Developing a broader scientific foundation for river restoration: Columbia River food webs

Robert J. Naiman[a,b,1], J. Richard Alldredge[c], David A. Beauchamp[d], Peter A. Bisson[e], James Congleton[f], Charles J. Henny[g], Nancy Huntly[h], Roland Lamberson[i], Colin Levings[j,k], Erik N. Merrill[l], William G. Pearcy[m], Bruce E. Rieman[n,2], Gregory T. Ruggerone[o], Dennis Scarnecchia[p], Peter E. Smouse[q], and Chris C. Wood[r]

[a]*School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195;* [b]*Centre of Excellence in Natural Resource Management, University of Western Australia, Albany WA 6330, Australia;* [c]*Department of Statistics, Washington State University, Pullman, WA 99164-3144;* [d]*US Geological Survey, Washington Cooperative Fish and Wildlife Research Unit, School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195;* [e]*US Department of Agriculture Forest Service, Pacific Northwest Research Station, Olympia, WA 98512;* [f]*US Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit, University of Idaho, Moscow, ID 83843;* [g]*US Geological Survey (Emeritus), Forest and Rangeland Ecosystem Science Center, Corvallis, OR 97331;* [h]*Ecology Center and Department of Biology, Utah State University, Logan, UT 84322;* [i]*Department of Mathematics, Humboldt State University, Arcata, CA 95521;* [j]*Fisheries and Oceans Canada* (*Scientist Emeritus*)*, Centre for Aquaculture and Environmental Research, West Vancouver, BC, Canada V7V 1N6;* [k]*University of British Columbia* (*Adjunct Faculty*)*, Institute for Resources, Environment and Sustainability, Vancouver, BC, Canada V6T 1Z4;* [l]*Northwest Power and Conservation Council, Portland, OR 97204;* [m]*Oregon State University, College of Oceanic and Atmospheric Sciences, Corvallis, OR 97331;* [n]*US Department of Agriculture Forest Service, Rocky Mountain Research Station, Seeley Lake, MT 59868;* [o]*Natural Resources Consultants, Seattle, WA 98199;* [p]*Department of Fish and Wildlife Sciences, University of Idaho, Moscow, ID 83844;* [q]*Department of Ecology, Evolution and Natural Resources, Rutgers University, New Brunswick, NJ 08901; and* [r]*Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, BC, Canada V9T 6N7*

Edited by Peter M. Kareiva, Nature Conservancy, Seattle, WA, and approved October 31, 2012 (received for review August 6, 2012)

Well-functioning food webs are fundamental for sustaining rivers as ecosystems and maintaining associated aquatic and terrestrial communities. The current emphasis on restoring habitat structure—without explicitly considering food webs—has been less successful than hoped in terms of enhancing the status of targeted species and often overlooks important constraints on ecologically effective restoration. We identify three priority food web-related issues that potentially impede successful river restoration: uncertainty about habitat carrying capacity, proliferation of chemicals and contaminants, and emergence of hybrid food webs containing a mixture of native and invasive species. Additionally, there is the need to place these food web considerations in a broad temporal and spatial framework by understanding the consequences of altered nutrient, organic matter (energy), water, and thermal sources and flows, reconnecting critical habitats and their food webs, and restoring for changing environments. As an illustration, we discuss how the Columbia River Basin, site of one of the largest aquatic/riparian restoration programs in the United States, would benefit from implementing a food web perspective. A food web perspective for the Columbia River would complement ongoing approaches and enhance the ability to meet the vision and legal obligations of the US Endangered Species Act, the Northwest Power Act (Fish and Wildlife Program), and federal treaties with Northwest Indian Tribes while meeting fundamental needs for improved river management.

Recent years have seen substantial expenditures and sustained efforts by government agencies, indigenous people, and nongovernmental organizations to restore rivers and their declining fish stocks. These activities are under increased scrutiny to show that goals and objectives are being met (1, 2). In general, past river restoration has focused on recreating structural attributes (e.g., channel width, complexity) based on the assumption that associated ecological functions will follow (3–6). However, contemporary evidence suggests that ecosystem structure alone does not necessarily reflect how it functions in supporting life. For example, field experiments in the US Pacific Northwest have shown that trophic manipulations (e.g., nutrient additions or salmon carcass introductions) that boost the abundance of potential prey organisms also boost subsequent fish growth (7–10). In contrast, restoration of physical habitats by creating pools or adding structures yields ambiguous evidence that such efforts increase subsequent fish abundance and biomass (11–17). Although it may be premature to conclude from these studies that food availability and species interactions are more limiting to fish than the quality or quantity of the physical habitat, evidence is mounting that many habitat restoration activities are not always as effective in meeting stated goals and objectives as originally anticipated.

Nationwide, river restoration practices tend to target the effects of dams, flow manipulation, and channel structure. More than $1 billion/y has been spent since 1990 on river restoration in the United States, with limited evidence of success (1). It has been argued that successful restoration should focus on restoring processes that support ecosystem services and monitoring how processes respond within an adaptive management framework (3, 18, 19). We suggest here that a balance between physical habitat restoration and an understanding of trophic processes supporting biotic communities would improve restoration effectiveness.

The Food Web as a Component of Restoration

Food web structures and the processes that drive them determine how system components act collectively—and often synergistically—to underpin the resilience and productivity of the larger ecosystem (*SI Text*, section 1). Each food web component, whether a primary producer, an external input of organic matter, a microbial decomposer, or a secondary consumer, responds to changes in environmental conditions. Furthermore, when a predator impacts its prey, the influence can reverberate through the entire food web as a "cascading trophic interaction" (20, 21). Connectivity across the entire river network also allows organisms, such as fish, to link subfoodwebs, thereby imparting an adaptive structure and stability to food webs (22, 23).

Despite their complexity and limited general application, food webs have been

Author contributions: D.A.B. performed research; R.L., W.G.P., and G.T.R. analyzed data; and R.J.N., J.R.A., D.A.B., P.A.B., J.C., C.J.H., N.H., C.L., E.N.M., W.G.P., B.E.R., G.T.R., D.S., P.E.S., and C.C.W. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

[1]To whom correspondence should be addressed. E-mail: naiman@uw.edu.

