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Stock-catch analysis of carp recreational fisheries in Czech reservoirs: insights into fish survival, water body productivity and impact of extreme events

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Abstract

In culture-based fisheries, managers strive for high stocking efficiency, the ratio between the total weight of caught and stocked fish. Here we present a new time series approach to examine the dependence of reported anglers' catches on stocking and external events, using data on carp (Cyprinus carpio L.) from 14 reservoirs in the Czech Republic. Average stocking efficiency varied between 0.25 and 2.2, with values close to unity in most reservoirs. The lowest efficiencies occurred in three reservoirs receiving cold hypoxic water from a large upstream reservoir, while the highest efficiencies were found in two shallow, highly productive reservoirs. Analyses further indicate that stocked carp are typically caught during the year of release or the year after; but also that the mean time lag between stocking and capture increases with reservoir area. External events can be important: major floods in the years 2002 and 2006 were in many cases followed by large, up to 10-fold, increases in catches in subsequent years; we attribute the surplus catch to carp washed down from upstream aquaculture and river stretches. In contrast, the "Velvet Revolution" (demise of the communist regime in 1989) had no discernible effect on catches in subsequent years. In conclusion, the proposed method can simultaneously estimate the likely mean survival time of stocked carp and identify the impact of major environmental and societal events on recreational fisheries. The approach thus sheds light on the performance of current stocking practices at individual reservoirs, and could be used to monitor and improve stocking strategies and management of culture-based recreational fisheries.

Keywords: management, time series, stocking, recreational fisheries, floods

Running head: Stock-catch analysis of carp recreational fisheries

1. Introduction

Stocking is a widespread tool in fisheries management (Cowx, 1998; Welcomme and Bartley, 1998). It is regularly used in recreational fisheries to satisfy angler expectations and demands, including increased catches and availability of multiple fish species for exploitation (Arlinghaus and Mehner, 2005; Baer et al., 2007; Britton et al., 2007). Stocking may be used to enhance or supplement natural reproduction or to create culture-based fisheries, i.e. fisheries based predominantly on the recapture of stocked fish (Lorenzen et al., 2001).

The common carp (Cyprinus carpio L.) in the Czech Republic provides a prime example of a culture-based fishery. Czech carp breed extremely rarely in the wild (Baruš and Oliva, 1995), yet they are the most popular target among anglers, and constitute the largest part of catches at most ponds and reservoirs (e.g., Jankovský et al., 2011). Local carp populations are actively managed by regular stocking, and long-term records of the amount of stocked and caught carp are maintained by many regional offices of the two major recreational fishing organisations, Czech Anglers' Union and the Moravian Anglers' Union. Catches of carp account for 75–80% of the total annual yield reported by anglers in the Czech Republic (e.g., Vostradovský and Mráček, 1996). During 1990–2010, the ~320,000 individual anglers registered in the two unions caught on average 3,000 tonnes of carp each year; this figure excludes fish that were immediately released back and were hence not recorded. The participation rate of ~3% in recreational fishing and the annual per-capita catch of ~10 kg of carp are comparable to those in many other European countries outside Scandinavia (Aas, 2008; EIFAC, 1996; Wortley, 1995).

The relationship between annually stocked and caught fish can be used by local fisheries managers and contribute to cost-effective stocking. However, there is no established rigorous method that would be used in such assessments. Statistical analyses aimed to elucidate the dynamics of stocking have investigated general relationships between yield and stocking weight/rate, between yield per unit area and the size of the stocked system, between yield and effort, and between yield and various physico-chemical factors as proxies for habitat productivity (e.g., De Silva, 2001, 2003; Sugunan & Katiha, 2004; Welcomme & Bartley, 1998). However, these studies have been motivated mainly by the need to achieve highly productive culture-based fisheries in developing countries. The resulting relationships are based on long-term averages and comparisons across multiple systems, which limit their utility to describe more closely a stock-catch relationship in a given water body. Time series analyses could provide useful tools in this task, but are used to build predictive models in the context of freshwater fisheries only rarely (Allen et al., 2006; Loomis and Fix, 1998; Skehan and De Silva, 1998).

Managers in the Czech Republic and elsewhere often assess the return rate of stocked fish on an annual basis by comparing the total amount of caught fish (expressed in weight or numbers) to the amount of fish stocked in the same year or the year before (e.g., De Silva et al., 1992; Pivnička and

Rybář, 2001). This simple approach is reasonable in the absence of better knowledge about average time to recapture. Indeed, stocking events can result in high catches shortly after the stocking because they attract increased attention and lead to temporarily higher fishing effort by the anglers and because the newly-stocked fish are often easy to catch (Baer et al., 2007; Pivnička and Čihař, 1986). Improved statistical methods, such as lag-correlation analysis, can identify most likely time lags between stocking and harvest (e.g., Quiros and Mari, 1999). Nevertheless, the drawback of correlation analyses is their inability to provide a full overview of the stock-catch relationship as they consider each of the lags separately and, furthermore, neglect any additional prominent features of the time series such as residual long-term trends. Contributions of fish stocked in different years to the catch in a given year are thus difficult to determine.

The aim of this paper is to propose a relatively simple time series analysis that can reconcile the aforementioned problems and, in addition, help identify attributes of each reservoir that are of high relevance to fisheries managers. In particular, we ask the following questions: can linear models capture long-term relationships between stocked and caught fish in culture-based fisheries? Do such models imply any differences between individual water bodies? Can we use long-term data to indirectly estimate survival patterns of the stocked fish, assess the reservoir productivity, and identify the impact of extreme events, such as large floods, on the catches? The questions are framed in the context of carp recreational fisheries in the Czech Republic, but the methods developed here are general and applicable to any other culture-based fishery.

2. Material and methods

2.1. Data sources

We use time series of stocked and caught carp from 14 reservoirs (Table 1), collated from annual reports provided by regional offices of the Czech Anglers' Union and Moravian Anglers' Union. The reservoirs vary greatly in age (ca. 20–80 years old) and surface area (14–4870 ha) and represent four distinct groups: relatively small urban reservoirs (from the smallest to the largest: Papež, Džbán and Hostivař), canyon-shaped and relatively cold, moderately productive reservoirs on the Vltava River (Kořensko, Hněvkovice, Slapy, Orlík and Lipno) and three productive reservoirs on the Dyje River (Mušov, Vranov and Nové Mlýny). Finally, three of the reservoirs on the Vltava River (Štěchovice, Kamýk and Vrané) are located immediately downstream of a large and deep reservoir (Orlík or Slapy; see Table 1) and receive cold hypoxic water from their hypolimnion, causing low productivity (referred to as a "cascade effect"). Draštík et al. (2004), Kubečka (1993) and Lusk and Krčál (1983) provide maps and further details on the reservoirs.

Data for each reservoir cover a period of 16–52 years (Table 1). The variables available from all reservoirs are the total weight and number of stocked carp and the total weight and number of caught carp. We use only weight in the analyses because it is the primary variable in stocking statistics; to our knowledge, only a subset of the stocked carp is weighed individually to obtain an estimate of the numbers of stocked carp. On the other hand, both total weight and total number of caught carp is calculated directly from the anglers' catches and thus represent relatively precise (bar any errors in reporting) primary data. Stocking usually consists of 2-year old carp, which are largely invulnerable to local piscivorous fish (pike, pikeperch and wels catfish). Younger fish were sometimes stocked in 1960s and early 1970s, and older fish have sometimes been stocked in recent years. We combine only the weights of stocked 2-year-old and older fish in the analyses as the weight of 1-year-old carp was usually much lower compared to the older fish and it is likely that these small carp suffered high natural mortality from predation and overwintering (Vostradovský, 1974). Sufficiently long time series (> 10 years) of effort, measured as the total number of fishing trips per year, are available for only three reservoirs, all of them located in southern Moravia (Table 1).

