

Fish, Productivity

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Introduction

Fishes are a highly diverse group that occupy a wide array of habitats and perform many ecological roles in aquatic systems. Because of the economic and social importance of this varied group, understanding factors that limit their ability to convert food resources into biomass (i.e., fish production) is of broad interest to ecologists and managers working in these systems. Moreover, because fish production represents the total amount of tissue elaborated over time, it is a useful metric to evaluate the status of a population. This article reviews methods of estimating fish production and provides a synthesis of theoretical and empirical evidence of factors that regulate the production of fishes in inland waters.

A general definition of fish production is the total quantity of tissue elaborated by a population over a period of time, regardless of whether or not all of it survives to the end of that time (e.g., $\text{g m}^{-2} \text{ year}^{-1}$). This includes all new biomass accrued by a population during the course of a year via birth and growth minus biomass losses, which might result from factors such as death or starvation and accounts for losses or gains resulting from immigration and emigration. The basic premise is that primary production is converted to fish tissue through a variety of trophic pathways. Although measures of fish standing stock or biomass are not a direct measure of fish production, a review of studies that quantify these variables is also relevant because biomass can be a strong predictor of fish production (Figure 1). In addition to characterizing a fish population with production, the ratio of production to biomass (P/B ratio) is often used to indicate the turnover rate of tissue.

Studies that include estimates of fish production in lakes or streams have been published since the 1950s. There was a surge of research in this emerging field in the 1960s, in association with the International Biological Program, which focused on the productivity of biological resources and human adaptability to environmental change. This ambitious program resulted in several important volumes that provide a comprehensive coverage of methods for estimating fish production as well as comparative studies across systems (see Further Reading). In addition to refining methods, early studies in this field were

largely centered on using this information to benefit the production of sport or commercial fisheries. More recent work has focused on general ecological hypotheses and tests of factors regulating fish production.

The efficiency of converting food to tissue is largely dependent on the individual characteristics of each species. Some species acquire their energy directly from algae or plants; thus, their productivity can be tightly linked to these primary producers. Other fishes may directly consume detritus and, depending on the source of detritus, their growth and production may not be linked to the primary productivity of their immediate habitat. Most fish species are secondary, tertiary, or even higher-order consumers that rely on the availability of organisms that have already assimilated energy from primary producers or detritus. Those consumers can still be tied to autotrophic production, but this association may be weakly linked, as this energy is assimilated over larger spatial and temporal scales. In addition to these food web dynamics, the habitat template in which a fish species lives will often mediate the efficiency of this conversion of energy into body tissue. Moreover, many fishes are capable of migrating among habitats with vastly different levels of primary productivity for forage or escape mortality (e.g., predation or undesirable conditions), further decoupling the linkage between primary production and fish production.

Estimating Fish Production

Secondary production may be estimated in terms of weight, nitrogen content, energy content, and so on. Although energy is the most applicable unit of measure from an ecosystem context, most production estimates are based on weight measurements, which can secondarily be converted into more applicable units for any given context (e.g., carbon, energy, etc.). The basic information needed to estimate secondary production is routinely collected by aquatic ecologists, yet there are several methods that can be used to calculate production. Three methods for estimating secondary production in fishes are reviewed here: two graphical approaches and a numerical approach. These approaches vary in complexity and

thus have associated benefits and limitations. In general, production (P) of any fish population over a time period is expressed as

$$P = (G - Z)B$$

where G is the instantaneous rate of increase in biomass, Z is the instantaneous decrease in biomass, and B is the mean population biomass.

Several population parameters are necessary for estimating fish production: number of individuals, average individual weight, and age structure of a population. The number of individuals in a population (N) can be estimated using a variety of techniques depending on habitat. For example, population sizes of stream-dwelling fishes are typically estimated by simple Petersen–Lincoln mark–recapture methods. In lakes and reservoirs, methods such as hydroacoustics, trawling, or rotenone surveys are used to derive population estimates. Because all estimators of fish production require estimates of mean individual weight and population size, it is logical to measure individual fish length and weight during a population census.

