

Effects of stocking-up freshwater food webs

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The establishment of exotic game fishes to enhance recreational fisheries through authorized and unauthorized stocking into freshwater systems is a global phenomenon. Stocked fishes are often top predators that either replace native top predators or increase the species richness of top predators. Many direct effects of stocking have been documented, but the ecosystem consequences are seldom quantified. New studies increasingly document how species and community shifts influence ecosystem processes. We discuss here how predator stocking might increase top-down effects, alter nutrient cycles and decrease links between aquatic and surrounding terrestrial ecosystems. As fisheries management moves beyond species-specific utilitarian objectives to incorporate ecosystem and conservation goals, ecologists must address how common management practices alter food-web structure and subsequent ecosystem-level effects.

Stocking of predatory, recreational fishes

Widespread and long-term fish stocking of lakes and streams, and the subsequent invasion of nearby aquatic systems, has shifted species assemblages and food-web structure in freshwater systems globally. Many fish introductions into freshwater systems were intended to create recreational fisheries, whereas only a few targeted the conservation of threatened species [1]. Largemouth bass *Micropterus salmoides*, smallmouth bass *Micropterus dolomieu*, rainbow trout *Oncorhynchus mykiss*, brown trout *Salmo trutta*, brook trout *Salvelinus fontinalis*, northern pike *Esox lucius*, walleye *Stizostedion vitreum* and striped bass *Morone saxatilis* have been stocked in lakes throughout North America [1,2] and European countries [3,4], resulting in more homogenous fish fauna with either increased species richness of top predators or introduced predators replacing native species. Additionally, fisheries management often involves annual fish stocking, potentially maintaining higher predator populations than would occur naturally [5]. Much of the motivation for stocking is economic because abundant game species are highly sought after by sport anglers who support lucrative tourism operations.

Stocking can cause the loss of genetic variation within species, as well as changes in populations and community structure [6,7]. Few studies have quantified the impacts of stocking on food-web or ecosystem function, but those that do often find pervasive and strong effects [8,9]. For example, cascading effects of supplementing top predators are frequent enough that predator stocking has been incorporated into management strategies for controlling primary producers in Europe and China [8,10]. Currently, fisheries practices are being reevaluated (e.g. stocking trout in high alpine lakes [11]) and management goals are being broadened to include non-game objectives, such as the maintenance of biodiversity and ecosystem function [12]. A better understanding of how management practices influence food-web and ecosystem processes is needed to achieve these goals.

Here, we review how stocking fish predators alters food-web and ecosystem processes and we evaluate the wider implications of intentional and unintentional stocking based on case studies and current theory. We conclude with suggestions for future research directed at gaps in our ecological understanding that would help set goals and expectations for future management.

Common outcomes of stocking fish predators

The establishment of exotic predators typically leads to one of two outcomes: replacement of native predators or an increase in predator species richness. Exotic fishes often replace native invertebrate and fish predators through predation and competition. In western North America, exotic lake trout *Salvelinus namaycush* and brook trout are displacing native bull trout *Salvelinus confluentus* [13,14]. In Australian and New Zealand streams, introduced brown trout and rainbow trout often reduce or eliminate native galaxiid fishes [6] (Box 1). Nile perch *Lates niloticus* introduced into African lakes have replaced most piscivorous fishes, including haplochromis species (Cichlidae) and catfish *Bagnis* spp. [15]. Stocking trout into small, high-altitude, historically fishless lakes throughout Europe and western North America has eliminated large invertebrate predators and amphibian species, and produced subsequent effects that have altered food-web structure and nutrient cycling [16] (Box 2).

When exotic predators do not replace native predator(s) in an ecosystem, they increase the number of top predators.

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Glossary

Bottom-up control: resource regulation of growth and production typically beginning with biogeochemical control of photosynthesis

Diel: daily, referring to events that recur at intervals of 24 hours or less with no connotation of either daytime or nighttime.

Epilithion: biofilm (bacteria, algae) that grows on rocks and stone surfaces.

Food-web structure: refers to the organisms and pathways by which energy is transferred through the community trophic levels.

Functional redundancy: species that fill the same role or function in food-web structure and ecosystems.

Habitat coupling: the connection among different habitats through the transfer of nutrients

Hypolimnetic: the hypolimnion is the lower, cooler, non-circulating water in a thermally stratified lake in the summer.

Littoral: the littoral region is the interface between the land and the open water of lakes. Littoral fishes include those that are found along the shores of a lake from the edge of the water down to the rooted vegetation.

Metamorphs: amphibians that have just transitioned from their aquatic larval stage (e.g., tadpole) to an adult life form, which is often terrestrial.

Ontogenetic shifts: changes in diet, habitat use and/or other ecological trait associated with an organism growing from the newborn or larval stage to adulthood.