In one of the reservoirs, Lake Lipno, commercial fishing with seine nets was carried out in 1959–1996; the commercial catch exceeded 5% of the total catch only during 1959–1971, with a maximum of 44% in 1961. We include the commercial yield in the catch data and treat it as equivalent to anglers' catches: preliminary analyses showed that the commercial catches were otherwise "missing" in the anglers' data (not shown).

2.2. Statistical analyses

The analyses of stock-catch relationships for carp in different reservoirs are based on generalized least squares regression (Zuur et al. 2009). We first standardize the total weights of stocked and caught carp from each reservoir by dividing them by the reservoir's area.

The basic model is,

$$Y_T = \sum_{i=j}^{k} p_i \, S_{T-i} + \varepsilon_T \,, \qquad (1)$$

in which the total weight Y_T of carp caught in year T per unit area is related to total weight S_{T-i} of stocked carp per area in the same year ($i = 0$) and/or in selected preceding years ($i = 1, 2, \ldots, k$). Specifically, the models simultaneously consider time lags ranging between j and k years that separate the stocking and capture events. Because the fish are stocked at or only slightly below harvestable size, we primarily consider models where the shortest time lag is $j = 0$ (part of the biomass is harvested the same year in which it has been stocked) but put no constraints on the longest lag k. In addition, we include the case $j = k = 1$, which assumes that all biomass is harvested the year after stocking. Coefficients p_i, termed annual return ratios, express the fraction of the stocked biomass that is fished out i years later. The ratios combine natural mortality with biomass gain due to individual growth of the fish. They may also be affected by systematic biases in reporting, e.g. due to inaccuracies that might arise when the anglers convert the length of the fish into weight using standardized conversion tables supplied by the Czech Anglers' Union, but there is not enough data to investigate such biases.

We also consider alternative models with increased complexity,

$$Y_T = B + \sum_{i=j}^{k} p_i \, S_{T-i} + \varepsilon_T \,, \tag{2}$$

$$Y_T = \sum_{i=j}^{k} p_i \, S_{T-i} + F_{\hat{T},T} + \varepsilon_T \,, \tag{3}$$

$$Y_T = B + \sum_{i=j}^{k} p_i \, S_{T-i} + F_{\hat{T},T} + \varepsilon_T \,, \tag{4}$$

$$Y_T = \sum_{i=j}^{k} p_i \, S_{T-i} + c\left(T - \bar{T}\right) + \varepsilon_T \,, \tag{5}$$

$$Y_T = B + \sum_{i=j}^{k} p_i \, S_{T-i} + c\left(T - \bar{T}\right) + \varepsilon_T \,, \tag{6}$$

$$Y_T = \sum_{i=j}^{k} p_i \, S_{T-i} + F_{\hat{T},T} + c\left(T - \bar{T}\right) + \varepsilon_T \,, \tag{7}$$

$$Y_T = B + \sum_{i=j}^{k} p_i \, S_{T-i} + F_{\hat{T},T} + c\left(T - \bar{T}\right) + \varepsilon_T \,, \tag{8}$$

In models (2), (4), (6) and (8) we add a time-independent biomass change term B, which combines the effects of biomass loss due to time-and stocking-independent mortality of individual carp (which might arise, e.g., through a constant population of predators and/or poachers) and biomass gain, e.g. due to downstream migration of fish. In models (3) and (4) we also use indicator variables $F_{\hat{T},T}$ to estimate the impact of an external event in year $\hat{T}$ on catches in year T. We a priori identified three events that could have influenced the stock-catch relationship. The Velvet Revolution in 1989 could have led to lower fishing effort and consequently lower catches in early 1990s. The other two events, extreme floods in 2002 and 2006 on the Vltava and Dyje Rivers, concern only the riverine reservoirs: they could have led to either lower or higher catches depending mainly on the outflow and mortality of resident fish and the influx of escapees from upstream river stretches and aquaculture. Models (5) and (6) include time as predictor to capture any long-term trends over the entire time series in catches that cannot be ascribed to stocking; $\bar{T}$ denotes mean year of the series and c the annual rate of change in catches. Finally, models (7) and (8) combine the three external events as in models (3)–(4) with long-term trends as in (5)–(6).

The error term $\varepsilon_T \sim N(0, \sigma^2)$ in models (1)–(8) is assumed either to be uncorrelated in time or to represent a first-order auto-regressive [AR(1)] process with $\mathrm{cov}(\varepsilon_t, \varepsilon_s) = \Phi^{|s-t|}$. Positive values of the autocorrelation coefficient Φ would arise if longer periods with catches higher than predicted would mostly alternate with periods of low catches, indicative of underlying long-term processes in the dynamics of stocking and fishing and carp survival and growth.

Models (1)–(8) assume that variation in catches is primarily driven by variation in stocking, not variation in effort (apart from the possible effect of the Velvet Revolution in two of the models). Variation in effort, if random and uncorrelated with stocking, would thus merely increase unexplained variability in catches. More systematic trends in effort could be indirectly detected, e.g., as long-term trends in the residuals of models (1)–(8).

For the three Moravian reservoirs with sufficiently long time-series of fishing effort data, we also investigate two additional sets of alternative models. The first one has the same structure as models (1)–(8) but links catch per unit effort (CPUE, kilograms of fish caught per fishing trip) to total weight of carp stocked in previous year(s) and to external events. In this case, the intercept measures a hypothetical CPUE under no stocking and the model coefficients express the increase in CPUE after i years for every tonne of stocked carp. The second and more complex set of models directly investigates the interaction between stocking, effort E_T, measured as the total number of reported fishing trips in year T, and catches:

$$Y_T = \sum_{j=0}^{k} p_j \left(E_T S_{T-j} - \sum_{i=1}^{k-j} E_{T-i} S_{T-i-j} \right) + \varepsilon_T . \qquad (9)$$

Models (10)–(16) are defined analogously to models (2)–(8), but with the simple summation in model (1) replaced with that in model (9); we do not list them here for brevity. These hybrid, biomass-and-effort based models take into account gradual depletion of each released cohort in subsequent years. All parameters have the same interpretation as in the basic models (1)–(8) except the model coefficients p_i, which express the contribution of every tonne of stocked carp to CPUE i years after the release.

Akaike Information Criterion with small sample size correction (AIC_c) is used to select the best-fitting models (Burnham and Anderson, 2002). Since the models differ in complexity, we always use only data from the years for which all compared models give predictions. We first compare models (1)-(8) with $k = 1$, i.e. with time lags of 0 and 1 years, and continue to increase k as long as the added time lags do not lead to higher AIC_c. The main text reports models with the lowest AIC_c value for each reservoir and a few selected models for which the difference of the AIC_c value from the lowest value, ΔAIC_c, is at most 2 and hence their evidence ratio does not deviate too strongly from unity (Burnham and Anderson, 2002). We also provide Akaike weights for the models. Since our model set is not a priori constrained (k could be arbitrarily large), we restrict it to the best fits of models (1)–(8) with $j = 0$, k varying between 0 and the value selected for the best fit (or 1, whichever number is higher), and present/absent autocorrelation error term. We further include variants with $j = k = 1$ in the model set, but the corresponding model variants (3)-and (4) with flood contribution(s) are included only if the contribution is significant in at least one of these variants. Fits of models (3) and (4) are otherwise very similar to the fits of corresponding models (1) and (2), i.e. we would effectively spread the Akaike weights over multiple models with the same lag structure. Inclusion of models (5)–(6) and (7)–(8) follows the same rules, and the same procedure applies to models (9)–(16). More comprehensive summary of the fitted models is given in Supplementary data (Tables S1–S3). We then inspected the residuals of the best fit to reveal abrupt changes in local stocking and/or exploitation patterns over the entire period. Finally, prediction intervals for models in which the error term is uncorrelated in time are based on a linear regression model.

