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Hansen, Henry H.; Andersen, Ken H.; Bergman, Eva

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Projecting fish community responses to dam removal – Data-limited modeling

Henry H. Hansen a,*, Ken H. Andersen b, Eva Bergman a

a Department of Environmental and Life Sciences, Karlstad University, Karlstad, Sweden
b Centre for Ocean Life, National Institute of Aquatic Resources (DTU Aqua), Technical University of Denmark, Copenhagen, Denmark

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ABSTRACT

Modeling fish community responses to dam removal is an emerging field of study as dam removals become more common, but uncertainties concerning recovery time and community stability remain. In Europe, an EU-wide biodiversity strategy plans to restore around 25,000 km of rivers to free-flowing status, which emphasizes the importance of being able to predict fish community responses after dam removal. We developed a multi-species size spectrum model for a fish community in the Mårrum River in Sweden to identify possible outcomes after a dam was removed in 2020. Electrofishing monitoring before the dam removal was used to calibrate the model. We projected multiple scenarios into the future to explore patterns of community stability, individual species responses, and recovery time while varying parameters related to dam removal mortality, base resource rate change, and maximum recruitment change. We created 30 hypothetical scenarios using an abrupt change perspective (parameters are step-based) and 30 scenarios using a gradual change perspective (parameters are smooth). In both perspectives, dam removal mortality and a decreasing resource rate reduced community biomass and delayed recovery time compared to pre-dam removal conditions. Our results demonstrate that recovery from a dam removal scenario is not necessarily a benefit for all species. In scenarios where dam removal practices or dam failures cause high mortality events and sustained impacts on base trophic level resources, recovery of pre-removal biomass may take decades, while community stability may be unstable for twice that time-period. Our study shows that size spectrum models can be applied to dam removal scenarios to explore potential recovery outcomes, particularly from a risk avoidance perspective. A benefit of using such an approach is the relatively low data requirements needed to perform projections (e.g., present species, fish growth rates, relative fish abundance). Implementing this model in other river systems, particularly at the reach scale, can help river restoration and management assess tradeoffs associated with different habitat restoration approaches prior to committing to a dam removal plan.

1. Introduction

Dams have been and will continue to be a common feature within river systems around the globe (Zarfl et al. 2015). They have provided a variety of societal benefits, often at the cost of local biodiversity and ecosystem services (Dugan et al. 2010). As water based infrastructure—such as dams—age and their integrity deteriorates, society must either act proactively, including dam removal and culvert replacement (Neeson et al. 2018), or in a reactive manner, including dam failure (Hansen et al. 2019). Given that both planned dam removals and dam failures are expected to increase in the next century for various dams (Grabowski et al. 2018), questions concerning recovery time and ecological effects remain, particularly about biodiversity. Previous literature concerning small dams in temperate landscapes demonstrated a variety of restoration outcomes (e.g., ecosystem transition, biodiversity changes, geomorphological responses) at different rates that span from a single year or upwards of multiple decades (Bednarek 2001). Potential causes for the variety of outcomes arise from the multi-faceted nature of dams themselves, such as dam size, operation, age, and their overall lack of ecological classification (Poff and Hart 2002). Multiple ecological linkages and feedbacks among both biotic and abiotic factors underpin the quantitative challenges related to the scale and relations of impacts for upstream, immediate, and downstream reaches (Pizzuto 2002, Bellmore et al. 2019). The complexity of this issue is further
complicated by the multiscale nature of watersheds. The land cover and use along with other water management structures (i.e., culverts, weirs, diversions) interact and influence biophysical dynamics at a variety of scales. As biodiversity goals continue to become a universal standard for restoration, attempts to model dam removal recovery times with a focus on fish diversity has become a top priority (Bellmore et al. 2019).

Existing dam removal models typically use a: 1) food-web perspective (Bellmore et al. 2017) and optimization techniques (Kuby et al. 2005), 2) habitat suitability index models (Tomisc et al. 2007), or 3) statistical models (Poulos et al. 2014). But such approaches model outcomes over short time spans, as post-dam removal data collection is rarely required when dam removals occur. Many projects assume dam removal is inherently beneficial, but so far studies predicting fish responses has been limited to single species (Stanley and Doyle 2003) and cannot predict outcomes related to fish diversity and community composition. Modeling potential outcomes of fish diversity and community composition before dam removal occurs could both add ecological insight and be of practical importance when designing a dam removal. This is particularly relevant for cases where dam removal may cause new environmental issues such as systems that may contain invasive species (Teréncio et al. 2021), systems prone to societal conflict (Lejon et al., 2009), or systems that contain immense quantities of sediment (Bushaw-Newton et al. 2002). One unexplored means of filling this gap is to apply a deterministic size spectrum modeling approach that incorporates multiple fish species and food-web interactions.

