1. Introduction

The importance of interspecific competition as a force shaping ecological communities has been debated for a long time (e.g., Connell 1983, Begon et al. 2006). However, most examples of competition usually concern relatively closely related species, e.g. species within a genus or family (Schoener 1983). Much less is known of intertaxon competition (Rosenzweig & Abramsky 1993), although there are some examples of competitive interactions between different phyla, e.g. rodents, birds, and frogs vs. insects (Brown & Davidson 1977, Morin et al. 1988, Aho et al. 1999).

Fish and ducks are often limited by the same key environmental factors, such as lake productivity (Paszkowski & Tonn 2000). Many ducks feed on the same invertebrate prey as fish do and, hence, there is a potential for competitive interactions between the two groups. In freshwater aquatic ecosystems, invertebrate-eating fish are known to strongly affect the distribution and abundance of their prey (Gilinsky 1984, Zimmer et al. 2002, Batzer 2013).

Community structure, abundance and species richness of aquatic invertebrates clearly differ in lakes with and without fish. Fishless lakes harbour more macroinvertebrates and higher macroinver-



tebrate diversity than lakes with fish (Mallory *et al.* 1994, Schilling *et al.* 2009).

Fish predation on invertebrates usually acts more effectively in simple, non-vegetated habitats (Heck & Crowder 1991, Diehl & Kornijów 1998), and this top-down regulation especially affects the abundance and size distribution of prey living in the water column (Evans 1989, Diehl 1992, Tate & Hershey 2003). This pattern is pronounced in boreal areas, where lakes typically have a habitat structure with a relatively sparse shore vegetation zone (Haapanen & Nilsson 1979, Nummi & Pöysä 1993).

Boreal wetlands form a relatively coherent group with regards to habitat structure and productivity, and we will therefore focus in our review on fish-duck competition research done in this area. Many ducks also feed on plants but here we focus on competition for invertebrate prey because, as far as we know, studies addressing specifically fish-duck competition for plants have not been done. We include all the Eurasian boreal areas described by Taggart and Cross (2009) covering the whole of Fennoscandia, the northern parts of the Baltic States, and continuing throughout Russia to the Pacific Ocean and the northeastern parts of China. For North America we follow the descriptions of Mack and Morrison (2006), according to which the boreal ranges from Alaska and eastwards throughout all of Canada; however, differing from their classification, we also include the boreal transition zones in this study. We used the literature survey by Holopainen et al. (2015) as our main data base to find scientific articles published about fish-duck competition in the boreal. In total, we found 14 papers concerning the subject (Table 1). All the studies come from Fennoscandia and Canada, and we didn't find a single one from the Russian boreal. Likewise, many boreal duck species have not been included in the studies performed so far (see also Holopainen et al. 2015).

The most abundant Holarctic boreal ducks are Mallard (*Anas platyrhynchos*), Pintail (*Anas acuta*), Common Goldeneye (*Bucephala clangula*) and Velvet Scoter (*Melanitta fusca*). In the Palearctic boreal Common Teal (*Anas crecca*), Wigeon (*Anas penelope*), Tufted Duck (*Aythya fulicula*) and Smew (*Mergellus albellus*) are numerous (Valkama *et al.* 2011). In the Nearctic boreal Green-winged Teal (*Anas carolinensis*), American Wigeon (*Anas americana*), American Black Duck (*Anas rubripes*), Ring-necked Duck (*Aythya collaris*), Lesser Scaup (*Aythya affinis*), and Hooded Merganser (*Lophodytes cucullatus*) abound (Mack & Morrison 2006). Table 1 shows which of the species have been studied in the duck–fish context. Of insectivorous fish, Eurasian Perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) are common species in the Palearctic, and Yellow Perch (*Perca flavescens*), Brook Stickleback (*Culaea inconstans*), Fathead Minnows (*Pimephales promelas*) and White Sucker (*Catostomus commersoni*) in the Nearctic (McNicol *et al.* 1987, McNicol & Wayland 1992, Rask *et al.* 2010).