Finally, identifying cohorts within a population is essential to estimate production of a single age-cohort, or when using the age-cohort approach for estimating annual production for the whole fish population as discussed below. There are several methods for characterizing age classes. Perhaps the simplest approach is the length–frequency analysis, which involves plotting the frequency of individuals as a

function of fish length. Different age groups can then be separated based on size, assuming fish length within each age group is unimodally distributed. Because older fish grow at a slower rate than do younger fishes, it is often difficult to clearly distinguish older age classes, particularly for long-lived fishes. A second, relatively easy and inexpensive method for estimating aging fishes in a population is by counting annual marks left on scales, bones, or spines during periods of slow growth. However, such marks are present only in fish that live in systems with notable seasonal variation in growth rates (such as the temperate climates). Also, hard part examination can be easily executed with modest investment of time and energy.

Graphical Approach

Allen's Graphical Method

Allen's graphical method requires the population or cohort size (N_t) to be plotted as a function of mean individual size (w_t) for successive periods of time (Figure 2). Typically, the number of individuals in a cohort decreases over time as a result of mortality (both natural and fishing mortality; Z), and the average weight of individuals in the cohort increases over time as a result of growth (G). Because the area between the x -axis and the trend line $\Delta N \Delta w$ is equivalent to the net rate of increase in biomass ($G - Z$) as a

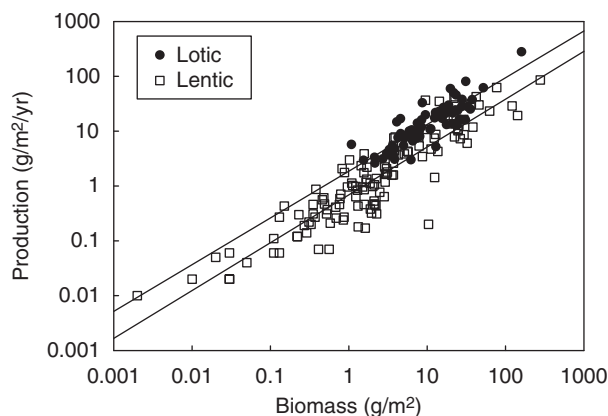


Figure 1 Relationship between fish biomass and production for lotic and lentic waters. Data were compiled from Downing JA and Plante C (1993). Production of fish populations in lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 110–120, Randal RG, Kelso JRM, and Minns CK (1995) Fish production in freshwaters: Are rivers more productive than lakes? *Canadian Journal of Fisheries and Aquatic Sciences* 52: 631–643, and Kwak TJ and Waters TF (1997). Trout production dynamics and water quality in Minnesota streams. *Transactions of the American Fisheries Society* 126: 35–48.

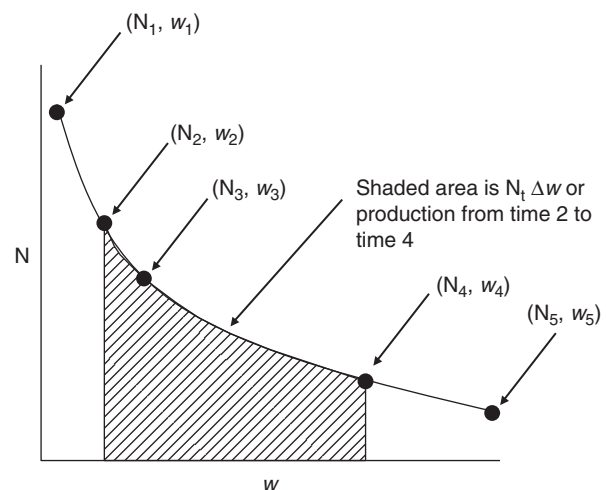


Figure 2 Theoretical example of Allen's graphical method based on five separate estimates of N and w . Adapted from Chapman DW (1971) Production. In: Ricker WE (ed.) *Methods for Assessment of Fish Production in Fresh Waters: International Biological Programme Handbook Number 3*, pp. 199–214. Oxford: Blackwell.

function of mean biomass B (i.e., $P = GB$), fish production can be estimated as function $N_t \Delta w$ or the total area under the curve between any two consecutive time periods.

There are two ways to estimate the area under the curve produced from this approach. If the formula for the curve is known for any sample interval (Δt), the area falling below this curve can be calculated by integration. Alternatively, the area under the curve can be calculated by increment-summing for Δw for any period of time because as the increment Δw approaches zero the function $N_t \Delta w$ approaches P for that time period. Thus, P for any length of time can be approximated by the summation of all small increments of Δw within that time.