Assessing future changes in aquatic ecosystems requires a food-web perspective, as ecosystem-based management becomes more popular and species interactions a greater priority (Andersen et al. 2015, Geary et al. 2020). The uptake of one specific class of food web models called size spectrum models are becoming increasingly more prevalent among modelers and practitioners in the marine environment (Blanchard et al. 2017). One of the more profound advantages of size spectrum models over existing aquatic food web models (e.g., Ecopath/Ecosim) is their derivation from well-established ecological mechanisms and a physiological, size-based theory for fish populations, and rather lower data requirements needed to make them operational. The size based distinction explicitly links feeding and growth to the population feedbacks shown in ecosystems (Sprules and Barth, 2016). These linkages provide a flexible and transferable means to understand food web dynamics and thus makes it possible to adapt it to freshwater systems without compromising on performance. Existing size spectrum studies in lotic systems focus on evaluation of stressors that include both macroinvertebrates (Mehner et al. 2018) and fish (Murry and Farrell 2014, Kopf et al. 2019), but these are almost exclusively statistical methods to explain size spectra changes and not process-based model investigations. The prospect of using size spectrums as a basis in lotic systems, produces a compelling opportunity for both theoretical and applied ecologists to coalesce existing empirical understandings of lotic stressors with a flexible deterministic modeling framework.

An additional advantage of using size spectrum models is the intuitive indicators that can help one understand the complexity of a food web and community dynamics at different levels of biological organization (e.g., individual species, fish community) (Marín et al., 2023). For example, the dynamics of species richness, biodiversity, and functional diversity all operate at the ecosystem scale, but such indicators tell us very little about the function of the food web and how each species plays a role. A size spectrum model instead uses community biomass, community weighted mean of a particular trait, deviation of size spectra slope, size spectra elevation, and size spectra linearity to provide valuable insight on community dynamics (Avolio et al. 2019, Sprules and Barth, 2016). Predator–prey relations, growth trajectories, population size structure, and resource dependence provide insight on species dynamics (Benoit et al. 2021). Connecting these indicators to the projections from a size spectrum model may help uncover crucial food-web changes before dam removal operations begin. Understanding the time-scale relationship between the ecological disturbances of a removal and its recovery process can help identify the time and thus budgetary commitment needed to restore a river system.

The aim of this work is to present a first assessment of fish community responses to varying dam removal scenarios using a size spectrum model. Specifically, we explored how abrupt or gradual changes in 1) mortality associated with the dam removal, 2) resource rate change (e.g., macroinvertebrate abundance), and 3) maximum recruitment change for fish; could affect a resident lotic fish community in southern Sweden after the dam was recently removed. For each ecological response above, we implemented a variety of dam removal scenarios from best-case to worst-case. Here best-case is a scenario that has no adverse affects to the resident fish community and only improve resources and recruitment potential through time. Worst-case is defined as a scenario where no recruitment is improved, resources are limited and slow to recover, and mortality from the dam removal persists for years after the event. We modeled 1) how specific responses independently or synergistically could affect the community at equilibrium, and 2) how a range of best to worst case conditions over short to long temporal scales could affect both the entire community and individual species.

2. Materials and methods

2.1. Model overview

We built a size spectrum model for 18 resident freshwater fishes of the Môrrum river in Sweden using the R package ‘mizer’ (Scott et al. 2014). The theoretical background of size spectrum models now support a range of applications for single species, trait-based, and multi-species approaches to answer questions related to fisheries (Blanchard et al. 2014, Andersen et al. 2016) (Fig. 1). In layperson terms, a size spectrum model is a deterministic model that allows a user to project how a fish community changes over time, based on size-based predator–prey interactions and individual fish species physiology. These predator–prey interactions start from egg and grow all the way to the maximum size of a species, this is the “size” part of size spectrum. The “spectrum” part is jargon for describing the abundance of every size for a species, which means for every size, there is an associated abundance. The resulting relation between size and abundance results in a line called a species size spectrum. When all species spectra are added together at each size, this is a community spectrum (the combined abundance of every species for each size).

The unique shape and position of a species size spectra is based on the growth of every individual from egg to adult, where growth depends on 1) available resources (e.g., prey), 2) reproduction characteristics, and 3) mortality (e.g., fishing, predation, external) up to an asymptotic size. Given an initial understanding of a species growth rate, maximum size, reproductive capacity, and prey preference, the model projects how the community will respond to external perturbations (i.e., mortality). Mortality events such as fishing are species and size specific, thus removing abundance from particular regions of a species-spectrum. Similarly, one can adjust the mortality to encompass other forms, such as dam removal mortality in our case. Individual components can also be adjusted to become time-varying to reflect environmental change as we have done for resource rate change and maximum recruitment change. A more formal definition and equations for the base size spectrum model are provided in Appendix S1. It is important to note that this model provides projections of a fish community which show possible outcomes rather than a precise prediction of future events.

