TOPICAL REVIEW

Meta-analysis of environmental effects of beaver in relation to artificial dams

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Abstract

Globally, artificial river impoundment, nutrient enrichment and biodiversity loss impair freshwater ecosystem integrity. Concurrently, beavers, ecosystem engineers recognized for their ability to construct dams and create ponds, are colonizing sites across the Holarctic after widespread extirpation in the 19th century, including areas outside their historical range. This has the potential to profoundly alter hydrology, hydrochemistry and aquatic ecology in both newly colonized and recolonized areas. To further our knowledge of the effects of beaver dams on aquatic environments, we extracted 1366 effect sizes from 89 studies on the impoundment of streams and lakes. Effects were assessed for 16 factors related to hydrogeomorphology, biogeochemistry, ecosystem functioning and biodiversity. Beaver dams affected concentrations of organic carbon in water, mercury in water and biota, sediment conditions and hydrological properties. There were no overall adverse effects caused by beaver dams or ponds on salmonid fish. Age was an important determinant of effect magnitude. While young ponds were a source of phosphorus, there was a tendency for phosphorus retention in older systems. Young ponds were a source methylmercury in water, but old ponds were not. To provide additional context, we also evaluated similarities and differences between environmental effects of beaver-constructed and artificial dams (767 effect sizes from 75 studies). Both are comparable in terms of effects on, for example, biodiversity, but have contrasting effects on nutrient retention and mercury. These results are important for assessing the role of beavers in enhancing and/or degrading ecological integrity in changing Holarctic freshwater systems.

Introduction

Maintenance and restoration of the ecological integrity of freshwater ecosystems is a major global challenge due to anthropogenic hydrogeomorphological alterations, nutrient enrichment and loss of biodiversity (Vörösmarty et al 2010). Increased demand for water, flood control and hydropower energy has resulted in a steady increase in the number of artificial dams in streams and rivers (Downing 2010, Vörösmarty et al 2010, Lehner et al 2011, Zarril et al 2015). In addition, beavers (Castor canadensis and Castor fiber), ecosystem engineers known to build dams and create ponds, are recovering across much of the Holarctic after near or partial extirpation, which started in southern and central Europe as early as the medieval times and in northern regions in the 19th century. Recovery is evident from substantial increases in population size, distribution range expansion in North America (C. canadensis) and Eurasia (mainly C. fiber, but also C. canadensis), and introduction to new areas (e.g. southern Patagonia) (Naiman et al 1988, Baldini U et al 2008, Halley et al 2012). Today, beavers are included in reintroduction programs aimed at rewinding and/or restoring degraded landscapes all over the Holarctic (Foreman 2004, Pereira and Navarro 2015).
While artificial dams disrupt the ecological integrity of streams (Nilsson et al. 2005, Vorösmarty et al. 2010), beaver dams are considered to increase it by re-naturalizing degraded stream systems (Törnblom et al. 2011). The validity of this latter assumption, however, has never been tested as, to our knowledge, there is no comparison between the environmental effects of artificial and beaver impoundments. Artificial dam construction causes a multitude of environmental changes in freshwater environments, e.g. alterations of hydrogeomorphology (including environmental flow), biogeochemistry, ecosystem functioning, and biodiversity (reviewed by Foley et al. 2017). For example, in 2000, 12% of the global river phosphorus (P) was trapped in artificial impoundments, a level of retention that is predicted to increase to 17% in 2030 due to an increase in the number of artificial dams (Maavara et al. 2015). Further, artificial dams result in increased concentrations of mercury (Hg) and methyl Hg (MeHg) in biota (Bodaly et al. 2007, Hall et al. 2009), a general decrease in fish abundance and diversity and an increase in the number of barriers to fish migration (Gehrke et al. 2002, Vorösmarty et al. 2010, McLaughlin et al. 2013, Mazumder et al. 2016).

While some similarities are to be expected between the effects of beaver dams and artificial dams, it is not certain that the effects of beaver dams will be as severe. Beavers have been present in the Holarctic for more than 20 M years (Rybczynski 2007). Many Holarctic species have co-evolved with beavers and are adapted to natural temporary barriers. Beaver dams may be more ephemeral than artificial dams as they are frequently damaged or even destroyed during high flow events (Hillman 1998, Butler and Malanson 2005). Although beaver dams solidify when aging (Meentemeyer and Butler 1999), not all dams in a beaver territory are necessarily equally maintained (reviewed in Gurnell 1998). Hence, it can be expected that the effects of beaver dams on, for example, migrating fish are less severe than those caused by artificial dams.

Beaver dams have been reported in streams up to fourth order (Westbrook et al. 2006, Smith and Mather 2013, Burchsted and Daniels 2014), while dams for flood control and hydropower generation are generally located on streams of higher order (e.g. streams reviewed by Nilsson et al. 2005, Maavara et al. 2015). Individual beaver ponds are generally small (often less than 1–2 ha and rarely exceeding 50 ha: see for example Alexander 1998, Klotz 1998, Nyssen et al. 2011) and often significantly smaller than artificial reservoirs (mean = 8000 ha for the 155 artificial impoundments reviewed by Maavara et al. 2015). On the other hand, beaver pond density can be high, sometimes exceeding more than 10 ponds per km of stream length (Naiman et al. 1986, Woo and Waddington 1990, Burchsted and Daniels 2014). Despite their smaller size, the frequency and density of beaver ponds motivate a comparison of their environmental effects with those of artificial reservoirs. Furthermore, there is a pressing need to further our knowledge of such small waterbodies since their role in global biogeochemical processes has been unduly neglected in the past (Downing 2010).

