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Secondary production is an underutilized metric to assess restoration initiatives

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ABSTRACT

Secondary production is an integrative measure of the accumulation of heterotrophic biomass through time and can be a valuable tool to design, implement, and assess restoration initiatives. To highlight applications of secondary production in restoration contexts, we identify recent papers from the literature, use these to make generalizations about how the concept is applied, and examine why it may not be utilized more commonly. We identified 21 papers that empirically quantified secondary production to compare pre/post-restoration or assess restored sites relative to reference ones. Every study was aquatic, suggesting that secondary production is an underutilized tool in terrestrial restoration studies. We discuss various ways that food web perspectives inform restoration secondary production outcomes, such as through shifts in aquatic basal resource pools and alleviation of nutrient limitation, changes which ripple through food webs supporting higher trophic level production. Despite challenges inherent to calculating secondary production, the approach holds much promise—it is a composite metric simultaneously reflecting components of ecosystem structure and dynamics that restoration initiatives target.

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1. Introduction

The science of restoration ecology is associated with many focal study areas, including biodiversity (and links to ecosystem function), community structure, abiotic-biotic feedbacks, connectivity, and ecosystem service provision (Benayas et al., 2009; Hobbs and Norton, 1996; Palmer et al., 2005; Suding et al., 2004). This complexity necessitates the use of simplified and accessible metrics that best encapsulate the results of a given restoration initiative. Choosing these metrics (and quantifying them accurately) is a core challenge in restoration ecology. Simple community metrics (e.g., species richness) may not reveal aspects of ecosystem function, whereas those reflecting ecosystem service provision (e.g., carbon sequestration) may be difficult to adequately measure over relevant spatial and temporal scales. Metrics that integrate ecosystem characteristics, yet are practical to measure, are desired when allocating limited resources for restoration projects.

Secondary production, the formation of heterotrophic biomass through time, is an integrative metric that links aspects of population, community, and ecosystem ecology. Biomass is a representative measure at a given point in time, whereas production is dynamic (defined mathematically as a flux) and while correlated with biomass, it is an integration of numerous processes and rate functions. Secondary

production incorporates measures of density, biomass, growth rates, reproduction, mortality, and development time—all of which are tied to the ability to procure and assimilate resources. As such, secondary production encapsulates underlying energy acquisition and trophic relationships (Benke and Huryn, 2017). Food web ecology is thus intricately linked to the underlying drivers of secondary production, and food webs can be used to predict dynamics of production associated with ecosystem conservation and management strategies. Furthermore, production can be calculated at different levels of ecological organization (e.g., individual, population, and community) and across scales, providing insight into ecosystem patterns more generally (e.g., Rypel and David, 2017). To highlight applications of secondary production in restoration contexts, we identify recent papers from the literature, use these to make generalizations about how the concept is being applied, and discuss why it may not be utilized more commonly.

2. Approach

We conducted a Science Citation Index Web of Science search (1993–July 2020) with the keywords “secondary production” and “restoration” that yielded 73 articles. The date of the oldest article was established based on the search results. Of these, 18 explicitly quantified secondary production and used it to assess a restoration initiative (using either a before/after design or contemporary reference/control sites) (Table 1). Other studies (see the full list in Supplementary Material

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Table 1) did not empirically quantify secondary production, used production data for planning future restoration projects, or were literature reviews or perspective pieces. Table 1 also lists three additional studies (Able et al., 2008; Cardoso et al., 2005; Grilo et al., 2009) that were identified by performing a forward search of a seminal paper that outlined the utility of secondary production for planning and evaluating restoration projects (Peterson and Lipcius, 2003). Studies focused on diverse invertebrate and vertebrate taxa (see Table 1), with two providing insights into bacterial secondary production in restoration contexts (Hein et al., 1999; Peter et al., 2012).