2.2. Study site

The Môrrum River is a temperate river in southern Sweden that drains to the Baltic Sea (Fig. 2). It supports a variety of diadromous, anadromous, and resident fish species and some parasitic fishes. It has three primary barriers on its main stem: the Marieberg Dam (which was removed in 2020) and is the dam removal modeled in this paper, see...
3. Parameterization & calibration

To parameterize our model, information on resident fish species, fish growth, initial abundance, and predator–prey interactions are needed. Resident fish species were identified using annual and individual electrofishing censuses (sites depicted as points in the map in Fig. 2) which occurred throughout the study area between 2004 and 2020 during the non-winter months when wade electrofishing is safe to conduct. We sourced growth parameters for the included species from FishBase, as local information on fish growth is not available (Froese and Pauly 2021) (Table 1). To calibrate biomasses of each species within the community, observed abundances of fishes were calculated from the electrofishing censuses. Electrofishing density estimates (number per 100 m²) were multiplied by the area of the study area and then scaled by proportion of census events in which species was detected (e.g., a fish with an estimated density of 10 individuals per 100 m² but was only observed in 1 of 100 censuses was multiplied by 0.01). Observed biomasses were calculated using the observed abundances multiplied by the geometric mean of sampled fish weights for each species. More precise abundance information from stock assessments for Atlantic salmon Salmo salar and brown trout Salmo trutta were available for smolts, thus biomass for these species were scaled by the average number of smolts estimated for the river (ICES 2020), multiplied by the average weight at which smolts depart the river (provided by an ongoing fish tagging study).

Parasitic species, brackish species, hybrid species (only 1 type present in field data: salmon-trout hybrid) and migratory behavior are not included in our model’s 18 species community due to incompatibility with size spectrum assumptions (i.e., depredation is proportional to size thus larger fish eat smaller fish, fish stay within the model system area). A caveat to this view is that the migrant species are included in their resident form (i.e., trout and salmon up to smolt size and adult eels). We modified the model to include resident versions of migrants. For eels, we only assumed that eels in the river existed at the size of return from the sea (Appelbaum et al. 1998). We assumed all species in the community interact equally since all species are present within the study area and capable of occupying any portion of the river. One exception to this community wide parameterization, is that Atlantic salmon and brown trout do not consume top piscivore predators, as such interactions are typically rare.

To scale the model to the appropriate amount of biomass for each species we used observed biomasses and assumed equal reproductive efficiency (fraction of eggs that survive) to infer density-dependent relationships for each species until steady state model outputs approximated observed biomasses. For species that went extinct under projected...
initial conditions, we increased their reproductive efficiency until extinction was no longer possible. For smolts, we decreased their reproductive efficiency until the ratio between density-dependence and maximal reproduction rate reached 0, to mimic them leaving the system.

We used the correlation between model biomass and observed biomass for model calibration (Appendix 1, Fig. S1.1). Although refinement of community parameters that deal with biomass and reproduction can be continually adjusted to reduce relative error, such values would require reproductive output that is not biologically feasible.

Coexistence for all species in the community is necessary for a...
calibrated model which is in part influenced by natural mortality. All fishes were assumed to have a conservative external mortality of 0.15 yr⁻¹ (in addition to the predation mortality that emerges in the model) which is approximately half the allometrically scaled mortality estimate for riverine fish (Lorenzen 1996). This value assumes that total mortality is equal to natural mortality when exploitation are unknown in rivers. Since this value is impossible to estimate with available data, we assessed the sensitivity of this value (Appendix S2).

3. Theory

3.1. Generalizing the process of dam removals and failures

There is a multitude of unstudied responses that can influence a fish community as a dam removal occurs which makes bringing them within a modeling environment difficult (Hart et al. 2002). Despite this, the typical phases that occur during a planned dam removal and how such phases correspond to a fish community’s stable state through time can be demonstrated. For the Mörrum River we identified four such phases along with practitioners (Fig. 2), but alternative phase descriptions exist in other regions (e.g., ‘blow-n-go’) (Magilligan et al. 2016, Duda and Bellmore 2022). Phase 1 focuses on lowering the reservoir in a stable and controlled manner, phase 2 deals with development of physical structures to aid in demolition, phase 3 is the actual demolition of the dam, and phase 4 is the restoration work that follows the dam removal. For the study system this occurred in a single year, but for larger and more complex systems, these phases—especially phase 4—can take multiple years, even decades. In the case of dam failure, the first and third phase happen simultaneously and instantly while phase 2 does not occur, and phase 4 is an optional event in both removals.

We contend that three fundamental ecological responses are linked to these phases that ultimately govern the trajectory of a fish community. These are: 1) dam removal mortality, 2) resource rate change, and 3) recruitment maximum change that can be viewed from either an abrupt change or gradual change perspective (Fig. 3). The abrupt change perspective is where the response persists for a constant period of time and then settles to a new value (often the original stable state value), while the gradual change view provides a more idealized, non-linear representation where responses change gradually over time. An abrupt change perspective would be appropriate in very data-poor situations, whereas the gradual change perspective is appropriate in situations with empirical data or other information that can identify potential non-linear relationships. For the gradual change perspective, we chose non-linear responses that correspond to typical dam removal case studies, but in actuality, any non-linear relationship for the gradual change scenarios can be used in the model.