Following widespread beaver reintroductions into Europe and North America, several reviews have been written on their hydrogeomorphological, biogeochemical and/or biodiversity effects (Smith et al. 1991, Gurnell 1998, Collen and Gibson 2001, Hering et al. 2001, Rosell et al. 2005, Anderson et al. 2009, Stoffyn-Egli and Willison 2011, Kemp et al. 2012, Parker et al. 2012, Gibson and Olden 2014, Janiszewski et al. 2014, Stringer and Gaywood 2016). Despite the large amount of data available, few studies have systematically quantified the environmental effects of beaver dams and ponds (see Romero et al. 2014 in relation to the biodiversity effects of ecosystem engineers in general). Many assessments of the environmental effects of beaver dams are ambiguous. For example, there is no consensus as to whether beaver ponds are P sources or sinks (Maret et al. 1987, Correll et al. 2000, Harthun 2000), or whether beaver dams adversely affect fish communities (Collen and Gibson 2001, Kemp et al. 2012). Given the ongoing eutrophication (Vorösmarty et al. 2010) and also oligotrophication (Lucas et al. 2016) of freshwater ecosystems globally, it is important to understand the role of beavers in nutrient cycles in general and the potential role of beaver ponds in retaining or releasing nutrients.

Conservation efforts target restoration of stream continuity and flow regimes via, for example, removal of artificial dams (reviewed by Palmer et al. 2014). However, recovering populations of beavers increase discontinuities in streams by either building new dams or renewing dams in previously abandoned systems, leading to a system of dams of varying age and colonization history that affect stream network continuity and flow regimes.

The environmental effects of damming are likely linked to intrinsic properties of the impounded areas. Beaver ponds trap sediment and decrease stream velocity and discharge; processes that appear to be age-dependent, with older systems displaying signs of stronger effects, likely due to increased solidification and decreased permeability of older dams (Meentemeyer and Butler 1999). Hence, it can be expected that old beaver ponds will more closely resemble artificial reservoirs in many respects; including, for example, effects on hydrogeomorphology and nutrient retention. Despite early recognition of the importance of beaver pond age on environmental impact (Naiman et al. 1986), age-dependent effects have rarely been reported except for vegetation succession (e.g. Johnston and Naiman 1987, Wright et al. 2003) and MeHg concentrations in water (Roy et al. 2009a, Roy et al. 2009b, Levanoni et al. 2015).

Quantification of the potential negative effects of beaver dams is crucial to balance out potential environmental benefits including those for species dependent on dead wood (Thompson et al. 2016) and/or threats...
resulting from beaver reintroductions (for example, those related to MeHg in biota; Painter et al. 2015).

In a meta-analysis, we evaluated the effects of the impoundment of streams and lakes by beavers on 16 environmental factors related to hydrogeomorphology, biogeochemistry, ecosystem functioning and biodiversity. Our research posed four main questions:

(i) Do beaver impoundments have consistent environmental effects?

(ii) Are these environmental effects stronger in systems with artificial dams compared to beaver dams?

(iii) What is the importance of system age as a controller of environmental effects?

(iv) Based on these analyses, what direction should be pursued in future for research and sustainable management of currently expanding beaver populations, especially in North America and Europe?