The primary benefit of Allen's graphical method is that growth and mortality estimates are indirectly estimated from ΔN and Δw over time. Thus, selection of appropriate growth and mortality models is not necessary. However, the correct shape of the so-called Allen curve, as defined by the function $N_t \Delta w$, is critical for accurately estimating production between any two periods in time. Although a minimum of two consecutive estimates of N and w are needed to produce a curve (i.e., a straight line), a more accurate production estimate can be made with more estimates of N and w during the time interval of interest. Production estimates derived from monthly estimates of N and w over the course of a year are ideal, as this will allow the investigator to quantifying temporal variation in productivity in relation to environmental conditions.

The shape of the Allen curve can also vary across cohorts. For example, fish growth rates decline with age. Likewise, production estimates will vary across age-cohorts. Thus, for accurate fish production estimates, one must follow individual cohorts through time while monitoring decreases in N and increases in w for each age-cohort, which can be summed within cohorts across a time period to achieve an estimate of total fish production. Moreover, it may be difficult to precisely estimate N in young cohorts because it may often be difficult to capture these fishes with traditional sampling gear.

Age-Cohort Method

The age-cohort method differs from Allen's graphical method because it requires only one sample period, which typically is taken at time of annulus formation in the spring in temperate environments (i.e., the beginning of the growing season), and is used to estimate population size (N) and mean weight of each age-cohort comprising the population. Population size (N) of each age-cohort comprising the population is plotted against mean weight for that

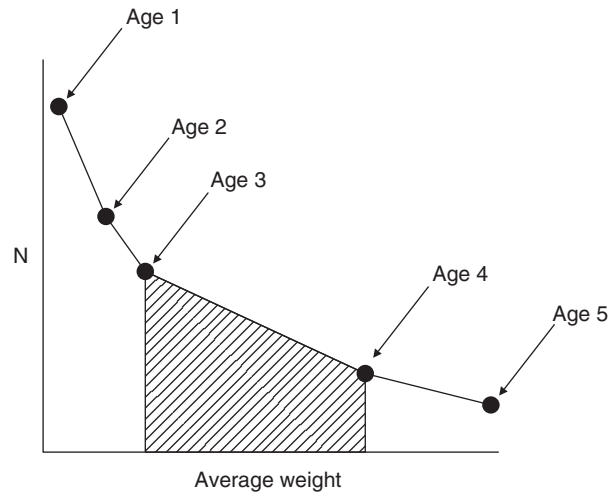


Figure 3 Hypothetical example of the age-cohort method for estimating fish production. The shaded region represents production for 3-year-old age-cohort.

corresponding age-cohort (Figure 3). The difference in N and mean weight across cohorts is used as an indirect estimate of fish growth and mortality. Thus, the slope of the line connecting any two consecutive age-cohorts represents annual mortality and annual increase in average biomass per cohort. Similar to Allen's graphical method, annual production for each age-cohort is estimated as the area under the curve between any two consecutive points and annual production for the whole population is estimated as the total area under the curve.

The age-cohort approach for estimating annual production is computationally simplistic and advantageous when it is difficult or impossible to make repeated estimates of N and w over time. However, an important assumption of this method is that population size and average weight of each age-cohort is similar across years because the change in N and mean weight of different age cohorts is used as a surrogate for repeated samples as in Allen's graphical method. This assumption might be invalid, which will limit the accuracy of the estimate, under a variety of circumstances, particularly when varying environmental conditions differentially affect population growth and recruitment from year to year.

Numerical Approach

Instantaneous Growth Rate Method

Similar to the graphical methods, the instantaneous growth rate method also requires estimates of population abundance (N_t) and average individual fish weight (w_t) over consecutive sample times; however, the instantaneous growth rate method relies on

computation of G and Z using instantaneous models. For this method, the instantaneous coefficients G and Z are estimated as

$$G = \log_e w_2 - \log_e w_1 / \Delta t$$

$$Z = -(\log_e N_2 - \log_e N_1) / \Delta t$$

where w_1 , w_2 and N_1 , N_2 are the mean individual weights and total numbers of fish at times t_1 and t_2 , respectively, and Δt is the time interval between t_1 and t_2 .