3.2. Dam removal mortality

Phase 1, 2, and 3 all influence dam removal mortality on the fish community but do so in different ways. In the dam removal context, Phase 1 has the potential to increase mortality from existing conditions for reservoir fishes as the volume of the reservoir is reduced to the original river bed, causing stranding, crowding, and stress if lowering occurs too fast (Cattaneo et al. 2021). As phase 2 and 3 commence, increased turbidity, release of toxic sediments, and reductions of water quality can occur for the downstream reaches of the dam (Thompson et al. 2020, Parente et al. 2021). In severe circumstances, river reaches inundated with compromised sediment can continue to inflict mortality on benthic or young-of-year fish (Magilligan et al. 2016). Similarly, dam removal can incur mortality on adult fish if demolition occurs during periods of spawning for anadromous fish or the structure is left in a state (e.g., partial decommission/removal) that causes additional mortality over time by inhibiting movement. In the gradual change scenario, dam mortality (μ damning) is modeled as a decreasing sigmoid function to reflect the decreasing nature of mortality overtime while still allowing for adjustment of intensity of recovery:

\[
μ_{\text{dam}}(t) = k \left(1 - \frac{1}{1 + e^{a+bt}}\right)
\]

where t is time and a, b, and k are constants.

Fig. 3. Conceptual illustration of possible dam removal functions that can be used to capture dam removal responses, dam removal mortality (left), resource rate (middle), and maximum recruitment (right). The abrupt change scenario is modeled using simple step changes whereas the gradual change scenario uses non-linear functional relationships (equations (1), 2, 3). Each color represents a different possible input into the dam removal model across time that affects the resident fish community based on anticipated dam events and actions. Warm colors indicate pervasive impacts while cool colors indicate transitory impacts.
### 3.3. Resource rate change

Lasting effects of sediment being emptied from the reservoir can inhibit production of lower trophic levels over time by reducing photosynthesis, blanketing macroinvertebrate habitat, and introducing noxious chemicals (Bednarek, 2001; Mahan et al., 2021). Macroinvertebrates are often especially sensitive to the turbidity and chemical composition of suspended sediment (Moran et al. 2017). Depending on the amount and toxicity of the reservoir sediment, the impact on total resource production can be impacted for years or decades (Parente et al. 2021). To model this response, a resilience function corresponding to a single perturbation was used (Arnoldi et al. 2016, Madni et al. 2020, 2021). To model this response, a resilience function corresponding to a single perturbation was used (Arnoldi et al. 2016, Madni et al. 2020, Capdevila et al. 2020). The output of this function is then supplied to \( r_{p_b} \) (Coefficient of the intrinsic resource birth rate) throughout the project management plan of a system would be longer than such a time period and the associated transients of the model. Again, we projected 30 different scenarios. For dam removal mortality (eq (1)), the parameter \( b \) used evenly spaced values between \(-3\) and \(-0.05 \text{ yr}^{-1}\), which controls the time at which mortality returns to pre-dam conditions. A value closer to \(-3 \text{ yr}^{-1}\) indicates that dam removal mortality will return to 0 in less than 2 years and a value of \(-0.05 \text{ yr}^{-1}\) will return to 0 at approximately year 200. Parameter \( a \) (sigmoid change rate) was fixed to 5 and \( k \) (starting value of dam mortality) to 0.5 \text{ yr}^{-1}. For resources (eq (2)), we supplied evenly spaced values \( u \) from \(-1 \text{ yr}^{-1} \) to \(-0.05 \text{ yr}^{-1}\) which controls the depth of the resource rate during its disturbance period. Parameter \( m \) was fixed to 10 (settling value of resource), \( b \) to \(-1 \) (rate of return to settling value), and sequence extraction values of 0.01 to 10 (translates the function into a vector the model can use). For recruitment maximum (eq (3)), we supplied evenly spaced values from 3 \text{ yr}^{-1} \) to 0.01 \text{ yr}^{-1} for parameter \( I \) (controls height of logistic function) and \( l \) (logistic growth rate) to 0.5, and \( t_0 \) (midpoint of logistic function) to 10. The synergistic combination of these responses results in an best-case outcome of return to 0 mortality in a short time period, only a minor negative deviation of resources, and high recruitment potential, whereas the last scenario of the series corresponds to a worst case scenario that spans almost two centuries before all responses return to pre-dam values.