2. Observations and experiments

The 14 papers (Table 1) described 152 individual cases of fish variables explaining duck variables, e.g. lake use of Mallard pairs explained by small fish and large fish occurrence in the same study makes two cases. These cases are usually independent between studies and among species and stages within a study. Only three cases out of 152 found positive interactions between fish occurrence and ducks, while 42 found negative ones; negative interactions were more frequent than positive ones (binomial test, P < 0.001).

At a general level, presence/absence data of fish show that ducks in all stages of the breeding cycle may be negatively affected by fish presence, both in Europe (Eriksson 1979, Elmberg et al. 2010) and in North America (McNicol et al. 1987, Parker et al. 1992, Epners et al. 2010). Also duck species richness has been shown to be negatively associated with fish occurrence (Elmberg et al. 2010). Paszkowski and Tonn (2000), however, found different results in their study of community concordance of fish and waterbirds in Canada. Occurrence and species richness of both groups were affected by the same environmental factors, such as lake size and productivity. And, competition between birds and fish appeared to play a much smaller role in shaping the two assemblages (Paszkowski & Tonn 2000).

More intensive research with data on both fish and duck density have supported the findings of extensive presence/absence studies. These have looked especially at competition between Eur-

Fish species/ variable type	Study type	Reference
Fish density	Descriptive	Eriksson 1983
YE, density	Descriptive	Eadie & Keast 1982
Fish occurrence	Descriptive	Pehrsson 1984
Fish occurrence	Descriptive	McNicol et al. 1987
Fish occurrence (cyprinids, YE)	Descriptive	McNicol & Wayland 1992
Fish occurrence	Descriptive	Parker <i>et al.</i> 1992
Fish community	Descriptive	Paszkowski & Tonn 2000
Fish occurrence	Descriptive	Elmberg <i>et al.</i> 2010
Fish occurrence	Descriptive	Epners <i>et al.</i> 2010
Total fish, PE, RO, PI	Descriptive	Väänänen <i>et al.</i> 2012
Fish occurrence	Descriptive/	Eriksson 1979
and manipulation	experimental	
BR, manipulation	Experimental	DesGranges & Rodrigue 1986
PE, density and manipulation	Descriptive/ experimental	Pöysä <i>et al.</i> 1994
PE, density and manipulation	Descriptive/ experimental	Nummi <i>et al.</i> 2012
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Table 1. Studies of fish-duck competition in the boreal region.

Species abbreviations. Ducks: MA = Mallard, BL = Black Duck, TE = Common Teal, RI = Ring-necked Duck, GO = Goldeneye, HO = Hooded Merganser; Fish: PE = Eurasian Perch, YE = Yellow Perch, RO = Roach, PI = Eurasian Pike, BR = Brook Trout.

asian Perch (hereafter Perch) or Yellow Perch and Common Goldeneye (hereafter Goldeneye). These studies have been conducted both in different parts of a large lake (Eadie & Keast 1982) and within a group of lakes (Pöysä *et al.* 1994, Nummi *et al.* 2012, Väänänen *et al.* 2012).

Competition between Goldeneye and Perch has also been tested with field experiments. Eriksson (1979) divided a fishless lake into two parts and introduced Perch to one part. He also eradicated the fish populations from another lake. Goldeneye brood use responded positively to fish eradication but not negatively to fish introduction. Nummi *et al.* (2012) introduced Perch into three lakes which had become fishless in the 1980s because of acidification. After the perch population increased in the experimental lakes, lake use by Goldeneye broods decreased (see also Rask *et al.* 2001) whereas the number of pairs were not much affected. This pattern was similar in an experimental lake which was divided in two with a plastic curtain and in which one half became fishless (Pöysä *et al.* 1994): Goldeneye brood use of the fishless side clearly increased whereas pairs did not respond to the loss of Perch.

Age-specific differences in the response of Goldeneye to changes in invertebrate populations have been found in experimental settings (Pöysä *et al.* 1994, Nummi *et al.* 2012). It has been suggested (Nummi *et al.* 2012) that the lack of response of Goldeneye adults to Perch introduction could have been due to the concealed benthos that may not be affected as strongly by the visually oriented Perch as the visible nektonic invertebrates (Estlander *et al.* 2010). Adult diving ducks presumably can use benthos since they are effective benthic foragers (see Tome 1988). This age-related difference has not been found in descriptive studies (Pöysä *et al.* 1994, Nummi *et al.* 2012).