The difference between the instantaneous coefficients (i.e., $G - Z$) is the estimated rate of increase in the biomass of the population during any time period (Δt). These coefficients are used in a separate exponential model to estimate average biomass of the population (B) during Δt . The exponential models for increasing or decreasing average biomass, respectively, are calculated as

$$B = B_1(e^{G-Z} - 1) / G - Z$$

$$B = B_1(1 - e^{-(Z-G)}) / Z - G$$

where B_1 is biomass of the population at time 1. Thus, from these independent calculations of exponential coefficients, G , Z , and B , production (P) can simply be calculated as

$$P = GB$$

Because the numerical method is based on exponential growth and mortality rates, this method is an ideal approximation only when exponential conditions are met. However, periods of exponential growth and mortality may be rare, applying only to specific cohorts, over short periods of time or during specific seasons. For example, exponential growth often is the case for young fishes, particularly during the first year of life, and may apply to fishes (particularly young) during a growing season. Thus, G likely is an accurate coefficient under these circumstances. Exponential mortality rates also are likely to apply only under specific conditions. For example, mortality rates of older fishes or during harsh time periods may very well approach an exponential rate. Therefore, much like the graphical method, the exponential method is probably most accurate when the time intervals (Δt) between estimates of N and w are relatively small. However, as Δt becomes very small, the exponential coefficients G and Z become linear and B can simply be expressed as the linear function

$$B = B_1 + B_2/2$$

where B_1 and B_2 are the biomass of the population at t_1 and t_2 , respectively.

Estimates of P using the instantaneous growth rate method may be accurate over longer periods of time between estimates of N and w (e.g., 1 year or more) if G and Z vary in a comparable manner. However, the possibility of G and Z varying similarly over longer time periods is relatively rare. As a result, more complex production models that combine exponential mortality and the von Bertalanffy growth model, which allow for production estimates to be made over longer time periods, are recommended.

Factors Regulating Production

Factors that Affect Growth and Survivorship (Bottom-Up Effects)

The rate of fish production increases when individuals in a population grow faster or have a higher probability of survival. In habitats where energy for fish production originates within the water body of interest, it is reasonable to assume factors limiting the conversion of sunlight into chemical energy would also limit fish growth and survivorship. Accordingly, oligotrophic systems with low primary production also have lower fish production. This pattern is well documented for lakes, as fish production is positively correlated with phosphorus concentrations (Figure 4).

Other abiotic factors that may stimulate primary production, such as physical characteristics of aquatic habitats, alkalinity, total dissolved solids (TDSs) and temperature, may also enhance physiological

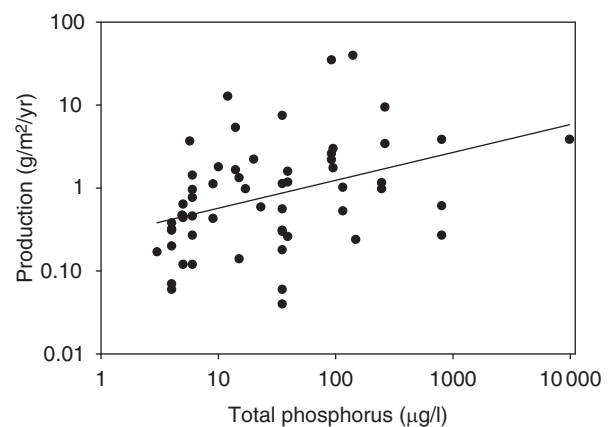


Figure 4 Relationship between total phosphorus and fish production in lakes. Based on data from [Tables 1 and 2](#) from Downing JA and Plante C (1993) Production of fish populations in lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 110–120, and Kelso JRM and Johnson MG (1991) Factors related to the biomass and production of fish communities in small, oligotrophic lakes vulnerable to acidification. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 2523–2532.

performance of fishes and can be positively associated with fish production. For example, shallow lakes with a high proportion of littoral habitat also tend to have higher fish production than do deeper lakes. Rivers with high abundances of shallow off-channel habitats such as side channels and flooded backwaters are also expected to have high fish production. In addition, increased abundance of coarse woody debris in rivers are hot-spots of invertebrate production and can stimulate fish production. Although total fish production is generally positively associated with abiotic factors that stimulate production at lower trophic levels, these relationships are likely unimodal, as fish production should decline in hyper-eutrophic systems because of harsh abiotic conditions that increase mortality rates (e.g., hypoxia, sedimentation on spawning grounds).