### 3.4. Recruitment maximum change

As systems recover from dam removal, the reservoir should return to a natural river state (Bellmore et al. 2019). Depending on the size of the reservoir and number of years of siltation, the recovered riverbed should increase carrying capacity and thus recruitment into the future for fish once the original river bed is exposed (Katopodis and Aandland 2006). Similarly, now that access to upstream reaches of the river system are no longer impeded, recruitment should also increase as spawning migrations can be readily fulfilled (Duda et al. 2021). Post dam-removal monitoring of native fishes suggest that as the reservoir transitions to a new lotic equilibrium, a logistic relationship is typical when new spawning habitats become saturated (Doyle et al. 2005). The resulting function is a proportional increase of the recruitment maximum \( R_{\text{max}} \) for the calibrated community for each species. For example, a value of \( I \) would mean a 100% increase in recruitment maximum for the species:

\[
R_{\text{max}}(t) = \frac{1}{1 + e^{k(t-t_0)}}
\]  

(3)

### 4. Calculation

#### 4.1. Projections

We tested 30 different scenarios for response independently using the abrupt change approach and then combined all three functions to assess the synergistic effects for all 30 independent scenarios. The choice of these scenarios is to explore individual effects of each response on the community with varying impact magnitudes under a relatively short time frame (50 years). For dam mortality, we projected 30 scenarios evenly spaced between values of 0 and 2 \text{ yr}^{-1} that lasted only 5 years. For resource rate, we projected 30 scenarios evenly spaced between values of 10 and 0.1 \text{ yr}^{-1} that lasted 20 years and then returned to the calibrated value of 10. For recruitment max, we projected 30 scenarios evenly spaced from 5 to 0 that occurred 1 year after resources recovered (year 6). Individually this shows a variety of potential negative and positive outcomes for the system. Synergistically, the first scenario of the series reflects a best case outcome of no mortality, consistent resources, and high recruitment potential, whereas the worst scenario of the series corresponds to decades with high mortality, low resource renewal and low recruitment. Each scenario was projected for 50 years into the future. Here, projections are limited to 50 years as we expect no management plan of a system would be longer than such a time period and that any restoration measures that would take place would occur during that time frame.

The purpose of the gradual change scenarios is to explore the widest range of dam removal responses under long time-scales (200 years) and the associated transients of the model. Again, we projected 30 different scenarios. For dam removal mortality (eq (1)), the parameter \( b \) used evenly spaced values between \(-3\) and \(-0.05 \text{ yr}^{-1}\), which controls the time at which mortality returns to pre-dam conditions. A value closer to \(-3 \text{ yr}^{-1}\) indicates that dam removal mortality will return to 0 in less than 2 years and a value of \(-0.05 \text{ yr}^{-1}\) will return to 0 at approximately year 200. Parameter \( a \) (sigmoid change rate) was fixed to 5 and \( k \) (starting value of dam mortality) to 0.5 \text{ yr}^{-1}. For resources (eq (2)), we supplied evenly spaced values \( u \) from \(-1 \text{ yr}^{-1} \) to \(-0.05 \text{ yr}^{-1}\) which controls the depth of the resource rate during its disturbance period. Parameter \( m \) was fixed to 10 (settling value of resource), \( b \) to \(-1 \) (rate of return to settling value), and sequence extraction values of 0.01 to 10 (translates the function into a vector the model can use). For recruitment maximum (eq (3)), we supplied evenly spaced values from 3 \text{ yr}^{-1} \) to 0.01 \text{ yr}^{-1} for parameter \( I \) (controls height of logistic function) and \( l \) (logistic growth rate) to 0.5, and \( t_0 \) (midpoint of logistic function) to 10. The synergistic combination of these responses results in an best-case outcome of return to 0 mortality in a short time period, only a minor negative deviation of resources, and high recruitment potential, whereas the last scenario of the series corresponds to a worst case scenario that spans almost two centuries before all responses return to pre-dam values.

#### 4.2. Metrics

There are two primary scales of metrics used to evaluate model projections; the first is community characteristics across time, and the second is species characteristics across time. These metrics address the questions of how the productivity of the system will change and which species that will succeed or fail after the dam removal. The community metrics focus on the total biomass of the community, mean weight, proportion of large fish (over 100 g), size spectra slope, size spectra elevation, and size spectra linearity relative to the stable state community prior to removal (Marin et al., 2023). Species metrics look at rank of species biomass over time.

### 5. Results

#### 5.1. Individual mechanistic effects and their synergy

An abrupt change implementation of dam removal demonstrates across all scenarios that biomass can recover to original biomass in less than 10 years and no perturbations to biomass are present after recovery when only dam removal mortality is acting on the community (Fig. 4 A). A abrupt change implementation of resources causes an immediate decrease in biomass and then returns close to initial biomass when resources have recovered after 20 years (Fig. 4 B). Once recovered, scenarios that were more resource limited not only take longer to recover (up to 5 years), but the community also tends to overshoot initial community biomass (Fig. 4 B). A change in recruitment maximum causes an expected increase in biomass but higher values tend to settle at slightly lower values from their peak (Fig. 4 C). When all dam removal effects are combined, the best case scenario (purple) shows no decrease in biomass during the dam-removal impact period and an increased biomass once recruitment improves. In the worst-case scenario, the combination of dam mortality and reduction of resources nearly eliminates all biomass in the community. As responses return to original conditions, larger biomass swings occur compared to better conditions (Fig. 4 D).