To compare the stock-catch relationship across reservoirs, we used the best fits of models (1) or (3) and calculated the stocking efficiency, defined as $r = \sum_{i=j}^{k} p_i$, relative annual return ratios $\tilde{p}_i = p_i / r$, and mean return lag $\overline{\Delta T} = \sum_{i=j}^{k} i\, \tilde{p}_i$. The lag can be used as proxy of the mean survival time of the stocked fish if there is no further source of input of the fish into the system. Models (2) and (4) with $B \neq 0$ as well as models (5)–(8) with temporal trends unattributed to stocking are thus omitted from this comparison. On the other hand, this approach separates a potential impact of floods from stocking: a significant contribution of floods in year $\hat{T}$ to catches in year T will appear as positive value of $F_{\hat{T},T}$ in model (3). The resulting stocking efficiency and mean return lags are compared across reservoirs with linear models including log-transformed value of the area and/or the length of the fitted time series as predictors. All analyses were implemented in R version 2.10.1 (R Development Core Team, 2009) and significance level in all tests was set at 0.05.

3. Results

Annual stocking and catches across the 14 reservoirs span three orders of magnitude (~0.1–100 tonnes of carp), and stocking density and catch per area vary similarly (~1–1000 $kg.ha^{-1}$; Fig. 1). Larger reservoirs are stocked with more fish, but the stocked and caught biomass per area decline with the reservoir area. Despite the overall good correspondence between catches and the amount of fish stocked in the same year (diagonal lines in Fig. 1 indicate perfect correspondence), annual catches in some reservoirs and years were as much as ~10 times higher or lower than the biomass of stocked fish.

3.1. Overall performance of time series models

The amount of stocked carp and the catches have increased significantly over time in all but two reservoirs, sometimes as much as 10-fold over the entire period (Fig. 2). Models suggest that the increasing catches have been primarily driven by enhanced stocking: for all reservoirs except Kořensko, at least one of models (1)–(4) with at least one non-zero annual return ratio p_i provided a biologically meaningful description of the relationship between the stocked and caught biomass of carp (Table 2). Similarly, at least one of the models provided a biologically meaningful description of the relationship between the stocked biomass and CPUE (Fig. 3a-c and Table 3) and between stocking, effort and catches (Fig. 3d-f and Table 4).

Residuals from models (1)–(4) fitted to the entire time series from Štěchovice indicated a shift in the stocking/exploitation patterns in mid 1990s, as the average stocking efficiency during 1995–2009 was about 3.2 times larger than during 1971–1994. We detected a similar shift with a twofold increase in stocking efficiency in the data from Vrané after 1992. We thus treated the early and late part of the time series from these two reservoirs as separate (Tables 2 and S1; Figs. 2d and 2h). Setting the divide a year later or earlier led to very similar results.

Models with autocorrelated error terms ε_T were favoured over models with uncorrelated errors for four reservoirs (Štěchovice before 1995, Vrané after 1992, Lipno and Nové Mlýny; Tables 2-4).The correlation was positive in all four cases: the model residuals tended to remained positive or negative for several consecutive years.

Our time series analyses indicate that stocking-independent factors are mostly unimportant for carp catches. Models (1) or (3) without the production term yielded poorer fits than models (2) or (4) with non-zero production term B (in the sense of the best model without the production term having $\Delta AIC_c > 2$) only for Štěchovice before 1995, Kořensko, Hněvkovice and Nové Mlýny (Tables 2 and S1). However, the fits of the data at Štěchovice before 1995, Kořensko and Nové Mlýny were generally poor (Figs. 2d, 2e and 2n). A strong support for non-zero production, e.g. through downstream fish migration, thus seems limited to Hněvkovice. On the other hand, the link between stocking and CPUE seems more loose: models (2) and (4) relating CPUE to stocking with non-zero intercept were favoured over models (1) and (3) for two of the three reservoirs with CPUE data (Vranov and Nové Mlýny; Tables 3 and S2). Results from models (9)–(16) are intermediate in this aspect. The model with non-zero intercept gave better results only for Vranov but not for Mušov and Nové Mlýny data (Tables 4 and S3).

3.2. Impact of major external events and long-term trends in stocking and exploitation patterns

We have already mentioned that we had to divide the data from two reservoirs, Štěchovice and Vrané, into the early and late part of the time series to accommodate a clear shift in the stocking/exploitation patterns. More generally, models (1)–(4) did not provide any compelling evidence for impacts of external events (i.e., Velvet Revolution and floods) and for gradual or abrupt changes in local stocking and/or exploitation patterns at four reservoirs: Papež, Džbán, Hostivař and Mušov. The first three are small catchment areas with no significant sources of fish drift, while the latter, Moravian reservoir was largely unaffected by the floods in 2002 and 2006. Catches at the remaining eight reservoirs bear clear signatures of one or more irregularities.

First, some of the catches peak conspicuously in early 2000s. The fitting procedure captured sharp increase in catches after the 2002 floods at five reservoirs on the Vltava River: Kořensko, Hněvkovice, Kamýk, Slapy and Orlík. Catches immediately after the floods were ca. 2–10 times higher than expected without the flood contribution and the effect lasted until 2003 or 2004 (Table 2 and Figs. 2e, 2f, 2h, 2i and 2j). Similar effect of the 2002 and 2006 floods at the Dyje River is discernible in catches and CPUE data from Vranov (Tables 2–4 and Figs. 2m, 3b and 3e). On the other hand, we did not find any significant change in the stock-catch pattern at any reservoir in early 1990s, after the Velvet Revolution.

Second, we detected long-term trends in the catches at three reservoirs (Kořensko, Lipno and Nové Mlýny) that were not captured by stocking, fishing effort and effect of floods. Catches at the Kořensko increased by about 5.6±1.8 $kg.ha^{-1}.yr^{-1}$ over the study period (mean±SD; model (8), Table 2), while catches at Nové Mlýny declined by approximately 2.0±0.7 $kg.ha^{-1}.yr^{-1}$ (model (6), Table 2; AIC_c value slightly higher than that of the most favoured model of constant catch) and CPUE by 0.026±0.007 $kg.trip^{-1}.yr^{-1}$ (model (6) relating CPUE to stocking, Table 3). Finally, model (5) fitted to the Lipno data indicates a small but significant increase in catches over the years, about 0.06±0.03 $kg.ha^{-1}.yr^{-1}$ (Table 2).