Pelagia: the open water of lakes or marine systems.

Riparian: pertaining to a stream or river bank.

Seston: particulate matter in the water column, such as algae.

Spiraling: typically, nutrients are thought of as cycling between abiotic and biotic compartments of an ecosystem. In streams, however, advective transport stretches nutrient cycles into spirals because nutrients are transported downstream as they cycle between organic and inorganic forms. The length of an idealized spiral is the sum of the distance a dissolved nutrient atom travels before it is taken up by an organism plus the distance it travels as it passes through the food chain before it is returned to a dissolved inorganic state.

Top-down control: generally refers to predation influencing community structure of the trophic level below it that, in turn, might influence its feeding efficiency on seston.

Trophic cascade: the propagation of predation-driven indirect control among nonadjacent levels in a food chain ultimately altering the expression of primary production.

Trophic efficiency: the proportion of energy that passes from one trophic level in a food chain to another.

Uptake length: the average downstream distance a nutrient travels before being removed from the water column.

Uptake rate: the area-specific rate at which a nutrient is removed from the water column.

For example, northern pike, rock bass and largemouth bass have been stocked in many North American lakes and have increased species richness. Whether bass displace native species depends upon several factors, including the ecology of the native top predator and the food web of the receiving water body [17]. In addition, recreational fisheries are often stocked with multiple predatory fish species. For example, multiple salmonid species have been introduced into the Great Lakes and five have established populations [18](Box 3). Thus, heavily stocked freshwater ecosystems might have higher top predator species richness than those that are similar but unstocked.

Food-web consequences of introduced fish predators

Numerous case studies demonstrate food-web consequences of stocking. Effects include increased top-down control (see Glossary), altered food-web structure, modified food-web linkages, as well as both increased and decreased coupling of habitats and ecosystems.

Increased top-down control

Case studies (e.g. [19,20]) and trophic models (e.g. [21]) of predator introductions vary in outcome, predicting top-down, bottom-up, and/or co-limitation by consumers and resources. However, multiple studies demonstrate

Box 1. Stocking brown trout into New Zealand streams

Brown trout have been stocked into New Zealand streams and have subsequently displaced many native fishes in the family Galaxiidae [57]. Historically, galaxiids were common top predators, but are now restricted to trout-free reaches above waterfalls and other barriers to migration. In these reaches, galaxiids feed on invertebrate grazers consuming 18% of invertebrate production. Invertebrates, in turn, feed on benthic algae and consume 75% of annual net primary production (Figure 1a). Conversely, brown trout annually consume nearly 100% of invertebrate production and, because trout are effective visual predators, reduce the willingness of invertebrates to forage during the daytime or on top of rocks. As a result, invertebrates consume only 21% of annual net primary production in trout streams (Figure 1b). Consequently, trout streams support nearly five times the algal biomass and six times the primary production of galaxiid-dominated streams and non-consumptive processes (e.g. nutrient limitation and sloughing of algae) have become more important limits on standing stock in trout streams. In fact, export of algae from trout streams might be an important subsidy for downstream ecosystems.

By injecting a stable isotope ($^{15}\text{NH}_4\text{Cl}$) tracer into two streams, one with native galaxiids and one with brown trout, Simon *et al.* [58] tested the hypothesis that these large differences in energy flux would be accompanied by altered nutrient dynamics. Uptake of ammonium differed little between the two streams, probably because background ammonium concentrations were so low; however, nitrate (NO_3^-) uptake rates were greater and spiraling lengths shorter in the trout stream. Additionally, trout induced a shift in the location of nitrogen demand in streams. In galaxiid streams, where rates of primary production were universally low, nitrogen demand differed little between riffles and pools. Conversely, in trout streams, where rates of primary production were high, epilithion in riffles had faster turnover times and higher nitrogen-specific uptake rates than in pools. As a result, the epilithion in riffles took up ammonium more rapidly than did any of the other compartments in either stream. Surprisingly, whereas trout did affect where nitrogen was retained, they did not affect whole-stream nitrogen retention. This change in the location of nitrogen storage could affect how much nitrogen is exported if the two compartments are differentially susceptible to export during floods.