The response of fishes to abiotic factors will likely vary among different functional groups of fishes. For example, omnivorous fishes may respond positively to increased lake trophic status because they benefit from increased abundance of algae and detritus. Alternatively, if abundance of large zooplankton declines with increasing trophic status, because of increased abundance of inedible algae, planktivores or juvenile predators that forage on those zooplankton may also decline. Similarly, stream fishes that rely on allochthonous sources of energy (e.g., terrestrially-derived nutrients) may have a weak or no response to increases in nutrient loading within a stream. Recent work on resource subsidies has highlighted the importance of this allochthonous energy to consumers and the implications for food web dynamics. Herbivorous consumers (i.e., grazing fishes) should be most responsive to increases in primary production. For example, riparian canopy removal that increases light availability to algae also increases abundance and growth of grazing fishes. In addition, nutrient fertilization experiments in streams that increase ambient nutrient concentrations result in large increases in production of invertivorous fishes.

Factors that Limit Growth and Survivorship

Factors that increase mortality or decrease growth would reduce fish production if mortality is not accompanied by compensatory gains in weight of remaining individuals. Size-selective mortality, in particular, is expected to have a strong effect on fish production. The selective removal of large individuals may increase or have no effect on production, whereas factors that remove small individuals are likely to have the greatest negative effect on production because P/B is highest for small or young fish (Figure 5). Apex predators in aquatic systems are

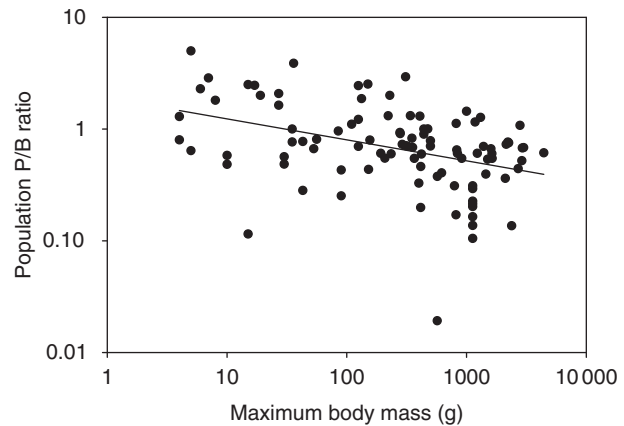


Figure 5 Relationship between the ratio of production to biomass and maximum body size of fishes. Reproduced from Downing JA and Plante C (1993) Production of fish populations in lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 110–120, with permission from National Research Council Canada.

often size selective and have the potential to influence the production of their prey. For example, selective mortality of small individuals may decrease productivity because only larger, slower-growing individuals are left in the population. Alternatively, if large individuals are removed from the population, this might increase overall production by favoring smaller individuals with rapid growth. Exploitation of fishes by humans can act in a similar manner if fishers selectively harvest large individuals, which are the least productive portion of the population. Alternatively, if the threat of predation or consumptive mortality is great, the general effect of a predator would reduce productivity of its prey. This has been demonstrated in small streams and lakes in which a generalist predator altered the behavior of prey, resulting in lower growth rates.

Stochastic disturbances such as water level fluctuations, flooding, or drought can reduce fish production by decreasing recruitment and growth of fish populations as well as mediating the transfer of allochthonous materials. For example, fish production in the tailwaters of reservoirs can decline after the construction of dams as a result of increased fluctuation in flows and trapping of organic matter in the reservoir. However, some studies have observed increased production of nonnative fishes in tailwaters, which are attributed to cooler water temperatures released from the impoundment. Reduced hydrological variability of flows also can reduce the connectivity of a river and its floodplain, limiting the production of fishes. Much work on the role of altered hydrology in shaping river nutrient dynamics and fish production is needed to help manage these impacted river systems.