3.3. Stocking efficiency and residence time of released carp in individual reservoirs

Average stocking efficiency (the ratio of caught to stocked biomass, r) estimated by model (1) or (3) over the entire period varied between 0.5 and 2.2 (Fig. 4). Most reservoirs had a stocking efficiency close to or larger than unity. However, low stocking efficiency (r ~ 0.5–0.7) was found in the three reservoirs with the cascade effect: Štěchovice, Kamýk and Vrané. The stocking efficiencies in Štechovice and Vrané were extremely low until early 1990s (r ~ 0.25–0.35) after which they increased to r ~ 0.75–0.9. Stocked biomass was more or less recovered (r ~ 0.92–1.04) in the reported catches at four reservoirs: Papež, Hostivař, Slapy and Lipno. Biomass of reported catches surpassed substantially the stocked biomass ($r > 1.1$) only in Džbán, Kořensko, Orlík, Hněvkovice and in all three productive reservoirs on the Dyje River (Vranov, Nové Mlýny and Mušov). Overall, stocking efficiency did not depend significantly on reservoir area ($r = 0.63 + 0.071 \cdot \ln(\tilde{A})$, nondimensionalised area $\tilde{A}$ obtained by dividing area A in hectares by $A_0 = 1\,\text{ha}$: $R^2 = 0.06$, $df = 13$, $P = 0.37$; dashed line in Fig. 4a) or time series length (not shown).

Mean return lag $\overline{\Delta T}$ could be compared across 13 reservoirs except Kořensko, for which models (1) and (3) provided no meaningful fit of the time series. In addition, the early and late part of the time series from Štěchovice and Vrané were treated as separate data in this analysis. Mean return lag varied between 0.32 and 1.51 and increased significantly with reservoir area, $\overline{\Delta T} = 0.49 + 2.2 \cdot 10^{-4} \cdot \tilde{A}$, $R^2 = 0.78$, $df = 13$, $P < 10^{-4}$ (dotted line in Fig. 4b) and $\overline{\Delta T} = -0.11 + 0.14 \cdot \ln(\tilde{A})$, $R^2 = 0.53$, $df = 13$, $P = 0.002$ (dashed line in Fig. 4b). Adding the length of the time series as an additional predictor had no significant effect on the relationships (not shown).

Examining this comparison in more detail, the stocked carp were probably fished out fastest at Vrané in 1971–1992 and at the small urban reservoir of Džbán. These two time series are consistent with an intensive exploitation pattern under which, on average, about two thirds of the reported biomass are removed in the stocking year and the remaining third is caught in the next year (Tables 2 and S1). At most other reservoirs, about half of the stocked biomass was caught the same year ($\tilde{p}_0 = 0.40$–0.57; Papež, Hostivař, Štěchovice, Vrané after 1992, Hněvkovice, Slapy, Orlík and Mušov). Less than one third was retrieved the same year at Kamýk, Lipno, Vranov and Nové Mlýny ($\tilde{p}_0 = 0$–0.32). The estimated value of relative annual return ratio one year later, $\tilde{p}_1$, was similar to $\tilde{p}_0$ at Papež, Hostivař, Štěchovice, Vrané after 1992 and Mušov ($\tilde{p}_1 = 0.43$–0.60). The estimated value of $\tilde{p}_1$ was considerably larger than $\tilde{p}_0$ at the two largest Moravian reservoirs (Vranov and Nové Mlýny) and much lower than $\tilde{p}_0$ only at two large reservoirs on the Vltava River (Slapy and Orlík). The fitted models did not indicate any significant returns after two years or later, except for three of the four largest reservoirs (Slapy, Orlík and Lipno: $\tilde{p}_2 > 0$, range 0.24–0.53; $\tilde{p}_3 > 0$ only at Lipno). However, analogous interpretation of results from model (9) suggests significant biomass returns two years later also from Mušov and Nové Mlýny ($\tilde{p}_2 = 0.61$–0.65, see Table 4).

4. Discussion

Enhancement of carp fisheries through stocking in Central Europe dates back several centuries (Balon 1995). Nowadays, carp forms the backbone of Czech recreational fisheries and many anglers catch very few or no other fish (Jankovský et al., 2011). Strong emphasis on carp might have unwanted consequences for aquatic ecosystems. Stocked carp could compete with other planktivorous and benthivorous fish for food, which might be one of the causes of observed long-term declines in catches of bream and other smaller cyprinids (e.g., Adámek & Jurajda, 2011). Increased stocking of carp could also indirectly add more fishing pressure on other species as substantial numbers of Czech anglers are probably generalists and catch multiple species (Jankovský et al., 2011).

Surprisingly, a proper assessment of the stocking programmes has not been attempted earlier in the Czech Republic. Such a step is crucial to develop optimal stocking policies that would ultimately take into account the full range of management and environmental issues associated with recreational fisheries (Arlinghaus et al., 2002; Cowx, 1998). In addition, a detailed study of the carp recreational fisheries in the Czech Republic can provide general insights that could be applied elsewhere, given that few rigorous studies of stock-catch relationships exist (Welcomme and Bartley, 1998). Previous research has addressed various aspects of the stocking process such as the survival of stocked fry and juvenile fish (e.g., Aprahamian et al., 2003; Hervas et al., 2010), relative contributions of wild and stocked fish to catches (e.g., Baer et al., 2007; Heard, 2003), and the interplay between stocking, yield and abiotic and biotic factors across reservoirs (e.g., Allen et al., 2006; De Silva, 2001, 2003; Nguyen et al., 2005). As we show here, time series of annually stocked and caught fish alone can be used to unravel the long-term dynamics of culture-based recreational fisheries.

4.1. Similarities in stock-catch relationships across Czech reservoirs

The 14 reservoirs included in this study range from systems in which most fish species (other than carp) reproduce naturally to extensive culture systems. Stocking of carp in these reservoirs is consistent with patterns observed elsewhere: the density of stocked fish and yield per area decline with the size of the reservoir (Welcomme and Bartley, 1998).

Models with an autocorrelated error term were the most preferred description of the stock-catch relationship in only four out of the 16 time series (considering early and late part of the series for Štěchovice and Vrané as separate data). This suggests that processes with strong temporal correlations may be atypical in the recreational fisheries for carp in the Czech Republic, admitting that we might have failed to detect autocorrelation in some of the time series because they were too short. Nevertheless, all four significantly non-zero autocorrelation error terms were positive. This speaks against the scenario in which overfishing in one year leads to below-average yield in the next year (and would hence appear as negative autocorrelation term with one-year lag).

Models without a time-independent production term provided a comparable or better fit than those with such a term for 12 out of 16 time series. The respective carp populations can be thus characterized as closed without any time-independent immigrations from upstream areas of the catchment (except during floods) and losses, for example through time- and density-independent mortality or poaching.

4.2. Patterns in stock-catch relationships: outlining possible causes

Comparison of stocking efficiency across all reservoirs supports the notion that productive, eutrophic water bodies offer prime conditions for carp growth (Kottelat and Freyhof, 2007): the highest efficiencies were achieved at Orlík, Vranov, Nové Mlýny and Mušov, all of which are highly eutrophic. Moreover, Mušov and Nové Mlýny are shallow and warm, and thus offer the best growth conditions for carp among all reservoirs included in this study.

On the contrary, three reservoirs (Štěchovice, Kamýk and Vrané) displayed very low stocking efficiencies. They are all characterized by the cascade effect (i.e., inflow of cold and hypoxic water) leading to low biomass production; furthermore, fishing effort in these reservoirs is low (Draštík et al., 2004; Jankovský, 2009). The abrupt increase in stocking efficiency at Štěchovice and Vrané in early 1990s can be attributed, at least partly, to increasing average weight of the stocked fish (not shown): larger fish are harvestable sooner, and might better cope with the environmental conditions. However, we cannot rule out additional explanations for which data are not available: major change in reporting (including errors), improved conditions in the reservoirs, release from competition with other fish species, cessation of illegal fishing, or increase in legal fishing pressure.