Duckling behavior, growth and survival have also been studied in relation to fish density. DesGranges & Rodrigue (1986) found that Ameri-

	Fishless	Cyprinid	Perch, Yellow Perch
Benthic inverts Nectonic inverts Duck species affected negatively	Positive Positive –	Positive Negative Ring-necked Duck Common Teal Mallard	Negative Negative Goldeneye Ring-necked duck Black Duck (Common Teal)

Table 2. The effects of different fish communities on aquatic invertebrate groups and ducks.

can Black Duck ducklings spent more time foraging but gained less weight in lakes with abundant fish. This finding is corroborated by studies outside the boreal: one in Maine, USA (Hunter *et al.* 1986), and another in England where Tufted Duck brood size increased after fish removal from gravel pit lakes (Giles 1994).

3. Species affected

In general, it appears that habitat use by diving ducks foraging in more open water is more affected by fish competition than that of dabbling ducks (Table 1). Of 70 cases of diving duck-fish associations, 26 found evidence of competitive interactions, while the corresponding figures for dabbling ducks and fish were 71 and 12, implying that competitive interactions were more frequent in diving ducks than in dabbling ducks ($\chi^2 = 7.336$, df = 1, P = 0.007). Of the diving ducks, the Goldeneye (Eriksson 1983, McNicol & Wayland 1992, Elmberg et al. 2010, Väänänen et al. 2012), Ring-necked Duck (McNicol & Wayland 1992, Paszkowski & Tonn 2000) and to some extent Hooded Merganser (McNicol & Wayland 1992) has been found to be affected by fish.

However, there appears to be some differences in the response to fish among dabbling ducks. Common Teal with habitat use not associated with vegetation, seems to be more affected by fish, whereas Mallards show the weakest response to fish presence as they forage in the shore vegetation where fish are sparse (Elmberg *et al.* 2010, Väänänen *et al.* 2012).

Interestingly, American Black Duck appears to resemble teal in its response: a negative fish effect on its presence, or growth and behavior, has been found both in descriptive (McNicol & Wayland 1992) and experimental studies (DesGranges & Rodrigue 1986).

The structure of the fish community also affects competition with ducks. The effects of Cyprinid and Perch dominated fish communities have been considered separately in some studies (Table 2, McNicol & Wayland 1992 [see below], Väänänen *et al.* 2012). When Perch and Roach were considered separately in oligotrophic lakes, a negative association, suggesting food competition, was found between Perch and Common Teal and Goldeneye. The role of Roach as a food competitor, again, seemed to have minor importance in oligo- and mesotrophic lakes (Väänänen *et al.* 2012).

4. Food and habitat related processes

4.1. Food

The competitive effect of fish on ducks is assumed to act via a reduction in the abundance of aquatic invertebrates in oligotrophic lakes. In eutrophic lakes also habitat structure may be of great importance (Diehl 1992, Diehl & Kornijów 1998). As already mentioned above, insectivorous ducks and fish consume similar invertebrate foods and diet overlap in certain circumstances may be considerable (Giles et al. 1990, Krapu & Reinecke 1992, Paszkowski & Tonn 2000, Nummi & Väänänen 2001, Estlander et al. 2010). In the Goldeneye and Yellow Perch, this assumption was verified with a study by Eadie & Keast (1982) showing a considerable diet overlap (71%) in the two species (for Perch and Goldeneye, see Pöysä et al. 1994). Furthermore, in fishless situations, ducklings of Goldeneye and Hooded Merganser ate more nektonic prey, e.g. Dytiscids, than in lakes with

fish (Bendell & McNicol 1995). Large nektonic insects such as Dytiscids are known to be susceptible to fish predation (Diehl 1992, see below).