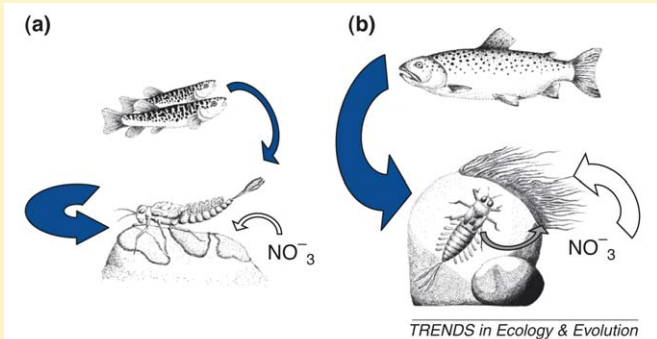


Figure 1. Contrasting food webs in New Zealand streams with native fishes (a) and with introduced brown trout (b). Blue arrows indicate direct predation by fishes or invertebrates, while arrow thickness indicates the strength of the interaction. Brown trout not only have a strong effect on benthic invertebrate biomass, but also affect their willingness to forage on the surface of rocks. White arrows indicate nitrate uptake rates by algae. Arrow thickness is proportional to uptake rate.

increased top-down effects, manifested as shifts in prey species richness, composition (shifting dominance) and/or abundances. Effects of these shifts in prey can cascade to primary producers, although whether effects result in an increase or decrease in algal biomass depends on the number of trophic levels. The addition of planktivorous fishes to the top of the food web often reduces competitively

Box 2. Effects of stocking game fishes into fishless alpine lakes

Stocking of fishes into fishless aquatic systems has occurred throughout western North America for decades [59]. As a result, fishes have been stocked into at least 60% of western mountain lakes [59] and 20% of Canadian Rocky Mountain lakes [60], many of which were historically fishless. Trout introductions typically shift community composition and often result in the loss of native species, particularly amphibians, benthic macroinvertebrates and large zooplankton (Figure 1) [61]. By consuming large zooplankton species that naturally dominate zooplankton assemblages without fish predators, trout enable smaller zooplankton to increase in abundance, potentially increasing overall zooplankton species richness by enabling smaller zooplankton to coexist with competitively dominant larger species [22]. Because many herbivorous zooplankton are gap

limited, suppression of large zooplankton in lakes can stimulate phytoplankton by reducing grazing pressure [62], although such trophic cascades do not always result [63]. Thus, trout can stimulate pelagic primary production by increasing nutrient availability. By feeding on benthic invertebrates and excreting waste in the pelagic zone, trout transfer nutrients, particularly phosphorus, that were trapped in the sediment to the water column (Figure 1) [48].

The effects of fish stocking can also alter the flux of energy and nutrients beyond the lake margin. For example, in many Sierra Nevada lakes, introduced trout have dramatically reduced mountain yellow-legged frog *Rana muscosa* populations, which, in turn, have led to declines in mountain garter snakes *Thamnophis elegans elegans* that prey predominately on amphibians [64].