None of the 21 papers that quantified secondary production in a restoration context was terrestrial. Only 2 of the 73 identified papers in the overall search were conducted in a terrestrial ecosystem (Leidinger et al., 2017; Teague and Dowhower, 2003), with one focused on aquatic-terrestrial linkages (Compson et al., 2016). There is no fundamental reason why secondary production is less relevant to the study of terrestrial ecosystems. It could be that different terminology is employed in terrestrial studies which resulted in fewer identified in the search. It was not practical to conduct all searches that encompass specific terms that could indicate focal consumers (e.g., ungulate) or products (e.g., meat) in terrestrial secondary production studies. Yet, additional targeted searches of the terrestrial restoration literature further suggested a lack of application of secondary production tools. We also note that Web of Science searches do not identify non-English papers or those outside the primary academic literature (e.g., agency or NGO reports). But based on results of the survey approach, we do not address terrestrial restoration studies further herein. In the next section, we offer two explanations for the apparent bias toward aquatic restoration-secondary production studies.

3. Bias toward aquatic studies

Some of the aquatic papers identified in the literature search involve determining the economic value of natural resources, specifically those with existing market values, such as for fisheries (e.g., Able et al., 2008; Minello et al., 2012; Weinstein and Litvin, 2016; Weinstein et al., 2014). Production is well-suited to the study of exploited/restored populations, and early production approaches have given rise to what are now standard methods for modeling fishery population dynamics (Ricker, 1946; Rypel et al., 2018; Walters and Martell, 2004). Further, secondary production calculations are especially useful because, with an existing biomass-based market price, it is a simple translation to convert production into a dollar value that non-scientists can readily interpret. For example, the annual value of increased penaeid shrimp production (relative to open water) from nine constructed wetlands in Galveston Bay, Texas, USA, was \$425–690 ha⁻¹. Valentine-Rose et al. (2007) and Valentine-Rose and Layman (2011) suggested a production-based economic fishery valuation showing that even small (<2 ha) tidal creek restoration projects could yield thousands of dollars in annual snapper (Lutjanidae) production, substantially exceeding the costs of the restorations. More broadly, conservation initiatives in marine systems often are framed in the context of increasing economic yields of fishery species for which calculation of secondary production is the primary tool (Claisse et al., 2014; Peterson and Lipcius, 2003; Powers et al., 2003). The lack of a direct link to species with existing economic markets may result in terrestrial studies instead having a focus on other ecosystem services that are related to restoration (de Groot et al., 2012).

Second, the aquatic focus of secondary production may reflect important contributions, more than 35 years ago, central to the ecological study of freshwater systems (Benke, 1979; Benke et al., 1984; Benke and Wallace, 1980; Elliott, 1981; Menzie, 1980; Waters, 1977; Waters, 1983; Waters and Crawford, 1973). These early studies provided methodological and conceptual frameworks that remain in place in current freshwater research programs (e.g., Dorff and Finn, 2020; Embke et al., 2019; Entekin et al., 2020; Schmid-Araya et al., 2020; Zilli and Del Barco, 2020). Benke and Huryn (2017) provide a thorough summary of

calculating secondary production in freshwaters, highlighting production/biomass calculations, field methodological details, statistical approaches, and various assumptions that frame the discipline. We refer a reader to that paper, as well as other citations in the paper, for extensive detail on the intricacies of secondary production quantification. Here we highlight ways in which secondary production and food webs are natural complements to one another in restoration contexts.

4. Empirical examples

With the historical context in mind, it is not surprising that many studies applying secondary production to restoration efforts are focused on macroinvertebrate production in freshwater systems. For example, the link between coarse woody debris and invertebrate productivity is a common area of study (Dolph et al., 2015; Entekin et al., 2020; Entekin et al., 2009; Vandermyde and Whiles, 2015). Entekin et al. (2020) showed that the addition of large wood increased the proportion of gross primary productivity and coarse benthic organic matter consumed by the macroinvertebrate community in a headwater stream, suggesting fundamental shifts at the base of the food webs that were elucidated via secondary production calculations. Vandermyde and Whiles (2015) examined how removing riparian trees (and thus decreasing organic matter input and increasing light penetration) restored more natural conditions of tallgrass prairie streams, thereby increasing macroinvertebrate production. These contrasting examples (wood addition vs. removal) within streams highlight the importance of system- and taxa-specific contexts in designing successful freshwater restorations as quantified via invertebrate production. The utility of benthic invertebrate production metrics to assess restoration also extends to estuarine and coastal systems (Cardoso et al., 2005; Dolbeth et al., 2011; Grilo et al., 2009; Wilber et al., 2012; Yang et al., 2017).

