PERSPECTIVE

Approaches for studying fish production: Do river and lake researchers have different perspectives?

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Abstract: Biased perspectives of fisheries researchers may hinder scientific progress and effective management if limiting factors controlling productivity go unrecognized. We investigated whether river and lake researchers used different approaches when studying salmonid production and whether any differences were ecologically supported. We assessed 564 peer-reviewed papers published between 1966 and 2012 that studied salmonid production or surrogate variables (e.g., abundance, growth, biomass, population) and classified them into five major predictor variable categories: physical habitat, fertility (i.e., nutrients, bottom-up), biotic, temperature, and pollution. The review demonstrated that river researchers primarily analyzed physical habitat (65% of studies) and lake researchers primarily analyzed fertility (45%) and biotic (51%) variables. Nevertheless, understudied variables were often statistically significant predictors of production for lake and river systems and, combined with other evidence, suggests that unjustified a priori assumptions may dictate the choice of independent variables studied. Broader consideration of potential limiting factors on fish production, greater research effort on understudied genera, and increased publication in broadly scoped journals would likely promote integration between lentic and lotic perspectives and improve fisheries management.

Résumé : Les perspectives biaisées de chercheurs du domaine des pêches pourraient faire entrave à des avancées scientifiques et à une gestion efficace, si cela devait se traduire par la non-reconnaissance de facteurs qui limitent la productivité. Nous avons vérifié si les chercheurs travaillant en rivière, d'une part, et en lac, d'autre part, utilisent des approches différentes pour étudier la production de salmonidés et si certaines différences sont appuyées par des considérations écologiques. Nous avons examiné 564 articles évalués par des pairs publiés de 1966 à 2012 et portant sur la production de saumons ou des variables substitutives (p. ex. abondance, croissance, biomasse, population) et les avons classés selon cinq grandes catégories de variables explicatives, soit celles reliées à l'habitat physique, à la fertilité (c.-à-d. nutriments, effet ascendant), au biote, à la température et à la pollution. Cet examen démontre que les chercheurs travaillant en rivière analysent principalement l'habitat physique (65 % des études), alors que les chercheurs travaillant en lac analysent principalement des variables associées à la fertilité (45 %) et au biote (51 %). Cela étant, des variables sous-étudiées constituent souvent des variables explicatives statistiquement significatives de la production de systèmes lacustres et fluviaux ce qui, combiné à d'autres observations, semble indiquer que des hypothèses a priori non justifiées pourraient dicter le choix des variables indépendantes étudiées. Une plus grande prise en considération de facteurs qui pourraient limiter la production de poissons, plus de recherche axée sur des genres sous-étudiés et un nombre accru de publications dans des revues à grande portée favoriseraient probablement l'intégration des perspectives lentique et lotique et amélioreraient la gestion des pêches. [Traduit par la Rédaction]

Introduction

One of the primary objectives in the study of freshwater ecosystems is to better understand controls on primary and secondary production, particularly the production of fish species of economic, recreational, and conservation importance (Moyle and Cech 2003). Despite novel challenges and opportunities posed by unidirectional flow in rivers, freshwater biota in all aquatic systems face some similar growth and survival challenges. Consequently, it seems logical that people who study streams and rivers (lotic systems) and those who study lakes and reservoirs (lentic systems) would evaluate a relatively similar set of factors controlling fish production. Although fish are adept at moving across these ecosystem boundaries, the frequent separation of lentic and lotic research in textbooks, university courses, scientific societies, and peer-reviewed literature suggests that many scientists are not as adroit.

Here, we analyze primary literature on salmonid production in lotic and lentic systems to better understand the degree to which

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individual researchers think differently about the two systems. If lentic and lotic researchers do in fact conceptualize fish production processes differently, it follows that they would study different predictors or controls of freshwater fish production and use different research methods. This is important because the scarcest resource is generally most limiting to production (Liebig 1852; Sprengel 1839). Applying the Liebig–Sprengel Law of the Minimum as the conceptual framework, fish production may be visualized as a wooden barrel filled with water (Fig. 1). The amount of water and, hence, the number of fish in the barrel, is limited by the shortest stave — where each stave represents an independent control of fish production such as physical, water quality, or biotic variables. If certain staves are a focus of research in rivers but not in lakes (or vice versa), managers are unlikely to target some potentially important factors and may be ineffective as a result.

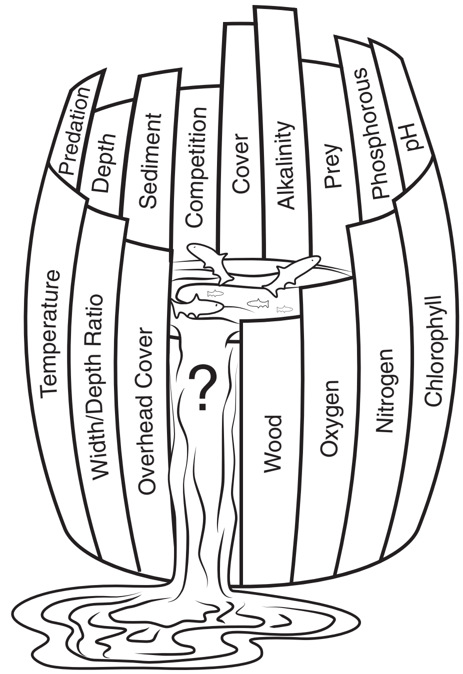
A division in research focuses between lotic and lentic systems could originate from real differences in factors controlling production in the two systems. Alternatively, differences could simply reflect the training of scientists in these similar, but often separate, systems. Regardless, the lack of cross-system research may inhibit system understanding and lead to a narrowed, and perhaps unsubstantiated, focus on particular factors controlling fish production and ecosystem processes (Chase 2000; Menge et al. 2009; Steele 1991). If the science community is fundamentally — and perhaps arbitrarily — compartmentalizing lentic and lotic systems, we may be limiting our research, skewing results, and impeding knowledge development. Additionally, there may be approaches used by researchers in one system that could be applied to the other or to both systems concurrently.

Although it is difficult to identify the temporal and conceptual origins of the lentic–lotic schism, the divide is evident in seminal texts concerning standing and flowing waters. Hutchinson's *A Treatise on Limnology* (Hutchinson 1967) and Hynes' *The Ecology of Running Waters* (Hynes 1970) virtually excluded discussion of other freshwater systems. Much of the early work in lakes addressed ecosystem-level questions such as controls on primary production (Kalff 2002), which led to a focus on trophic status as an important distinction between lakes. In contrast, early ecological work in rivers focused on specific biotic components such as benthic insect communities or particular fish species (Kalff 2002; Minshall et al. 1985), which resulted in a focus on physical habitat requirements for different groups of organisms (Fisher 1997). Vannote et al.'s (1980) classic river continuum paper describing stream structure and function used a physical template based on gradients in stream size to describe the presence, distribution, and growth of species. The same paper failed to even address the roles that water chemistry and nutrients might play in controlling productivity.