**Methods**

**Selection of studies**

We evaluated the effects of beaver and artificial dam construction on the following environmental factors, which are relevant for understanding biogeochemical and ecological processes in freshwater ecosystems: concentrations of nitrogen (N), P, carbon, dissolved oxygen, Hg and MeHg in water, methane emission, water temperature, hydrology (velocity, water area and volume), sedimentation, dead wood, ecosystem functioning, macroinvertebrates, fish and Hg concentrations in biota. We searched Web of Science™ on 22 April 2016 for peer-reviewed literature listed in Journal Citation Reports using ‘beaver’ and the aforementioned factors as title keywords combined with the following topic keywords: For ‘N’, we used ‘nitrite’, ‘nitrate’, ‘ammonium’, ‘water chemistry’, ‘water quality’; for ‘P’, we used ‘phosphate’, ‘water chemistry’, ‘water quality’; for ‘carbon’, we used ‘total organic carbon’, ‘dissolved organic carbon’, ‘organic matter’, ‘total dissolved solids’ and ‘total suspended solids’; for ‘hydrology’, we used ‘runoff’, ‘flood’, ‘water storage’, ‘water retention’ and ‘hydromorphological alteration’; for dead wood, we used ‘woody debris’; ‘ecosystem function’, ‘ecosystem process’; and for ‘macroinvertebrates’, we used ‘macroinvertebrate’*. We did not use ‘dissolved oxygen’, ‘temperature’, ‘mercury’, ‘methane’, ‘sedimentation’ and ‘fish’ as these were used as unique keywords. We also identified suitable literature on artificial dams focusing on the following six environmental factors: P and Hg concentrations in water, Hg concentrations in biota, ecosystem functioning, macroinvertebrates and fish. For all environmental factors (except P), we used the keywords listed above combined with the following to identify artificially dammed systems: For the title, we used ‘dams’, ‘damming’, ‘impoundment’ or ‘reservoir’ and for topic, we used ‘hydropower’, ‘hydroelectric’ or ‘regulat’*. For P in artificial systems, all data were taken from Maavara et al. (2015). After selecting potential articles using the listed keywords, we made a pre-selection, excluding articles from further analysis that dealt with topics not related to this review, such as beaver morphology, physiology, genetics and foraging strategy. All remaining articles were screened for quantitative data on the respective factors. Several of the initially identified studies were unsuitable due to, for example, lack of empirical data, being either reviews or having results that were potentially impacted upon by confounding effects from intensive disturbances such as mining. We only selected studies that allowed for a comparative approach, i.e. included data from at least two locality types (upstream and downstream [U–D], upstream/reference and impoundment [U–I] or impoundment and downstream [I–D]). Based on our selection criteria, we identified 164 scientific articles that included quantitative data suitable for our meta-analysis, representing studies from 30 countries (11 countries for data from beaver systems) and six continents (three continents for data from beaver systems).

Our intention was to include only studies on small artificial impoundments. Unfortunately, the study of small freshwater systems (especially those <0.01 km²) is underrepresented in the literature (Downing 2010). Whenever possible, we focused on smaller artificial impoundments (median area 1367 ha) and excluded studies from the largest systems (e.g. Three Gorges Dam: 1084 km²).

We included studies on both beaver species. *C. canadensis* has a slightly higher litter size, but both species have otherwise similar life history, ecology and behaviour (reviewed by Parker et al. 2012) and build dams with similar frequency (Danilov and Fyodorov 2015). Hence, we expect similar environmental effects of their dam-construction activity even though, to our knowledge, this has not formally been tested (see Parker et al. 2012 for a review). To ensure our results are not biased by beaver species type, we also analysed differences in effects between species.

**Extraction of data**

If available, we extracted raw factor values from each study; otherwise, mean or median values were registered. If data were only available in figures, they were mainly digitized using WebPlotDigitizer (Rohatgi 2016). For each pair of data (U–D, U–I, I–D), we registered (when available) the following: country of study, system age(s), distance of sampling sites to impoundment, season, number of studied streams/systems and number of observations. System age was classified as young (<10 years) or old (≥10 years). For beaver systems, we recorded colonization status (pioneer versus recolonized: see Levanoni et al. 2015 for details) and species (*C. canadensis* or *C. fiber). We assigned each pair of data to one of three main study designs. The first design followed an upstream-impoundment-downstream approach (Design I, figure S1 available at stacks.iop.org/ERL/12/113002/mmedia), where a
system either included one (Design 1a) or multiple impoundments (Design Ib, figure S1). The second design included at least two systems that were either paired (streams part of the same stream network: Design Ila) or un-paired (streams not part of the same stream network: Design IIb, figure S1). The third type of studies followed a temporal approach that studied the effect of impoundment either before and after establishment (Design IIIa), or before and after removal/collapse of a dam (Design IIIb). For studies that did not apply a paired approach (beaver compared with non-beaver systems or artificial impoundments compared with natural ponds: Design II, figure S1), we registered the lowest number of systems in either of the groups.

Hydrology, sedimentation and fish data were divided into subgroups. For hydrology, we differentiated between effects on velocity (including discharge) and area (including surface area, water depth and water volume). Sediment was divided into ‘coarse’ (substrate with diameter larger than sand) and ‘fine’ (substrate with diameter equal to or smaller than sand), respectively. As substrate diameter was rarely provided in the studies, we used substrate type as classified in the respective studies instead. We applied the substrate divisions since we expected beavers to have contrasting effects on these factors. For example, dam-construction results in a higher proportion of substrate with small diameter and lower proportion of substrate with large diameter in the impoundments. Fish data were analysed as one group, but for analyses focusing on the barrier effects of dams, salmonid response was also analysed separately.

For macroinvertebrates and fish, extracted data on diversity included taxa richness and indices accounting for abundance (e.g. Simpson index, Shannon entropy and evenness indices) (see Tuomisto 2012 for a review of the different indices). It should be noted that diversity and abundance are often inter-correlated and may be confounded (Gotelli and Colwell 2010, Tuomisto 2012). Limited sample size and insufficient raw data precluded the partitioning of diversity into different components.

Quantifying the effect of dam construction

The effect size of beaver-constructed and artificial dams on the studied factors was assessed using the response ratio suggested by Osenberg et al (1997):

\[
\Delta r_1 = \ln \left( \frac{X_D}{X_U} \right)
\]

with \(X_D\) representing mean, median or raw downstream values and \(X_U\) representing mean, median or raw upstream values.

\[
\Delta r_2 = \ln \left( \frac{X_I}{X_{UR}} \right)
\]

with \(X_I\) representing mean, median or raw impoundment values and \(X_{UR}\) representing mean, median or raw upstream or reference values. Reference values were obtained from studies identified during the literature search of sites not affected by beaver or artificial impoundments (see figure S1 for the different study designs).

