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Culling Prey Promotes Predator Recovery—Alternative States in a Whole-Lake Experiment

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Many top-predator fish stocks in both freshwater and marine systems have collapsed as a result of overharvesting. Consequently, some of these communities have shifted into seemingly irreversible new states. We showed, for predators feeding on prey that exhibit food-dependent growth, that culling of fish prey may promote predator recovery. We removed old stunted individuals of a prey-fish species in a large, low-productive lake, which caused an increase in the availability of small-sized prey and allowed the predator to recover. The shift in community state has been sustained for more than 15 years after the cull ended and represents an experimental demonstration of an alternative stable state in a large-scale field system. Because most animals exhibit food-dependent growth, shifts into alternative stable states resulting from overcompensating prey growth may be common in nature and may require counterintuitive management strategies.

Rapid changes observed in many ecological systems, such as the collapse of major fish stocks (1–4), have prompted an increased interest in alternative stable states during recent years (5, 6). Theoretical studies (7, 8) suggest that size-selective predation (9–11) may be a major mechanism behind shifts between alternative stable states if reduced competition for resources among remaining prey (6, 12) accelerates prey growth. Predation on small individuals in this case leads to an overcompensating response because surviving prey mature more rapidly and achieve higher population reproductive outputs. Counterintuitively, densities of

small prey hence increase and not decrease when predators forage on such small prey individuals (7, 13). Thus, size-selective predators shape the biotic environment to their own advantage. These predator-prey systems are, however, prone to irreversible collapse of the predator if overharvested. A drop in predator density causes prey to grow and reproduce more slowly and consequently produce lower abundances of vulnerable, small-sized prey. This change in prey-size distribution subsequently prohibits recovery of the predator, making the collapse seemingly irreversible (7, 8). Next to the predator-prey state the community thus possesses an alternative stable state with only prey (7). Size-selective harvesting of prey may offer a route to predator recovery, because it should stimulate rates of prey growth and reproduction and thereby shift prey-size distribution toward smaller individuals. Once the prey-size constraint for recovery is lifted, the recovered predator population should itself be able to sustain the system in the new state.

In the early 1900s, the top-predator brown trout (*Salmo trutta*) was the only species in the low-productive Lake Takvatn, in northern Norway (14–16). Overharvesting reduced trout to low levels, and Arctic charr (*Salvelinus alpinus*)—prey for, but also a potential competitor of, small brown trout for invertebrates (14, 16–19)—was introduced in about 1930. The charr soon dominated the fish community, and by 1980 trout were almost absent (Figs. 1 and 2, A and D). To improve lake fisheries, 666,000 charr (31.3 metric tons) were removed during 1984 to 1989 (14, 15). By 1991 charr density had decreased by 80%, subsequently rebounded to less than half its 1984 density, and ultimately exhibited a decelerating decrease toward a new steady state (1992 to 2006, regression $F_{1,14} = 14.7$, $P = 0.002$) (Fig. 1). Trout density increased from 1989 to 1992, remaining steady afterward (1992 to 2006, regression $F_{1,14} = 0$, $P = 0.99$). On average (1992 to 2006), the trout density was 12% of the charr density, similar to the value of 15% observed in a control lake (16). Although charr may compete with small trout for food (14, 17, 18), we found no evidence for a negative density-dependent effect of either total charr density or density of charr <150 mm in size on the body condition of 100-mm trout (regressions, $F_{1,16} = 0.10$ to 2.27, $P > 0.1$).

We generated seven testable expectations of this prey-culling management strategy with an existing resource-prey-predator, food-chain model (7, 13), in which prey exhibit food-dependent growth and reproduction and predators forage on small prey only. At low densities, invading predators cannot increase in density in the stable prey-resource state (Fig. 3). Culling prey induces oscillations in prey density and strong pulses in prey recruitment, which allow predators to increase in numbers and reach high densities. Predators can subsequently control the prey, driving the system toward an alternative, stable resource-prey-predator equilibrium (Fig. 3) characterized by (1) lower prey density (smallest-size

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classes excluded), (2) higher predator density, (3) broader prey-size distribution, (4) higher individual prey growth rate, (5) higher density of small-size classes of prey, and (6) improved body condition of predators (7, 13). Finally, the route to the new equilibrium state occurs via harvesting-induced oscillations (7) (Fig. 3).