Biomass- and CPUE-based models as well as hybrid biomass-and-effort based models were available for three reservoirs on the Dyje River. For Nové Mlýny, biomass- and CPUE-based models found no effect of stocking on catches and fitted the observed pattern poorly compared to the hybrid model. For Mušov, CPUE-based and hybrid models estimated that at least one third of the stocked biomass survives for two years in the reservoir, a result that was not detected by the biomass-based models. Estimated lag structure for Vranov differed qualitatively between the biomass-based and CPUE-based model: the latter found no significant effect of stocking, possibly due to the shorter time series available to this model. Alternatively, CPUE might have not depended on fish density over densities experienced during the study period. Based on this limited comparison, the hybrid models seem to perform best. The conclusion should be seen as tentative: the amount of carp stocked in each of the three Moravian reservoirs was relatively stable between years, which could have diminished the performance of the biomass-based and hybrid models. Data from additional seasons and reservoirs are needed to better understand the interactions between stocking and effort and their impact on carp recreational fisheries.

Overall, our time series analyses suggested that long-term patterns in catches could be explained by changes in stocking or in effort. However, in three reservoirs, Lipno, Nové Mlýny and Kořensko, long-term patterns remained. CPUE at Nové Mlýny declined from its peak value (~1.2 $kg.trip^{-1}$) in 1994–1995 to about a half in 2005–2008. Stocking was similar in both periods and the effort declined over time. Hence, anglers should not have been increasingly more limited by the amount of stocked carp. The residual decline in catches and CPUE at Nové Mlýny is therefore probably caused by long-term habitat changes or the impact of natural predators, mainly cormorants (Adámek, 1991). Gradual increase in catches despite a declining amount of stocked carp at Kořensko could be driven by growing fishing effort at a relatively new fishing ground. The reservoir was established in 1991, three years before the start of the time series, but effort data are lacking to confirm the hypothesis. The much smaller but significant residual increase in catches at the largest reservoir, Lake Lipno, has been presumably driven by a gradual increase in the size of stocked fish, growing fishing effort (parts of the lake were in the border zone and hence closed to fishing before 1990) and eutrophication. The residual increase in overall catches further correlates with the decline in commercial fishing but the link seems purely circumstantial.

Survival time of released fish (i.e., time between release and (re)capture) is an important parameter for management. It can be directly studied in mark-and-capture experiments (e.g., Adlerstein et al., 2008; Britton et al., 2007; Jensen et al., 2009; Kerr and Lasenby, 2000; Prokeš et al. 2009, 2010; Vostradovská, 1975). As we have shown here, analyses of time series of stocked and caught biomass provide an alternative method in the absence of direct or sufficiently precise observations. Overall, our results indicate that most carp in Czech reservoirs are caught the year of release or the following year. A similar conclusion was reached for fisheries yields at three Chinese reservoirs (De Silva et al., 1992). In addition, we found that survival time of stocked carp increases with reservoir area and a significant proportion of fish survive for more than two winters in the largest reservoirs. In large reservoirs the density of the stock is smaller and the fish can spread out over larger distances (Vostradovská, 1975) than in ponds and smaller reservoirs. Carp in large reservoirs are thus probably more difficult to locate and lure by feeding as done by many carp anglers (Lusk and Krčál, 1983; Pivnička and Čihař, 1986; Vostradovský, 1974). However, we emphasize that the detected time lags between stocking and catch refer to long-term, population-level averages. This does not rule out that individual fish may survive much longer. For example, Prokeš et al. (2009) found that 93 out of the 100 tagged fish released during an experiment in Nové Mlýny were caught the same or the next year, but one fish survived for five years.

4.3. Can stock-catch relationships reveal events seemingly unrelated to fisheries?

Finally, we have taken our analyses one step further and asked how various perturbations to the society and environment could influence recreational fisheries. We have hypothesized that the average stock-catch relationship at the studied reservoirs could have been affected by two major events, the fall of the communist regime (‘Velvet Revolution’) in late 1989 and the extreme floods in 2002. The Velvet Revolution could have led to lower effort in early 1990s, as people suddenly faced entirely new challenges in their lives and had the chance to travel abroad and take part in many other new, exciting activities (e.g., Duke, 1994; Hraba et al., 2000; Kubička et al., 1995). Since the earliest effort data come from 1991, a potential dip in effort could be observed only indirectly through lower catches in early 1990s. That is, models (1) and (2) would predict much higher than observed catches in one or more years in early 1990s, or models (3) or (4) with negative values of F_n in those years would be favoured. As none of the seven reservoirs with sufficiently long time series yielded such result, we conclude that the fall of communism had no tangible effects on recreational fisheries for carp in the Czech Republic.

On the contrary, the extreme floods in August 2002 left a strong footprint in the fishery. The event affected most of the Vltava River basin, and large amounts of fish were washed downstream into the reservoirs (Kubečka et al., 2004). Only catches from Lipno, the most upstream reservoir on the river, and from two downstream reservoirs with the cascade effect (Štěchovice and Vrané) were not visibly affected by the floods. Carp catches at five other reservoirs on the river (Kořensko, Kamýk, Hněvkovice, Slapy and Orlík) increased sharply in 2002 and 2003, and the effect lasted at least until 2004 at Orlík and Kamýk. We estimate that 34–630 tonnes of the reported catches at each of the five reservoirs came from carp that drifted downstream. Similarly, floods on the Dyje River in 2002 and 2006 increased the reported catches at Vranov by about 9 and 14 tonnes in the respective year.

4.4. Conclusions

We propose to replace the common practice of regressing yield against the amount of fish stocked in the current or previous year with more general regression analyses of long-term data. These analyses can provide new insights into the dynamics of culture-based recreational fisheries and highlight the influence of external events on the yields. In our case study on Czech carp, we have exposed the differences in exploitation and production rates in different reservoirs and were able to isolate and quantify the impact of external events such as extreme floods in the data. The results also suggest that, in the long run, politics has little effect on recreational fisheries. It seems that anglers—at least Czech ones—go fishing no matter what political turmoil surrounds them.

Since these analyses require sufficiently long time series, we emphasize the great and often overlooked value that lies in old reports, meticulously assembled by successive generations of local fisheries managers. In addition, we highlight the need for long-term data on effort in recreational fisheries, which should be routinely collected whenever possible. Statistical analyses of effort, stocking and catch data, such as those proposed in this paper, can shed light onto long-term dynamics of culture-based fisheries, of which carp in the Czech Republic is a prime example.

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Figure legends

Figure 1. Relationship between the amount of stocked carp and carp caught in the same year across the data for all 14 reservoirs expressed as (a) total biomass and (b) biomass per area. Diagonal (dashed line) = equal amounts of stocked and caught carp. Symbol size proportional to log-transformed area of the reservoir.

Figure 2. Time series of stocking and catches and the best stock-catch regression models summarized in Tables 2 and S1. Thin lines = stocking; thick lines = catches; dashed lines = best fit of the data; grey areas = 95% model prediction intervals. For 1971–1994 data in panel (d), 1993–2009 data in (g) and data in (n), prediction interval and R^2 value are based on model with uncorrelated error terms (dotted line in (g), overlapping with dashed line in panels (d) and (n)); R^2 values in panels (d) and (g) given separately for early and late part of the time series.