Fish Production in Lotic and Lentic Habitats

Several studies have contrasted fish production among lakes, reservoirs, and streams. Fish community production is generally three times greater and *P/B* ratios about 1.5 times higher in lotic than in lentic systems (Figures 1 and 6). These differences may be attributed to the increased biomass and smaller average size of individual fishes in rivers. In addition, allochthonous energy inputs increase from lakes to reservoirs to streams. Lakes and reservoirs have smaller allochthonous energy inputs because they have a larger wetted surface area relative to their shoreline than does lotic ecosystems, and their major energy source is driven by autochthonous production of phytoplankton or macrophytes growing in the littoral zone. Rivers have much smaller ratios of surface area to shoreline length and thus receive relatively more allochthonous materials. Reservoirs are intermediate between lakes and rivers in the relative contributions of autochthonous and allochthonous energy sources, and so, may also be expected to have intermediate fish production between lakes and streams. Thus, higher fish production in lotic versus lentic systems may be due to the added availability of allochthonous energy to lotic systems.

Fish production in lakes within and among regions can be affected by morphometric, edaphic, and climatic factors. Accordingly, various studies report associations between fish production and temperature,

phosphorus concentration, pH, and physical habitat. In addition, fish production has been associated with primary production and with the number of fish species. The positive relationship of productivity with nutrient concentrations and primary production has already been discussed. In addition, commercial fish production can be inversely correlated with mean depth of lakes, which is attributed to greater availability of littoral habitats in shallow lakes. Temperature effects on fish production are linked to the physiological optimum of the species under consideration. In general, extreme cold temperature limits growth and extreme high temperatures increase mortality, but the exact relationships between temperature and productivity of fish communities are not well understood for many species.

Fish production in reservoirs has been related to water exchange rates (i.e., flushing rate) and the morphoedaphic index (MEI; Figure 7), which in its most common form predicts yield based on the mean depth and TDSs; however, the MEI typically works best in regions with similar climatic conditions. The positive association of fish yield with TDS and exchange rates indicates the reliance of reservoir production on allochthonous nutrients that stimulate production or external sources of organic matter. Because watersheds of reservoirs can be large relative to their surface area, their reliance on materials from inflowing rivers is not surprising. However, autochthonous production within a reservoir can be substantial and can sustain the secondary production of some reservoirs.

There is a strong conceptual basis for evaluating variation of fish production in lotic systems. In river

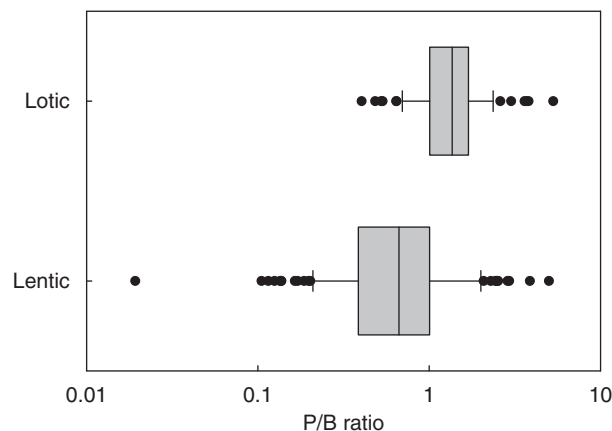


Figure 6 Comparison of the production to biomass ratio of fish populations in lotic and lentic systems. Data were compiled from Downing JA and Plante C (1993) Production of fish populations in lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 110–120; Randal RG, Kelso JRM, and Minns CK (1995) Fish production in freshwaters: Are rivers more productive than lakes? *Canadian Journal of Fisheries and Aquatic Sciences* 52: 631–643, and Kwak TJ and Waters TF (1997) Trout production dynamics and water quality in Minnesota streams. *Transactions of the American Fisheries Society* 126: 35–48.

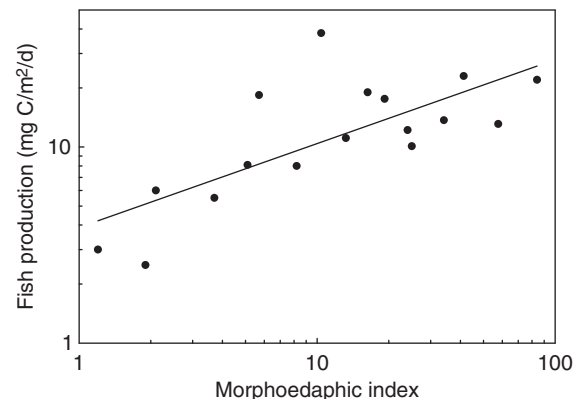


Figure 7 Relationship between reservoir fish production and a MEI based on mean depth and total suspended solids. Reproduced from Adams SM, Kimmel BL, and Ploskey GR (1983) Sources of organic matter for reservoir fish production: A trophic-dynamics analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 40: 1480–1495, with permission from National Research Council Canada.