[2]Retired.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1213408109/-/DCSupplemental.

used in successful restoration efforts (7, 24, 25) and manipulated at large scales to improve water conditions and recreational fisheries (20, 26, 27). At the same time, ill-advised manipulations have resulted in serious environmental problems [the introduction of opossum shrimp (*Mysis diluviana*) into freshwater lakes being a particularly pernicious example (28)]. Food webs are often considered to depend on habitat, but habitat alone does not determine the food web; many other factors shape its internal organization, linkages, productivity, and resilience. Species diversity, mix of native and nonnative species, chemical contaminants, phenologies and seasonal production cycles, carrying capacity, disturbance, nutrient delivery and cycling, competition, predation, disease, and other processes all shape food webs (29). Management actions affecting any one of these components often cascade through food webs to influence community and ecosystem characteristics.

A food web perspective can reveal insights into basic properties underpinning productivity and resilience that cannot be obtained from an exclusive focus on hydrosystem, habitat, hatcheries, and harvest (referred to as the four Hs)—the cornerstones of the Columbia River and many other river restoration programs. Restoration activities traditionally focus on flows and physical habitat, and assume that local habitat structure, quality, and amount dictate fish production (3, 4, 5, 18, 19). Traditional freshwater food web illustrations have typically conveyed the notion that most fish food is produced within the local aquatic habitat. In reality, much food comes from external or very distant sources—including subsidies from marine systems borne by returning anadromous fishes, headwater tributaries that transport prey downstream, adjacent riparian and floodplain habitats (30, 31), and disturbance that can influence the flux of nutrients and other materials (32, 33) (*SI Text*, section 2).

Setting

We use the Columbia River to illustrate the importance of food webs in restoration. Examining the Columbia River restoration program, in light of river restoration in general, provides insights into factors underpinning successful activities (e.g., improved survival at dams for juvenile salmonids) (34) as well as less successful efforts (35). The Northwest Power and Conservation Council (NPCC) Fish and Wildlife Program for the Columbia River seeks to establish and maintain an ecosystem that sustains an abundant, productive, and diverse community of fish and wildlife (36). From 2009 to 2011, the Independent Scientific Advisory Board, a committee of scientists reporting to the NPCC, National Oceanic and Atmospheric Administration, and the Columbia Basin Tribes, conducted an extensive review of information on riverine food webs in light of ongoing restoration activities, and made recommendations to refocus some research and restoration actions. The process involved evaluating over 1,000 peer-reviewed published and unpublished reports, conducting public briefings, and receiving correspondence from >40 government agencies, tribal biologists, university researchers, and private sector scientists (29). The Columbia River serves as the illustrative example for which we synthesize our conclusions and recommendations, but the problems and potential solutions are applicable to river restoration in general. Recognizing that restoration goals often represent political, cultural, and societal choices, not just scientific decisions, the US Endangered Species Act mandates the ecological restoration of federally listed fish. The NPCC Fish and Wildlife Program plays a central role in the restoration effort (*SI Text*, section 3).

Today's Columbia River ecosystem, including the estuary and uplands, represents a vestige of the historical ecosystem (37). Dam construction, water storage and withdrawals for irrigation, flood control, changing land uses and climate (38, 39), and introduction and expansion of numerous nonnative species (40) have resulted in significant landscape-scale modifications of the river and its tributaries. In particular, the relatively recent and widespread construction of water impoundments throughout the Basin (Fig. 1*A*) has attenuated peak springtime river flows, which historically aided migrations of juvenile salmon and transported large quantities of sediments, nutrients, cold water, and associated materials downstream. Collectively, these alterations have fundamentally altered food web structures and processes in tributaries, the mainstem river, the estuary, and coastal marine environments. The net result is that many populations of once abundant salmon and other fishes have sharply declined and are now listed as endangered or threatened under federal laws, resulting in legal obligations to protect critical habitat [Endangered Species Act 16 USC §§ 1531–1544; ESA §3 (6) defines critical habitat for a threatened or endangered species] (*SI Text*, section 4).

Current Columbia River restoration activities are diverse, but a high priority is placed on habitat restoration, and its dominance is reflected in the Program's expenditures. [The Program states (p. 7):

> This is a habitat-based Program. The Program aims to rebuild healthy, naturally producing fish and wildlife populations by protecting, mitigating, and restoring habitats and the biological systems within them. Artificial production and other non-natural interventions should be consistent with this effort and avoid adverse impacts to native fish and wildlife species.

Much of the species- and habitat-centric focus can be attributed to the Endangered Species Act and federal treaty obligations with numerous Northwest Indian Tribes. They are an important part of the political landscape and likely to remain so.] About 40% of the ∼$311 million spent annually goes to acquiring, restoring, and monitoring habitat, removing passage barriers, providing diversion screens for migrating fish, assisting with riparian habitat protection, improving water quality (temperature and sediments), and conducting transactions and conservation activities to maintain ecologically desirable instream flows and other actions aimed at reestablishing more natural habitat processes (41). A relatively small portion of the budget is focused on removing, relocating, or controlling native and nonnative predators, a key element of food webs that is likely to affect interactions within communities.

Although these efforts are viewed as beneficial, none explicitly addresses protection or restoration of food webs. Food webs are integral to the four Hs, because they provide the fuel and direct the flow of energy and material for both productivity and resilience over the long term. In the past, a traditional threat analysis approach has been used to relate habitat, hatcheries, harvest, and hydropower operations to salmon (42, 43). Within that context, size-dependent survival, density-dependent growth, and dependence of growth on the interplay between temperature and food availability as well as other important life history parameters could be viewed as consequences of trophic processes. Habitat and food web approaches are compatible, and if better integrated, they could improve restoration effectiveness and possibly avoid unanticipated consequences of management actions for target species, such as habitat actions that inadvertently facilitate invasion by nonnative predators or competitors and cause unanticipated, often destructive and unwanted, changes in food webs (28, 44, 45). Despite the long history of research on the Columbia River and many thousands of restoration actions, there is still little information on how food webs (Fig. 2) and their processes underpin restoration (*SI Text*, section 5).