In total, we calculated 2131 effect ratios (ERs) for the 16 environmental factors (table 1). Most ratios were calculated for macroinvertebrates in beaver and artificial systems, followed by concentrations of N and P in beaver systems, diversity and/or abundance of fish in beaver systems and ecosystem functioning in artificial systems (table 1). Most effect ratios (63%) for the environmental effects of beaver dam construction were derived from studies of C. canadensis (table 1). Details on all included studies and ERs are given in table S2.

For macroinvertebrates and fish in beaver systems, we also estimated the unique contribution of impoundments to species richness by calculating, if possible, the number of species present in the impoundments that were absent in upstream/reference and downstream sites.

Statistical analyses

We used 95% confidence intervals (CIs) for pairwise comparisons of ERs (Zar 1996). CIs are sensitive to sample size, with smaller samples generally resulting in wider CIs, while larger samples generally result in more narrow CIs (Zar 1996). Despite this limitation, we used CIs because response ratios showing this statistic instead of others (e.g. standard deviation or standard error) simplify interpretation because overlapping CIs and/or CIs of response ratios including zero indicate non-significance (see also Romero et al 2014). Response variables where the sample size was less than three were excluded from the analyses. The overall results were the same irrespective of whether statistical analyses were unweighted, or were weighted either by the number of observations per ER or by number of systems per ER (results not shown). Therefore, we present non-weighted results only. We tested potential publication bias with funnel plots showing that positive, negative and neutral effect sizes were satisfactorily represented in our meta-analysis (figure S3). Among the potential explanatory variables (season, distance of localities from dams, beaver species and system age), sample size was only sufficient to allow for statistical analyses of beaver species and system age. All statistical analyses were performed in Statistica (Dell Inc. 2015).
Table 1. Number of effect sizes calculated per factor in beaver (divided for C. canadensis, C. C. and C. fiber, Cf) and artificial systems for comparisons between upstream and downstream, upstream/reference and impoundments and between impoundments and downstream. Main studied variables per factor are given in descending order of number of associated effect sizes.

| Factor Variables | Cc | Cf | Total |
|------------------|----|----|-------|
| Nitrogen (N) Nitrite-Nitrate, Ammonium, Tot-N | 178 | 50 | 228 |
| Phosphorus (P) Beaver Phosphate, Tot-P | 174 | 21 | 195 |
| Artificial Tot-P | 149 |
| Carbon (C) DOC, POM, Suspended C, TSS, TOC | 91 | 24 | 115 |
| Dissolved oxygen Dissolved oxygen | 34 | 32 | 66 |
| Mercury (Hg) in water Beaver Hg, MeHg | 42 | 17 | 59 |
| Artificial Hg, MeHg | 21 |
| Mercury (Hg) in biota Beaver MeHg | 3 | 0 | 3 |
| Artificial Hg, MeHg | 144 |
| Methane Flux, evasion, proportion | 10 | 0 | 10 |
| Temperature Temperature | 40 | 32 | 72 |
| Hydrology—Area Surface area, water depth | 7 | 27 | 34 |
| Hydrology—Velocity Discharge, velocity | 17 | 35 | 52 |
| Sediment—Coarse Percentage cover, density | 18 | 1 | 19 |
| Sediment—Fine Percentage cover | 21 | 9 | 30 |
| Dead wood Number of felled trees per area | 5 | 0 | 5 |
| Ecosystem functioning Beaver Chl-a, abundance of faecal microbes, litter breakdown | 14 | 8 | 22 |
| Artificial Litter breakdown, fungal biomass, Chl-a, carbon turnover time, accumulation of benthic POM | 173 |
| Macrionvertebrates Beaver Diversity, abundance, proportion | 98 | 177 | 275 |
| Artificial Diversity, density | 254 |
| Fish Beaver Diversity, abundance | 108 | 73 | 181 |
| Artificial Diversity, abundance | 24 |
| Total | 860 | 506 | 2131 |

* Chl-a: Chlorophyll-a; DOC: Dissolved organic carbon; MeHg: Methylmercury; POM: Particulate organic matter; Suspended C: Suspended carbon; TOC: Total organic carbon; Tot-N: Total nitrogen; Tot-P: Total phosphorus; TSS: Total suspended solids.