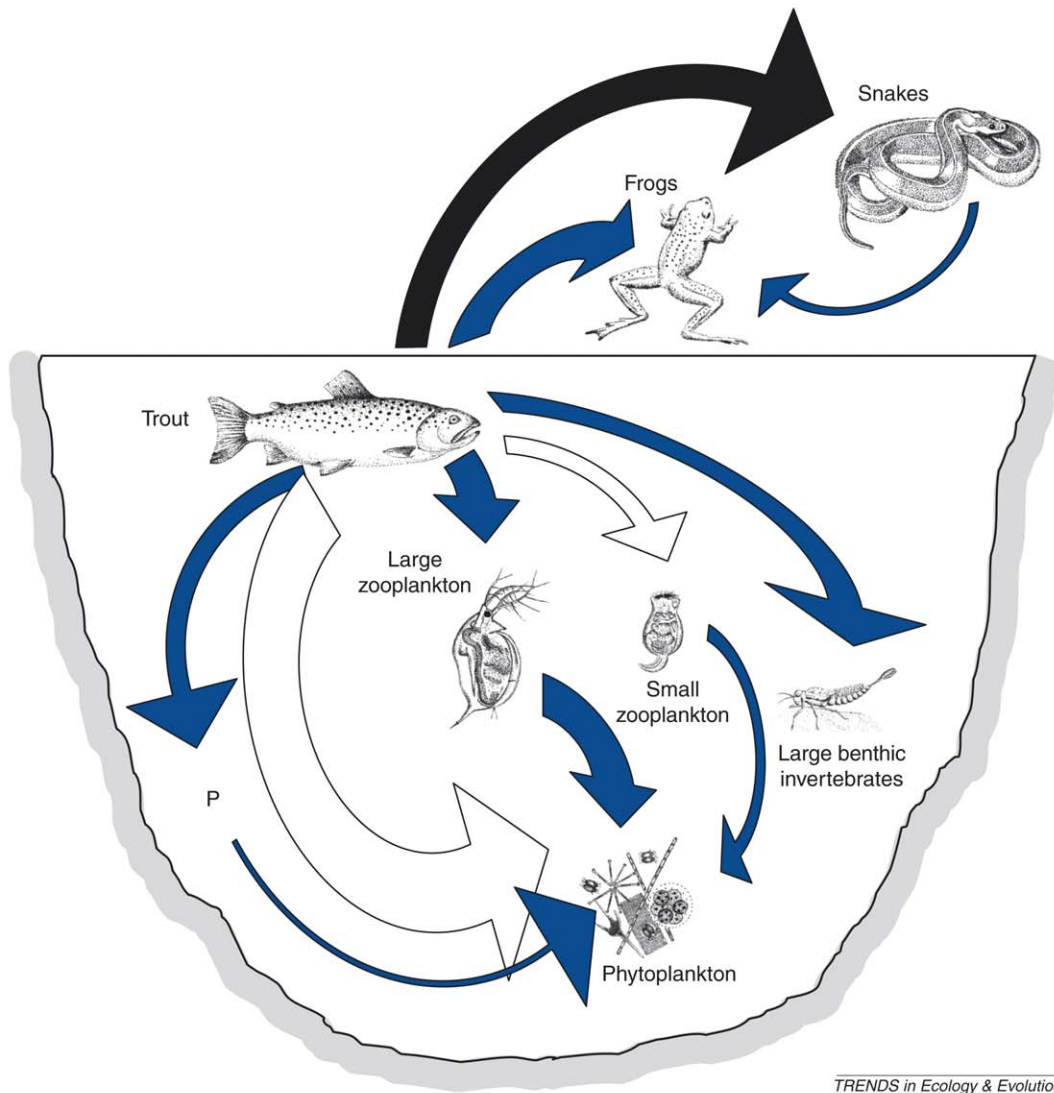


Figure 1. Effects of stocking trout on food webs of Sierra Nevada lakes. Stocking fishes into fishless lakes results in a series of effects that cascade through the food web. Blue lines denote direct consumption or, in the case of phosphorus, uptake and excretion. White and black lines indicate the positive and negative indirect effects of trout, respectively. Arrow thickness provides a coarse indication of the relative strength of the interaction.

dominant, large-bodied zooplankton, enabling the coexistence of smaller zooplankton, thus increasing overall zooplankton species richness [22]. Because smaller zooplankton are less efficient grazers, phytoplankton biomass can increase (e.g. [9]). Conversely, addition of piscivorous fishes into aquatic systems often decreases the

species richness and biomass of non-piscivorous fishes [23], releasing large-bodied zooplankton from predation and resulting in reduced phytoplankton biomass [24] (Box 2). These top-down effects have been repeatedly demonstrated in temperate lake systems in North America and Europe [25,26]. Similarly, in the Great Lakes, stocked

Box 3. The Great Lakes ecosystem

Offshore, coldwater food webs in the Great Lakes have changed dramatically over the past century. By 1960, this system had lost most of its native coregonid (whitefish) assemblage and the major piscivore, lake trout. These lakes gained many exotic species (e.g. stocked salmonids *Oncorhynchus mykiss*, alewife *Alosa pseudoharengus* and smelt *Osmerus mordax*). Currently, exotics comprise up to 45% of the total number of species, including eight different stocked salmonid species [18]. These gains and losses have substantially altered the structure of the fish community, leading to changes in the food web and community structure of the lakes. Specifically, the planktivorous:piscivorous fish ratio has decreased in each lake (Figure 1). For example, food webs in Lake Michigan had ~16 planktivorous versus two piscivorous species (ratio of eight) during the early 1930s. The ratio is currently 1.3 [18]. As the species richness per planktivore increased, the diversity in the diets of the top predators decreased (Figure 1). During the 1930s, lake trout were consuming approximately eight different types of prey in Lake Michigan [65] whereas top predators currently have an average of three prey species

in their stomachs, predominately alewife [66]. In Lake Ontario, the planktivorous fish community is dominated by alewife, declines in the numbers of which led to growth declines of top predators as there were no available prey species to compensate for the reduction in alewife numbers [67]. Whether this loss of functional redundancy in the food web is impacting ecosystem processes is currently unknown.

Food-web effects

Increase in top-down control of the Great Lakes ecosystem is associated with the stocking of salmonids; the subsequent decrease in the alewife population changed the size structure of the zooplankton population, impacting water clarity [9]. Original predators found in these lakes (burbot *Lota lota* and lake trout) were part of deep-water food webs, whereas stocked Pacific salmon are primarily found in the shallower waters. Thus, this new food-web structure shuttles carbon through a pelagic pathway but with a loss of avenues through the deep-water community. This results in a loss of carbon making its way into the deep-water benthic community [68].