Priority Issues for Riverine Ecosystems

In our review, three critical issues—carrying capacity, chemical contaminants, and hybrid food webs—were consistently

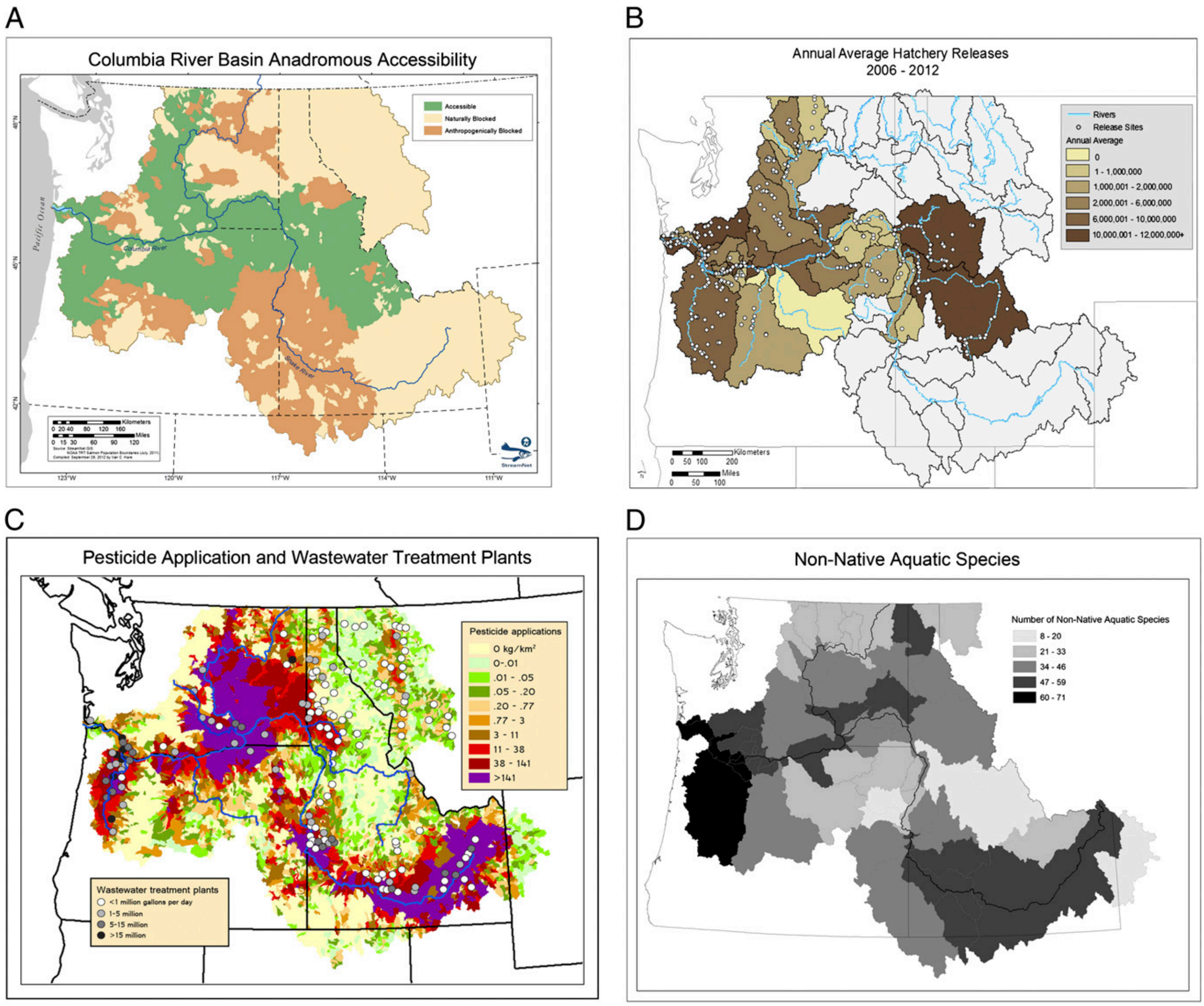

Fig. 1. In addition to the construction of major dams, the Columbia River Basin has undergone substantial transformations in many other ways. Examples include (*A*) blocking of anadromous fish passage over large areas (StreamNet), (*B*) substantial releases (annual average of 2006–2012) of hatchery-raised fish (Fish Passage Center, Portland, OR), (*C*) widespread application of pesticides (246 compounds evaluated; average of 1999–2004) and construction of wastewater treatment plants, and (*D*) establishment of numerous nonnative aquatic species (note that the number and distribution of nonnative riparian species are not known). White areas, outside Columbia River Basin.

identified as having high priority for research, management, and river restoration programs. River restoration programs could be greatly improved by incorporating food web considerations into the four Hs to better understand and address these three critical issues. Incorporating food web considerations into project implementation could be especially important in determining whether sufficient foods and suitable thermal conditions are available to support adequate growth and bioenergetics in juvenile salmonids, whether pesticides and other chemicals are impacting food supplies as well as reducing the ability of organisms to adequately function (e.g., altered behaviors, slower growth, increased disease susceptibility), and whether nonnative species or hatchery fish are competing for prey with native fishes. These three issues are rarely addressed, and they represent potentially huge problems for the recovery of federally listed species that could easily derail the success of many habitat, harvest, and hatchery programs.

Uncertainty About the Carrying Capacity of Rivers. There is little understanding of the carrying capacity of altered or natural habitats for aquatic organisms (46). We define carrying capacity as the maximum abundance or biomass of species of concern that can achieve adequate somatic growth needed to support population growth given the accessible quantity and quality of food available through time. Managers and biologists in the Columbia Basin have rarely considered this limitation, although it may seriously constrain the success of their programs (e.g., survival of large numbers of stocked fish).

It simply is not clear whether the Columbia River, or any other river, can provide sufficient food to support large populations of artificially raised fishes and other organisms for the long term. Consider the massive annual releases of juvenile fish from Columbia River hatcheries and how they potentially affect food webs and stocks of wild fish (Fig. 1*B*). There are ∼130–150 million hatchery salmon and steelhead added to the river annually from >200 hatcheries at a cost of >$50 million (29, 41, 47). The food used to raise them (most originating from outside the Basin) as well as the thousands of metric tons of natural foods required to sustain them in the river certainly affect the capacity of the Columbia River to