Another indication of the schism between the two fields is the different approaches used to classify water bodies. Lake classification systems are usually based on nutrient and phytoplankton status (i.e., oligotrophic, eutrophic, etc.) or thermal mixing cycles (e.g., cold dimictic; Wetzel 2001). Rarely are physical characteristics other than mixing cycles incorporated into lake classification systems. In contrast, river classification systems frequently rely upon physical characteristics such as stream order, gradient, sinuosity, and width-to-depth ratio (e.g., Brierley and Fryirs 2008; Montgomery and Buffington 1997; Rosgen 1994), and they do not incorporate chemical or biological parameters of the stream. In contrast with lakes, rivers are only rarely described as oligotrophic or eutrophic (but see Dodds 2006). If these classification systems reflect the perception of researchers' concern with dominant processes within a system, it can be concluded that researchers in lentic and lotic systems have different ideas about important factors driving systems and, thus, fish productivity.

Previous reviews of fish production literature in lakes and rivers generally reflect the different perspectives of lentic and lotic researchers. In reviewing predictive models of stream fish standing crop, Fausch et al. (1988) found researchers commonly assumed physical habitat limited production without testing other factors such as competition, fishing mortality, or nutrients. Similarly, Kiffney and Roni (2007) argued that restoration of physical habitat in streams is often undertaken even where productivity at lower trophic levels limits fish production. Reviews of fish production in lakes have generally found weak effects of physical variables such as lake area and depth and stronger effects of temperature and chemical factors, such as phosphorus concentration and pH (Downing et al. 1990; Downing and Plante 1993). However, a recent meta-analysis found a direct link between physical habitat and fish biomass and abundance in both lentic and lotic systems (Smokorowski and Pratt 2007). Additionally, Randall and Minns (2002) and Randall et al. (1996) found strong correlations between physical habitat variables and fish production in the Laurentian Great Lakes. Randall et al. (1995), one of the few reviews to integrate fish production parameters in both lakes and rivers, found that fish biomass was strongly correlated with total phosphorus concentrations in both lakes and rivers and that a given phosphorus concentration predicted a similar fish biomass in both types of ecosystems. Finally, reviews of fish production in either lakes or rivers have generally not taken water pollution into account, even though water quality has been a growing societal issue in recent decades (Mason 2002; Warren 1971).

Fig. 1. Liebig–Sprengel's barrel showing how different independent predictor variables might influence fish production. In this conceptualization, the most limiting resource (e.g., wood, nitrogen) or the dominant control factor (e.g., temperature, predation) is the one that actually controls fish production. Fishery researchers may design studies without really evaluating what the most important predictor variables are for fish production.



Given the mostly separate treatment of lake and river systems in the aquatic science literature, we hypothesized that there are differences in the predictor variables evaluated by lake and river scientists in fish production studies and that these differences are often driven by unsubstantiated a priori assumptions. To evaluate this hypothesis, we reviewed papers from the fish production literature in both types of systems and classified them according to five major predictor variables studied: physical habitat, fertility, biotic, temperature, and pollution. To understand existing patterns in publication activity among freshwater scientists, we evaluated changes in publication rates and determined the degree of separation in journal use between lentic and lotic researchers. Additionally, we identified data gaps and opportunities for improved integration between lotic and lentic systems for fish production research.

Because research efforts between lakes and rivers could differ as a result of the taxa evaluated, we limited this review to the Salmonidae family. This family of fish is ideal for our study because many of these species inhabit both lotic and lentic systems, occupy similar and limited ecological niches (e.g., cold, clean water), and are ecologically, economically, and culturally important. Additionally, similarities among these fishes decrease the likelihood that evolutionary variability in the species evaluated would result in observed differences between lake and stream research.

Fish production: definition and controlling factors

Ecologically, fish production is defined as the elaboration of fish tissue per unit time per unit area, regardless of whether or not the tissue survives to the end of a given time period (Warren 1971). It is usually calculated as the product of mean growth rate and initial biomass of a fish size class, summed over all sizes. As a broad measure, fish production integrates individual fish growth and processes that drive demographic change in fish populations (birth, immigration, death, emigration). Therefore, processes that control growth (e.g., physiology; Fry 1947) and operate at the population level (e.g., density-dependent mortality; Hairston et al. 1960; Murdoch 1994) determine the potential for fish production. Growth of individual fish is a function of food consumption and energetic expenditures (Hayes et al. 2000; Kitchell et al. 1977), which are both influenced by competition for prey resources (Jenkins et al. 1999; Nakano 1995) and aspects of the physical environment, including water temperature and light availability (Dionne and Folt 1991; Hokanson et al. 1977; McCullough et al. 2009). Population size is regulated by density-dependent and density-independent mechanisms, including presence of predators (e.g., Hansen et al. 1995), refuge from predation (e.g., Tabor and Wurtsbaugh 1991), physical conditions (Jensen and Johnsen 1999; Labbe and Fausch 2000; Lobón-Cerviá and Rincón 2004), and resource availability (Hixon et al. 2002). Furthermore, trade-offs between resource availability and predation threat may lead to complex dynamics whereby individual survival (Walters and Juanes 1993) or growth potential (Gilliam and Fraser 1987) is dependent on the relative resource availability in refugia or high-risk habitats.

Although basal food resources and biotic interactions (e.g., competition, predation) are critical factors determining fish production in a system, the importance of bottom-up and top-down controls are often site-specific, mediated by characteristics of the physical environment (e.g., refuge habitat, flow regime), water temperature, and pollutants. Physical characteristics of fish habitat can impact resource availability (Benke et al. 1984; Hawkins et al. 1983; Suttle et al. 2004), energetic costs for growth (Fausch 1984), and death from harsh environmental conditions (Brown 1986; Cunjak and Power 1986). Water temperature controls many physiological processes that determine both growth and survival (Fry 1947; Golovanov 2006) and require fish to use a greater variety of habitats to complete their life history (Goniea et al. 2006; Nielsen et al. 1994). Finally, the presence of pollutants can force fish to allocate resources away from growth (Silby 1996) and directly reduce survival (Hollis et al. 1999).

Methods

Literature search

To investigate the approaches and predictor variables used to study salmonid production, we searched for peer-reviewed papers on salmonid production in both lentic and lotic systems. Papers were identified using Web of Knowledge (Thomson Reuters, New York City, New York, USA) and the following keywords and Boolean operators: (lentic or lake or reservoir or pond or lotic or stream or river or creek) and (trout or Salmo* or char or grayling or *Oncorhynchus* or *Salvelinus* or *Thymallus*) and (producti* or biomass or abundance or density or standing crop or yield). The search period was 1966–2012. Using Web of Knowledge produced a temporal bias of papers found because prior to the early 1990s, the database only includes paper titles, whereas both titles and abstracts are included after the early 1990s. Consequently, we were less likely to encounter relevant keywords prior to the early 1990s.

We did not limit our review to papers that measured fish production as it is strictly defined because this would have reduced the number of papers from which to draw insights. Rather, we included papers that focused on related measures of population size (biomass, abundance, density, standing crop, and yield) and growth, because these surrogate measures are likely to reflect the factors that are important in controlling fish production. We did not include the term "population" in our search criteria because we wanted to avoid reviewing studies that focused on describing specific fish populations or stocks (e.g., Chinook salmon (*Oncoryhnchus tshawytscha*) in the Snake River), but which did not evaluate factors controlling production. Likewise, we did not include "growth" in our search terms to avoid studies focused on individual fish and those that reported on physiological rates that influence consumption and growth (e.g., gastric rates of evacuation). However, we did retain papers that focused on population or growth as primary response variables in our final analyses, provided that they investigated how these parameters responded to independent predictor variables (see Predictor variable categories used by researchers section below).