#### 5.2. Gradual change impacts on the community

Gradual change based implementation showed similar patterns to abrupt change scenarios when comparing community biomass (Fig. 5...
A). Deviation of size spectra slope are only visually noticeable for the worst case scenarios (Fig. 5 B). The lowest size spectra values typically occurred decades after community biomass was already recovering indicating hampered fish growth. Ecologically, this suggests that the relation between species abundance and size weakens and responds slowly under the most severe conditions. For community mean weight, scenarios are distinct within 10 years after dam removal but then overlap decades after before separating again (Fig. 5 C). The reduction of mean weight for the best case scenarios is due to an increase of young of year fish from improved recruitment while the reduction of mean weight for the worst case scenarios is from a loss of large fish. A disproportionate loss of large fish and their biomass is also apparent in the size spectra linearity, an indicator of trophic efficiency. The worst case scenarios which have lost many large predators begin to amass large quantities of smaller-bodied fishes that do not have comparable number of predators to pre-dam conditions. The proportion of large fish (over 100 g) plot confirms this by highlighting the highest proportion for the best case scenarios and lowest for the worst case scenarios (Fig. 5 E). The transition towards increased large fish proportions becomes slower as intensity of the worst scenario increases, taking almost two centuries to return to original levels. Size spectra elevation, an indicator of carrying capacity, grows as recruitment improves for the best case scenarios. Cases with little to no improvement of recruitment only obtain carrying capacity similar to pre-dam conditions after dam mortality subsides (Fig. 5 F).

5.3. Gradual change impacts on individual species

Inspecting the best-worst scenario comparison shows how biomass rank for each species changes across time (Fig. 6, A,B). In the best scenario, there is only one dramatic shift in the community where eel decreases from position 4 to position 15 in the community. Some skepticism should be applied to the predictions of eel, as empirical evidence would suggest that dam removal helps anadromous and diadromous similarly, but the entire migration process is not captured in this model. Additionally, eels are supported by stocking and assisted migration in reality but such actions are not in the model. For all other species, the rank difference from the start of the projection to the end was typically only one or zero. Under the worst scenario, multiple species drop multiple ranks while others capitalize on these shifts. Brown trout goes from position 2 to last position by the end of the projection. Many top predators, such as pike Esox lucius and burbot Lota lota, initially drop to the lower half of the community but tend to recover after year 25. While predators declined, the community becomes dominated by smaller fish species such as bleak Alburnus alburnus, ruffe Gymnocephalus cernua, and alpine bullhead Cottus poecilopus up until year 100. The result for the first 25 years would be a community dominated by salmon but also by small-bodied fishes which agrees with the large fish proportion plot (Fig. 5 E).

6. Discussion

We showed that dam removals have the potential to improve the river ecosystem in terms of fish production and stability while maintaining community composition, and that the worst case scenario can negatively affect the ecosystem and introduce a vastly different community. In addition, these changes (positive or negative) exhibited a range of timespans that usually took a decade or more before the ecosystem stabilized. Over short time scales our results showed the possibility of substantial changes in biomass which corroborates empirical studies in other dam removal evaluations (Bubb et al. 2021). Additionally, individual species reacted differently with respect to the entire community, regardless of the type of the event and its severity, suggesting that fish habitat tradeoffs will be more prevalent than an all-fish-will-benefit scenario (Ishiyama et al. 2018). Both results highlight the biodiversity risk of typical restoration strategies that 1) favor a few species (e.g., salmonids, eels) as metrics of success (Verhelst et al. 2021), and 2) lack funding for restoration, or monitoring follow-up outside of the time of the event (Duda and Bellmore 2022). Thus, a long-term community view of resident fishes may be a more meaningful metric of success that reflects the possibility that some fish species will fare worse after the dam is gone. From the worst case scenario perspective, waiting for the system to “heal” or “let nature take its course” (Belovsky et al. 1994) might require multiple decades, if not a century when dam removals are implemented poorly. Our model has the potential to be implemented prior to dam events so that commitments to proper preparations regarding funding, monitoring, and restoration are resolved before events occur, and also respect the long-term support a river system might need.