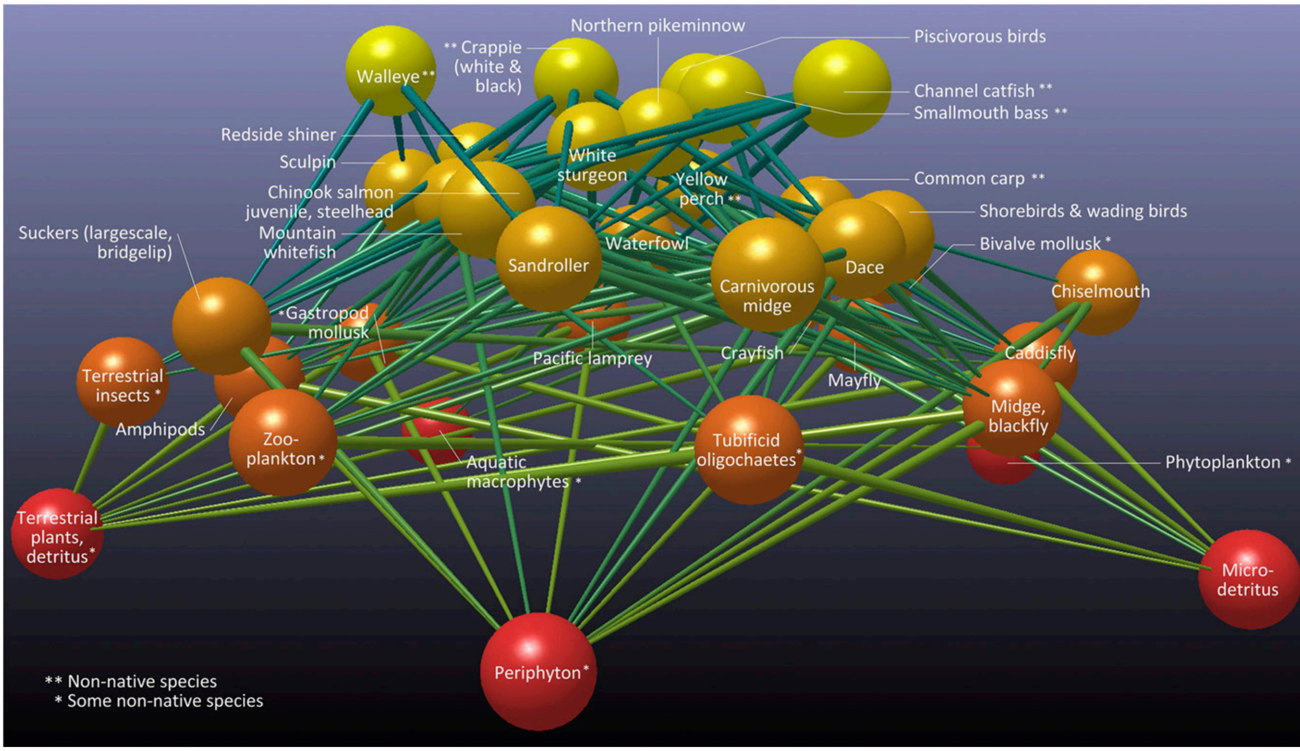

Fig. 2. Food web structure in the Hanford Reach of the Columbia River (considered a relatively well-known site). The weak food web resolution illustrates the lack of fundamental knowledge. Note the prevalence of nonnative species. The depicted food web is only a rudimentary subset of the actual web, despite being a well-studied site; there is little empirical understanding of the diversity of food web elements and critical linkages. The basal nodes of the food web—terrestrial plants, periphyton, detrital-associated organisms, aquatic insects, and zooplankton—are aggregates of a huge diversity of organisms; in contrast, the higher nodes are usually composed of single species. Red, primary producers; orange, primary consumers; yellow, secondary consumers; green, tertiary consumers (created in Network3D; RJ Williams, 2010, Network3D Software; Microsoft). *Taxonomic groups containing some nonnative species. **Nonnative species.

support naturally produced native fishes. Evidence suggests that nearly two times as many salmon smolts (mostly hatchery fish) are produced in the Columbia Basin today as were present during the period before major hatchery and mainstem dam construction (29). Furthermore, nonnative American shad (*Alosa sapidissima*) (Fig. 3) have greatly increased since the mainstem dams were built, and they are potentially competing subyearling Chinook (*Oncorhynchus tshawytscha*) smolts (29, 40). Bioenergetic modeling suggests that the greatest potential spatial and dietary overlap of shad with age 0 Chinook is in July, when both species feed primarily on *Daphnia*. Depending on the consumption demand between warm and cool years, an estimated 14–16 mt *Daphnia* are consumed for every 1 million subyearling Chinook compared with 2.4–4.0 mt of *Daphnia* consumed for every 1 million larval–juvenile shad present during July in John Day reservoir, one of the primary spawning sites of adult shad. Although accurate estimates are not available for the abundance of larval–juvenile shad, there are orders of magnitude more shad than subyearling Chinook feeding in the reservoir. Consequently, the total consumption demand for *Daphnia* by the shad population exceeds the consumption by Chinook by a considerable but currently unknown amount during the final month of premigration growth. There are also another 85 nonnative fish species and a poorly inventoried suite of nonnative plants and invertebrates in the Columbia River (48, 49) that impact the food supply in unknown ways. The lack of routine monitoring of key food organisms like *Daphnia* precludes the ability to compare temporal food supply with consumption demand by the major consumers. Consequently, understanding of the carrying capacity of specific habitats and how the carrying capacity for salmonids might change in response to variability in climate, hatchery practices, or populations of consumers or prey is still quite limited.

We believe that there is a fundamental need to consider sustainable food web structures and carrying capacity for broad habitat types in catchments (e.g., tributaries, mainstem rivers, lakes, reservoirs, estuary, and wetlands). For each habitat type, including healthy and degraded examples, a blueprint for what to protect and what to restore for maintaining carrying capacity is paramount. Establishing reasonable and measurable carrying capacity targets for key species allows one to gauge ongoing success in preservation and reclamation efforts. In addition to abundance estimates or counts already recorded at dams, migrant traps, and hatchery releases, other measurable metrics might include relationships among thermal regimes, size (length and weight) or condition of smolts and other juvenile stages to stage-specific survival rates or adult returns, and temporal trends in diets or stable isotope values as a reflection of food sources.

Some of this information is already being collected, but general access to data remains problematic. There are ongoing efforts to improve data availability and sharing through emerging monitoring programs (e.g., Fish Passage Center: www.fpc.org; Data Access in Real Time: www.cbr.washington.edu/dart; Pacific Northwest Aquatic Monitoring Partnership; www.pnamp.org), but ongoing effort is needed to collect and report food web-relevant information. For example, access to these data is essential for determining the relationship between carrying capacity and performance and resilience of specific stocks and monitoring the food demands of wild and artificially propagated native and nonnative fishes.