Our initial search yielded 7016 peer-reviewed papers, of which 2742 addressed lentic and 4274 addressed lotic ecosystems. We then reviewed abstracts to determine if salmonid production or related measures of production were actually foci of the papers. This narrowed the number of papers from 7016 to 564, which were read and classified according to six major categories: journal, year published, study system (lentic, lotic, or both), taxa studied, main study approach (correlation, experimental, modeling, or descriptive), and predictor variables measured, which were further categorized into five major categories (see section below and Table 1). We also assessed whether researchers found a statistically significant effect of each predictor variable on salmonid production or a related measure.

To determine the main study approach used in each paper, we adopted the following definitions. Correlation approaches involved quantitative analysis relating salmonid production (growth, density, etc.) to quantitative measures of predictor variables (e.g., amount of chlorophyll *a*, cover). Descriptive approaches were similar, but did not involve a quantitative assessment of the strength of the independent and dependent variables. Modeling approaches included bioenergetics applications and studies that used simulations to determine limiting factors on salmonid populations. Finally, experimental approaches involved quantitative modification of one or more predictor variables relative to a control and related measures of salmonid production.

Predictor variable categories used by researchers

Five major categories of predictor variables were identified: physical, temperature, fertility, pollutants, and biotic (Table 1). Although individual variables could often have been placed in multiple categories, we placed each variable into a single category based on our understanding of the most common application of variables in the freshwater science literature. The physical category included predictor variables such as depth, cover, and geomorphic structure (e.g., riffle–pool sequences). We chose to categorize water temperature separately from other physical variables because it influences organisms in fundamentally different

Table 1. Four major categories examined in salmonid production studies and variables associated with these categories.

Variable	Lentic %	Lotic %
Physical	***n* = 40**	***n* = 260**
Depth; light	37	26
Size; width; area	15	21
Velocity; gradient; discharge	0	44
Cover; undercut banks; large woody debris; artificial structures (habitat); macrophytes; physical complexity	22	58
Substrate	10	18
Riffle–pool	0	19
Land use (not pollutant focused)	5	15
Barriers (culverts, dams, etc.)	5	5
Other physical	32.5	16
Fertility	***n* = 73**	***n* = 88**
Prey abundance	55	50
Phosphorus; nitrogen	34	34
Alkalinity; conductivity; total dissolved solids; salinity	14	16
Terrestrial subsidies	0	16
Phytoplankton production	12	2
Chlorophyll	7	3
Other fertility	7	18
Pollutants	***n* = 18**	***n* = 43**
pH	56	35
Sediment	0	49
Pesticides; herbicides; organics	22	7
Land use (pollutant focused)	0	9
Metals	11	2
Other pollutants	6	16
Biotic	***n* = 82**	***n* = 116**
Competition	46	75
Predation	35	5
Introduced species	27	15
Fishing; angling	26	6
Other biotic	1	9

Note: Temperature, a fifth major category, is not included here, because it had only one variable (temperature). Percentages indicate the proportion of studies in each independent predictor variable within each major category. These sum to more than 100% because researchers sometimes studied more than one variable. Two papers that studied both lentic and lotic systems are not included.

ways than other physical factors such as depth and substrate. Furthermore, there is no consensus among researchers regarding the classification of water temperature; it may be included with bioenergetics and food availability, treated as a pollutant, or combined with other water quality criteria that affect the chemical composition of lakes and streams. The fertility category included direct measures of nutrient levels and surrogate measures such as alkalinity. It also included metrics of primary production and prey availability. Thus, "fertility" as used here is similar to the "bottom-up" terminology used by many ecologists and "edaphic factors" sometimes used in limnology. The pollutants category included both human-introduced contaminants and naturally occurring compounds whose levels are often altered by human activities (e.g., pH was included in the pollutants category because it is often altered by industrial pollution). The biotic category reflected species interactions other than prey availability. Within this category, we included studies that investigated predation, competition (interspecific or intraspecific), angling, and invasive species. Many studies addressed more than one of the five categories and more than one predictor variable within a category. For instance, a study may have focused on depth as a physical habitat variable, as well as competition with an invasive species. In these cases, we recorded each predictor variable included in the study.

Data analysis

We calculated publication rates on fish production by counting the number of studies published per year over specific time intervals. Beginning in 2012, we worked backward in 5-year increments and grouped those published between 1978 and 1992. Additionally, we calculated publication growth rates for lentic and lotic studies and compared them with an estimated publication rate for the natural sciences (Larsen and von Ins 2010). Owing to the potential temporal bias associated with using Web of Knowledge, we estimated the publication growth rate based on articles published only between the years 1990 and 2012.

To determine if researchers studying salmonid production in lentic and lotic systems published in different venues, we calculated the Bray–Curtis dissimilarity index (BC; Bray and Curtis 1957) using journals as "species" to determine how different the two groups were

$$BC = \frac{\sum |x_{ij} - x_{ik}|}{\sum (x_{ij} + x_{ik})}$$

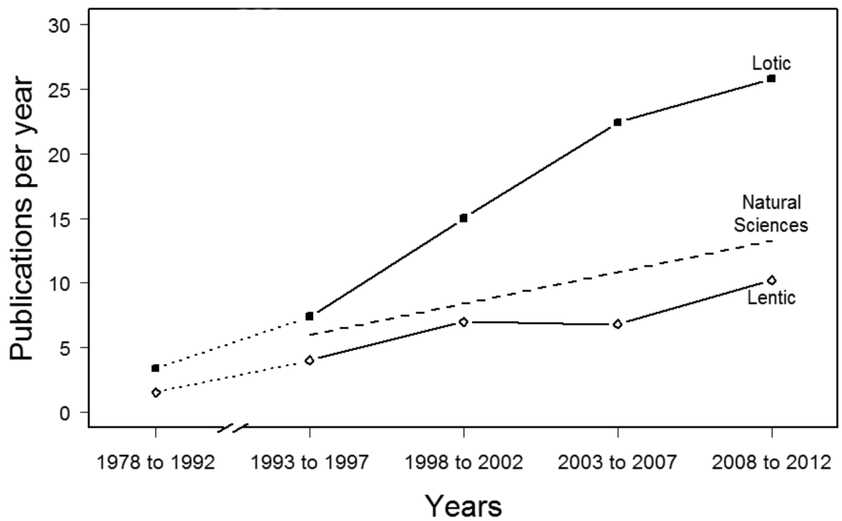
where x_{ij} and x_{ik} refer to the quantity of species i (journals) and systems j and k (river or lake). Using this index, a value of 0 would indicate that lentic and lotic researchers published in the exact same journals, while a value of 1 would indicate no overlap between journals.

To investigate whether river and lake researchers evaluated similar controls of fish production, we calculated the proportion of all lotic and lentic articles that investigated each of the major control variable categories (Table 1). In addition, we examined temporal trends in the frequency with which major control variables were studied.