Figure 3. Comparison of CPUE-based and biomass-and-effort based models for three Moravian reservoir. (a)-(c): time series of CPUE and the best stock-CPUE regression models summarized in Tables 3 and S2; (d)-(f): time series of catches and the best biomass-and-effort based models summarized in Tables 4 and S3. All panels: thick lines = data (CPUE or catches); dashed lines = best fit of the data; grey areas = 95% model prediction intervals. Prediction interval based on model with uncorrelated error terms (indistinguishable from dashed line) in panels (c) and (f).

Figure 4. Relationship between reservoir area and (a) stocking efficiency w and (b) mean return lag $\overline{\Delta T}$. Points = data for individual reservoirs; dashed lines and dotted curve = regression lines. See text for details.

Table 1. Summary of available data for carp in selected Czech and Moravian reservoirs. Stock/catch data = period with available stock and catch data; effort data = period with available effort data. Stock/catch data available as total weight; effort available as total number of reported fishing trips. Cascade effect = reservoir receiving cold water with low oxygen concentrations from another large and deep upstream reservoir. * = the pond was last emptied in 1987 or before; [a] = missing 1976 and 1979 stocking data; [b] = missing 1999 stocking data.

reservoir	**area (ha)**	**main characteristics**	**year built**	**stock/catch data**	**effort data**
Papež	14	small urban reservoir (pond)	1987 *	1987–2009	
Džbán	18	small urban reservoir (pond)	1971	1982–2007	
Hostivař	44	small urban reservoir	1963	1980–2009	
Štěchovice	115	reservoir on the Vltava River (river km 84), cascade effect	1944	1971–2009 [a]	
Kořensko	120	reservoir on the Vltava River (river km 200)	1991	1994–2009	
Kamýk	195	reservoir on the Vltava River (river km 135), cascade effect	1962	1993–2009	
Vrané	251	reservoir on the Vltava River (river km 71), cascade effect	1936	1971–2009 [a]	
Hněvkovice	268	reservoir on the Vltava River (river km 210)	1991	1991–2009	
Slapy	1392	remote reservoir on the Vltava River (river km 92)	1955	1971–2009 [a]	
Orlík	2730	remote reservoir on the Vltava River (river km 145)	1961	1990–2009	
Lipno	4870	remote reservoir on the Vltava River (river km 330)	1960	1958–2009 [b]	
Mušov	530	shallow reservoir on the Dyje River (river km 56), highly productive	1978	1991–2007	1991–2007
Vranov	761	reservoir on the Dyje River (river km 162), productive	1934	1991–2008	1996–2008
Nové Mlýny	1668	shallow reservoir on the Dyje River (river km 41.5), highly productive	1988	1991–2008	1991–2008

Table 2. Summary of best fits of stock-catch regression models (1)–(4). AR = models with AR(1) autocorrelation error term Φ; w = Akaike weight (see text for details); B = production term (kg.ha^{-1}); p_n = proportion of stocked biomass caught n years later; F_T = contribution of floods in 2002 (all riverine reservoirs) and 2006 (reservoirs on the Dyje River) to catches in year T (kg.ha^{-1}); c = slope of long-term temporal trend in catches (kg.ha^{-1}.yr^{-1}). Parameter values followed by standard error in parentheses; values significantly different from zero ($P < 0.05$) given in bold.

				parameter estimates										
reservoir	**model**	**note**	w	B	p_0	p_1	p_2	p_3	F_{2002}	F_{2003}	F_{2004}	F_{2006}	c	Φ
Papež	(1)	-	0.71	0	**0.47** (0.12)	**0.57** (0.12)	-	-	-	-	-	-	-	-
Džbán	(1)	-	0.51	0	**0.77** (0.12)	**0.39** (0.12)	-	-	-	-	-	-	-	-
Hostivař	(1)	-	0.40	0	**0.48** (0.12)	**0.55** (0.12)	-	-	-	-	-	-	-	-
Štěchovice (1971–1994)	(2)	AR	0.34	**4.50** (0.85)	-	-	-	-	-	-	-	-	-	0.50
Štěchovice (1995–2009)	(1)	-	0.23	0	**0.50** (0.17)	**0.37** (0.17)	-	-	-	-	-	-	-	-
Kořensko	(8)	-	0.23	**124.2** (8.5)	-	-	-	-	**92.0** (31.8)	**186.9** (31.9)	-	-	**5.57** (1.84)	-
Kamýk	(3)	-	0.52	0	-	**0.50** (0.06)	-	-	**139.2** (11.8)	**415.0** (11.2)	**73.6** (11.7)	-	-	-

Vrané (1971–1992)	(2)	-	0.37	**5.32** (2.28)	**0.23** (0.05)	-	-	-	-	-	-	-	-	-
	(1)	-	0.22	0	**0.24** (0.05)	0.11 (0.06)	-	-	-	-	-	-	-	-
Vrané (1993–2009)	(1)	AR	0.98	0	**0.37** (0.07)	**0.36** (0.07)	-	-	-	-	-	-	-	0.93
Hněvkovice	(4)	-	0.49	**58.9** (12.8)	**0.70** (0.12)	-	-	-	**197.0** (20.7)	**130.0** (20.0)	-	-	-	-
Slapy	(3)	-	0.32	0	**0.45** (0.09)	**0.27** (0.12)	**0.23** (0.10)	-	**10.8** (4.7)	**27.2** (4.7)	-	-	-	-
Orlík	(4)	-	0.38	**8.81** (3.58)	**0.79** (0.18)	-	-	-	**40.1** (4.58)	**45.4** (4.55)	**20.5** (4.56)	-	-	-
	(3)	-	0.21	0	**0.54** (0.22)	0.09 (0.19)	**0.69** (0.24)	-	**32.5** (5.15)	**43.1** (4.37)	**22.0** (4.25)	-	-	-
Lipno	(5)	-	0.29	0	**0.18** (0.07)	**0.26** (0.08)	**0.31** (0.07)	**0.15** (0.06)	-	-	-	-	**0.055** (0.020)	-
Mušov	(2)	-	0.20	31.4 (16.5)	-	**1.19** (0.51)	-	-	-	-	-	-	-	-
	(1)	-	0.17	0	0.88 (0.49)	**1.32** (0.47)	-	-	-	-	-	-	-	-
Vranov	(3)	-	0.37	0	**0.54** (0.20)	**0.80** (0.20)	-	-	**8.8** (2.7)	= F_{2002}	-	**19.4** (3.7)	-	-
Nové Mlýny	(2)	AR	0.57	**34.7** (9.99)	-	-	-	-	-	-	-	-	-	0.72