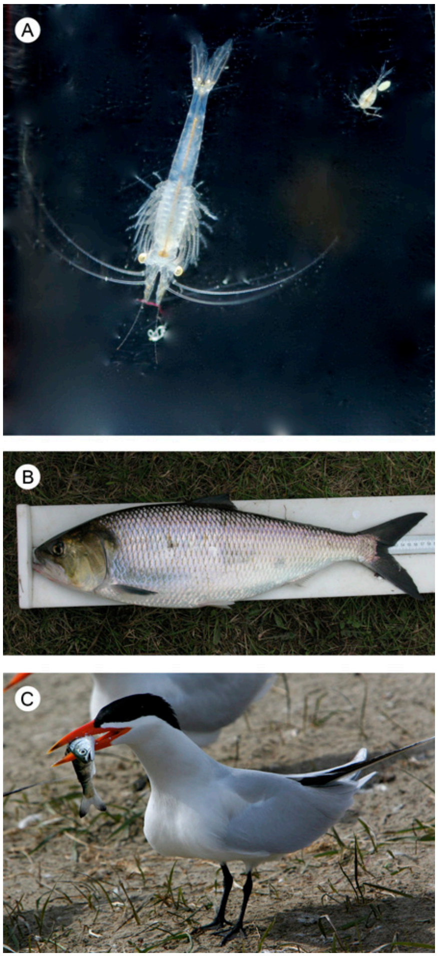

Fig. 3. Hundreds of nonnative aquatic species are now established in the Columbia River Basin, and many have changed food webs in unanticipated and unwanted ways by shifting predation pressure or fundamentally altering fluxes of energy and nutrients. (*A*) *M. diluviana* and (*B*) American shad (*A. sapidissima*) are abundant and important competitors with planktivorous salmonids and potentially serve as a nonnative energy source, thus expanding predator populations and increasing predation mortality on resident and anadromous salmonids. Furthermore, altered environmental conditions are allowing the expansion of many native predators, including (*C*) Caspian terns (*H. caspia*), thereby directly altering food webs and increasing predation on native salmonids (48, 49). Photos courtesy of (*A*) www.flickr.com/photos/wontolla_jcb/2475661498/, (*B*) D. Hasselman, and (*C*) Bird Research Northwest.

An Example: Bioenergetic Simulation of Food Demand and Feeding Rate by Spring–Summer Chinook Smolts. Growth and feeding rates of spring–summer Chinook salmon during peak migration of smolts illustrate their food demands and the potential effects on both wild and hatchery-reared fish. Using bioenergetic modeling, we estimated the food demands of wild and hatchery-reared Chinook that were passive integrated transponder (PIT)-tagged at Lower Granite Dam and recovered 461 km downstream at Bonneville Dam from April to July of 2008. The bioenergetics modeling simulations are based on empirical inputs for the average initial and final weights measured over the simulation period, estimated diet composition, thermal experience, and energy density of major prey in the diet.

The simulations indicated that, to grow from the observed 15.0 g at Lower Granite Dam on May 5 to 18.2 g at Bonneville Dam on May 19, yearling Chinook needed to feed at 78% of their theoretical physiological maximum consumption rate given the diet composition and thermal regime experienced during migration. Over that period, individuals consumed an estimated 23.1 g food, with a growth efficiency (grams of growth per grams of food consumed × 100) of 14%. Assuming 64% survival between Lower Granite and Bonneville dams (e.g., 80% survival from Lower Granite to McNary and 80% survival from McNary to Bonneville; approximated from figure 25 and table 35 in ref. 50), for every million yearling Chinook passing Lower Granite Dam, 18.5 mt of prey would have been consumed over the 13-d migration. This consumption demand was composed of 3.7 mt dipterans, 5.8 mt other insects, 4.3 mt *Daphnia*, and 4.7 mt amphipods (many nonnative). Given the population abundance index of 9 million hatchery and wild yearling Chinook at Lower Granite Dam during 2008 (ref. 50, tables 16–18), the total consumption demand by yearling Chinook passing Lower Granite Dam would have been 166.5 mt prey consumed over the 13–14 d migration, comprising 33.3 mt dipterans, 52.1 mt other insects, 38.8 mt *Daphnia*, and 42.2 mt amphipods (*SI Text*, section 6).

Proliferation of Chemicals and Contaminants. Although there is widespread and abundant use of synthetic chemicals in nearly all river basins (*SI Text*, section 7), data on use of artificial chemicals in the Columbia Basin provide ample cause for concern. The most recent tally of pesticide use (average for 1999–2004) lists 182 chemicals, with an aggregate application rate of ~46,000 mt active ingredients annually; these chemicals are concentrated mostly in agricultural lands along water courses (Fig. 1*C*). In addition, there are a variety of manufactured and natural organic compounds, such as pharmaceuticals, steroids, surfactants, flame retardants, fragrances, and plasticizers detected, especially in waters in the vicinity of municipal wastewater discharges and livestock agricultural facilities (51, 52).

There is an urgent need to quantify and map the spatial patterns of these chemicals, assess their transfer and accumulation rates, and document the vulnerabilities of food webs to them. Additional investigations on the ecotoxic potential of their mixtures on food webs are also required (51, 52). Bioaccumulation and biomagnification of chemical contaminants affect species that are critical components of the food web (e.g., microbes, sensitive invertebrates, and top consumers), herbicides can cause direct loss of food sources such as aquatic plants and algae (leading to food shortages for higher trophic levels), and exotic chemicals can reduce the ability of species and individuals to cope with normal predation risk and environmental stresses (because of altered behaviors, slower somatic growth, and increased disease susceptibility) (29). If the basal layers of food webs are being depleted by the rapidly expanding presence of contaminants (53, 54), it could negate many ongoing restoration efforts. Furthermore, fish migrating from the oceans to freshwater transport persistent industrial pollutants acquired at sea. The net balance between positive feedback of marine-derived nutrient additions from spawning adults (55) and negative feedback from pollutant delivery from the ocean is unclear and needs careful documentation (56).

Recognizing Hybrid Food Webs and Maintaining Productivity. The continuing introduction and proliferation of nonnative species and their still poorly understood impacts on the native biota heighten the need to manage what have been termed novel, hybrid, or no-analogue food webs (the terms novel, hybrid, and no-analogue are used synonymously here) for which we have no historical precedent (57). Rather than focus on restoring pristine food webs, it would be prudent to identify and maintain the most productive and resilient food webs (i.e., those food webs with the capacity to buffer and recover from mild perturbations). Food webs containing both new and old biotic elements can collectively retain function, productivity, and resilience (58). Attempts to return to pristine food webs often involve use of herbicides, pesticides, or other control measures that can have unintended effects. Contemporary rivers often contain a diverse assemblage of fishes and other species, and resilience does not imply that each species should be abundant at all times. The biological portfolio is dynamic, with species waxing and waning according to environmental conditions.