We employed a series of analyses to address whether differences between lentic and lotic researchers were justified ecologically or based on a priori assumptions. First, we calculated the proportion of papers that examined multiple categories of predictor variables. Our rationale for this analysis was that if researchers are harboring a priori assumptions about important variables controlling salmonid production, they are more likely to focus on a single control variable category. In contrast, researchers are more likely to examine multiple predictor categories if they do not harbor a priori assumptions. Second, we looked at the distribution of study approaches (correlation, modeling, experimentation, or descriptive) to determine whether lentic and lotic researchers used approaches with similar frequency. Given the relative strength of experiments in assessing causation, we were especially interested in how frequently experimental approaches were used to study fish production relative to correlative, modeling, and descriptive approaches. We also examined the distribution of predictor categories within studies that used only experimental approaches. Our reasoning for this was that if researchers base their choice of control variable(s) on biologically justified controls on fish production, then researchers should be assessing all variables equally in controlled experimental settings, which would provide supporting data that one or a few variables are dominant controls on fish production.

Finally, we looked at the proportion of papers in both lentic and lotic systems that reported significant or nonsignificant results for each of the five predictor categories. Here, our null hypothesis was that the most frequently evaluated control variables should also be the variables that most frequently have significant effects on salmonid production. We also performed this same analysis for a subset of papers that examined multiple control variable categories in a single study. In these analyses, we considered a paper to report significant results for a variable category if at least

Fig. 2. Growth in the number of publications on salmonid production appearing in Web of Knowledge between 1978 and 2012 in lentic (lake and reservoirs) and lotic (river and stream) systems. The mean publication trend for natural sciences is from Larsen and von Ins (2010), and its *y*-axis intercept was arbitrarily assigned so that the slope could be shown. Note that data points prior to 1993 cover a 15-year period and that these numbers are biased downward because of the keyword structure of Web of Knowledge (see text).



one of the individual variables studied within a category was found to significantly impact salmonid production.

When appropriate, we used Pearson χ^2 tests or goodness-of-fit χ^2 tests to gauge the statistical significance ($\alpha < 0.05$) of observed differences between lentic and lotic systems. In some cases, groups in χ^2 analyses were not strictly independent, primarily because individual papers sometimes studied more than one predictor variable category. In such cases, the sample size was inflated and thus we interpreted any borderline significant results cautiously. These statistical analyses gauged whether some control variables limit fish production in both lake and river systems, which variables were routinely ignored in either lake or river systems, and highlighted whether variables that were significant in either lake or river systems should be assessed across system type.

Results

Patterns in publication activity

Papers that evaluated salmonid production in lotic and lentic systems increased markedly between 1978 and 2012 (Fig. 2). The number of papers published per year on salmonid production was 2.5 times higher for lotic systems than lentic systems. The mean annual growth rate of salmonid production publications from 1990 to 2012 was 5.6% and 8.3%·year^{-1} for lentic and lotic, respectively. The growth rate of publications for lentic systems was similar to the journal publication growth rate for natural sciences (5.3%·year^{-1}) for the period 1997–2006 (Larsen and von Ins 2010), but the growth rate for lotic systems was greater.

Articles focused on salmonid production were published in a wide range of journals ($n = 94$). However, several journals served as more typical outlets. A substantial proportion of the 564 papers we reviewed were published in *Transactions of the American Fisheries Society* (27%), *Canadian Journal of Fisheries and Aquatic Sciences* (17%), or *North American Journal of Fisheries Management* (8%). Combined, articles from these three journals comprised 43% of lentic studies and 46% of lotic studies. Approximately half of the journals included in our analysis had only one paper on salmonid production, indicating those journals publish papers on broad or varied topics or that fish productivity is not an emphasis of the journal.

Lentic and lotic researchers often published in different journals, as reflected by our calculated value for the Bray–Curtis dissimilarity index (BC = 0.58). The observed lack of overlap may be partially explained by journal focus and target audience. For example, *River Research and Applications* has an obvious focus on lotic systems, whereas *Journal of Great Lakes Research* is generally more focused on lentic systems and likely targets a broader audience of freshwater biologists. Nevertheless, for several journals, the proportion of studies on lentic and lotic systems was unequal for unexplained reasons. For example, *Fisheries Research* has published six lentic studies, but no lotic studies. In contrast, the *Journal of Applied Ecology* and *Ecological Research* both have published four lotic studies but no lentic studies.

Papers addressing lotic and lentic systems studied a range of salmonid species; however, we observed several distinct and significant differences in the genera that were studied (Fig. 3; χ^2 = 73.4, df = 6, $P < 0.005$). The biggest difference we found was that there were far more studies of *Salvelinus* in lentic systems than expected under a random distribution and fewer studies of *Salvelinus* than expected in lotic systems. The difference was largely due to a large number of studies on lake trout (*S. namaycush*) in lakes, a species that is seldom observed in rivers. We also found many more studies focused on the *Salmo* and *Oncorhynchus* genera in lotic compared with lentic systems.

Do river and lake researchers evaluate similar fish production predictors?

As we hypothesized, predictor variables differed significantly between lotic and lentic researchers (Fig. 4; χ^2 = 73.5, df = 4, $P < 0.001$). Papers considering physical variables comprised 65% of lotic studies but only 25% of lentic studies. Biotic variables (e.g., competition and predation) were the most frequently studied variables in lentic systems (51%) and were the second most important variable group in lotic systems (29%). Fertility factors such as nutrients and prey abundance were studied frequently by lentic researchers (45%), but less often by lotic researchers (22%). Temperature was studied relatively equally by lentic and lotic researchers (17% and 22%, respectively). Pollutants were studied infrequently by researchers studying fish production in either lentic (11%) or lotic (11%) systems.

The distribution of predictor variables studied in lentic and lotic systems has been relatively consistent through time (Fig. 5). A 2 × 5 contingency table analysis of predictor variable distribution through five time periods during 1978–2012 indicated that there was no significant temporal difference for either lentic (χ^2 = 11.5, df = 16, $P = 0.78$) or lotic systems (χ^2 = 14.0, df = 16, $P = 0.60$).

Fig. 3. Salmonidae genera studied in production analyses of lentic and lotic systems. The "Various" category includes studies where more than one genus was analyzed. The asterisk (*) indicates that the obsolete taxon, *Salmo gairdneri*, was categorized as *Oncorhynchus* in our analyses. The genus *Prosopium* was examined in only one instance from a lotic system and is not shown in the figure.

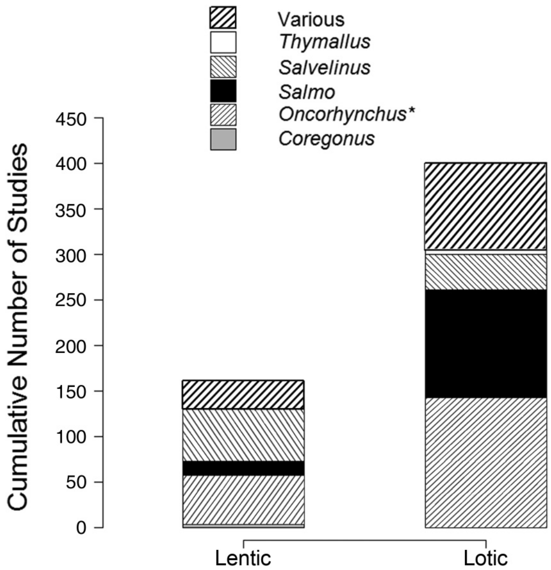


Fig. 4. Percentage of studies that examined different major categories of predictors of fish production in lentic (lakes and reservoirs) and lotic (streams and rivers) systems. The term fertility refers to nutrient and prey abundance variables and is considered synonymous with "bottom-up" controls. Within each system (lentic or lotic), percentages sum across study factors to more than 100% because researchers sometimes studied variables in more than one category. Numbers above histogram bars show the total count of papers for each category.