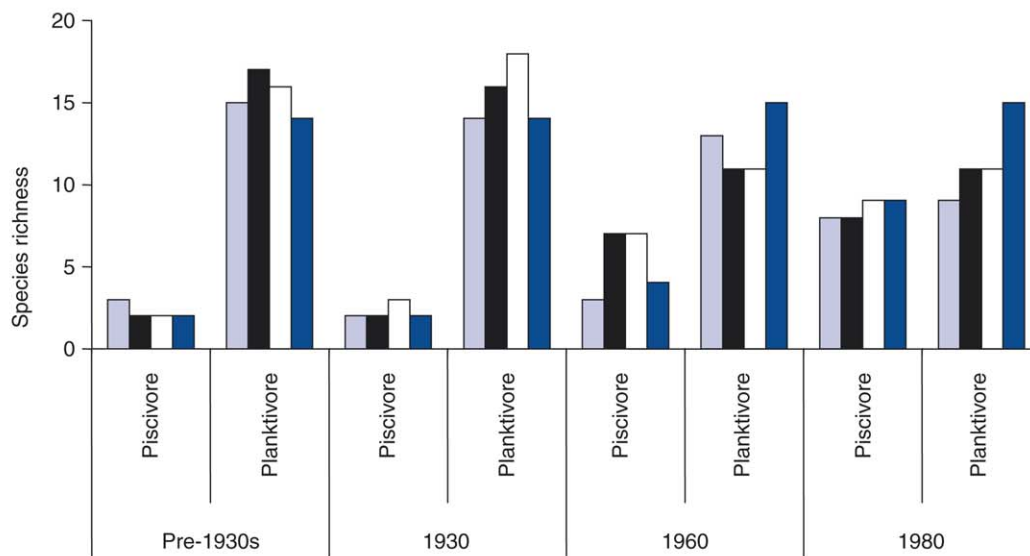


Figure 1. Change in number of planktivore species and piscivore species in Lake Ontario (light-blue bars), Lake Michigan (black bars), Lake Huron (white bars), and Lake Superior (dark-blue bars) over the past 80 years [18].

salmonid species reduced exotic planktivorous alewife populations, increased the size structure of zooplankton populations and subsequently increased water clarity apparently as a result of increased phytoplankton grazing [9] (Box 3).

Increased top-down control can change flows between food-web components, altering where productivity accumulates. Specific mechanisms driving changes in primary production are varied [26]. For example, declines in algal biomass as a consequence of adding fishes to lakes [24] have been linked to: (i) nutrient limitation resulting from decreased planktivorous fish biomass and commiserate reduction in recycling rates [27]; (ii) increased grazing pressure owing to increased abundance of larger zooplankton species; and (iii) phosphorus limitation owing to shifts in zooplankton composition and subsequent enhanced phosphorus sedimentation rates [28]. These mechanisms are not mutually exclusive, so it is often difficult to identify which are responsible for the observed shifts in algal communities.

Although trophic cascades have been observed frequently in lake ecosystems [25], their prevalence has been debated [26,29]. For example, evidence for top-down control is equivocal in streams, as the response of benthic communities to the presence of fishes varies from one experimental study to the next. Although effects of fish predation on stream invertebrates are often purported to be weak [30], stream invasions by brown trout in New Zealand have resulted in strong trophic cascades [31] (Box 1). Even though nutrient state and ecosystem size (i.e. lake depth) can influence whether stocking of top predators alters phytoplankton species composition [32] and where productivity gets expressed, trophic cascades are not completely restricted by ecosystem type, diversity, habitat complexity or assemblage [26].

Altered food-web structure

Introduced predators can alter food-web structure: if introduced predators replace multiple species at the same trophic level or decrease the diversity of lower trophic

levels, simplification of the food-web structure results. For example, Nile perch in African lakes have simplified the food web by replacing hundreds of native consumers [15]. By contrast, predators might shift which trophic level contains the greatest diversity of species. In the Great Lakes, stocking and invasions have substantially changed the offshore cool-water food-web structure, reducing both the planktivorous: piscivorous fish ratio and the species richness of piscivorous fish diets (Box 3). Although implications of these changes for aquatic communities are not yet known, previous studies have demonstrated that ecosystems with less functional redundancy are most vulnerable to disruption of food-web structure and ecosystem function [33].

Changes in habitat coupling

With species replacements and increases in species richness, changes are often seen to food-web linkages and, subsequently, to habitat coupling. For example, stocking fishes into historically fishless lakes often decreases amphibian richness and abundance [34,35], while the loss of metamorphs emerging from aquatic sites severs links between lakes and surrounding terrestrial habitats (Box 2). Similarly, stocking arctic char *Salvelinus alpinus* into streams can reduce the emergence of benthic insects eaten by spiders and birds in the riparian zone [36,37], potentially decreasing the flux of carbon from aquatic to surrounding terrestrial ecosystems [38]. Additionally, a reduced flux of aquatic invertebrates can indirectly affect riparian communities by reducing the pollination of terrestrial plants [39].