About 1,000 nonnative species of plants and animals, of which 326 are documented aquatic species (Fig. 1*D*), inhabit the Columbia Basin. Many others are expected to invade and be transported to the Basin (48, 49). Agencies have dramatically increased prevention measures against invasions by zebra and quagga mussels (*Dreissena polymorpha* and *D. bugensis*) into the Basin through border inspection, cleaning stations, and required invasive species tags for boats. Such programs could be expanded to other aquatic invertebrates, vertebrates, and macrophytes to complement intervention with existing problematic nonnative species. The stark reality is that hybrid food webs will persist; nonnative species are widely established, and eradication will be difficult, if not impossible. The challenges are exemplified by introductions of opossum shrimp, lake trout and brook trout (*Salvelinus namaycush* and *S. fontinalis*), and various other nonnative fishes into the upper Columbia (28), which have fundamentally altered aquatic communities and jeopardized recovery of bull trout (*S. confluentus*) and other native species (Fig. 3).

A Basin-wide monitoring program is needed to address the temporal pace and spatial extent of continuing nonnative introduction, invasion, and establishments and identify impending problems while they are still manageable. As a start, it would be prudent to reevaluate ongoing stocking practices for nonnative species that are inconsistent with the conservation of native biota and their food webs. Identifying which nonnative species may support or disrupt important functions and processes is essential for successful restoration of federally listed species and important ecological services. Improved public education is also needed to help prevent future introductions of nonnative species through aquarium releases, ballast water discharges, live seafood, boat trailers, and ornamental plants.

Other Important Food Web Concerns. Biotic conservation is most successful where actions are aimed at protecting ecosystems rather than restoring or reclaiming them after the damage is done. For the Columbia and other rivers, the need for a concerted effort to protect the food webs of critical environments is increasingly recognized. A robust strategy would preserve food web diversity, which includes access by species to a mosaic of connected habitats (for reproduction, growth, refuge, and migration) with different productivities and mixtures of native and nonnative species, even while steering degraded systems to more productive status. A broad range of additional food web issues needs to be addressed and will allow the more complete understanding necessary for effective management. These issues include understanding the consequences of altered nutrient, organic matter (energy), water, and thermal sources and flows, reconnecting critical habitats and their food webs, and restoring for changing environments (*SI Text*, section 8).

Incorporating a Food Web Perspective into Management

Incorporating food web considerations into management helps test restoration assumptions and leads to discovery of species interactions that influence management success. Although the construction and modeling of complete food webs may be difficult, there are approaches that can yield useful results relatively quickly. Specifically, we suggest a tractable framework that focuses on key processes and interactions that affect growth and survival of salmonids. First steps could include (*i*) use of focal species to quantify interactions with prey, competitors, predators, pathogens, and parasites and environmental conditions; (*ii*) use of stable isotopes and diet analysis to quantify food-related interactions, especially with predators, invasive species, or hatchery-reared salmonids; (*iii*) use of bioenergetic models to estimate demands on food supplies by intra- and interspecific competitors and diagnose the interplay between temperature, food availability, and quality within the growth environment of key species; (*iv*) consideration of density dependence in growth and survival associated with artificially elevated abundance through hatchery stocking; and (*v*) understanding the effects of chemicals and toxins on specific food web structures and processes. These and other targeted approaches can identify interactions or environmental conditions that impact restoration goals, allowing managers to focus on critical processes at relevant locations and times.

Furthermore, food web modeling, like habitat modeling, has an important place—if for no other reason than the development of testable hypotheses that can be confirmed or refuted. In the Columbia, linked trophic and population models have been essential in understanding the scope of predation by northern pikeminnow (*Ptychocheilus oregonensis*) and nonnative predators in the mainstem river reservoirs (59–62), impacts of predation by gulls (*Larus* spp.) and Caspian terns (*Hydroprogne caspia*) on migrating juvenile salmon (63–66), impacts of nonnative mysids and lake trout on kokanee and native salmonids in lakes (28, 67), complex species interactions (68), and stage-specific growth and survival of some juvenile salmon populations during freshwater and early marine rearing (69, 70). General statistical and population models have been used to explore density dependence and carrying capacities in lake- and stream-rearing populations (71–74). More broadly, trophic modeling has greatly improved the understanding of lake conditions in North America (20, 26). A comprehensive food web model should be general enough that the inputs can be changed to accommodate variability in thermal regime, feeding, diet, and growth at appropriate temporal and spatial scales to both forecast what would happen and update inputs when experience suggests key components are missing.

Specifically for the Columbia, whether restoration actions are effective cannot be known for many years. However, NPCC, state and federal agencies, and Columbia River tribes are actively involved in discussions about implementation of food web considerations—and the availability and sharing of data—within the existing Fish and Wildlife Program. Most importantly, this discussion has raised awareness of the key roles of food webs in restoration. The needs to consider carrying capacity, chemical impacts, hybrid communities, future conditions, and data transparency are paramount when prioritizing expensive restoration activities. Implementing a food web perspective for the Columbia River complements the four Hs and thereby, enhances the ability to meet the vision and legal obligations of the US Endangered Species Act and the need for improved river management.

ACKNOWLEDGMENTS. We thank K. Barnas, B. Chockley, M. DeHart, M. Ford, B. Muir, D. Roby, J. Ruff, P. Roger, B. Sanderson, L. Sutton, and V. Hare for supplying critical information; the numerous individuals and organizations who graciously responded to requests for information; J. Dunne for providing Network3D software; and L. Robinson and E. Schrepel for keeping the committee on task, organizing drafts, preparing graphics, and compiling references.

1. Bernhardt ES, et al. (2005) Ecology. Synthesizing U.S. river restoration efforts. *Science* 308(5722):636–637.
2. Palmer MA, et al. (2005) Standards for ecologically successful river restoration. *J Appl Ecol* 42:208–217.
3. Palmer MA, Filoso S (2009) Restoration of ecosystem services for environmental markets. *Science* 325(5940):575–576.
4. Palmer MA (2010) Beyond infrastructure. *Nature* 467:534–535.
5. Humphries P, Winemiller KO (2009) Historical impacts on river fauna, shifting baselines, and challenges for restoration. *Bioscience* 59:673–684.
6. Good TP, Harms TK, Ruckelshaus MH (2003) Misuse of checklist assessments in endangered species recovery efforts. *Conserv Ecol* 7(2):12.
7. Warren CE, et al. (1964) Trout production in an experimental stream enriched with sucrose. *J Wild Manage* 28:617–660.
8. Shortreed KS, et al. (1984) Periphyton biomass and species composition in 21 British Columbia lakes: Seasonal abundance and response to wholelake nutrient additions. *Can J Bot* 62:1022–1031.
9. Slaney PA, Perrin CJ, Ward BR (1986) Nutrient concentration as a limitation to steelhead smolt production in the Keogh River. *Proc Ann Conf West Assoc Fish Wild Agency* 66:146–155.
10. Bilby RE, et al. (1998) Response of juvenile Coho salmon (Oncorhynchus kisutch) and steelhead (Oncorhynchus mykiss) to the addition of salmon carcasses in two streams in southwestern Washington, USA. *Can J Fish Aquat Sci* 55:1909–1918.
11. Frissell CA, Nawa RK (1992) Incidence and causes of physical failure of artificial habitat structures in streams of western Oregon and Washington. *N Am J Fish Manage* 12:182–197.
12. Hilborn R, Winton J (1993) Learning to enhance salmon production: Lessons from the Salmonid