Results

Effects of beaver dams

Overall, the net effects of beaver dams (comparing upstream and downstream sites) were small in contrast to comparisons between upstream/reference sites and impoundments and between impoundments and downstream sites (figure 1). Not surprisingly, beaver dams increased water area and volume and negatively affected flow velocity (figures 1(a) and (b)). While beaver dams had no net effect on sediment properties (figure 1(a)), ponds were characterized by finer sediment than upstream/reference and downstream sites (figures 1(b) and (c)). Temperature increased from upstream to downstream (figure 1(a)). Concentrations of dissolved oxygen were higher upstream compared with downstream and impoundments (figures 1(a) and (b)), but did not differ between impoundments and downstream sites (figure 1(c)). Organic carbon concentrations (dissolved organic carbon, DOC; particulate organic matter, POM; suspended carbon; total suspended solids, TSS; and total organic carbon, TOC) were higher downstream than upstream (figure 1(a)), and higher in impoundments than at upstream/reference and downstream sites (figures 1(b) and (c)). Methane concentrations were higher in impoundments compared to downstream sites (figure 1(c)) with a tendency towards higher concentrations in ponds compared to upstream/reference sites (four out of five ERs were positive, figure 1(b)). Neither N nor P were affected by beaver activity in any of the comparisons (figures 1(a)–(c)). Concentrations of Hg in water and biota showed a net effect of beaver dams with higher concentrations downstream (figure 1(a)) and higher Hg concentrations in impoundments compared with upstream/reference and downstream sites (figures 1(b) and (c)). The effects were, however, stronger for MeHg than for total Hg (THg). Comparing upstream sites with downstream sites, the effect size for MeHg in water was twofold that of THg (MeHg: mean ER_U–D = 0.99, CI = 0.54–1.45, n = 21; THg: mean ER_U–D = 0.50, CI = 0.05–0.94, n = 10). When comparing impoundments with upstream and downstream sites, calculated effect sizes for concentrations in water in figures 1(b) and (c) are attributable to differences in MeHg since sample sizes for THg were low (n = 2 for ER_U–I and ER_I–D). There was a tendency towards more dead wood in impoundments than reference sites; in fact, all ERs for this factor were positive, but highly variable (figure 1(b)).
Figure 1. Effect ratios (means ± 95% CI) for the effect of beaver dams on 16 environmental factors and comparing (a) upstream with downstream sites (positive ratios indicate higher factor values downstream), (b) upstream/reference sites with impoundments (positive ratios indicate higher factor values in impoundments), and (c) impoundments with downstream sites (positive ratios indicate higher factor values downstream). The number of calculated effect ratios is given in parentheses.
Values for ecosystem functioning combine data for three indicators (viz. concentrations of chlorophyll-a (Chl-a), faecal microbial abundance and litter breakdown) and were higher in impoundments compared to both upstream/reference sites and downstream sites (figures 1(b) and (c)). There was a net decrease in diversity and/or abundance of macroinvertebrates and fish from upstream to downstream (figure 1(a)). However, ERS for salmonids failed to support a hypothesis of overall adverse effects of beaver dams on migration as effect size confidence intervals overlapped zero (figure 1(a)). Effect sizes did not differ between impoundments and upstream/reference and downstream sites even though there was a tendency for higher abundance/diversity of macroinvertebrates in upstream and downstream sections compared to impoundments (figures 1(b) and (c)). Comparing environmental effects resulting from *C. canadensis* and *C. fiber* activity did not reveal any consistent differences (figure S4).

For 10 of 17 analysed comparisons of macroinvertebrate species richness between impoundments and upstream/reference and downstream sites, impoundments had between one and 15 more species. In all fish comparisons, impoundments contained one species that was not found in either upstream/reference or downstream sites.

**Comparison between beaver and artificial dams**

Artificial impoundments showed P retention, while beaver ponds generally released P (figure 2(a)). Both artificial and beaver impoundments displayed higher Hg concentrations in water and biota in downstream sites compared to upstream sites (figure 2(a)).
mean effect on Hg in biota was, however, more than twice as high in artificial systems compared to beaver systems (figure 2(a)). Values for ecosystem functioning (table 1) were higher in both artificial and beaver impoundments compared to upstream systems (figure 2(b)). Values were also higher in impoundments than downstream sites, but only for beaver systems (figure 2(c)). Focusing on Chl-a alone, which was the only functional indicator with adequate sample sizes in both system types, there was a net increase of concentrations in artificial systems, but not beaver systems from upstream to downstream (mean ER(U-D),Artificial = 0.89, CI 0.16–1.62, n = 9; mean ER(U-D),Beaver = 0.43, CI = 0.12–0.98, n = 6). The effects of dam construction on macroinvertebrates differed between system types, with artificial systems generally having higher diversity and/or abundance in upstream sites in comparison to downstream sites, while the opposite was seen for beaver systems (figure 2(a)). For fish, there were no overall differences between artificial and beaver systems (figures 2(a)–(c)).

Effect of age dependency

Consideration of the system age revealed interesting patterns. Both young and old artificial impoundments showed P retention (figure 3). Young beaver impoundments were a source of P (positive ER), but there was a tendency towards P retention in old systems (figure 3). Both young and old beaver systems showed a greater release of Hg in water downstream compared to upstream systems regardless of age (mean ER(U-D),Young = 1.13, CI 0.54–1.73, n = 11; mean ER(U-D),Old = 0.69, CI 0.24–1.14, n = 19). This net effect was even more pronounced for MeHg concentrations (mean ER(U-D),Young = 1.25, CI 0.42–2.08, n = 8; mean ER(U-D),Old = 0.89, CI 0.23–1.54, n = 12). The Hg concentrations in young, but not old, beaver systems increased from upstream to downstream sites (mean ER(U-D),Young = 1.11, CI 0.76–1.45, n = 7; mean ER(U-D),Old = 0.04, CI = –0.1–0.17, n = 7) and decreased from pond to downstream sites (mean ER(U-D),Young = −0.45, CI −0.73–−0.18, n = 6; mean ER(U-D),Old = 0.01, CI = −0.04–0.06, n = 6). This effect was mainly due to MeHg (mean ER(U-D),Young = 1.21, CI 0.91–1.51, n = 6; mean ER(U-D),Old = 0.03, CI = −0.14–0.2, n = 6), indicating a high net Hg methylation within impoundments in young beaver systems.