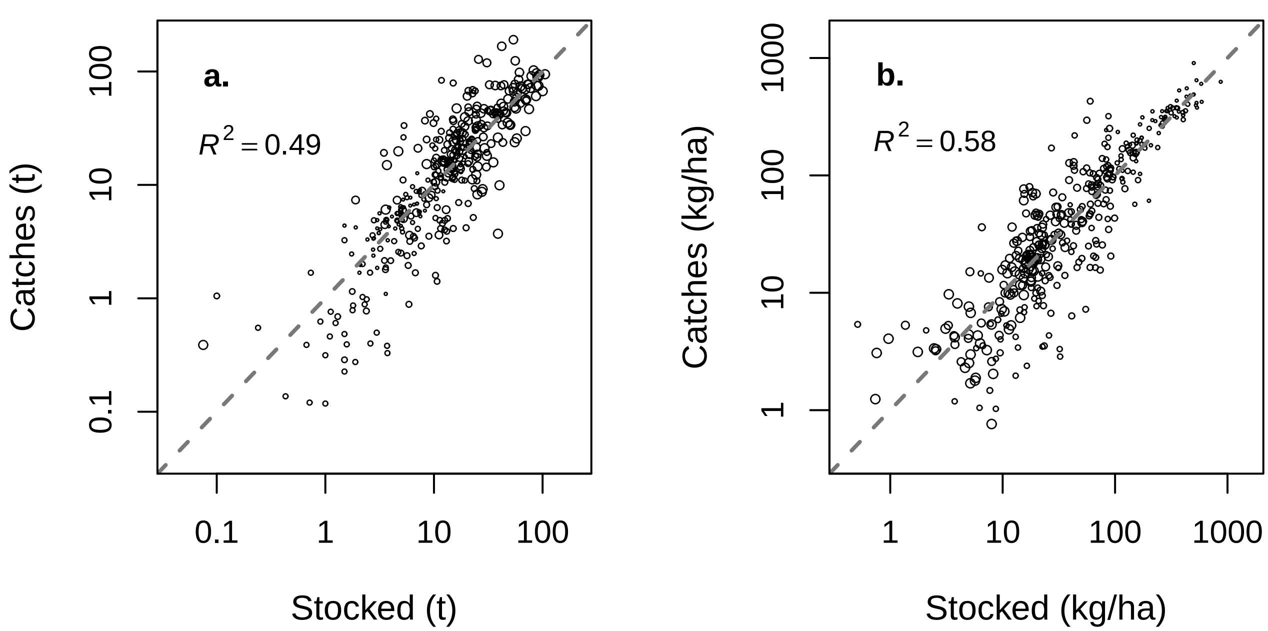
Table 3. Summary of best fits of regression models of the form (1)–(4) describing the relationship between CPUE (kg.trip^{-1}) and total weight of stocked carp (tonnes); B = baseline CPUE; p_n = contribution of stocking to CPUE after n years (kg.trip^{-1}.t^{-1}); F_T = contribution of floods in 2002 and 2006 to catches in year T (kg.trip^{-1}). Other symbols as in Table 2.

				parameter estimates								
reservoir	**model**	**note**	w	B	p_0	p_1	p_2	F_{2002}	F_{2003}	F_{2006}	c	Φ
Mušov	(1)	-	0.31	0	0.010 (0.005)	0.011 (0.005)	**0.012** (0.005)	-	-	-	-	-
	(2)	-	0.26	**0.27** (0.09)	-	**0.016** (0.005)	-	-	-	-	-	-
Vranov	(4)	-	0.31	**0.30** (0.01)	-	-	-	**0.09** (0.03)	$= F_{2002}$	**0.22** (0.04)	-	-
Nové Mlýny	(6)	-	0.26	**0.84** (0.04)	-	-	-	-	-	-	**-0.026** (0.007)	-

Table 4. Summary of best fits of hybrid regression models (9)–(16). p_n = contribution of stocking to CPUE after n years (kg.trip^{-1}.t^{-1}). Other symbols as in Table 2.

				parameter estimates								
reservoir	**model**	**note**	w	B	p_0	p_1	p_2	F_{2002}	F_{2003}	F_{2006}	c	Φ
Mušov	(9)	-	0.64	0	0.005 (0.002)	**0.019** (0.003)	**0.038** (0.003)	-	-	-	-	-
Vranov	(12)	-	0.21	**14.3** (4.8)	**0.009** (0.003)	-	-	**8.0** (2.9)	$= F_{2002}$	**20.5** (3.9)	-	-
	(11)	-	0.09	0	**0.020** (0.001)	-	-	-	-	**19.5** (5.8)	-	-
Nové Mlýny	(9)	AR	0.77	0	**0.004** (0.002)	**0.008** (0.002)	**0.022** (0.003)	-	-	-	-	0.83

Figure 1



a.
R² = 0.49
Catches (t)
Stocked (t)
0.1
1
10
100
b.
R² = 0.58
Catches (kg/ha)
Stocked (kg/ha)
1
10
100
1000