Enhancement Program. *Can J Fish Aquat Sci* 50:2043–2056.
13. Reeves GH, et al. (1997) *Watershed Restoration: Principles and Practices*, eds Williams JE, Wood CA, Dombeck MP (*American Fisheries Society*, Bethesda, MD), pp 335–359.
14. Ward BR (2000) Declivity in steelhead (Oncorhynchus mykiss) recruitment at the Keogh River over the past decade. *Can J Fish Aquat Sci* 57:298–306.
15. Thompson DM (2006) Did the pre-1980 use of in-stream structures improve streams? A re-analysis of historical data. *Ecol Appl* 16:784–796.
16. Stewart GB, et al. (2009) Effectiveness of engineered in-stream structure mitigation measures to increase salmonid abundance: A systematic review. *Ecol Appl* 19:931–941.
17. Whiteway SL, et al. (2010) Do in-stream restoration structures enhance salmonid abundance? A meta-analysis. *Can J Fish Aquat Sci* 67:831–841.
18. Poff NL, et al. (1997) The natural flow regime: A paradigm for river conservation and restoration. *Bioscience* 47:769–784.
19. Hoeltje SM, Cole CA (2009) Comparison of function of created wetlands of two age classes in central Pennsylvania. *Environ Manage* 43:597–608.
20. Carpenter R, Kitchell JF, Hodgson JR (1985) Cascading trophic interactions and lake productivity. *Bioscience* 35:634–639.
21. Terborgh J (2010) *Trophic Cascades*, ed Estes JA (Island Press, Washington, DC).
22. Rooney N, McCann KS (2012) Integrating food web diversity, structure and stability. *Trends Ecol Evol* 27(1): 40–46.
23. McCann KS, Rooney N (2009) The more food webs change, the more they stay the same. *Philos Trans R Soc Lond B Biol Sci* 364(1524):1789–1801.
24. Mundie JH, McKinnel SM, Traber RE (1983) Responses of stream zoobenthos to enrichment of gravel substrates with cereal grain and soybean. *Can J Fish Aquat Sci* 40:1702–1712.
25. Stockner JG, ed (2003) *Nutrients in Salmonid Ecosystems: Sustaining Production and Biodiversity*, Symposium 34 (American Fish Society, Bethesda, MD).
26. Carpenter SR, Kitchell JF (1988) Consumer control of lake productivity. *Bioscience* 38:764–769.
27. Carpenter SR, Chisholm SW, Krebs CJ, Schindler DW, Wright RF (1995) Ecosystem experiments. *Science* 269 (5222):324–327.
28. Ellis BK, et al. (2011) Long-term effects of a trophic cascade in a large lake ecosystem. *Proc Natl Acad Sci USA* 108(3):1070–1075.
29. ISAB (Independent Scientific Advisory Board) (2011) *Columbia River Food-Webs: Developing a Broader Scientific Foundation for Fish and Wildlife Restoration. Northwest Power and Conservation Council (NPCC) Report ISAB 2011-1, Portland, Oregon*. Available at www.nwcouncil.org/library/isab/2011-1/. Accessed November 13, 2012.
30. Naiman RJ, Décamps H, McClain ME (2005) *Riparia: Ecology, Conservation and Management of Streamside Communities* (Elsevier/Academic, San Diego).
31. Jardine TD, et al. (2012) Fish mediate high food web connectivity in the lower reaches of a tropical floodplain river. *Oecologia* 168(3):829–838.
32. Malison RL, Baxter CV (2010) The fire pulse: Wildfire stimulates flux of aquatic prey to terrestrial habitats driving increases in riparian consumers. *Can J Fish Aquat Sci* 67:570–579.
33. Wipfli MS, Baxter CV (2010) Linking ecosystems, food webs, and fish production: Subsidies in salmonid watersheds. *Fisheries (Bethesda, Md)* 35:373–387.
34. Levin PS, Tolimieri N (2001) Differences in the impacts of dams on the dynamics of salmon populations. *Anim Conserv* 4:291–299.
35. Berntson EA, et al. (2011) Diminished reproductive success of steelhead from a hatchery supplementation program (Little Sheep Creek, Imnaha Basin, Oregon). *Trans Am Fish Soc* 140:685–698.
36. NPCC (Northwest Power and Conservation Council) (2009) *Columbia River Basin Fish and Wildlife Program: 2009 Amendments. Northwest Power and Conservation Council, Portland, Oregon, USA. Document 2009-9*. Available at www.nwcouncil.org/library/2009/2009-09/Default.asp. Accessed November 13, 2012.
37. Williams RN, ed (2006) *Return to the River: Restoring Salmon to the Columbia River* (Elsevier, Amsterdam).
38. ISAB (Independent Scientific Advisory Board) (2011B) *Using a Comprehensive Landscape Approach for More Effective Conservation and Restoration. Northwest Power and Conservation Council (NPCC) Report ISAB 2011-4, Portland, Oregon*. Available at www.nwcouncil.org/library/report.asp?d=640. Accessed November 13, 2012.
39. ISAB (Independent Scientific Advisory Board) (2007) *Climate Change Impacts on Columbia River Basin Fish and Wildlife. Northwest Power and Conservation Council (NPCC) Report ISAB 2008-2, Portland, Oregon*. Available at www.nwcouncil.org/library/report.asp?d=354. Accessed November 13, 2012.
40. ISAB (Independent Scientific Advisory Board) (2008) *Non-native Species Impacts on Native Salmonids in the Columbia River Basin (Including Recommendations for Evaluating the Use of Non-Native Fish Species in Resident Fish Substitution Projects). Northwest Power and Conservation Council (NPCC) Report ISAB 2008-4, Portland, Oregon*. Available at www.nwcouncil.org/library/report.asp?d=348. Accessed November 13, 2012.
41. NPCC (Northwest Power and Conservation Council) (2011) *Columbia River Basin Fish and Wildlife Program. Northwest Power and Conservation Council, Portland, Oregon, USA. Document 2011-04:47*. Available at www.nwcouncil.org/library/2011/2011-04.pdf. Accessed November 13, 2012.
42. Ruckelshaus MH, et al. (2002) The Pacific salmon wars: What science brings to the challenge of recovering species. *Ann Rev Ecol Syst* 33:665–706.