While both young and old artificial impoundments showed higher Hg concentrations in biota downstream compared to upstream, the increase was more than twofold in young systems compared to old systems (mean ER(U-D),Young = 1.42, CI = 1.25–1.6, n = 50; mean ER(U-D),Old = 0.57, CI 0.38–0.76, n = 53).

Discussion

It is widely acknowledged that beavers, as ecosystem engineers and keystone species, have profound environmental effects (Smith et al. 1991, Gurnell 1998, reviewed by, for example, Collen and Gibson 2001, Rosell et al. 2005, Kemp et al. 2012). In our meta-analysis, we were able to systematically quantify such effects for a variety of important environmental variables and processes and to identify interesting and important general patterns.

Overall, nutrients (N and P) were not retained by beaver dams. This is contradictory to previous findings on the role of beaver systems for nutrient dynamics in streams (e.g. Klotz 2010), but is consistent with studies identifying runoff and season as important determinants of nutrient retention in beaver ponds (Devito and Dillon 1993). According to our study, the retention potential of P increases with the age of the beaver systems. This age-dependent retention is likely to be induced by changes in sediment properties that, in turn, are related to the age-dependent input of organic material by beavers and beavers’ digging activity (as also suggested by Naiman et al. 1986, Devito and Dillon 1993). Flooding of forest soil introduces organic material and nutrients to the system, sources that will, however, be depleted with time (Devito and Dillon 1993). The identified differences in P retention between young beaver and young artificial
impoundments might be related to dam properties. Old beaver dams (if maintained) might develop greater solidity and thus end up resembling artificial dams more in terms of water permeability and nutrient retention, in contrast to young, relatively permeable beaver dams.

Eutrophication is a global threat to freshwater integrity (Vörösmarty et al 2010) that is especially pronounced in densely populated coastal areas (Rönnberg and Bonnordorf 2004). In such areas, old beaver dams could potentially mitigate this environmental problem. The overall effects of beaver impoundments versus artificial impoundments on landscape energy and nutrient budgets are dependent on the relative rates of carbon and nutrient export from the two kinds of systems. Given the impervious nature of typical artificial dam walls, it is possible that carbon and nutrient export downstream is lower for artificial impoundments than for beaver impoundments. Greater nutrient retention in impoundments might mitigate the risk of eutrophication in downstream lakes, estuaries and ultimately the sea, but might also reduce downstream productivity.

The properties of DOM differ between beaver ponds of different ages (Catalán et al 2017), and the availability of degradable carbon is important in mobilizing Hg associated with organic molecules (Ravichandran 2004). While the increase in carbon from upstream to downstream may result in increased concentrations of both inorganic and organic Hg downstream, net formation of MeHg within beaver impoundments will favour additional factors such as low oxygen concentrations, which are also induced by iron(III) and other electron acceptors in oxygen-limited conditions that are created when terrestrial land is flooded. It is, therefore, likely that age-dependent methylation rates in beaver systems have previously been identified as being dependent on age and/or colonization history (Roy et al 2009a, Levanoni et al 2015). In newly formed impoundments (both beaver and artificial ones) Hg methylation may be favoured by an initial release of labile carbon sources, sulphate, iron(III) and other electron acceptors in oxygen-limited conditions that are created when terrestrial land is flooded. It is, therefore, likely that age-dependent methylation rates in beaver systems and higher Hg concentrations in biota in young (compared to old artificial systems) are caused by the same mechanisms. Considering the profound effect of system age that we identified for P and Hg in beaver systems, it is unfortunate that this factor is rarely considered when evaluating the environmental effects of beaver dams.

Only six studies were identified that reported the effects of beaver dams on methane emissions. Available data suggest that emissions were generally higher in impoundments compared to upstream and downstream sites. This result was expected as beaver impoundments provide conditions favouring methane production by slowing water velocity, increasing flooded land area, retaining carbon, and providing anoxic conditions (Ford and Naiman 1988), i.e. processes similar to those promoting methylation. However, it is not known how system age might affect methane emission rates. As is the case with Hg methylation, we speculate that methane production slows as systems age due to, for example, changes in availability and input of labile carbon.