Figure 2

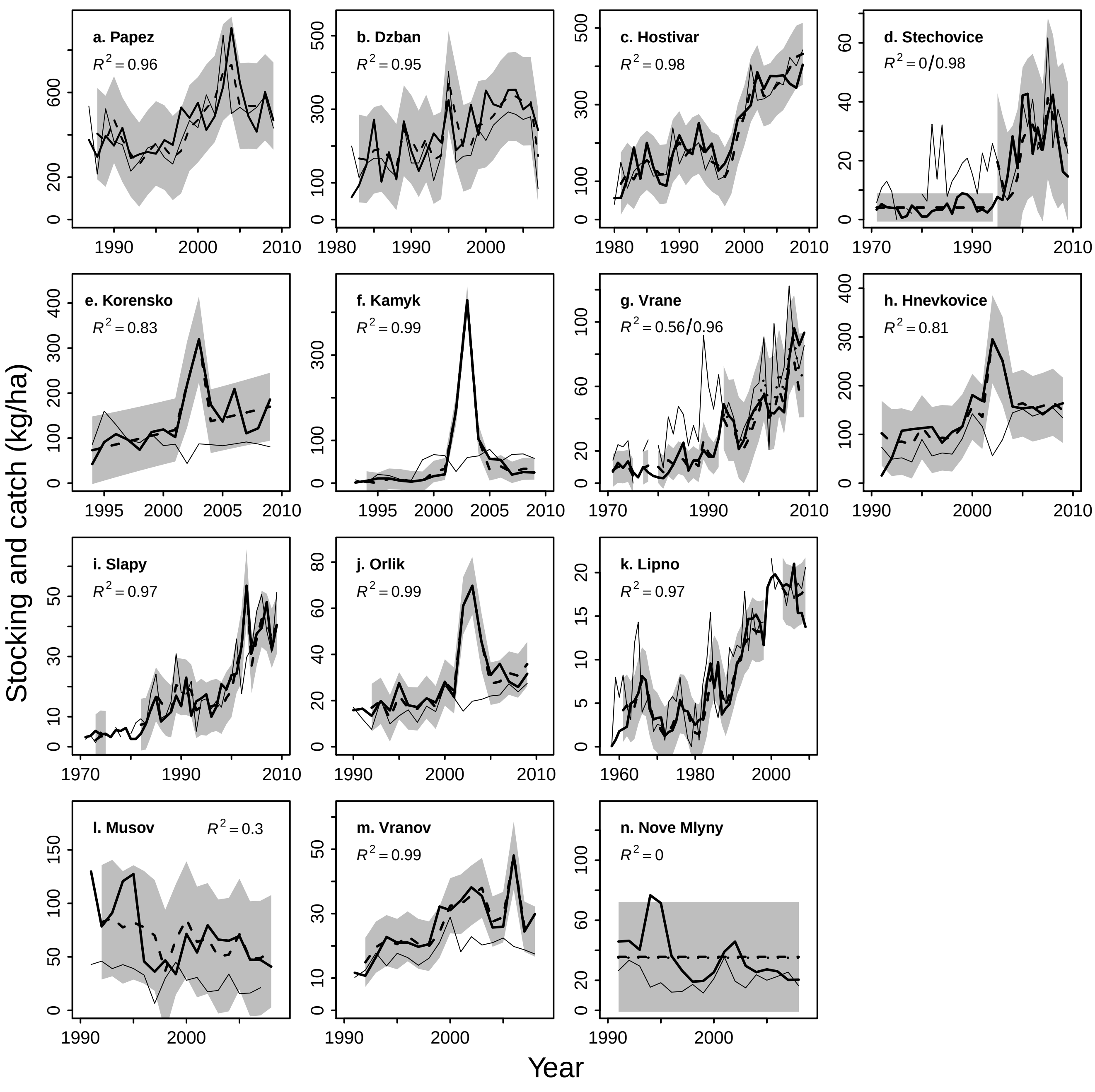
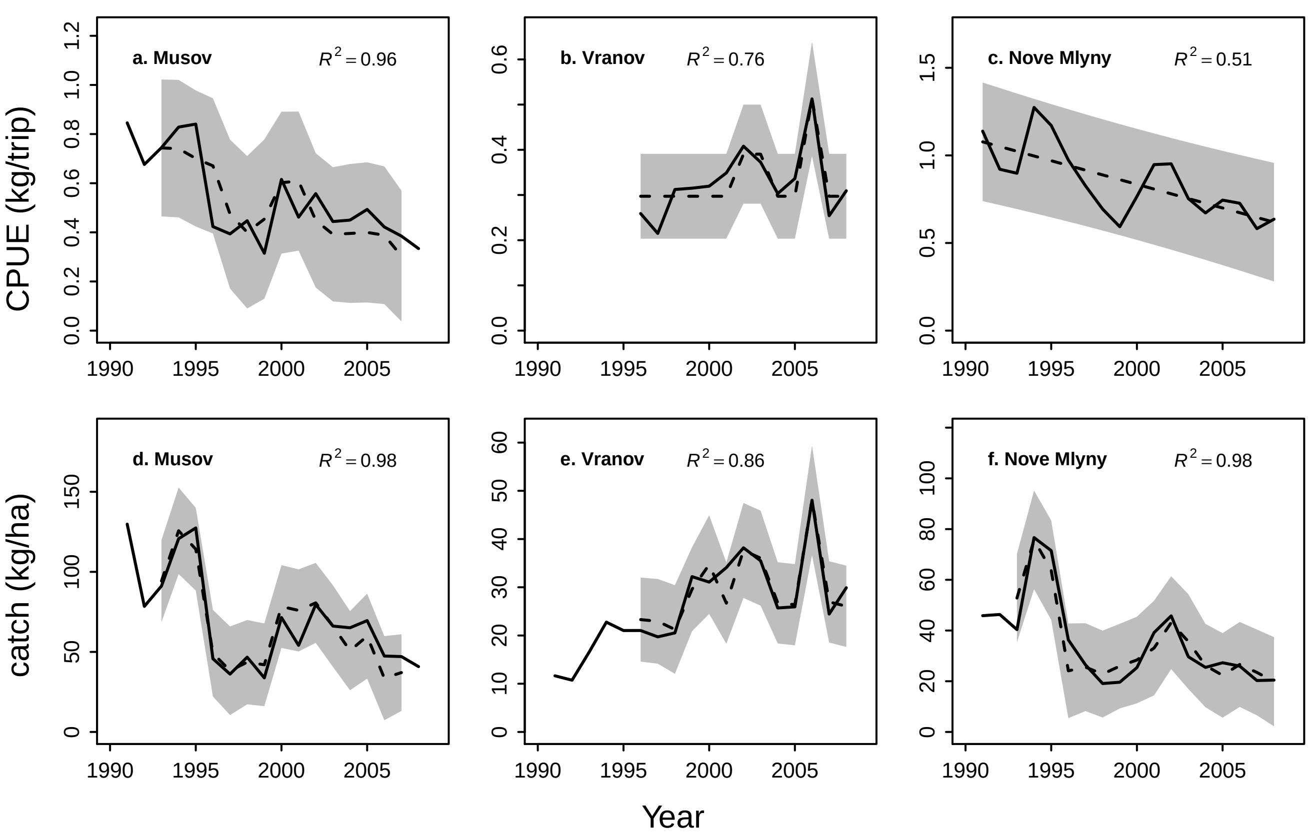
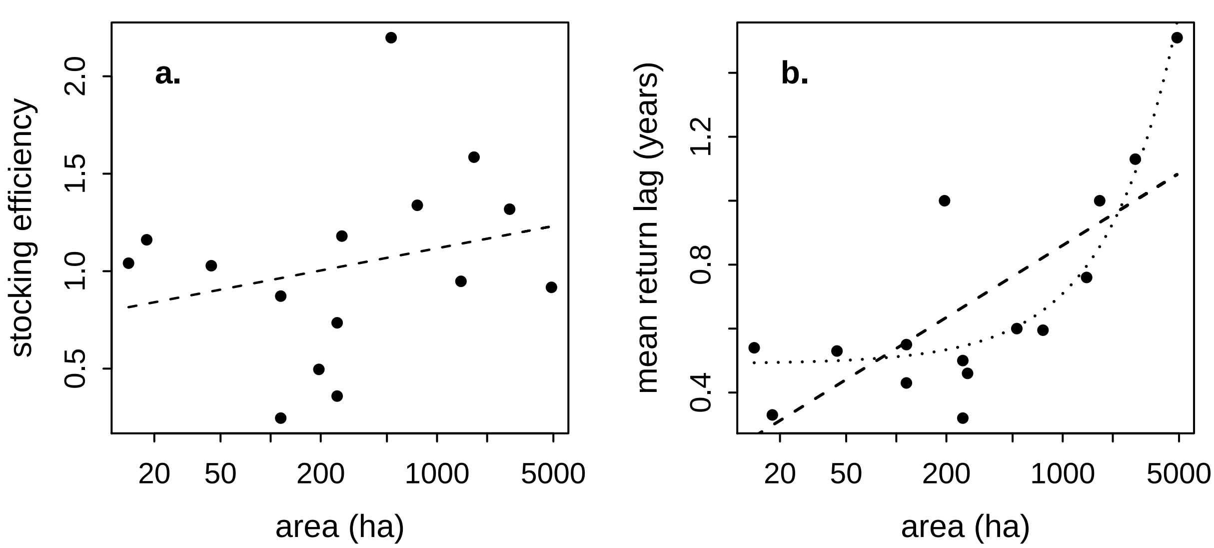

a. Papez
$R^2 = 0.96$
b. Dzban
$R^2 = 0.95$
c. Hostivar
$R^2 = 0.98$
d. Stechovice
$R^2 = 0/0.98$
e. Korensko
$R^2 = 0.83$
f. Kamyk
$R^2 = 0.99$
g. Vrane
$R^2 = 0.56/0.96$
h. Hnevkovice
$R^2 = 0.81$
i. Slapy
$R^2 = 0.97$
j. Orlik
$R^2 = 0.99$
k. Lipno
$R^2 = 0.97$
l. Musov
$R^2 = 0.3$
m. Vranov
$R^2 = 0.99$
n. Nove Mlyny
$R^2 = 0$
Stocking and catch (kg/ha)
Year

Figure 3



a. Musov
$R^2 = 0.96$
b. Vranov
$R^2 = 0.76$
c. Nove Mlyny
$R^2 = 0.51$
d. Musov
$R^2 = 0.98$
e. Vranov
$R^2 = 0.86$
f. Nove Mlyny
$R^2 = 0.98$
CPUE (kg/trip)
catch (kg/ha)
Year

Figure 4


a.
stocking efficiency
0.5
1.0
1.5
2.0
area (ha)
20
50
200
1000
5000
b.
mean return lag (years)
0.4
0.8
1.2
area (ha)
20
50
200
1000
5000