ecosystems, there is a gradual longitudinal change in the primary energy source (i.e., from primarily allochthonous sources of energy in headwaters to autochthonous sources in larger rivers), and primary productivity is generally greatest in the middle reaches. This pattern is influenced by the riparian canopy, not only as a source of energy, but as a mechanism for reducing light availability to primary producers. Production studies in forested streams that have had their riparian canopy removed highlight the importance of allochthonous inputs and light in regulating ecosystem processes. In large rivers, as the canopy opens, hydrology likely regulates the relative importance of autochthonous and allochthonous production. For example, fish production in floodplain rivers is generally reliant on allochthonous materials in the floodplain, whereas in more constrained rivers, it may be dependent on autochthonous production. In addition, the presence of coarse woody debris can also be a strong driver of secondary production in large rivers with open canopy.

The majority of fish production studies from lotic systems have focused on salmonids. Across large spatial scales (i.e., continents), salmonid production is positively correlated with alkalinity, suggesting pH balance is an important indicator of stream quality for such species. Although salmonid production is comparable to production estimates for nonsalmonids in warm and cold streams (Figure 8), more data from species occupying warm water streams are necessary to rigorously test differences among taxa and stream types.

Several studies of fish production in warm water streams have observed longitudinal patterns of fish production. Fish production in these streams was generally greatest in upstream riffle reaches because of high densities of young, generalized insectivores in these habitats. Production downstream was typically lower because of the development of large, stable pools that contain fewer, larger individuals with slower relative growth rates. Alternatively, in regions with variable climatic conditions, abiotic conditions may be unstable and production will be higher in lower, more stable reaches. In general, the major drivers of production in streams are the sources of energy as well as the size-structure and relative growth rates of the fish community.

Importance of Species Interactions

The relationship between community fish production and fish species richness is not well understood. Community production may increase with species richness because an assemblage of fishes occupying multiple niches would more efficiently convert existing energy

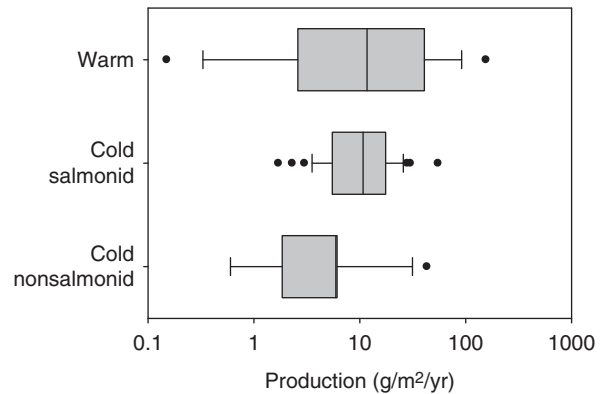


Figure 8 Comparison of fish production in streams for coldwater salmonids, coldwater nonsalmonids, and warm water fishes. Data were taken from Chapman DW (1971) Production. In: Ricker WE (ed.) *Methods for Assessment of Fish Production in Fresh Waters: International Biological Programme Handbook Number 3*, pp. 199–214. Oxford: Blackwell; Kwak TJ and Waters TF (1997) Trout production dynamics and water quality in Minnesota streams. *Transactions of the American Fisheries Society* 126: 35–48; and Neves RJ (1981) Fish production in warmwater streams. In: Krumholz LA (ed.) *The Warmwater Stream Symposium, American Fisheries Society special publication*, pp. 356–363. Bethesda: American Fisheries Society.

sources into production. Studies of salmonid production in streams support this hypothesis, in that total salmonid production is greatest when multiple species are present. In addition, differences in fish community productivity across broad geographic regions has been related to the species richness of those regions. Surveys of fish production in lakes show that some individual fish populations have greater productivity in lakes with more fish species, although overall fish community production is lower. More data on community productivity across systems with varying levels of species richness are needed to evaluate this relationship adequately.

