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Different approaches for studying fish production: A review

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Abstract
Biased viewpoints of fisheries researchers may impede scientific advancement and successful management if factors influencing productivity are not recognized. We analyzed 564 peer-reviewed published articles between 1966 and 2012 that looked at salmonid development or proxy factors (e.g. production, development, productivity, populace) and grouped these under five main explanatory variables classifications: physical environment, productivity (i.e. minerals, bottom-up), microbial, weather, and contamination. The review showed that river researchers predominantly examined physical habitat (65% of studies) and lake investigators actions are determined biodiversity (45%) and biotic (51%) factors. However, inadequately factors have also been statistically important predictors of output for lake and river systems and in conjunction with other data, indicate that unwarranted prior hypotheses can determine the selection of predictor factors evaluated. Increased awareness of possible limiting factors for fish production, increased research activity on under-studied genera, and increased publication in broad-based journals would likely encourage convergence between lentic and lotic viewpoints and enhance fisheries management.

Keywords: fish, production, microbial, weather, and contamination

Introduction

One of the primary main objectives in the study of fresh water ecosystems is to better understand controls on primary and secondary production, particularly the production of fish species of economic, recreational, and conservation importance [1]. Despite novel challenges and opportunities posed by unidirectional flow in rivers, freshwater biota in all aquatic systems faces 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 text books, 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 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 [2, 3, 4]. Applying the Liebig–Sprengel Law of the Minimum as the conceptual framework, fish production may be visualized as a wooden barrel filled with water. 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 [5, 6, 7, 8]. 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 [8] and Hynes' The Ecology of Running Waters [9] virtually excluded discussion of other freshwater systems. Much of the early work in lakes addressed ecosystem-level questions such as controls on primary production [10], 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 [11, 12, 13], which resulted in a focus on physical habitat requirements for different groups of organisms [14, 15] 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; [16]. Rarely are physical characteristics other than mixing cycles in corporate 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.,[17, 18, 19]), 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 [20]. 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, [21] found researchers commonly assumed physical habitat limited production without testing other factors such as competition, fishing mortality, or nutrients. Similarly, [22] 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 [23, 24]. However, a recent meta-analysis found a direct link between physical habitat and fish biomass and abundance in both lentic and lotic systems [25]. Additionally, [26, 27] found strong correlations between physical habitat variables and fish production in the Laurentian Great Lakes [28], 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 [29, 30]. 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 prior 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 in habit 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 [31]. 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; [32]) and operate at the population level (e.g., density-dependent mortality; [33, 34]) determine the potential for fish production. Growth of individual fish is a function of food consumption and energetic expenditures [35, 36] which are both influenced by competition for prey resources [37, 38] and aspects of the physical environment, including water temperature and light availability [39, 40, 41]. Population size is regulated by density-dependent and density-independent mechanisms, including presence of predators [42], refuge from predation [43], physical conditions [44, 45, 46] and resource availability [47]. Furthermore, trade-offs between resource availability and predation threat may lead to complex dynamics whereby individual survival [48] or growth potential [49] 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 [50, 13, 42], energetic costs for growth [53], and death from harsh environmental conditions [44, 15]. Water temperature controls many physiological processes that determine both growth and survival [56, 57] and require fish to use a greater variety of habitats to complete their life history [38, 49]. Finally, the presence of pollutants can force fish to allocate resources away from growth [50] and directly reduce survival [11].

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 (production 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. 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 chlorophylla, 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. 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.

Our reviewed literature results indicate that there has been tremendous growth in scientific efforts to understand controls on salmonid production over the last two decades. 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 in efficient; 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. 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.

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 [41, 42, 43] or lakes [44, 45, 46], 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 [47, 48, 49]; 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 [50, 41, 42].

Causes for differences in lentic and lotic perspectives

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 [23, 24, 25]. As a result, only 7.6% of the papers in our analyses were published prior to 1991. For example, in lake systems, the 1970s and 1980s were a major period for assessing how fish production was driven by bottom-up processes [36], and >33% of lentic papers. In river systems, the focus on physical habitat is suggested to have grown from studies on particular fish stocks and other aquatic organisms [47]. 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 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. 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). For example, [28] 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, [19] found that introduction of 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, 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 [10]. 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. Although many lotic researchers measured only physical factors, we found other predictors were just as likely to significantly influence salmonid production. For instance, [81] 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 [22, 23, 24]. We recognize that journal bias against publication of non-significant results [25] 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 [16, 17, 18]. 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., [49, 50]. 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. This new found awareness, coupled with the large amount of basic research on nutrient spiraling through streams and experimental evidence that nutrients can stimulate production at all trophic levels, 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 [92, 93], 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. Fishery managers working in lakes have long attempted to increase angling opportunities by adding physical refuges [14, 25, 36] or spawning habitat 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 [34, 45, 36]. 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. 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 [14, 19, 23]. Apparently, managers are relying heavily on laboratory-derived toxicological studies 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, 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 [44, 49, 50]. This low number of studies may reflect the fact that many marine-derived nutrients studies have focused on effects at trophic levels below fishes 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, 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 [44], and the other studied different salmonid species in lake and river habitats [49]. Our search terms did not target factors controlling spawning, which often plays an important role in regulating fish production [24]. Consequently, we likely underrepresented studies focused on species with adfluvial life history strategies, which are common among salmonids [34, 35, 46], 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*. 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 [36] 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.

Conclusion

However the suggestion that several predictor variables be considered when analyzing fish production is applicable to all taxa. Applying this suggestion would mitigate the pitfalls by discussing only preconceived and desired theories would result in a deeper understanding of the variables that influence fish development and potentially improve fish conservation by concentrating efforts on factors that currently limit fish output.

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