Many threatened and formally protected species depend on dead wood (Jonsell et al 1998, Tikkanen et al 2006, Stokland et al 2012). The formation of dead wood, either directly by tree felling or indirectly by forest flooding, has been identified as having one of the most profound environmental impacts in relation to beavers (reviewed by Rosell et al 2005). It is, therefore, surprising that we could only identify five ERs from the published literature. Even though all five ratios highlighted the significant increase in dead wood caused by beaver activity, there is a lack of studies on the cascading ecological effects of this input of woody debris at varying spatial and temporal scales. More generally, studies of the effect of beaver activity on aquatic-terrestrial linkages appear to be lacking in the literature. Such studies are needed if beaver managers are to successfully weigh potential biodiversity benefits against potential negative effects related to, for example, methane emissions and Hg methylation.

Sediment and hydrology-related effects were among the strongest and most consistent (measured as absolute values of ERs) detected in our study. Hydrology effects appear to be age-dependent, with stronger effects in older systems due to dam solidification (Meentemeyer and Butler 1999). Reduced water velocity downstream compared to upstream of dams, and increased water volume in impoundments (Green and Westbrook 2009, Nyssen et al 2011) are important ecosystem effects mediated by beavers, which contribute to regulating ecosystem services, for example, mitigating flood risk. Furthermore, beaver impoundments can sustain environmental flows in arid areas and during periods of low precipitation (Andersen et al 2011). Since environmental flow and management of flood risk are internationally prioritized (European Union 2007, Hirji and Davis 2009), it is timely to evaluate the role of beavers in environmental flow regulation at catchment, regional and national scales.

Changes in sediment properties induced by impoundment not only affect biogeochemical processes (like Hg methylation and methane production described above), but also alter habitat availability for benthic species. Previously, Collen and Gibson (2001) concluded that impoundment by beavers induces a loss and/or reduction in abundance of lotic (running water) macroinvertebrate taxa including Ephemeroptera (mayflies), Plecoptera (stoneflies) and Trichoptera (caddisflies) and that these changes are linked to changes in sediment properties. Generally,
in freshwater, coarse sediments (generally, but not exclusively, found in lotic sections) host more abundant and diverse macroinvertebrate communities than fine sediments (typical of lentic, i.e. still-water systems) (Mackay and Kalff 1969). Both artificial and beaver impoundments cause sedimentation of organic and inorganic material. Coarse sediments including gravel and cobbles that are an important substrate for EPT taxa (Verdonschot et al 2016) and potentially present in stream channels prior to impoundment will be buried by sedimentation following impoundment. We would, therefore, expect the negative effects of dam construction on benthic macroinvertebrates to be strongest in systems with coarse-sediment stream channels upstream of impoundments. These patterns were not evident or consistent in our study even though there was a tendency towards higher abundance/diversity in upstream and downstream sections compared to impoundments. At larger scales (multiple stream reaches), beavers increase habitat heterogeneity (reviewed by Rosell et al 2005). This, according to the ‘habitat heterogeneity hypothesis’, should increase species diversity across multiple stream habitats (Simpson 1949, MacArthur and Wilson 1967) unless the ‘ghost of land use past’ (Harding et al 1998) has depleted potential source populations. Thus, increased local-scale heterogeneity resulting from beaver impoundments could compensate for loss of coarse sediment and result in a neutral net effect on diversity and abundance of macroinvertebrates when comparing impoundments with upstream and downstream sections. Indeed, our meta-analysis revealed the unique contribution of impoundments to the total species richness of beaver systems.

At the landscape scale, beavers not only increase habitat heterogeneity, but their actions result in a higher frequency and total amount/area of lentic stream sections. Since beavers increase habitat diversity at local, stream-network, catchment and/or entire landscape scales, their dam-building activity has cascading ecological effects, especially in riverine landscapes low in either lentic or lotic sections (Naiman et al 1986). In riverine landscapes low in lentic habitats, impoundment will favour lentic species and their habitats, while in landscapes low in lotic systems, extensive impoundment may reduce the amount of lotic habitat, with negative consequences for the abundance and diversity of associated species. Our findings on the unique contribution of impoundments to macroinvertebrate and fish species richness suggest that, overall, beaver impoundments enhance landscape-scale species richness.

Barrier effects limiting species movement are among the main motivations for the removal of artificial dams and the restoration of longitudinal (upstream-downstream) stream connectivity (Liermann et al 2012). Indeed, our study identified a lower overall fish abundance/diversity upstream compared to downstream of beaver impoundments with the same tendency in artificial systems. However, focusing on salmonids in beaver systems, there was no adverse net effect on salmonid abundance due to beaver dams. It has been suggested that migrating fish, especially salmonids, are most negatively affected by artificial dam construction (reviewed by Quiñones et al 2015). For beaver systems, however, it has been shown that most reported negative effects (78% of all studies) on migrating fish due to dam construction are solely speculative (reviewed by Kemp et al 2012). In contrast to artificially regulated artificial dams, beaver dams are a) regularly flooded and surplus water bypasses dams by running through the riparian zone during periods of high precipitation, b) disturbed (partly or even entirely collapsing) through high floods (Hillman 1998, Butler and Malanson 2005), c) maintained to a varying degree (reviewed in Gurnell 1998) or d) potentially perforated by otters (Reid et al 1988). Hence, as supported by our study, we do not expect any significant effects on migrating fish species to be caused by beaver dams.