We compared these seven theoretical expectations with data from the whole-lake manipulation in Takvatn. First and second, the density of charr (young-of-the-year charr excluded) decreased and that of trout increased (predictions 1 and 2) (Fig. 1). After the perturbation, both populations approached new equilibrium densities sustained for more than 15 years (more than two generations), which is long enough to conclude that the new state represents an alternative stable state (20, 21). In addition, we found no relationships between the shift in the fish community and lake transparency or temperature, arguing against such environmental factors being responsible for the observed shifts (regressions, $F_{1,17} = 0.00$ to 0.19, $P > 0.1$). Moreover, thinning experiments with allopatric charr populations showed return times to the initial population structure within 5 to 8 years (22), i.e., in less than half

the post-thinning period in Takvatn. Third, the charr size distribution changed dramatically (prediction 3): Before manipulation, the charr population was densely packed with a high dominance of individuals 161 to 211 mm in size (1980 and 1981, Simpson's measure of dominance = 0.13 and 0.23, respectively) (Fig. 2A), which changed to a markedly reduced dominance of a few size classes (Simpson's measure of dominance: mean 0.05, range 0.02 to 0.08; comparison postperturbation years, 1990 to 2006, versus pre-perturbation years, 1980 to 1981, Mann-Whitney U test, two-tailed, $P = 0.022$) (Fig. 2, B and C). Fourth, compared with pre-perturbation years, the growth of individual charr increased substantially in all postperturbation years (prediction 4) (two-way analyses of variance, year class born in 1976 versus those born in 1984, 1989, 1994, and 1999, respectively, $F_{2,5} = 85.9$ to 245.5, $P < 0.001$) (Fig. 2D). It should be stressed that the growth curve for pre-perturbation years with its monotonic decrease with age and very narrow standard errors showed that the growth of Arctic charr was consistently low for the entire pre-perturbation period 1980 to 1984. In contrast, growth of individual Arctic

charr after perturbation showed temporal variation depending on charr density (15), although it was consistently higher than in pre-perturbation years (Fig. 2D). In contrast to the charr population in Takvatn, no changes in either size distribution or growth rate of charr were observed in the nearby control lake during 1979 to 1999, and both growth rates and size distributions (Simpson's measure of dominance = 0.06) were similar to that of post-thinning charr in Takvatn (fig. S1).

As a critical prediction for establishing the mechanism causing the alternative stable states, the availability of small-sized charr preyed upon by trout should increase (prediction 5). Indeed, on average, the charr available for a 400-mm trout [charr size range 4 to 160 mm, optimal size 80 mm (17)] almost doubled in size (Fig. 4A), with even larger increases for smaller trout (300-mm trout, 3.2 times; 350-mm trout, 2.7 times). Compared with pre-perturbation years (1980 to 1981), estimated trout encounter rates (Fig. 4A) with charr were higher in all but three post-perturbation years (1990 to 2006, except 1990, 1996, and 1998). Also consistent with expectations, we found harvesting-induced oscillations in the charr population (prediction 7) reflected in a very distinct periodicity in charr availability for brown trout (1990 to 2006, peaks: autocorrelation $\text{lag}_4 = -0.69$, $P = 0.017$; dips: autocorrelation $\text{lag}_8 = 0.45$, $P = 0.008$; peaks: partial autocorrelation $\text{lag}_4 = -0.69$) (Fig. 4B) and resulting from oscillations in charr recruitment [capture per unit effort (CPUE) of charr <150 mm, 1990 to 2006, peaks: autocorrelation $\text{lag}_8 = -0.40$, $P = 0.024$; valleys: autocorrelation $\text{lag}_4 = 0.66$, $P = 0.02$; valleys: partial autocorrelation $\text{lag}_4 = -0.568$] (Fig. 4, C and D). The abundance of charr <150 mm, including in the perturbation years, also clearly suggests that the system approaches an equilibrium through damped oscillations (Fig. 4C). Finally, the cyclic availability of charr after the perturbation allows us to test whether increased availability of charr results in