The effect of fish on invertebrate abundance has been studied in some duck–fish research. Parker *et al.* (1992) found that wetlands with the most invertebrates and most broods contained no fish. The pattern was clearest for young (1–36 days) American Black Duck ducklings. In a Goldeneye–Perch study, Nummi *et al.* (2012) found that Perch densities were negatively associated with invertebrate abundance and lake use by Goldeneye broods.

McNicol and Wayland (1992) found interesting differences in the way fish assemblages dominated either by Cyprinid or Yellow Perch affected different invertebrate groups. Yellow Perch suppressed both nektonic and benthic invertebrates whereas Cyprinids affected mainly nekton (Table 2). Thus, Cyprinid lakes were less attractive to waterfowl than fishless lakes because they harbored less nekton, but were more attractive than Perch lakes because they had more benthos. Kloskowski et al. (2010), again, found (in temperate Poland) that the age structure of Common carp (Cyprinus carpio) populations affected habitat use of Mallard and Tufted Duck. This has not been studied in the boreal, but considering the diet shift from invertebrates to fish of growing Perch, the age structure of fish populations may have an effect on ducks also there.

Clear-cut effects of fish predation on invertebrates have been found in two experiments. Eriksson (1979) found that after elimination of fish from a lake, the abundance of all invertebrate groups increased and lake use by Goldeneye ducklings increased. And, in an experiment by Nummi *et al.* (2012), invertebrate abundance and lake use by Goldeneye broods decreased upon introduction of Perch. Within the invertebrate groups, the decrease was especially sharp for large-sized Dytiscids, as predicted by Diehl (1992), for example.

4.2. Habitat features

Although boreal lakes generally are quite oligotrophic, their margins may be lined with emergent, and sometimes floating and submerged vegetation. Most studies on macrophytes, invertebrates and fish concern submerged vegetation (Heck & Crowder 1991, Diehl & Kornijów 1998) but one may assume that the structural complexity of emergent plants contain similar elements. It is generally assumed that because of less predation by fish, there are more large-sized macroinvertebrates in vegetated habitats (Mittelbach 1981, Diehl & Kornijów 1998). Herbivorous fish may also directly affect vegetation structure in eutrophic lakes, but very little of this is known from the boreal zone (but see Sammalkorpi *et al.* 2014).

Hornung and Foote (2006) studied how both aquatic vegetation structural complexity and fish presence predict the distribution of invertebrate biomass in boreal wetlands. The percent volume occupied by aquatic plants was positively associated with invertebrate biomass. Particular invertebrate functional feeding groups were correlated with different types of aquatic macrophyte architecture. Herbivorous invertebrate biomass was greater in more complex aquatic environments whereas predatory invertebrate biomass was greater in environments with simple plant architecture. Wetlands inhabited by Brook Stickleback (Culaea inconstans) had reduced invertebrate biomass of predatory and gatherer/collector functional feeding groups. Gatherer/collector, predator, and shredder invertebrates were negatively correlated with dissected leaved plant dominance in wetlands without fish. These invertebrate groups comprise the bulk of invertebrate protein available to nesting hen Mallards and their ducklings. Hornung and Foote (2006) suggested that the presence of Stickleback and/or dominance of dissected leaved plants in the wetlands resulted in decreased food supply for waterfowl. Concerning emergent plants, Nummi and Pöysä (1995) found that the number of aquatic invertebrates were clearly higher in patches of multistemmed Carex than within Phragmites with a more simple architecture.

Competitive fish-duck interactions can be modified by non-consumptive processes affecting habitat features. These include Muskrat (*Ondatra zibethica*) herbivory and increased water turbidity caused by fish. In a "natural experiment" setting, Nummi *et al.* (2006) found that there are differences in the occupancy of invertebrates and fish in a mosaic of Water Horsetail (*Equisetum fluvia*- *tile*)-open water stands after heavy Muskrat grazing. The habitat mosaic consisted of 1) clear-cut open-water area, 2) mixed floating and submerged vegetation and 3) undisturbed *Equisetum*. Invertebrates were more numerous and larger in size in *Equisetum* and mixed vegetation stands compared to clear-cut areas where the invertebrates were lower in numbers and smaller in size. Perch were found only in clear-cut areas. The change in the Water Horsetail habitat caused by Muskrat grazing rendered large-sized invertebrates more vulnerable to fish predation, but provided diverse habitat structure during the mixed vegetation phase.