Changes in macroinvertebrate production can, in turn, lead to increased growth rates and/or production of higher-order consumers. Kiffney et al. (2014) linked greater resource availability (via introduced tissue of adult Chinook salmon, *Oncorhynchus tshawytscha*) to increases in chironomid productivity, which supported the growth of juvenile Coho salmon (*Oncorhynchus kisutch*). Collins and Baxter (2020) demonstrated additions of salmon carcasses alleviated apparent food limitation and increased secondary production of rainbow trout (*Oncorhynchus mykiss*). This was attributed to direct foraging on carcasses, increased consumption of aquatic invertebrates, and consumption of terrestrial flies that colonize carcasses translocated to riparian zones. Combined, these studies highlight how restoration of food web subsidies from salmon carcasses underpin key trophic interactions, including the support of higher-order consumers of economic and conservation importance.

Cross et al. (2011) integrated secondary production and quantitative energy flow food web approaches in a system-wide study of experimental high-flow dam releases in the Colorado River, USA. Invertebrate biomass and secondary production declined significantly following the flood with most of the decline driven by reductions in two nonnative invertebrate taxa, New Zealand mudsnails (*Potamopyrgus antipodarum*) and the amphipod *Gammarus lacustris*. Yet, the production of rainbow trout increased substantially following the simulated flood, despite the large decline in invertebrate production. These results can be reconciled by drift concentrations of Chironomidae and Simuliidae prey that supported a large proportion of the trout production (but had relatively low localized secondary production). The message for restoration was that controlled floods may increase the production of nonnative rainbow trout, a factor that should be considered in management decisions in highly altered ecosystems like the Colorado River.

More broadly, detailed quantitative food webs, such as in Cross et al. (2011), depict trophic linkages based on energy production and subsequent flows of energy, greatly extending simplistic connectance food webs (Winemiller and Polis, 1996). Benke and Wallace (1980) first demonstrated an example of how the trophic basis of production

Table 1
Description of papers that quantified secondary production in a restoration context.