Our model offers a data-limited approach which provides projections of dam removal outcomes that are flexible to implement but the model strongly depends on many parameters that are expected not to change
Fig. 5. Output of 30 different gradual change projection scenarios visualizing from best case dam removal (purple) to worst case dam failure (yellow). Plots are an aggregate view of the community (all species abundance and size relations represented by a single line). Panel A shows biomass across time, panel B size spectra slope across time, panel C mean weight across time, panel D size spectra linearity across time, panel E proportion of large fish across time, panel F size spectra elevation across time.
across time. This assumption is inherent to projection style models so it is important to emphasize that the strength of our model is its ability to show a variety of possible outcomes to inform risk for species within an entire community (Smith et al., 2018). Recovery times, for example, should be viewed as "best estimates" as other factors that are not resolved may come in and further hinder or accelerate recovery. The model is not intended to provide exact predictions centuries into the future, as our parameters or other unmodeled aspects of the system will have likely changed by that point. Care should be taken to ensure that the unmodeled aspects of the system are justified (Quinn, 2008). For example, each species added to the model requires several parameters that need values and appropriate calibration. The addition of an alien species, such as pink salmon Oncorhynchus gorbuscha, a new invader to the Baltic Sea region could drastically change outcomes if it establishes in the Mörrum (Staveley and Ahlbeck Bergendahl, 2022). The inclusion of extremely rare species can also incorporate unexpected consequences as our model does not allow for extirpation since the resident species can emigrate from upstream. In other systems this may not be possible. If some species are endemic to a site and no colonization is possible from other regions, rare species may be extremely vulnerable to abiotic changes coupled with more favorable conditions for competitors (Dibble et al., 2021). Aspects of the system that are modeled but are uncertain or inherently dynamic should be explored with sensitivity analyses as we did for natural mortality (Appendix S2). This step can be done in a variety of ways but a straightforward technique for any questionable parameter is to assume a conservative value and perform a one-at-a-time sensitivity analysis to evaluate parameter influence (Hamby 1994).

A well-known issue for process-based/food web ecosystem models in both aquatic and terrestrial ecosystems is their uncertainty for both species specific and community level predictions as time spans increase (Newman et al., 2019; Geary et al. 2020). In our case, fish growth, predator–prey interactions, and natural mortality are aspects of the system that may naturally evolve over time which may be difficult or impossible to measure, let alone parameterize. The von Bertalanffy

Fig. 6. Individual species trajectories of biomass rank (purple for largest species, yellow for smallest species). This within-community view compares the best case scenario (most purple line from Fig. S; A) and worst case scenario (most yellow line from Fig. S; B).
growth coefficient is an influential parameter for model projections that requires care to ensure the correct values are used (Benoit et al. 2021). We used a database, as any data-limited approach would, but one could also rely on previous related studies that offer localized meta-analyses (for example – Rypel 2012). Other possibilities are to have a slightly more data intensive approach and use the estimation of growth using length frequency data for every species in the community (Taylor and Mildenberger 2017). The most reliable, but most logistically challenging and financially expensive approach would be to use classical age-based growth modeling from hard structures for the entire fish community (Campana 2005). Predator-prey interactions are another influential parameter that is time constant. In its data-limited form it is almost exclusively size determined, but one can incorporate specific prey preferences if such data exists (Scott et al. 2014). The last influential parameter is natural mortality which is extremely difficult to estimate for every size and every species in the community, although some ecosystem based estimates are available (Lorenzen 1996). There are a variety of data limited approaches for estimating natural mortality but their performance is questionable (Kenchington 2014). One can use von Bertalanffy growth parameters and environmental data to estimate mortality but such approaches require empirical data with robust sample sizes (Taylor et al. 2005, Brodzia et al. 2011).

The key mechanisms of dam removal also require scrutiny. Resource rate, dam mortality, and recruitment are crucial for the operation of this model but are difficult to quantify as these values are also expected to change over time. These changes are in the context of the projection scenarios which requires a different perspective on parameterization compared to the parameters of the fish community. Most experts that work with dams assume trends for these parameters, which is enough to implement the model, but usually lack empirical data to validate expectations (Magilligan et al. 2017). Instead, they rely on already established monitoring programs to facilitate this process (Bednarek 2001). Fortunately, in our system and the rest of Sweden, electrofishing is commonly used to monitor the fish community and the datasets are nationwide and open access (Comte et al., 2020), but there are biases such as sample location, size selectivity, and user experience that should be evaluated and quantified so estimation of community wide parameters is more robust. Rivers and reservoirs with deeper bathymetry may find electrofishing to be too biased towards near shore species and under sample pelagic or benthic species. One way to address this would be the implementation of a standardized fish sampling procedure that uses multiple capture methods (Bonnar et al. 2009). For other dam removal parameters, the proliferation of remote and automated monitoring techniques (i.e., fish counters/cameras, satellite remote sensing products, multi-parameter sondes) may allow much longer observational periods than what is typically used in dam removal studies (Besson et al. 2022).