43. Hoekstra JM, et al. (2007) Quantitative threat analysis for management of an imperiled species: Chinook salmon (Oncrhynchus tshawytscha). *Ecol Appl* 17: 2061–2073.
44. Minckley WL, et al. (2003) A conservation plan for native fishes of the lower Colorado River. *Bioscience* 53: 219–233.
45. Fausch KD, et al. (2009) The invasion versus isolation dilemma: Tradeoffs in managing native salmonids with barriers to upstream movement. *Conserv Biol* 23: 859–870.
46. Grossman GD (2012) Population regulation of brook trout (Salvelinus fontinalis) in Hunt Creek, Michigan: A 50-year study. *Freshwat Biol*, 10.1111/j.1365-2427.2012.02806.x.
47. Paquet PJ, et al. (2011) Hatcheries, conservation, and sustainable fisheries—achieving multiple goals: Results of the hatchery scientific review group's Columbia River Basin review. *Fisheries (Bethesda, Md)* 36: 547–561.
48. Sanderson BL, Barnas KA, Rub M (2009) Non-indigenous species of the Pacific Northwest: An overlooked risk to endangered fishes? *Bioscience* 59:245–256.
49. Carey MP, Sanderson BL, Barnas KA, Olden JD (2012) Native invaders—challenges for science, management, policy, and society. *Front Ecol Environ*, 10.1890/110060.
50. FPC (Fish Passage Center) (2009) *2008 Annual Report* (Columbia Basin Fish and Wildlife Authority, Portland, OR).
51. Focazio MJ, et al. (2008) A national reconnaissance for pharmaceuticals and other organic wastewater contaminants in the United States–II) Untreated drinking water sources. *Sci Total Environ* 402(2–3):201–216.
52. Morace JL (2012) Reconnaissance of contaminants in selected wastewater-treatment-plant effluent and stormwater runoff entering the Columbia River, Columbia River Basin, Washington and Oregon, 2008–10. *US Geol Surv Sci Invest Rept* 2012:5068.
53. Relyea R, Hoverman J (2006) Assessing the ecology in ecotoxicology: A review and synthesis in freshwater systems. *Ecol Lett* 9:1157–1171.
54. Fleishman ED, et al. (2011) Top 40 priorities for science to inform US conservation and management policy. *Bioscience* 61:290–300.
55. Naiman RJ, Helfield JM, Bartz KK, Drake DC, Honea JM (2009) *Challenges for Diadromous Fishes in a Dynamic Global Environment*, Symposium 69, eds Haro AJ, et al. (American Fish Society, Bethesda, MD) pp 395–425.
56. Krümmel EM, et al. (2003) Delivery of pollutants by spawning salmon. *Nature* 425(6955):255–256.
57. Hobbs RJ, et al. (2006) Novel ecosystems: Theoretical and management aspects of the new ecological world order. *Glob Ecol Biogeogr* 15:1–7.
58. Catford JA, et al. (2012) Predicting novel riparian ecosystems in a changing climate. *Ecosystems*, 10.1007/s10021-012-9566-7.
59. Beamesderfer RC, et al. (1990) Management implications of a model of predation by a resident fish on juvenile salmonids migrating through a Columbia River Reservoir. *N Am J Fish Manage* 10:290–304.
60. Rieman BE, Beamesderfer RC (1990) Dynamics of a northern squawfish population and the potential to reduce predation on juvenile salmonids in a Columbia River reservoir. *N Am J Fish Manage* 10:228–241.
61. Rieman BE, et al. (1991) Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. *Trans Am Fish Soc* 120:448–458.
62. Petersen JH, Kitchell JF (2001) Climate regimes and water temperature changes in the Columbia River: Bioenergetic implications for predators of juvenile salmon. *Can J Fish Aquat Sci* 58:1831–1841.
63. Ruggerone GT (1986) Consumption of migrating juvenile salmonids by gulls foraging below a Columbia River dam. *Trans Am Fish Soc* 115:736–742.
64. Roby DD, et al. (2003) Quantifying the effect of predators on endangered species using a bioenergetics approach: Caspian terns and juvenile salmonids in the Columbia River estuary. *Can J Zool* 81:250–265.
65. Collis K, et al. (2002) Colony size and diet composition of piscivorous waterbirds on the lower Columbia River: Implications for losses of juvenile salmonids to avian predations. *Trans Am Fish Soc* 131:537–550.
66. Antolos M, et al. (2005) Caspian Tern predation on juvenile salmonids in the mid-Columbia River. *Trans Am Fish Soc* 134:466–480.
67. Wiese FK, Parrish JK, Thompson CW, Maranto C (2008) Ecosystem-based management of predator-prey relationships: Piscivorous birds and salmonids. *Ecol Appl* 18(3):681–700.
68. Beauchamp DA, et al. (2007) *Analysis and Interpretation of Inland Fisheries Data*, eds Guy CS, Brown MJ (American Fish Society, Bethesda, MD), pp 765–842.
69. Zabel RW, Achord S (2004) Relating size of juveniles to survival within and among populations of Chinook salmon. Ecology 85:795–806.
70. Tomaro LM, et al. (2012) When is bigger better? Early marine residence of middle and upper Columbia River spring Chinook salmon. *Mar Ecol Prog Ser* 452: 237–252.
71. Rieman BE, Myers DL (1992) Influence of fish density and relative productivity on growth of kokanee in 10 oligotrophic lakes and reservoirs in Idaho. *Trans Am Fish Soc* 121:178–191.
72. Rieman BE, Maiolie M (1995) Kokanee population density and resulting fisheries. *N Am J Fish Manage* 15:229–237.
73. Crozier LG, et al. (2010) Interacting effects of density and temperature on body size in multiple populations of Chinook salmon. *J Anim Ecol* 79:342–349.
74. Zabel RW, et al. (2006) The interplay between climate variability and density dependence in the population viability of Chinook salmon. *Conserv Biol* 20:190–200.