Author and Date	Habitat type	Species	Restoration approach	Effect on secondary production	Link to the underlying food web
Collins and Baxter, 2020	Freshwater stream	Rainbow trout (<i>Oncorhynchus mykiss</i>)	Fish carcass addition	Increased	Alleviation of food limitation
Entrekin et al., 2020	Freshwater stream	Macroinvertebrates	Wood additions	Increased	Increased allochthonous and autochthonous carbon assimilation
Yang et al., 2017	Coastal wetland	Macroinvertebrates	Freshwater releases to a delta	Mixed depending on season and trophic level	No direct link to food web mechanisms
Weinstein and Litvin, 2016	Coastal wetland	Spot (<i>Leiostomus xanthurus</i>)	Ecosystem-scale restoration with multiple components	Increased	Comprehensive food web approach, with a focus on connectivity
Vandermyde and Whiles, 2015	Prairie stream	Macroinvertebrates	Riparian tree removal	Mixed depending on functional group	Shifts in available basal resource pools
Dolph et al., 2015	Agricultural stream	Macroinvertebrates	Boulder weirs and woody debris to alter hydrology	Increased	Habitat-related changes in food quality to some taxa
Kiffney et al., 2014	Experimental stream	Chironomids and baetids	Adding salmon or salmon analogs	Increased	Direct feeding pathway from salmon analogs to invertebrates to salmon
Weinstein et al., 2014	Coastal salt marsh	Multiple fish species	Ecosystem-scale restoration with multiple components	Increased	Comprehensive food web perspective
Minello et al., 2012	Coastal salt marsh	Penaeid shrimp	Constructed ridges/islands for marsh vegetation	Increased	No direct link to food web mechanisms
Peter et al., 2012	River	Bacteria community	Improved hydrologic connectivity and natural river morphology	Increased	Enhanced soil-groundwater coupling
Bellmore et al., 2012	River	Multiple invertebrates and three fish species	Restoring hydrologic connectivity with floodplain pools	Increased	Comprehensive food web perspective
Wilber et al., 2012	Oyster reef	Three resident crab species	Bags of recycled oyster shells	Not compared to reference sites	No direct link to food web mechanisms
Cross et al., 2011	River	Multiple aquatic invertebrates and rainbow trout	Experimental high-flow dam releases	Decreased for invertebrates; increased for trout	Comprehensive food web perspective
Dolbeth et al., 2011	Estuary	Multiple invertebrates	Decreased nutrient loading	Mixed depending on species and period	Linked to algal abundance
Valentine-Rose and Layman, 2011	Mangrove tidal creeks	Multiple fish species	Increased hydrologic connectivity	Mixed depending on creek	Enhanced foraging opportunities
Entrekin et al., 2009	Headwater stream	Macroinvertebrates	Wood additions	Mixed depending on stream identity and section	Change in basal resource pools
Grilo et al., 2009	Estuary	Amphipods	Increased hydrologic connectivity and reduced nutrient loading	Decreased	Loss of macroalgae food source
Able et al., 2008	Estuary	Mummichog (<i>Fundulus heteroclitus</i>)	Re-created tidal creek channels	Increased	Diet data show high similarity in restored and reference marshes
Cardoso et al., 2005	Estuary	Snail (<i>Hydrobia ulvae</i>)	Increased hydrologic connectivity and reduced nutrient loading	Increased	No direct link to food web mechanisms
Hein et al., 1999	River	Bacteria community	Re-establishing connectivity between river and floodplain	Increased	Shift from phytoplankton to bacterial production
Bell et al., 1993	Seagrass bed	Polychaete (<i>Kinbergonuphis simoni</i>)	Hand-planting seagrass	Increased	Increased survivorship in planted seagrass

could be used to understand net-spinning caddisflies in an Appalachian mountain stream. Benke and Wallace (1997) later presented a more complete example of how quantitative food webs can be built and used to understand energy flow in more complex ecosystems, such as subtropical floodplain rivers. Cross et al. (2007) used a control-treatment experimental design in a stream experimentally enriched with nutrients; patterns of food web connectance did not change, but the magnitude of material flows did. Thus, studies based on connectance alone would have missed the key ecological effects of the treatment. Similar applications of the trophic basis of production to restoration activities remain underutilized.

Other examples identified in the initial literature search show how secondary production studies inform on-going restoration modeling and decision-making, e.g., how river restoration responses vary with different food web configurations (Whitney et al., 2020). Whitney et al. (2020) built on Bellmore et al. (2012) who demonstrated that off-channel aquatic habitats (Yankee Fork Salmon River, Idaho, USA) are important for productivity in floodplains. They showed how the physical connectivity of habitats to previously restored river segments significantly increased invertebrate productivity. Then, using a bioenergetic model, they estimated overall invertebrate resources were much greater than the energy demand of fishes. This provided a case study where increased resource productivity generated through habitat restoration may not provide expected restoration outcomes (increased

salmon production). Here a resource-consumer food web perspective, as quantified and modeled via secondary production estimates, provided direct guidance for the allocation of funding for restoration/management initiatives.

Weinstein and Litvin (2016) and Weinstein et al. (2014) scale-up further, using whole-ecosystem and comprehensive food web perspectives to explore restoration initiatives in Delaware Bay, USA. They emphasized the role of spatial connectivity in restoration, i.e., that individual wetlands do not function in isolation but are functionally-connected habitat mosaics incorporating ecological processes driven by organism movement and resource pathways. Data used to frame these ecosystem-scale perspectives included stomach content analysis, stable isotopes, biochemical condition (e.g., fatty acids and lipids), reproductive measures, and movement data, highlighting the diverse tools that can be used to link shifts in secondary production to food web dynamics at ecosystem scales.