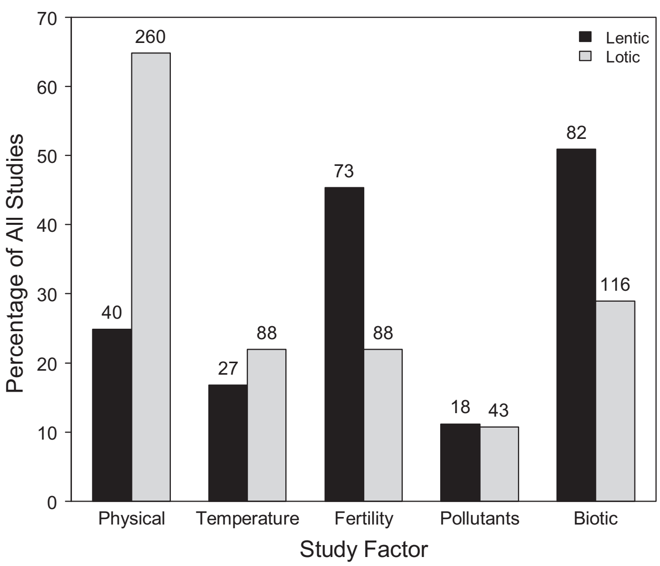
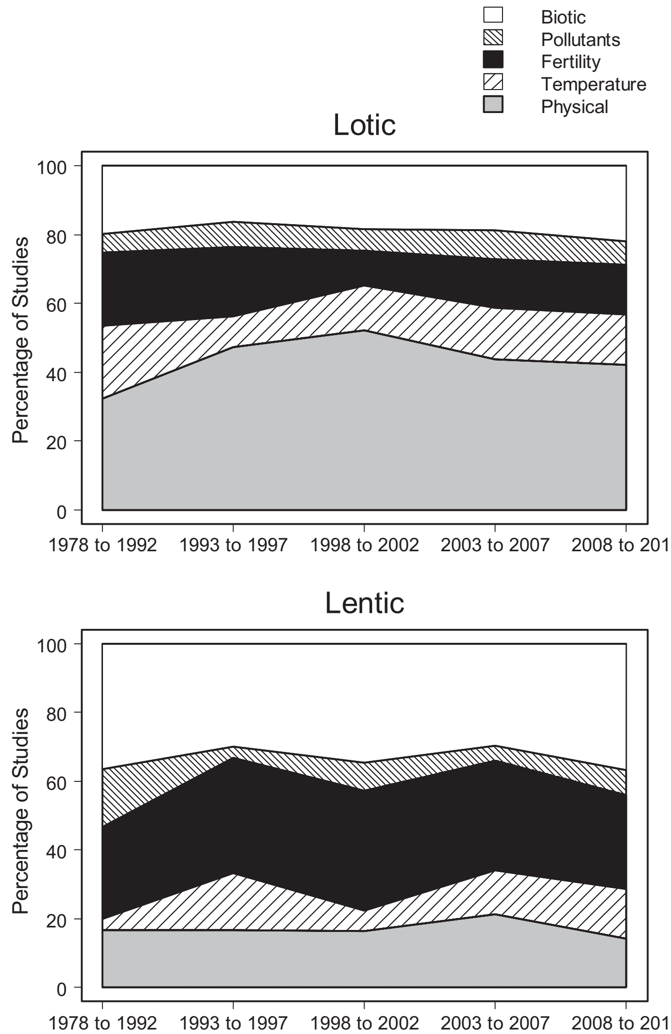


Fig. 5. Temporal trends in the frequency with which major categories of fish production controls were studied from 1978 to 2012. These trends were not significant for either lentic (P = 0.78) or lotic (P = 0.60) systems (χ^2 contingency table). Within each time interval, actual percentages summed to more than 100% because researchers sometimes studied more than one predictor category, but here the results were scaled to sum to 100%.



We found that lotic and lentic researchers focused on a single predictor category in 64% and 63% of studies, respectively. Thus, scientists were nearly twice as likely to limit their analysis to a single predictor category as they were to study multiple predictor categories simultaneously, regardless of whether they worked in rivers or lakes. In lotic systems, physical factors were studied most frequently in isolation, whereas in lentic systems, fertility or biotic factors were studied most often in isolation (Fig. 6). Of studies that examined multiple predictor categories, physical and fertility (25% and 27% in lentic and lotic systems, respectively), physical and biotic (22% and 33%, respectively), and fertility and biotic (46% and 12%, respectively) were the most common category combinations.

In both types of systems, researchers disproportionately used correlative approaches compared with descriptive, experimental, and modeling study methods (Fig. 7), as indicated by significant differences from a uniform distribution in both systems (lentic: χ^2 = 24.1, df = 3, P < 0.001; lotic: χ^2 = 269.5, df = 3, P < 0.001). Lotic researchers, in particular, relied on correlation analyses (60%) more than the other approaches. Within experimental studies, which comprised 24% and 22% of the studies in lentic and lotic systems, respectively, there were significant differences in the predictor variables that were studied (lentic: χ^2 = 19.9, df = 4, P < 0.001; lotic: χ^2 = 61.6, df = 4, P < 0.001). Lentic researchers most frequently modified fertility (e.g., nutrient level; 41%) and biotic factors (e.g., predator presence versus absence; 49%), whereas lotic

Fig. 6. Proportion of predictor variable categories reported in papers that examined only one predictor variable category (e.g., physical, biotic) in lentic and lotic ecosystems.

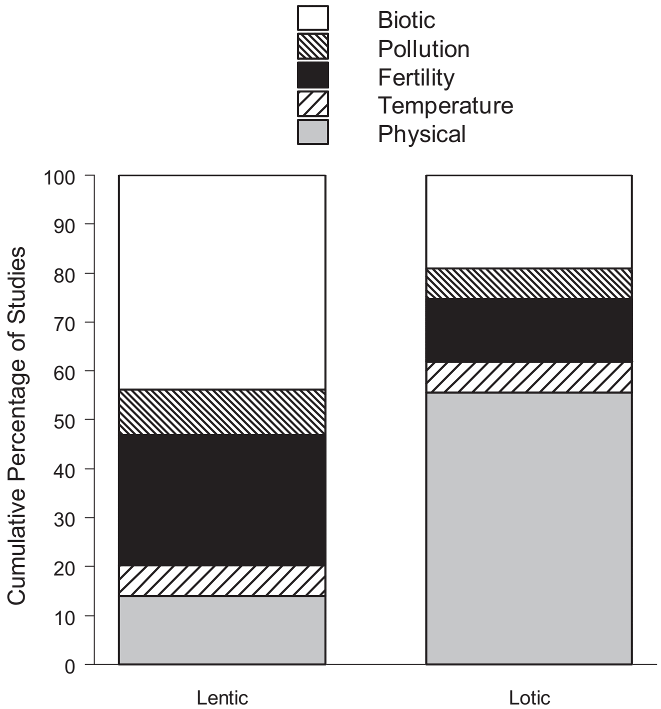
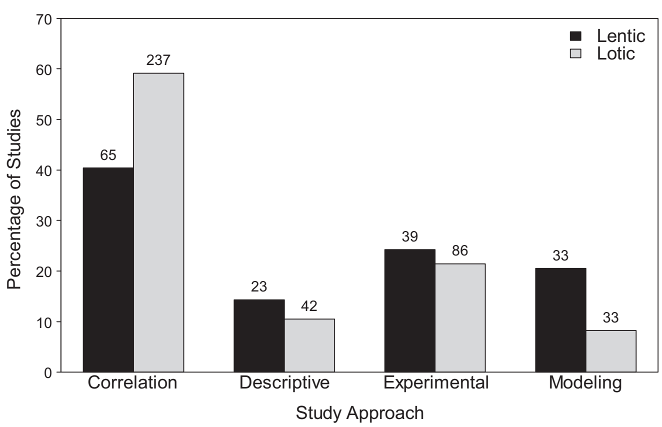