In Yellowstone Lake, WY, introduced lake trout consume Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri*, the native top predator of the system. Although ultimate effects of this introduction remain uncertain, lake trout have increased the number of trophic levels within the food web while reducing the abundance of cutthroat trout. Furthermore, lake trout and cutthroat trout also compete with each other, but they are not functionally equivalent. Lake trout remain within lakes for their entire life and occupy greater depths compared with cutthroat, which tend to spawn in tributaries and forage in shallower depths [40]. Consequently, lake trout are inaccessible to many consumers that routinely feed on native cutthroat, such as grizzly bears *Ursus arctos horribilis* and bald eagles *Haliaeetus leucocephalus*. Therefore, lake trout decrease or completely terminate the movement of as a nutrient vector between streams and lakes.

By contrast, when stocking increases predator species richness rather than replacing native species, it often results in novel food-web linkages and higher food-web complexity. Exotic species might use previously underutilized prey resources or force native species to rely on alternative prey. In small Canadian lakes where stocking has increased piscivore species richness, native predators experience shifting diets, habitats and/or trophic position. For example, lakes with native lake trout have been stocked with largemouth bass, rock bass and northern pike, causing a decrease in littoral prey fish diversity and abundance. Increased predation pressure in the

littoral zone has forced lake trout to occupy the pelagia, with concomitant decreases in their trophic position [17]. Thus, stocking fish predators can increase or decrease habitat coupling.

Increased total consumption by top predators

High stocking rates of predatory sports fishes have often resulted in an elevated abundance of top predators, leading to a potential imbalance between predator consumption and prey abundance [41]. This imbalance is likely to be greatest in less-productive reservoir systems [5], but has probably occurred in many freshwater ecosystems that receive high levels of regular stocking. Because measuring long-term trends in absolute abundance is difficult, deciphering whether stocking increases total predator demand or whether community compensation occurs is rarely evaluated quantitatively. The addition or removal of predators can induce changes in community composition or diet shifts that ensure the overall constant predation pressure on shared food resources is largely unaffected [42]. Whereas the functional responses of predators can reduce predation pressure, piscivorous fishes that feed on aggregated prey are often insensitive to changes in their prey base until prey reach very low densities [43].

Ultimately, whether survival rates of stocked and wild fishes compensate to maintain relatively stable predator abundances will depend on species characteristics, such as diet overlap of stocked and native species, ontogenetic diet shifts, life history and potential for use of alternative prey, as well as system characteristics, such as habitat heterogeneity and prey diversity of the receiving system. Ontogenetic diet shifts might enable more fishes to reach large sizes than the prey base can support. For example, young fishes feeding on zooplankton might have high survival rates, leading to high predation pressure of adult fishes feeding on macroinvertebrates and/or foraging fishes. In addition, alternative prey, such as large invertebrates, might maintain predator populations during periods of low prey fish abundances, maintaining higher predation levels [44]. Finally, stocking itself might help prop up a 'top-heavy' food web because many fishes are cannibalistic. Although these mechanisms could increase total predation pressure, how commonly this occurs has yet to be determined.

Ecosystem consequences of stocking top predators

Few case studies investigate the ecosystem effects of stocking top predators. Nevertheless, aquatic ecological theory and available case studies predict changes in trophic efficiency and to ecosystem resilience, and alterations to biogeochemical cycles.

Changes in trophic efficiency

Food-web structure can dramatically alter trophic efficiency. The efficiency of the first link of the food web (e.g. phytoplankton to consumer) is highly variable with energy transfer rates influenced by the quantity and quality of available food and the nutritional requirements of the grazer (e.g. [45]). A food quality index based on phytoplankton species composition and seston carbon:phosphorus ratios was a good predictor of the

production efficiency of *Daphnia rosea* [46]. In addition to stoichiometric considerations, changes to zooplankton size-structure and turnover rates can alter trophic efficiency between phytoplankton and their consumers. For example, decreases in zooplankton size structure produced by fish predation can release small-bodied phytoplankton, which have higher mass specific production rates. Furthermore, because small zooplankton are relatively inefficient grazers, a smaller proportion of primary production enters the food web when fishes exclude larger zooplankton. Therefore, food-web changes that decrease zooplankton size structure might be decreasing trophic efficiency [47].

Changes to biogeochemical cycling within aquatic systems

The addition of fish predators and the subsequent loss of planktivorous fish biomass can decrease total excretion by fishes. For example, in a planktivore-dominated lake, 90% of the recycled phosphorus was from fish excretion, whereas in the lake with piscivorous fishes it was only 20% [27]. Conversely, addition of fishes to fishless lakes can increase nutrient recycling rates. For example, increases in phosphorus regeneration rates resulting from the introduction of fishes into Sierra Nevada mountain lakes were approximately equal to the rate that phosphorus was supplied by atmospheric deposition, substantially increasing the phosphorus available to primary producers [48]. Additionally, shifts in zooplankton community composition (e.g. from cladocerans to copepods) resulting from fish introductions can alter residence times of carbon, phosphorus and nitrogen in the water column, producing shifts in the nutrient limitation [49].