When analysing the effects of impoundment on species diversity and abundance, it is important to account for species–area relationships. According to theory, larger habitats host more species than smaller ones (MacArthur and Wilson 1967) even though physical habitat structure is also an important determinant of biodiversity (Tews et al 2004). Through dam construction and digging, beavers significantly increase the surface area and volume of water along with sediment surface (Naiman et al 1986, Hood and Larson 2015). Hence, the higher diversity/abundance downstream compared with upstream of beaver ponds found in our study could simply be an effect due to habitat size. Future studies are needed to disentangle effects potentially caused by increased habitat heterogeneity from those caused by differences in the surface area of inundated habitat alone.

We were not able to distinguish between the effects of damming on diversity and abundance (see Methods), which might explain some of our ambiguous results for macroinvertebrates and fish. For practitioners, however, such a distinction is crucial and needs more attention as it might shed further light on whether damming affects, for example, the upstream abundance of single fish species and/or the diversity of whole communities.

Several of the environmental factors analysed here vary naturally with season. For example, stream velocity in the Holarctic is generally highest during spring, while water temperature is highest in summer and concentrations of dissolved oxygen in water are highest during spring and fall turnover (Wetzel 2001). Unfortunately, due to insufficient information in the source studies, we could not account for such seasonal variation in the meta-analysis.

The spatial extent of effects caused by damming and impoundment was not included as an explanatory variable in the meta-analysis as the requisite information was missing from most of the relevant literature (but see, for example, Virbickas et al 2015). Fencel et al (2015)
found geomorphological effects caused by small low-head dams, those that would be most similar to beaver dams considering size, over 7 km downstream of the dam structure. In contrast, we would probably expect demethylation of MeHg at such distances downstream due primarily to altered microbial communities and photodegradation. To assess whole-catchment impacts of artificial and beaver dams, future studies should, therefore, account for spatial scale.

The ecosystem functioning factor encompassed several metrics, which can be used as indicators of an ecosystem’s functional status. Planktonic primary productivity (here measured via Chl-a) is typically substantially higher in lentic than in lotic ecosystems, and thus was, unsurprisingly, consistently higher in beaver impoundments compared to upstream and downstream sites. This points towards the key role of beaver ponds in supporting a trophic food-web compartment (pelagic algal productivity) which is normally under-represented in lotic networks, and which may contribute to nutrient retention in ponds (e.g. in the form of consumer biomass), or the export of nutrients and energy downstream (e.g. in the form of dead algal cells or consumer faecal particles). The available set of ecosystem functioning indicators for artificial systems included Chl-a and other indicators of biological activity and system reteniveness, such as organic-matter breakdown, particulate organic-matter standing stocks, fungal biomass and carbon turnover time. Despite this variety of indicators and generally low sample size, the combined effect sizes often had surprisingly narrow confidence intervals, and showed similar patterns to those in the beaver systems, with higher values for the impoundments (reflecting, in particular, the large number of pelagic Chl-a measurements in the data set), though this was more clearly differentiated in the upstream-impoundment comparison than impoundment-downstream.

Our study identified important environmental factors that are significantly affected by beaver activity. Some of these effects are desirable from the perspective of ecosystem services, e.g. the high water-retention potential of beaver ponds that may reduce downstream flood risk. In contrast, other factors raise environmental concerns, e.g. Hg methylation and methane production. There are also effects that are ambiguous from a management perspective. Increased amounts of dead wood produced by beaver activity are valuable from a biodiversity perspective, but might be unacceptable from the perspective of forest productivity.

Meta-analyses such as the one presented here are a powerful tool for synthesizing large amounts of data and generating new insights, but they should not be the sole source of evidence for decision-making. Both experimental manipulations and modelling should also be used. Well-designed and properly executed experiments offer the possibility of making strong ecological inferences. Models can facilitate generalization of empirical results, upscaling to the regional level or projecting the potential effect of dam and pond construction on aquatic ecosystems.

Conclusion

Beavers are continuously increasing in number, expanding their distribution range and recolonizing former habitats. This increases the risk of human–beaver conflicts and is having a potentially profound effect on aquatic ecosystem functioning across the Holartic. The meta-analysis results presented here provide insight into the expected environmental outcomes of expanding beaver populations and can form the basis for future evidence-based management that is today lacking in many countries experiencing an increased incidence of beaver–human conflicts. Nevertheless, it is important to fill the significant gaps that remain in scientific knowledge related to the likely dependencies of environmental effect on the age and colonization history of beaver systems, and on seasonal variation and spatial context. Such knowledge would facilitate an improved quantification of the local and larger (i.e. stream reach to catchment and national) outcomes of the effects of beaver (and artificial) dams on freshwater ecosystems. When filling these knowledge gaps in relation to the effects of beavers, it is important to act with caution when making inferences from studies on the environmental impacts of artificial dam construction. As demonstrated here, results from artificial systems cannot be used directly to make inferences about the environmental effects of dam construction by beavers. The knowledge gaps relating to the environmental impacts of beaver dams and impoundments will need to be bridged if future beaver management is to successfully weigh environmental benefits against adverse environmental effects.

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