Fig. 7. Percentage of scientific approaches used for salmonid production studies in lentic and lotic ecosystems. Papers that used multiple study approaches (n = 4) and that studied both lentic and lotic systems (n = 2) are not included. Numbers above bars give the total number of papers in each category.

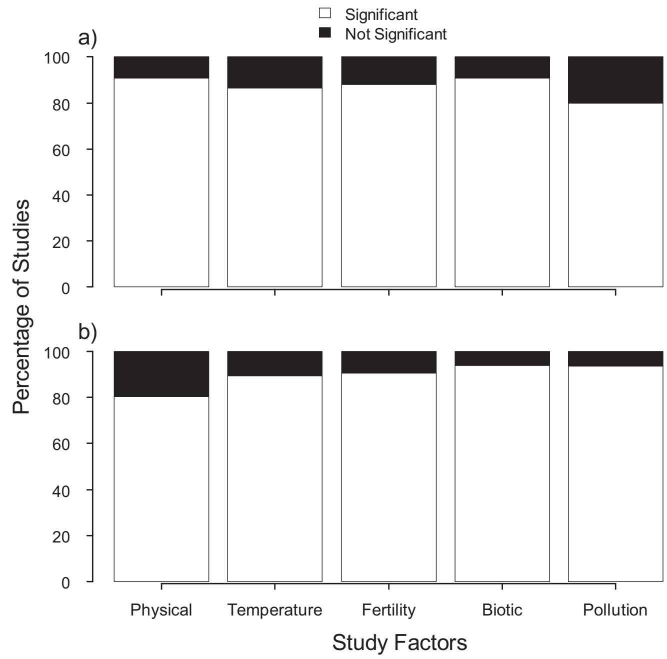


researchers most often experimentally manipulated physical factors (e.g., log and boulder addition; 49%) and, to a lesser extent, biotic factors (35%).

Are existing differences between lentic and lotic researchers justified ecologically?

Our review of published results indicated differences between the frequency with which predictor categories were studied and the frequency with which those categories produced significant effects on salmonid production. For example, many lotic researchers measured only physical factors, but our review indicated that temperature, pollution, and biotic variables were just as likely to influence salmonid production (Fig. 8*a*). In lotic systems, fertility predictors were reported to have significant effects in 88% of the

Fig. 8. Proportion of studies that reported statistically significant predictors of salmonid production by category type for lotic (*a*) and lentic (*b*) systems. Note the difference between the frequency of individual control variable categories that significantly affect salmonid production (this figure) and the frequency of individual control variable categories that were actually studied (Fig. 4).

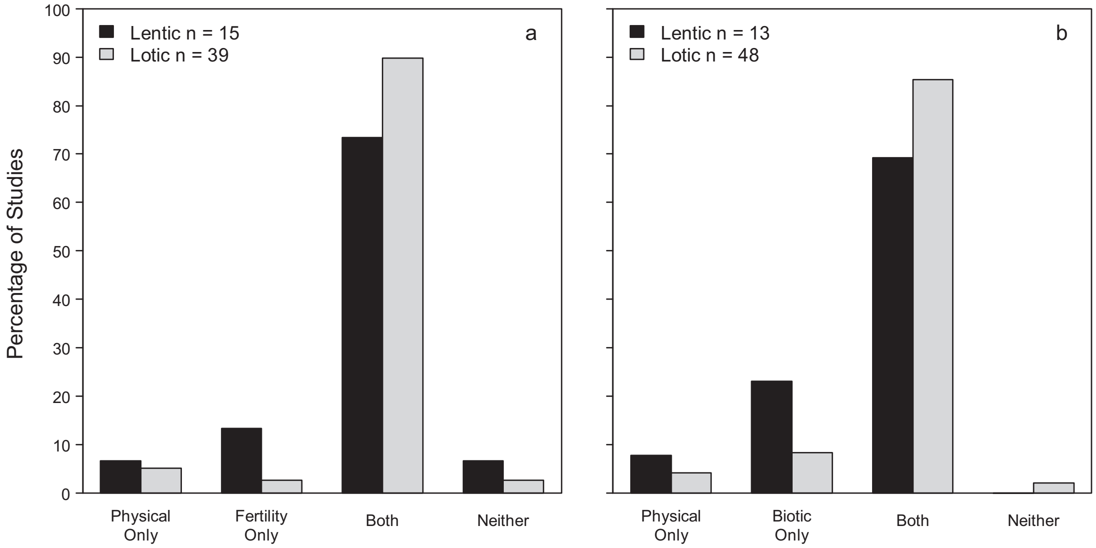


studies, whereas physical factors were only slightly more likely (91%) to be significant. Considering that lotic studies actually evaluated fertility factors in only 22% of their analyses, this discrepancy means that researchers often ignore factors that potentially limit salmonid production. Likewise, 80% of lentic studies evaluating physical predictors reported significant effects. This percentage is just slightly less than the reported significance for both fertility and biotic controls (Fig. 8*b*) and contrasts sharply with the proportion of lentic studies that evaluated physical controls (25%). When researchers did simultaneously evaluate more than one predictor category, they frequently found significant predictors in both categories. For example, when both physical and fertility factors were studied simultaneously (Fig. 9*a*), both predictors were significant in over 75% of the studies, and rarely was just one category of predictor variable found to be significant. Similar results were obtained when physical and biotic factors were studied simultaneously (Fig. 9*b*).

Discussion

Our results indicate that there has been tremendous growth in scientific efforts to understand controls on salmonid production over the last two decades (Fig. 2). However, trends stemming from a priori assumptions regarding which factors affect fish production in both lentic and lotic systems have potentially led researchers away from a holistic approach. If a considerable proportion of research effort has ignored potentially important predictor variables, fish population management will likely be inefficient; or, to return to our Liebig–Sprengel barrel analogy, much effort could go into fixing and raising unimportant staves without a coincident increase in fish production (Fig. 1). Our analysis indicates that there are marked differences in predictor variables studied by lake and river researchers and that these differences may have limited ecological justification.

Fig. 9. Percentage of salmonid production studies that reported significant effects of multiple control variable categories. For simplicity, we only show studies that evaluated both physical and fertility factors (*a*) and physical and biotic factors (*b*). Multiple control variable categories frequently were statistically significant predictors of salmonid production.