In more eutrophic boreal waters, benthivorous fishes, such as Cyprinids, increase water turbidity through resuspension of sediment. They also promote phytoplankton through nutrient recycling and suppression of large-bodied zooplankton (Schriver *et al.* 1995, Tátrai *et al.* 1997). These actions have negative effects on the availability of macroalgae, macrophytes and macroinvertebrates, and thus, have strong harmful effects on the food resources of ducks (Haas *et al.* 2007).

5. Consequences of competition

Food competition between fish and ducks occurs widely in the boreal and has strong effects on duck populations (e.g., Haas et al. 2007, Nummi et al. 2012). Competition between birds and fish is asymmetrical. If there is shortage of food, fish and ducks respond to "lean" times differently (Väänänen et al. 2012). Perch have a flexible diet, are effective at catching aquatic invertebrates and can tolerate food shortages much better than duck broods. If invertebrate abundance is a limiting factor, Perch decrease body growth (Alm 1946, Nyberg et al. 2010), and they can change to a fishdominated diet if possible (Horppila et al. 2000). Unlike fish, duck broods have to move to another lake or ducklings may die (see Sjöberg et al. 2000, Gunnarsson et al. 2004). Indeed, movement between lakes during the brood stage seems to be common in ducks especially if suitable feeding lakes are nearby (e.g., Paasivaara & Pöysä 2008 and references therein). However, such movements do not necessarily increase duckling mortality (e.g., Pöysä & Paasivaara 2006), suggesting that ducks are able to mitigate the negative effects of food competition at least to some degree.

6. Fish–duck competition in a changing world

During the last century the competitive interactions of fish with other species have faced many anthropogenic changes in fresh waters. One common activity worldwide has been to introduce fish to fishless lakes (Pister 2001, Denoel *et al.* 2005). In USA for example, thousands of formerly fishless lakes have been stocked, thereby effectively removing this habitat type from some regions (e.g. Schilling *et al.* 2009). Both in Europe and North America this has led to drastic decline in populations of Amphibians and those invertebrates which cannot cope with fish predation (Pilliod & Peterson 2001, Kats & Ferrer 2003).

The effect of these fish introductions on birds is less well known, but deducing from acidified lakes that have lost and then regained fish populations, we may assume that the effect might have been substantial (Eriksson et al. 1980, Nummi et al. 2012). The effects of fish on birds not only concern oligotrophic boreal habitats but extend to more eutrophic situations in the boreal zone, as shown in experiments in Germany, a little south of the boreal (Haas et al. 2007). The biomass of benthic macroinvertebrates as well as densities of waterbirds were reduced in Common Carp ponds compared to fishless ponds. There are also recent observations of the detrimental effects of introduction of the alien Prussian Carp (Carassius gibelio) on waterbirds (Sammalkorpi, pers. comm.). Epners et al. (2010) found that breeding waterfowl density was two times higher in fishless lakes than in lakes with fish, and in some duck species this effect was even more pronounced at the molting stage.

As discussed above, indirect anthropogenic effects also have played an important role in fishduck competitive interactions. Eutrophication process may have affected duck populations negatively either via impacts on water quality or by causing increases in cyprinid fish populations (see above and Pöysä *et al.* 2013, Lehikoinen *et al.* 2016). Sulphate deposition has been the major driving force of the acidification of boreal surface waters (e.g., Doka *et al.* 2003, Rask *et al.* 2014 and references therein). Sulphur emission reductions in Europe have induced a chemical recovery of acidified lakes in Finland and elsewhere since the late 1980s (Doka *et al.* 2003, Forsius *et al.* 2003, Arvola *et al.* 2010, Rask *et al.* 2014). This has resulted in the recovery of fish populations in formerly acidified lakes. For example, Rask *et al.* (2014) concluded that many Perch populations that were affected by acid deposition or became extinct in Finland by the end of 1980s have recovered following the chemical recovery of acidified lakes. This may have negative effects on duck populations, especially on Goldeneyes (McNicol *et al.* 1995, Rask *et al.* 2001). Interestingly, the breeding population of the Goldeneye in Finland has decreased since the mid-1990s (Pöysä *et al.* 2013).