Changes in phytoplankton biomass can alter phosphorus recycling and nutrient retention within lake systems. When phytoplankton biomass is low, sedimentation and decomposition rates might be reduced, resulting in high redox potential and low rates of phosphorus release from the sediment [28]. Furthermore, changes in the abundance and distribution of primary producers shift rates and locations of nitrogen retention in streams (Box 1). Thus, the introduction of top predators to streams can influence the location and rate at which nutrients cycle through ecosystems.

Many fishes are highly mobile animals that often feed in one habitat and excrete their wastes in another. For example, fishes that forage in the littoral zone can transfer nutrients to the pelagic zone [50]. The degree to which fishes transfer nutrients from one habitat to another is strongly influenced by fish species composition [50]. Stocking of fish predators can change lower trophic level species composition and behavior (or habitat use), decreasing this coupling. Specifically, introduced piscivorous fishes can limit planktivorous fishes to the littoral zone and subsequently decrease pelagic-littoral coupling. Similarly, by reducing benthic invertebrate abundances and amphibians, introduced trout can reduce the flux of energy and nutrients to surrounding terrestrial systems. Consequences of habitat decoupling, although poorly understood, are probably important, particularly if fishes transfer nutrients from previously inaccessible benthic or terrestrial sources [27], change organic carbon transfer to

the benthic community, or decrease transport of energy from aquatic to terrestrial food webs.

Change to global biogeochemical cycles

Repercussions of predation-driven shifts in primary production and nutrient cycling can extend beyond the lake. In addition to disrupting the flux of nutrients from aquatic ecosystems to adjacent terrestrial ecosystems, introduced fish predators can alter the exchange of carbon dioxide between lakes and the atmosphere [51]. Whether a lake acts a net source or sink of atmospheric carbon depends upon the balance between organic carbon burial and carbon dioxide evasion [52]. Lake carbon dynamics are affected by relative rates of gross primary production, carbon flux from terrestrial ecosystems and ecosystem respiration [51]. Food-web manipulations in a series of Wisconsin lakes demonstrated that primary production varies strongly with nutrient loading and trophic structure. In piscivore-dominated lakes, planktivorous fishes were eliminated and large-bodied zooplankton limited phytoplankton production and respiration. Food webs in these small lakes were fueled primarily by terrestrial carbon inputs, respiration exceeded organic carbon burial and the lake served as a source of carbon dioxide to the atmosphere. However, when piscivorous fishes were absent and planktivorous fishes dominated, large-bodied zooplankton were eliminated and primary production was no longer grazer limited. Such planktivore-dominated lakes were capable of depleting dissolved carbon dioxide in the water column and acted as net sinks for carbon dioxide [51]. Although introduced top predators can alter fundamental biogeochemical processes driving atmospheric carbon exchange in temperate lakes, the generality of this result and its impact on broader biochemical cycles remains unknown.

Changes to ecosystem resilience

Resilience has been defined as the capacity of a system to absorb disturbance and reorganize while undergoing change so as to retain essentially the same function, structure, identity and feedbacks [53]. Ecologists have argued that invasive species that alter food-web dynamics and ecosystem processes might be eroding the resilience of ecosystems [54]. Nutrient turnover time is often directly correlated with return time from a pulse nutrient addition [55], so any changes to food webs that alter nutrient turnover time probably also alter ecosystem resilience. Theoretical models predict changes to resistance and resilience associated with food-web simplification in structure and linkages, but these vary in their applicability to natural systems. Functional redundancy has been demonstrated to be a key factor in resiliency to acid stress for Canadian lakes [33]. Overall, we have little to no understanding of whether or how these food-web alterations influence the response and resilience of the ecosystem to common disturbances.

Conclusions

In comparisons of freshwater systems (increasing top predators) with marine systems (decreasing top predators), we see many of the same ecosystem components shifting

Box 4. Freshwater and marine comparisons

Fishing has removed many large predatory fishes from the oceans [69], posing potentially serious problems [70,71]. Predator loss and fishing on lower trophic levels has produced an estimated 50% decrease in mean trophic level of landings [72]. How pervasive these trends are is equivocal [73], but fishing pressure is changing the overall structure of marine food webs in several regions. As with freshwater systems, whether top-down forces are strong enough to have subsequent food-web and ecosystem effects remains a crucial question in marine systems [74]. If they do, there are several interesting questions addressing the differences and similarities of freshwater and marine ecosystems.