In studies of salmonid production, lake researchers have largely focused on fertility and biotic variables, whereas river researchers have focused primarily on physical attributes. This pattern emerges regardless of whether all the papers in our literature search are considered (Fig. 4) or just those that studied a single predictor category (Fig. 6). Further, a majority of studies focused on a limited number of specific predictors, particularly cover, velocity, and competition in lotic systems and prey abundance, nutrients, competition, and predation in lentic systems (Table 1).

Previous reviews on salmonid and total fish production have also revealed the parochial views of lentic and lotic researchers. First, nearly all previous reviews focused on either rivers (Almodóvar et al. 2006; Fausch et al. 1988; Hoyer and Canfield 1991) or lakes (Bachmann et al. 1996; Downing and Plante 1993; Hanson and Leggett 1982; Morgan 1980), but seldom on both. Focused reviews of fish production in lakes and reservoirs found that fertility factors such as phosphorus and primary production were positively correlated with fish production variables (Bachmann et al. 1996; Downing et al. 1990; Hanson and Leggett 1982; Morgan 1980); however, other than mean depth and area, lake researchers seldom investigated the influence of physical factors such as shoreline refuge habitat. In lotic systems, previous reviews found that researchers often assumed physical habitat was limiting and that managers targeted physical habitat for restoration without assessing alternative limiting factors such as nutrients (Fausch et al. 1988; Kiffney and Roni 2007).

Causes for differences in lentic and lotic perspectives

What has caused this divide in research focus between lake and river researchers? We considered two potential hypotheses. First, we assessed whether the skewed distribution of study approaches was simply an outgrowth of earlier publications that justified those foci. However, the foci in earlier time periods that we examined were no different than more recent decades (Fig. 5), yielding little support for this hypothesis. The Web of Knowledge biased our review toward publications after the mid-1990s when abstracts were searched for keywords in addition to article titles. The inability to search earlier abstracts potentially excluded important early studies assessing limitations to salmonid production, such as those by Binns and Eiserman (1979), Hyatt and Stockner (1985), Lebrasseur et al. (1978), and Oglesby (1977). As a result, only 7.6% of the papers in our analyses were published prior to 1991 (see online Supplemental Table S1[1]). However, the sample size of our study ($n = 564$) was sufficient to capture known trends in salmonid production literature prior to the 1990s, despite exclusion of particular studies. For example, in lake systems, the 1970s and 1980s were a major period for assessing how fish production was driven by bottom-up processes (LeCren and Lowe-McConnel 1980), and >33% of lentic papers in our analysis from this period included fertility factors (see Fig. 5). In river systems, the focus on physical habitat is suggested to have grown from studies on particular fish stocks and other aquatic organisms (Fisher 1997). Thus, while there may be some inaccuracies in the distribution of variables studied prior to the mid-1990s, there is no evidence that differences in factors studied by lentic and lotic researchers arose after many predictors were considered equally.

While there was little support for our first hypothesis, multiple lines of time-independent evidence suggest that differences in research foci between lentic and lotic researchers are often driven by a priori assumptions of important predictors of salmonid production. First, we found that the majority of studies in both lentic and lotic systems examined only one predictor variable category (Fig. 6). Unless such studies were based on unreported preliminary data that strongly implicated the studied variable as the primary control on salmonid production, other potential limiting factors necessarily went unrecognized. Furthermore, researchers who simultaneously examined multiple predictor categories frequently found both types to be significant influences on salmonid production (70%–80% of studies; Fig. 9). For example, Bilby and Bisson (1987) found that emigration of stocked salmon fry from streams in old-growth and clear-cut watersheds was primarily controlled by abundance of pool habitat, but that mortality rates when fry densities were high was primarily controlled by photosynthesis rate and food availability. Although lake researchers frequently focused on fertility factors, physical factors were frequently found to be important as well. For example, in Lake Michigan, Marsden and Chotkowski (2001) found that introduction of

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2014-0210.

artificial reefs attracted lake trout spawners and supported increased fry abundance, unless reefs became fouled with introduced zebra mussels (*Dreissena polymorpha*).

Our review indicated that researchers are using primarily correlation and descriptive analyses of salmonid production parameters (Fig. 7), with relatively little experimental work. The limited effort invested in determining causal relationships via experimentation suggests a greater opportunity for inherent biases to drive the choice of study variables and could lead to mismanagement of fishery resources by targeting correlative but not necessarily causative factors (Havens 1999). Lack of experimentation was particularly prevalent in lotic analyses, where 60% of the studies used correlation and 10% used descriptive approaches. Of course, correlation studies require less time and money than controlled experimentation, and the reliance on correlation approaches would be justified if experimental studies had consistently shown particular variables as the most influential factors regulating production. However, trends in this regard are not encouraging, as even within experimental studies, physical factors were the dominant predictor variable category in lotic systems and fertility and biotic factors the dominant predictor categories in lentic systems. If researchers were selecting study variables in an unbiased manner, we expected that experimental studies would have shown a more even distribution of predictor categories.

A final result supporting the view that lake and river researchers are biased with respect to the variables they choose to study is the focus on particular predictor categories in lotic and lentic systems does not reflect the proportion of studies reporting a significant relationship between the predictor categories and salmonid production (Fig. 8). Although many lotic researchers measured only physical factors, we found other predictors were just as likely to significantly influence salmonid production (Fig. 8). For instance, Bowlby and Roff (1986) examined physical, biotic, nutrient, and temperature factors as predictors of trout biomass in southern Ontario streams. Even though the authors measured over ten physical habitat variables generally considered important for salmonids, they found that fertility and temperature factors (including the biomass of the microbial community and benthic invertebrates and summer temperatures) explained a greater proportion of the variation in fish biomass. Models including these fertility factors explained 58% of the variance in biomass, whereas models that included only physical habitat factors explained less than 10%. Similarly, despite the primary focus of lentic researchers on nutrients, prey resources, and competition as key drivers, physical factors such as littoral and substrate complexity have often been shown to influence the growth and abundance of rainbow trout (*Oncorhynchus mykiss*) and other species in lakes (Fig. 8; Olden and Jackson 2001; Tabor and Wurtsbaugh 1991; Wurtsbaugh et al. 1975).

We recognize that journal bias against publication of nonsignificant results (Stanley 2005) likely underrepresented the number of predictor categories studied that did not yield significant results. Had we included non-peer-reviewed governmental reports, this bias likely would have been reduced. Nonetheless, potential publication bias does not negate the results of the many studies showing the importance to salmonid production of all of the major predictor categories considered here.

Merging lentic and lotic perspectives

Taken together, our results suggest that a priori assumptions are driving the divergent focus in controlling variables between lentic and lotic systems, as opposed to strong scientific justification based on controlled experimentation and consistent results demonstrating the primary importance of physical habitat variables in lotic systems and fertility and biotic factors in lentic systems. In cases where assumptions are not based on direct experience or knowledge of the system, they minimize the ability to detect the true drivers of salmonid production. The importance of taking a broad, objective view of potential factors controlling fish production has been emphasized in previous reviews (e.g., Fausch et al. 1988; Randall et al. 1995). We reiterate the suggestion of these authors that more integrated research is needed to better understand how different environmental factors influence fish productivity.