Along with the recovery of lake waters from acidification, water colour values have increased during the last decades (so-called 'brownification' process; Monteith *et al.* 2007, Arvola *et al.* 2010, Weyhenmeyer *et al.* 2014). Ecological consequences of water browning are not well known but it has been found that water colour affects benthic primary production, translating into effects on production and biomass of benthic invertebrates and fish (Karlsson *et al.* 2009). It remains to be studied whether the recent brownification process of boreal waters affects fish–duck competitive interactions.

7. Conclusions

The large amount of research done in boreal waters has shown that fish have asymmetric competitive effects on ducks. This has manifested especially in duck habitat use and lake occupation. Some studies suggest that fish competition may also affect reproductive success of ducks but this aspect has not been examined as thoroughly.

Fish introductions have reduced the suitability of aquatic habitats for many vertebrates, directly through competition, and indirectly through complex influences on aquatic communities (Bouffard & Hanson 1997). There is an urgent need to ensure the occurrence of fishless lakes, to protect fishless habitats from further fish introductions, and to restore wetlands where inappropriate fish introductions have been made in the past (Zimmer *et al.* 2002, Denoel *et al.* 2005, Schilling *et al.* 2009, Epners *et al.* 2010). Finally, the recent recovery of boreal lakes from acidification, and the concurrent browning of lake waters, may have unanticipated implications to fish–duck interactions. Freshwater ecosystems are in a continuous state of change, therefore research on fish–duck competitive interactions should continue into the future.

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Sorsien ja kalojen välinen kilpailu boreaalisilla järvillä

Sorsat ja kalat syövät molemmat paljon vesiselkärangattomia. Niinpä on mahdollista, että näiden ryhmien välillä on kilpailua ravinnosta. Kilpailu saattaa tulla erityisen hyvin näkyviin boreaalisilla järvillä: niissä on yleensä vain vähän kasvillisuutta selkärangattomien suojana, joten saalistus vaikuttaa selkärangattomiin voimakkaasti. Havaitsimme katsauksessamme, että vajaassa kolmasosassa tutkituista tapauksista kilpailua tosiaan esiintyi sorsien ja kalojen välillä.

Kilpailusta oli merkkejä niin töissä, joissa selvitettiin ilmiötä laajoilla esiintymiseen perustuvilla aineistoilla, kuin selvityksissä, joissa käytettiin hyväksi sorsien ja kalojen tiheyksiä. Sorsien ja kalojen välistä kilpailua on myös tutkittu kokeellisesti esimerkiksi istuttamalla kaloja lampiin, joista ne ovat hävinneet. Tällöin selkärangattomien väheneminen kalasaalistuksen seurauksena tuli selkeästi näkyviin. Nämä tutkimukset ovat useimmiten käsitelleet telkkää ja ahventa.

Katsaus paljasti myös kalojen vaikuttavan voimakkaammin avoimessa vedessä ruokaileviin sukeltajasorsiin, kuten amerikantukkasotkaan ja telkkään, kuin rannan tuntumassa viihtyviin puolisukeltajiin, kuten sinisorsaan. Kalayhteisön koostumuksella oli myös merkitystä vaikutuksen kannalta. Ahvenkalojen on todettu vaikuttavan sekä vesirungon selkärangattomiin että pohjaeläimiin, kun taas särkikalat vähentävät ennen kaikkea vesirungon eliöitä. Niinpä ahventen vaikutus sorsiin on voimakkaampi.

Johtopäätöksenämme on, että kalojen voimakas saalistus on syytä ottaa huomioon kosteikoiden hoidossa. Sellaisille paikoille, joissa ei alun perin ole kaloja, ei niitä tule missään nimessä istuttaa. Erityistapauksissa voidaan myös pyrkiä eroon istutetuista kaloista. Tällä tavoin turvataan niin lintujen, sammakkoeläinten kuin eräiden selkärangattomienkin elinmahdollisuudet kosteikoilla.

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