Conclusions

Fish production studies aid our understanding of factors that drive energy transfer to this ecologically and economically important group of organisms. Estimates of fish production have been widely used by fishery managers to designate harvest limits and by aquatic ecologists as an ecological response variable. Factors stimulating aquatic primary productivity typically stimulate productivity of higher trophic levels, but the efficiency of this transfer depends on the traits of the fish species and magnitude of eutrophication. There is a strong relationship between the mean size of individuals in a population or community and

fish production. In addition, systems that acquire energy through both autochthonous and allochthonous sources have greater fish productivity because of greater total energy input to the system. As lotic systems typically have greater abundance of small-bodied species and varied sources of carbon, they also tend to be more productive than do lentic systems. Freshwater fish production can be linked to a variety of abiotic and biotic processes and continued incorporation of this important ecosystem process into aquatic research and management will allow a more thorough understanding of anthropogenic impacts on inland waters.

Knowledge Gaps

Factors Driving Fish Production across Ecosystem Types

The reporting of fish production values has been constrained by the ability of scientists to acquire accurate population estimates across multiple time periods. As such, the literature is biased towards fish species that occupy habitats for which it is relatively easy to obtain population estimates (i.e., streams and small lakes). Recent advances in sampling methods (e.g., hydroacoustics and marking techniques) and statistical approaches should facilitate estimates of fish production in systems that are difficult to sample (e.g., large rivers and large lakes). Incorporation of production estimates into fisheries research across system types will likely yield important insight into the dynamics and management of fish populations.

Energy Sources Driving Fish Production

In the early 1950s, K.R. Allen concluded that macroinvertebrate production in streams was not adequate to support the production of local fish populations. More recent studies have found that detailed energy budgets, accounting for energy from subsurface and terrestrial habitats as well as cannibalism are able to account for fish production in streams. Nevertheless, factors driving fish production are poorly understood in many inland waters. In particular, the relative importance of autochthonous and allochthonous energy sources are often debated. Recent developments of time-integrated methodology, such as stable isotope analysis, will help ecologists characterize energy pathways driving secondary production.

The Role of Species Interactions in Regulating Fish Community Production

Interactions among species are likely to influence production, yet we have only a limited understanding

of these processes. For example, studies have reported positive associations between fish species richness and total production of the fish community. A plausible explanation for this relationship is the complementary use of resources by different species in the community. It is also possible that species negatively interact (i.e., through competition or predation), such that the occurrence of multiple species would reduce community fish production. Finally, the ability of particular species to exert a positive or negative feedback on primary production may indirectly affect production of other members of the fish communities. Further elucidation of these interactions will help refine our general understanding factors regulating fish production in freshwaters.

Characterizing the Role of Human Disturbances on Fish Production

Eutrophication and sedimentation are major impacts to aquatic systems that affect basal food resources, community composition, and diversity. Further research is needed to address the effects of anthropogenic disturbances on fish production. Are changes in biodiversity coincident with declines or increases in fish production? Are there thresholds for particular stressors at which fish production is drastically reduced? In addition to abiotic stressors, fish communities are becoming homogenized through the extirpation of species and the introduction of alien species. How will these changes, which alter food web interactions and resource availability, affect secondary production?

Glossary

Instantaneous growth rate – The natural logarithm of the ratio of final weight to initial weight of a fish or population in a unit of time.

Instantaneous mortality – The natural logarithm of the survival rate.

von Bertalanffy growth model – Describes the rate of change in length of a fish per unit of time and assumes that rate of change in length declines and will eventually become zero as a fish nears its maximum possible size.

See *also*: Biodiversity of Aquatic Ecosystems; Comparative Primary Production; Eutrophication of Lakes and Reservoirs; Fish, Characteristics; Fish, Populations; Lakes as Ecosystems; Phytoplankton Productivity; Regulators of Biotic Processes in Stream and River Ecosystems; Streams and Rivers as Ecosystems; Trophic Dynamics in Aquatic Ecosystems.

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Relevant Websites

- <http://www4.ncsu.edu/~tkwak/pp.html> – Population and production estimation software.
- <http://www.warnercnr.colostate.edu/~gwhite/software.html> – Population estimation software.