Fig. 1. Changes in abundance of Arctic charr (squares, solid lines) and brown trout (circles, dashed lines) in Lake Takvatn during 1984 to 2006. Trend lines are inserted for the period 1992 to 2006. Hatched area shows period of charr culling.

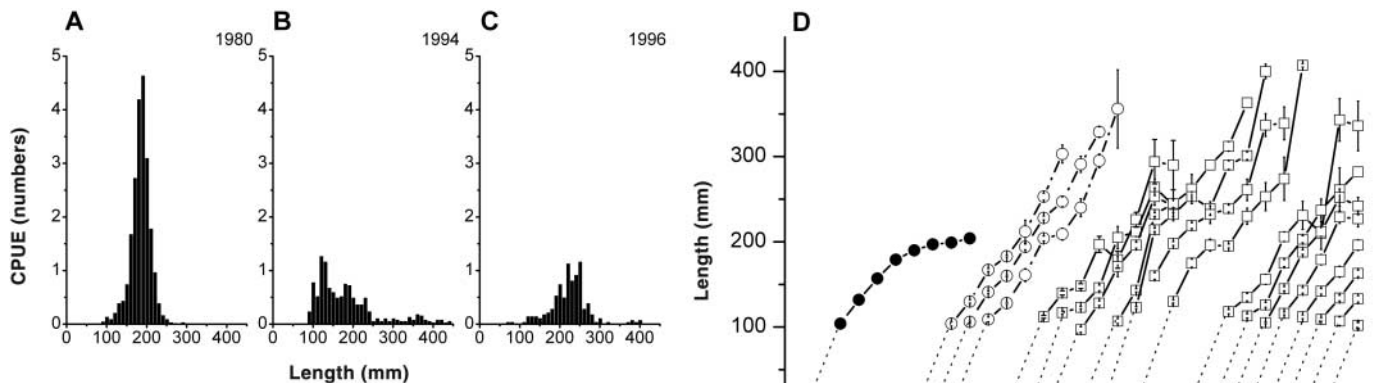
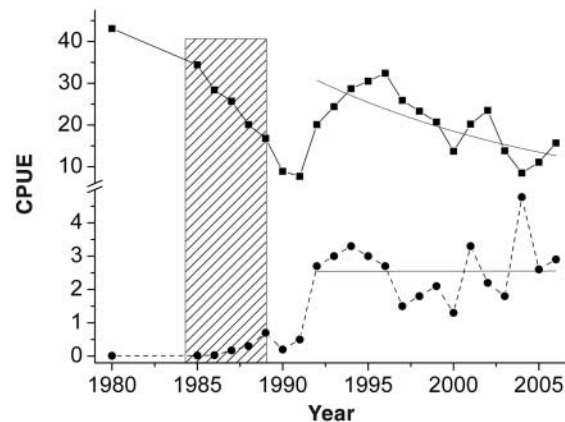


Fig. 2. Shifts in structure (size distributions, growth rates) of the charr population during 1976 to 2006. Size distributions of charr before [(A), 1980] and after [(B), 1994, and (C), 1996] the culling experiment. Size distributions for the postculling phase represent examples of years with high [(B), 1994] and low [(C), 1996] availability of small-size classes of charr. (D) Growth curves (means ± 1 SE) of charr from an age of 2 years before (closed circles, dashed line), during (open circles, dashed-dotted lines), and after (squares, solid lines) the perturbation of charr. Data from pre-perturbation period (year-class 1976) are based on samples from 1980 and 1981.

increased trout performance (prediction 6). In support of expectations, we found a positive relationship between charr availability and the body condition of trout in the same year (regression, $r^2 = 0.46$, $F_{1,16} = 12.5$, $P = 0.03$) (fig. S2). Furthermore, fluctuations in charr availability covaried with total trout abundance 2 years later (cross-correlation, $\text{lag}_2 = 0.59$), providing further support for the conclusion that competition between charr and trout was negligible.