An important constraint of our data-limited approach is the absence of spatial effects from the dam removal (Bellmore et al., 2019). Instead, our model consolidates resource rate, dam mortality, and recruitment maximum into generalized non-linear changes from a system wide perspective. For example, the network of our system can be symbolized as a single line where immediate impacts of the dam removal mortality would be localized only for the center (where the dam was) and decrease in impact further downstream. Recruitment improvements would only be expected for the top half of the line as hydropeaking disappeared at the dam and the upstream portions of the river could be reached for spawning activity. Resource rate would largely change at the reservoir as it transitions to natural river bed. Our case is relatively straight forward. Other systems are more complex as they will likely have significant tributaries, distinct communities between river and reservoir, and diverse water management actions which all test the limits of consolidating these mechanisms (Poff and Hart, 2002). Discussions with practitioners and dam removal specialists should emphasize that dam removal effects will have specific locations that are inherently spatially and temporally dynamic (Bellmore et al., 2019) but it is the summation of these effects that need to be reflected in the model.

There are many ways this model can be improved or extended to encompass fish diversity more completely. Firstly, in the case of the Mörrum River, inclusion of the migrant forms of eels, salmon and trout into the model would make it resemble the ecosystem more accurately. The challenge here lies in capturing the natural and fishing mortality of these migrants appropriately, as they encounter multiple fishing fleets and predators in each marine system (i.e., Baltic Sea, North Sea, Sargasso Sea) (Andersson et al. 2012). Moreover, human efforts to improve these species such as stocking and assisted migration would also need to be taken into consideration. For example, the scenarios we present do not include the stocking and trucked migrations for eels, and in the best scenario their biomass rank continued to decrease. Secondly, if one were to prioritize complete fish biodiversity and include parasitic fishes such as lamprey, as they are also threatened by habitat degradation in rivers (Almeida et al. 2021), this will violate the “big fish eat little fish” assumption of the model. Thus, the model would require a completely separate metabolic pathway to reflect these known physiological processes. We were fortunate for this system that the tributaries are rather small, but in larger river networks a “meta” size spectrum model that links different river communities together may offer a more realistic interpretation of fish communities and reflect practitioner priorities better (Null et al. 2014).

The practice of dam removal allows for ample flexibility to implement the four phases: phase 1 lowering the reservoir, phase 2 building and removing ancillary structures, phase 3 dam removal, and phase 4 restoration work. Overseers to the Marieberg dam removal contend that the Mörrum River has the potential to improve in a relatively short time period (less than 10 years) since near dam mortality was expected to be near 0. The dam removal went extremely well and below we list six practical measures that were included to prevent dam removal fish mortality and negative effects on resource rate change. First, the entire dam removal process requiring physical disturbances to water occurred under a very short timeframe of only 4 months (June 1st - September 30th). Second, lowering the reservoir started as early as April, only a maximum of 50 cm per week reduction was allowed. Third, just prior to the removal, reservoir sediment was measured for toxicity but no toxic agents were found. If toxic chemicals had been found, the sediment would have been dredged out. Fourth, the actual time of removal was approximately one month and occurred outside of typical spawning times for resident fishes. Fifth, free flowing passage for fishes was possible for most of this time period and regular turbidity readings were taken downstream and would force operations to stop if they surpassed typical conditions. This only occurred once for a single afternoon. Finally, the restoration process then followed for approximately one month after removal. Today the modeled portion of the river is now almost entirely free-flowing, only one dam with fish passage remains, and thus a return to a more historical flow regime suggests an increased resource rate and recruitment possibilities for fish. The removal of the hydropower turbine also means that hydropneaking will no longer have an impact on biotic and abiotic conditions downstream of the Marieberg powerplant. The increased connectivity will allow efficient passage of fish with migratory requirements. Future research can help develop techniques to translate the qualitative expertise of practitioners into quantitative measurements (Gosling 2018) that could go directly into the dam removal model.

7. Conclusion

Dam removals, be they planned or unexpected dam failures, produce a wide range of outcomes for the impacted ecosystem. While previous models have attempted to capture fish community responses to this process, data requirements and complexity usually make such models difficult to 1) parameterize, 2) transfer among systems, and 3) implement well before removal occurs. The deterministic model presented here overcomes those pitfalls by providing a standard set of responses,
dam mortality, resource rate, and recruitment, to help foster discussions about potential outcomes of the fish community and assess risk. For our dam removal case, we found the time scales of recovery about the age of maturation of the largest fish, and that we can expect to see both over- and undershoots of the final condition during the recovery process. These predictions are important input to stakeholder discussions. Our model also provides a solid foundation to incorporate more complexity when more information about the dam removal phases, dam removal responses, and fish community are available.

CRediT authorship contribution statement

**Henry H. Hansen:** Conceptualization, Methodology, Data curation, Formal analysis, Writing – original draft. **Ken H. Andersen:** Methodology, Formal analysis, Validation, Writing – review & editing. **Eva Bergman:** Data curation, Funding acquisition, Project administration, Supervision, Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Open Research Statement: All associated code and data is located in the following repository: 10.5281/zenodo.8240338.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.110805.

References