There are, however, some positive indications that researchers studying lentic and lotic systems are converging in their focus. First, some recent textbooks on limnology and aquatic ecology include treatments of both lentic and lotic systems (e.g., Dodds and Whiles 2010; Kalff 2002; Wetzel 2001). Consequently, future researchers and managers will appreciate the commonality of factors controlling production in both ecosystem types. Second, the demonstrated importance of marine-derived nutrients delivered to rivers is increasing awareness of the potential influence of fertility factors on fish production in river systems (e.g., Bilby et al. 1996; Cederholm et al. 1999; Kohler et al. 2013). This newfound awareness, coupled with the large amount of basic research on nutrient spiraling through streams (e.g., Hall et al. 2009; Mulholland et al. 2002) and experimental evidence that nutrients can stimulate production at all trophic levels (e.g., Johnston et al. 1990; Peterson et al. 1993; Slavik et al. 2004), indicates that lotic researchers are recognizing how fertility factors can control fish production. Third, lentic researchers are increasingly emphasizing the importance of the littoral zone in controlling ecosystem production processes (Vadeboncoeur et al. 2002; Vander Zanden and Vadeboncoeur 2002), which may lead to more work focused on how physical structure influences fish production in lakes. Fisheries researchers have also begun to quantitatively and experimentally assess the importance of physical structures in lakes for fish growth, survival, and abundance (Gaeta et al. 2014; Schindler and Scheuerell 2002; Tabor et al. 2011). Fishery managers working in lakes have long attempted to increase angling opportunities by adding physical refuges (Brown 1986; Ratcliff et al. 2009; Seaman and Sprague 1991; Tugend et al. 2002) or spawning habitat (Bolding et al. 2004; Fitzsimons 1996), but there have been few attempts to quantitatively assess whether overall fish production is increased by these activities.

Data gaps, limitations, and the future

Although we did not explicitly consider studies that focused on recruitment in our analysis, we recognize that factors affecting recruitment can impact production (Milner et al. 2003). For example, analyses of time-series data on salmonid populations suggest that a majority of variation in production rates (or year class production) can often be explained by variation in juvenile recruitment (Elliott 1994; Lobón-Cerviá 2005; Whalen et al. 2000). One implication of this body of research is that the controlling factors that influence salmonid production may be life-stage-specific, or at least those factors determining recruitment rates at early life stages may have legacy effects on population productivity that managers should consider. A post hoc addition of the term "recruitment" to our original search in Web of Knowledge indicated that this keyword increased the number of studies similarly for lotic (8%) and lentic (9%) systems. Therefore, recruitment has received similar attention in lentic and lotic systems. A future synthesis could explore the implications of past findings regarding the role of recruitment in fish production in lakes and streams.

Our review revealed several deficits in our understanding of factors controlling salmonid production where additional scientific effort could help integrate lentic and lotic research. Most surprising was the lack of studies addressing how pollution may limit fish production. Only 11% of both lentic and lotic studies included pollution variables as control factors, and most of these focused on pH (acid rain) or sediments (Fig. 4; Table 1). Although these percentages would have been higher if we had included temperature in the pollution category, the results nevertheless revealed a paucity of research analyzing pollution effects on salmonid production. Improved understanding and quantification of emerging contaminants of concern and threats to fish populations in freshwater systems is needed (Matthiessen and Sumpter 1998; Purdom et al. 1994). Apparently, managers are relying heavily on laboratory-derived toxicological studies (EPA 2006) without field-based analyses to infer how pollutants are influencing salmonid production.

We were also surprised by the lack of research on how fertility factors influence salmonid production in lotic systems (Fig. 5), given the recent focus on marine-derived nutrients as discussed above. Our analysis identified only nine studies that related marine-derived nutrients and salmon carcasses to fish production, despite the emphasis on this process in recent years (Kohler et al. 2013; Schindler et al. 2003). This low number of studies may reflect the fact that many marine-derived nutrients studies have focused on effects at trophic levels below fishes (e.g., Kohler et al. 2008; Tiegs et al. 2011; Wipfli and Baxter 2010), which would not appear in our literature review. The lack of growth in the proportion of water temperature studies in both systems was also surprising, given the likely importance of managing for altered temperatures under climate change (e.g., Keleher and Rahel 1996; Null et al. 2013), and suggests more effort may be needed to help manage fisheries in thermally dynamic environments.

Another deficit in our understanding is how longitudinally connected lentic and lotic ecosystems interact to control salmonid production. Our search produced only two studies where researchers simultaneously addressed salmonid production in both lentic and lotic systems, one of which studied fish in beaver ponds and the main channel on a river system (Lang et al. 2006), and the other studied different salmonid species in lake and river habitats (Hayes et al. 2009). Our search terms did not target factors controlling spawning, which often plays an important role in regulating fish production (Marshall 1996). Consequently, we likely underrepresented studies focused on species with adfluvial life history strategies, which are common among salmonids (Beauchamp and Van Tassell 2001; Brenkman et al. 2001; Noakes 2008), and this may explain the low number of integrated studies in our review. Even so, the rarity of non-spawning studies linking lentic and lotic systems suggests that integrated research could provide unique insights into salmonid production.

Finally, we found that the diversity of salmonids was not proportionally represented in the literature, which was dominated by studies on *Oncorhynchus*, *Salmo*, and *Salvelinus* (Fig. 3). This may be indicative of a geographic concentration of studies. In particular, *Salvelinus namaycush* is a focal species in the Great Lakes region, and *Oncorhynchus* is a focal genus in the Pacific Northwest, and both are regions of concentrated research efforts. Understudied systems, such as grayling (*Thymallus arcticus*) in Arctic environments, provide a unique opportunity to determine whether factors deemed important to salmonid production apply equally well to areas outside regions of intensive research.

We have identified a distinct difference in research focus between lentic and lotic systems with regard to salmonid production. In addition, we have provided evidence that in many cases, lentic and lotic scientists have preconceived assumptions about drivers of fish production and that these a priori assumptions subsequently influence the variables measured. This is reflective of divergent historical trajectories in lake and river science, with the former developing a focus on nutrient status as an important regulator of production at different trophic levels and the latter developing a focus on important physical habitat requirements for specific fish species.

Lentic and lotic researchers studying fish production have much to learn from each other's approaches, and our understanding of fish production would advance more rapidly if the perspectives of lake and river researchers were combined into a more unified and comprehensive view. Lentic researchers should avoid a strict focus on fertility and biotic controls and include the role of physical habitat, water temperature, and pollution as potentially important factors influencing fish production. Lotic researchers should more completely integrate fertility factors with traditional emphases on physical controls of production. We found that publications are somewhat separated by journal in the two disciplines, suggesting that special journal issues dedicated to integrated research could facilitate learning across systems and disciplines. Additionally, both groups should rely upon experimental analyses more frequently and endeavor to formulate multiple working hypotheses (Chamberlin 1965) to address what factor or factors are ultimately limiting fish production in their systems.

Our analysis focused on salmonid production, and the exact patterns we observed are likely to vary across different groups of fish. For example, salmonids tend to be pollution-sensitive, and much salmonid research has taken place in relatively pristine environments, where the role of pollution would naturally be de-emphasized compared with more pollution-tolerant groups. A more complete analysis of the literature will be needed to determine the generality of our conclusions across taxa. Nevertheless, the recommendation that multiple predictor variables be considered when studying fish production is applicable to all taxa. Applying this recommendation will minimize pitfalls from addressing only preconceived and favored hypotheses, yield a better understanding of the factors that control fish production, and ultimately improve fish management by focusing resources on factors that truly limit fish production.

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