Our experimental demonstration of alternative stable states in a large lake contrasts markedly in

scale with previous experiments restricted to laboratory or field enclosure systems (21, 23, 24). The results show that differences in charr size distribution induced by food-dependent growth were pivotal for creating an alternative stable state. Because the overwhelming majority of organisms exhibit food-dependent growth, including taxa such as insects, fish, reptiles, and amphibians (25, 26), overcompensation resulting from food-dependent growth could be a major mechanism giving rise to alternative stable states in many ecological systems. Our results are also

relevant to interactions where the average size differences between predator and prey are greater than those between brown trout and Arctic charr, because the main predatory effect may still be directed toward the smallest prey sizes (27), which is crucial for the alternative stable state to occur.

Many fish communities, including the Arctic charr–brown trout systems, simultaneously suffer from low levels (or indeed the complete absence) of top predators and stunting of prey. Both predator stocking and prey culling have been advanced as management tools to counteract this situation (1, 4, 28, 29). Our modeling studies (7, 13) suggest that piscivore stocking must be rather high to be successful, and hence this is not a practical management strategy in many cases. Prey culling may be a more realistic approach to improve the status of fish stocks in a sustainable way in large lakes such as Takvatn. We finally argue that the risk of irreversible collapse from overharvesting depends not only on the life history of the target species but also on the life history of its prey. Thus, changes in size distributions of prey fish may be a sensitive indicator for risk of collapse in predatory fish (7).

Fig. 3. Model predictions of culling size-structured prey on predator recovery. Continuous invasion of predators (solid line) until time = 1500 days is unsuccessful. At time = 1500 to 2000 days, heavy harvesting on prey (dotted line, vulnerable juveniles; dashed line, invulnerable juveniles and adults) is imposed (hatched area), leading to successful establishment of the predator. The perturbation induces oscillations in both predator and prey during a transient phase before the system reaches an alternative equilibrium.