- Do similar trophic cascades occur in marine ecosystems? The collapse of cod stocks in the North Atlantic produced effects that cascaded down to zooplankton and phytoplankton [75]. However, information about the effects associated with the loss of top marine predators is rare. Are changes in the densities and size structure of prey populations common? Does where and how productivity gets expressed shift? Are nutrient cycles altered?
- Are effects of removing trophic levels from marine systems more likely to be irreversible than the effects of stocking freshwater fish predators? Unlike freshwater systems that have demonstrated recovery with predator removal, there are common examples of persistence of an alternate state in both the North Atlantic and Caribbean coral reefs [74].
- What are the potential ecosystem impacts of these changes? Experimental evidence indicates grazers can buffer moderate increases in nutrient loading in coastal systems. Thus, if trophic cascades do shift species composition, we could expect ecosystem changes in carbon storage, nitrogen retention and in where productivity is expressed [76].
- Are marine food webs more connected than freshwater systems and, therefore, more robust? Recent studies have found that robustness can increase with food-web connectance [77]. Given that diverse estuarine and marine food webs are best described as food webs with many weak links, we might expect these species complexes to exhibit compensatory responses and to better maintain ecosystem functions.
- What can the introduction of fish predators to freshwater systems tell us about potential impacts of removing predators from marine ecosystems?
- How does widespread stocking of anadromous fishes influence marine food-web structure and ecosystem function? Populations of salmonids previously stocked in New Zealand and Patagonia are expanding naturally, while stocking of salmonids in the North Pacific continues at a rate of five billion smolts per year [78]. However, ecosystem-level consequences of this influx of fish predators remain poorly understood.

with anthropogenic manipulation. Given their smaller scale and relative isolation, small lakes are easier study sites for examining the cascading effects of food-web manipulations. By comparing across a gradient of systems from small, isolated lakes, with species-poor, simple food webs, to large systems with more complex food webs, we might better understand the ecosystem implications of anthropogenic manipulation and develop robust approaches to documenting complex changes that might be occurring in larger, less tractable marine systems (Box 4).

In many lakes and streams, fish stocking commonly results in food-web changes such as increased top-down control and food-web simplification, but we expect that characteristics that inhibit trophic cascades, such as low productivity of the ecosystem, large ecosystem size, presence of refuges, indirect effects of adaptive foraging, potential for compensation and organism physiology [26,32,56], would buffer some of the ecosystem effects.

Box 5. Outstanding questions

Understanding when and where to expect ecosystem consequences of stocking top predators is important for ecosystem management. Some common assumptions (e.g. large and more diverse systems are less likely to be impacted by exotic species) were not regularly supported by the case studies in this review. However, our review raised multiple questions about the effects of stocking on food webs and about how to connect fisheries management to ecosystem processes.

Food-web questions

- Does intense stocking increase predation pressure or is there functional and numerical compensation? Often stocked systems are also heavily exploited by recreational fisheries. Although there are only a few examples of overstocking [5,66], whether stocking increases predation pressure is not well-understood and worth pursuing.
- What is the role of compensation in number of trophic levels? Does stocking fishes at the top trophic level increase the number of trophic levels? Fishes introduced to high mountain lakes [22] and Lake Tahoe [79] replaced existing top predators. However, whether stocking piscivorous fishes commonly results in the replacement of native predators or ultimately increases the number of trophic levels has yet to be determined.
- What is the role of disturbance on whether stocked fishes have large food web and ecosystem effects?
- Are these food web changes irreversible? Although the return of native taxa after the removal of Nile perch [80] and exotic trout [61] suggests that some food-web changes are reversible, eradication of introduced fishes is a rare phenomenon. However, recent trends towards stocking hybrid, sterile fishes might influence whether these management actions are reversible. Furthermore, factors promoting recovery remain poorly understood.

Ecosystem questions

- Are ecosystem effects reversible or is there a point of no return (i.e. positive feedback that results in alternative stable states or in irreversible biogeochemical changes)?
- What systems are more or less vulnerable to ecosystem changes with stocking?
- What are the implications of altered nutrient cycles for nutrient retention and flux of nutrients to ecosystems?
- How are these changes influencing the role that these systems have in the landscape?
- Specifically, are these systems source populations for amphibians, fishes and invertebrates? Is the nutrient pathway from the aquatic to the terrestrial system important to nearby terrestrial communities?
- Do functionally equivalent species matter? Are highly connected communities more robust to changes in food-web structure (additions, as well as deletions)?
- Are changes to biogeochemical cycles large enough to be important beyond the immediate area?

Predator stocking often results in shifts in food-web energy and nutrient flows and, subsequently, the connectedness of habitats. But these effects on neighboring systems and geochemical cycles have rarely been examined. In addition, we do not yet know how these changes will alter the resilience of aquatic systems (Box 5). Given the long-term and widespread practice of stocking predators into freshwater systems, it is crucial to better understand its effects on food webs and ecosystem functioning.

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