5. Challenges and opportunities for applying secondary production

The relative paucity of studies estimating empirical production rates reflects the extensive data requirements required for calculation—or at least a prevailing perception of the extensive data needed. Mathematically, production is the product of size-based growth and biomass data. In many cases, ecologists study each of the component pieces

without calculating production itself. In the case of fisheries, managers focus on variables such as growth, mortality, and size, even though managing based on production would often be more direct and desirable (Ricker, 1946; Waters, 1992).

Streamlined production approaches ease concerns about data requirements and calculation burdens (Benke and Huryn, 2017). Models have been developed to predict secondary production based on readily available parameters, such as biomass, abundance, and temperature (Dolbeth et al., 2012; Hirst and Shearer, 1997; Plante and Downing, 1989). Conceptually, the most simple and accessible shortcut to estimating production (P) is the multiplication of biomass (B) by an estimate of P/B for the population or community in question. Waters (1992) demonstrated how this approach can be used to examine the production and harvest dynamics of trout in streams, and Rypel and David (2017) used this approach to explore geographic patterning of production in freshwater fishes at multiple spatial and organizational scales. In the absence of P/B estimates for a species or population, P/B can be provisionally estimated as 1/average lifespan for aquatic invertebrates and fishes (AC Benke personal communication, Myers et al., 2018). A further challenge is the acquisition of quantitative population data, especially for mobile taxa, yet methodological approaches are available within fisheries literature (Kwak and Waters, 1997; Myers et al., 2018; Parks and Rypel, 2018; Rypel et al., 2015). Such considerations should help alleviate concerns over the laborious nature of the metric and facilitate broader utilization of a production-based approach.

Whereas entire community-level secondary estimates are often not feasible because of the data demands for all species-specific estimates, careful selection of individual taxa that are linked to ecosystem function can inform restoration design. For example, Weinstein and Litvin (2016) used one species, spot (*Leiostomus xanthurus*), as a means to inform restoration efforts at an estuarine scale. This species was chosen because it reflected various aspects of the functioning of the linked habitats within the estuarine system. This same study also highlights the challenges posed by habitat connectivity, i.e., linkages via movement of organisms, nutrients, or other matter across arbitrary habitat boundaries. For example, many species use wetlands as nurseries and undergo ontogenetic shifts to other habitats as they grow. In this context, secondary production is a more appropriate tool than counting the number of individuals exported from one habitat to another, as secondary production better encapsulates the composite variables that affect both the growth and abundance of organisms. As such, using secondary production of indicator species can guide restoration projects beyond those focal species alone, as Weinstein and Litvin (2016) demonstrate.

Given the complexities inherent to designing, implementing, and monitoring restoration, perhaps it is not surprising study designs do not additionally focus on the measures required to calculate secondary production. However, viewed from an alternative perspective, secondary production may *simplify* the assessment of restoration when using appropriate study organisms and study designs. It is a composite metric representing many aspects of ecosystem structure and function, thereby obviating the need to quantify various population-, community-, and ecosystem-level metrics individually. Further, Benke and Huryn (2017) highlight how secondary production may provide a bridge between energy flow and functional views of food web structure (sensu Layman et al., 2015), a distinction that often is not well understood nor applied adequately when targeting specific restoration outcomes. Secondary production provides a means to assess both energy flow and functional aspects of food web structure using a single tool.

Secondary production has not been adopted more broadly likely because of the historical focus on macroinvertebrates in aquatic ecosystems and the perception of biologists regarding the effort necessary for obtaining secondary production data. Yet the careful choice of focal taxa and the use of innovative modeling approaches help overcome these challenges. There is obvious scope for broader application of the approach as a means to integrate aspects of ecosystem structure and function, drawing on insights provided by food web ecology. It is not

the only factor that needs to be considered in restoration designs but can provide a powerful component tool. Secondary production should be used more widely as a fundamental approach to plan and assess restoration initiatives, as well as to more broadly prioritize ecosystem management goals and outcomes.

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Declaration of competing interest

There are no conflicts of interest concerning our article.

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