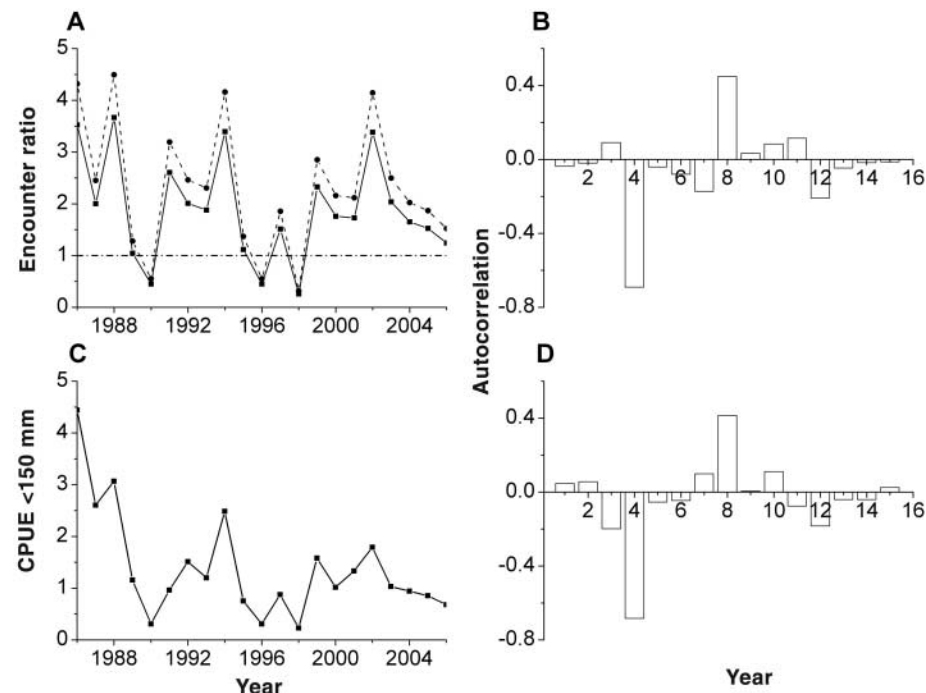
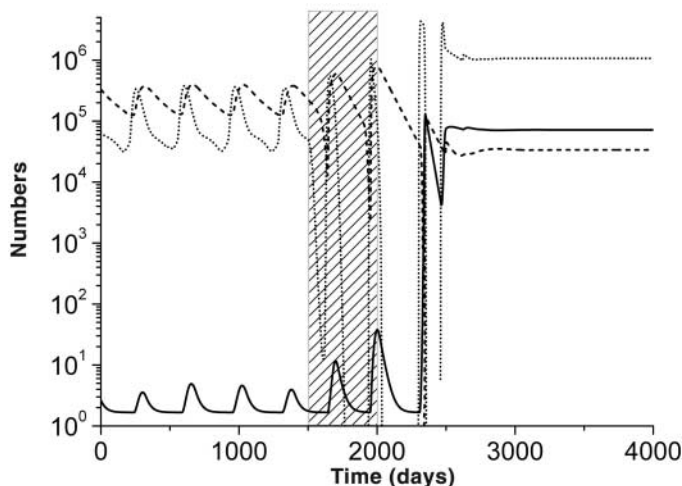


Fig. 4. Cyclic dynamics in charr availability. (A) Encounter rates of a 400-mm brown trout with charr in 1986 to 2006 relative to two pre-perturbations years (1980, squares and solid lines; 1981, circles and dashed lines) expressed as a ratio. (B and D) Autocorrelation in encounter rate (B) and charr <150 mm CPUE (D) for the period 1990 to 2006 showing an 8-year periodicity (negative correlations are peaks in availability, positive correlations are dips in availability). (C) Capture per unit effort (CPUE) of charr <150 mm.

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Figs. S1 and S2
References

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Influence of Phylogeny on Fungal Community Assembly and Ecosystem Functioning

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Ecology seeks to explain species coexistence and its functional consequences, but experimental tests of mechanisms that simultaneously account for both processes are difficult. We used an experimental mycorrhizal plant system to test whether functional similarity among closely related species (phylogenetic conservatism) can drive community assembly and ecosystem functioning. Communities were constructed with the same number of fungal species, but after 1 year of growth, realized species richness was highest where the starting species were more distantly related to each other. Communities with high realized species richness also stimulated plant productivity more than those with low realized species richness. Our findings suggest that phylogenetic trait conservatism can promote coexistence because of reduced competition between distinct evolutionary lineages and enhance ecosystem function because of functional complementarity among those same lineages.

Although it has long been recognized that ecological communities are not random collections of species, ecologists still seek to understand the processes that shape community assembly (1–4). One hypothesis that explains nonrandom species assemblages is that competitive interactions limit the long-term coexistence of species with similar fundamental niches (2, 5–7). If closely related species share a fundamental niche (niche conservatism), competitive exclusion will cause communities to be made up of species that are phylogenetically overdispersed, or more distantly related to each other than would be expected by chance (2, 5, 8–10). This hypothesis is difficult to test directly because the spatial and temporal scales of the critical processes in plant and animal communities are typically too large for manipulation (11). Recent research indicates that the degree of phylogenetic dispersion varies across communities and depends on the level of phylogenetic relatedness within a particular community and the spatial scale of species interactions (3, 10, 12–14). However, this evidence is correlative rather than causative because most previous studies have been confined to comparative analyses of existing communities (15, 16). In addition, the strength of a phylogenetic signal in the species assemblage of communities is often obscured by stochastic processes and dispersal limitations (8).

Using a model mycorrhizal plant community, we experimentally determined whether commu-

nity assembly depends on the phylogenetic relatedness of species. The model community consisted of sympatric arbuscular mycorrhizal fungi (AMF) growing on plant roots of *Plantago lanceolata* (17) (Fig. 1). The arbuscular mycorrhizal symbiosis is ideal for testing hypotheses about community assembly for two reasons. First, the small size and short generation time of the organisms allow us to manipulate and observe ecologically meaningful interactions in tractable experimental units on a short time scale. Second, most described AMF are confined to three distinct taxonomic families (Glomeraceae, Acaulosporaceae, and Gigasporaceae) within two orders (Glomerales and Diversisporales) (18) in which functional traits associated with spatial niche requirements are phylogenetically conserved (19) (Fig. 2). For example, the majority of fungal biomass in the Gigasporaceae is found in the hyphae that are located outside the plant root (Fig. 2, A and B). In contrast, the majority of fungal biomass in the Glomeraceae is found in hyphae growing inside the root (Fig. 2, A and B). The Acaulosporaceae form a third distinct group, because species in this taxon produce low biomass inside and outside the root (Fig. 2, A and B).

Species from these major evolutionary lineages were sampled to form experimental communities. We manipulated the level of phylogenetic relatedness in the species pool by constructing communities sampled from all three AMF families (relatively overdispersed) or from two or fewer families (relatively underdispersed) (Fig. 1). We predicted that species within each family were less likely to coexist with each other because of similar spatial niche requirements. In contrast, we

expected that taxa from distinct lineages such as the Gigasporaceae and the Glomeraceae should coexist because they each specialize on different spatial components of the rhizosphere.

We found that community assembly depended on phylogenetic relatedness. Experimental communities were constructed with eight AMF species, but after 1 year of growth, realized species richness was highest in those communities that were assembled using taxa from all three families as compared to those communities assembled using taxa from two or fewer families (Fig. 2C). Realized species richness after 1 year was >80% of the initial value in communities with representatives from all three families. In contrast, communities made up largely of species from one family retained <40% of the initial species pool. We also found that realized species richness in phylogenetically overdispersed communities was similar regardless of the identity of the sampled species within each family (Fig. 2C), a result consistent with our expectation that there is trait conservatism and therefore a degree of functional redundancy within each AMF family (Fig. 2, A and B, and table S1) (19).

We also tested whether the level of phylogenetic dispersion in an AMF community could be influenced by abiotic factors (1). If the abiotic environment acts as a habitat filter, permitting only those species with specific traits or ecological tolerances to co-occur (1, 2), then the conservatism for hyphal length and root colonization in AMF could produce communities that consist only of species that are closely related to each other, or phylogenetically underdispersed (2, 8–10). To determine whether this was the case, we sampled species richness in the old-field community from which the species pool of AMF was derived (17). We found that the community had species from all three AMF families, indicating that it was similar to our experimentally assembled species-rich communities (Fig. 2C). Thus, we conclude that the phylogenetically overdispersed experimental AMF communities we assembled were ecologically realistic.

Because of trait, and therefore niche, conservatism within the AMF (Fig. 2, A and B, and table S1) (19), our results suggest that the primary mechanism responsible for increased species richness in phylogenetically overdispersed communities is competitive exclusion preventing closely related and functionally similar species from co-occurring (2). Our results are therefore consistent with life-history and niche-based determinants of community assembly (4) as opposed to neutral models (20). Nevertheless, there is no clear consensus on the role of evolution in contemporary community assembly, in part because

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Culling Prey Promotes Predator Recovery—Alternative States in a Whole-Lake Experiment

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