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NOTE

Linking Historical Changes in Salt-Marsh Coverage to Lost Production of a Nektonic Bioindicator

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Abstract

Development reduces the amount of secondary biological production in coastal estuaries. However, the magnitude of this reduction remains largely unknown. We are not aware of studies that have quantified lost secondary biological production in estuaries as a result of interdecadal coastal development of salt-marsh habitats. Our objective was to demonstrate a technique that combined historical imagery, GIS, and secondary production estimates to quantify the magnitude of lost areal production arising from the development of tidal creeks. We estimated lost production of a dominant salt-marsh fish Mummichog *Fundulus heteroclitus* in Spooners and Pelletier creeks, two second-order tidal systems in coastal North Carolina. We georeferenced historical (1939) aerial imagery, digitized low-tide and high-tide features in historical and contemporary (2019) imagery, and compared the intertidal vegetated area of each creek between periods. The lost intertidal area was then multiplied by creek-specific published rates of areal production of larval and juvenile age-0 Mummichog in salt-marsh cordgrass *Spartina alterniflora* habitats. There was a loss of intertidal area and intertidal/subtidal vegetated edge of 72% and 54%, respectively, in Spooners Creek, and 47% and 4%, respectively, in Pelletier Creek. Losses of intertidal area over the last ~80 years translated into estimated annual losses of 44 and 8 kg of dry weight production (~695,000 and 186,500 individuals) for a single cohort in Spooners and Pelletier creeks, respectively. These estimates represent minimum losses, as some in-stream development was already visible in the historic imagery and a single cohort's production was used (not multiple cohorts). We encourage other researchers to use historic imagery to determine changes in aquatic habitats and link losses (or gains) in these habitats to the productivity metrics of important fishes.

Salt marshes are hydrologically dynamic and highly productive habitats (Valiela et al. 2004) that provide forage and refuge for nekton that are both resident (Weinstein 1979; McIvor and Odum 1988; Kneib 1997a; Teo and Able 2003a; Bretsch and Allen 2006) and tidally transient (Minello et al. 1994; Minello et al. 2003). Salt marshes are among the most threatened and frequently degraded coastal habitats around the world (Bromberg-Gedan et al. 2009), reducing coastal biodiversity, resiliency, and limiting the effectiveness of ecosystem system services (i.e., carbon sequestration, storm surge dissipation). Extensive salt-marsh area along United States coastlines has been lost to development (Kennish 2001) with loss rates that are 300–600% higher than that of human population growth in coastal zones (Beach 2002). The

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conversion of salt marsh to developed area reduces primary and secondary production (Dame et al. 2000; Svensson et al. 2007; Lowe and Peterson 2014) and has bottom-up effects on estuarine food webs (Svensson et al. 2007). Specific anthropogenic effects in the salt marshes that are located along the southeastern United States and Gulf of Mexico coastlines include benthic habitat destruction due to dredging (Bass and Turner 1997; Partyka and Peterson 2008), culvert construction and the associated fragmentation of formerly contiguous habitat patches (Eberhardt et al. 2011; Rudershausen et al. 2016), and shoreline armoring that reduces both salt-marsh area (Bilkovic and Roggero 2008; Gittman et al. 2015) and intertidal edge, a transitional interface for nekton access to the marsh surface (Peterson and Turner 1994; Minello 1999). Among estuarine waterbodies, small tidal creeks and their resident nekton may be the most threatened by development due to the proximity of these creeks to nearby developed lands (Krebs et al. 2014; Sanger et al. 2015).

Secondary biological production, a measure of tissue accretion per area and time, can be a useful indicator of the ecological integrity of estuaries. Researchers have estimated the biomass and production of a variety of nekton species in salt-marsh habitats (Nixon and Oviatt 1973; Valiela et al. 1977; Meredith and Lotrich 1979; Conover and Ross 1982; Teo and Able 2003b; Hagan et al. 2007) to evaluate the importance of these species in transferring energy from salt marshes to open water estuaries (Kneib 2000). Rudershausen and Buckel (2020) related secondary production in salt-marsh systems to landscape-level factors; they found that both creekwide production and areal production of the fish Mummichog *Fundulus heteroclitus* was lower in salt marshes that had lost area due to development. However, all of these studies of nekton production have been contemporary in that they have quantified biomass and/or production at specific times but not tracked longitudinal changes (through time) in habitat and their cascading effects on fish production.

In terrestrial systems, longitudinal studies of aerial and satellite imagery have been used to document habitat changes as well as the effect of these changes on associated biota. For example, Zahawi et al. (2015) documented a decline in tropical forest coverage. Brambilla et al. (2017) documented land-cover changes in northern Italy that resulted in effects on the distribution of a bird species. Sarhara et al. (2015) used remote sensing to estimate rates of forest encroachment on grasslands. Although longitudinal approaches have been used extensively in terrestrial systems, their use in aquatic systems to examine changes in biota is limited. Fish production was assumed to have dropped because of increased rice production in a Cambodian floodplain, but no calculation of lost fish production was made (Mahood et al. 2020). While there are numerous estimates of historical salt-marsh loss along U.S. coastlines compared with predevelopment levels (e.g., Dahl 1990; Kennish 2001; Bromberg and Bertness 2005), we are not aware of previous studies that have combined estimates of salt-marsh loss and its effects on associated biota or fish production.

In this study, we used published creek-specific rates of daily Mummichog production along with contemporary and historical imagery to link changes in areal production to changes in salt-marsh coverage. We then estimate the daily production lost due to eight decades of development in two tidal creeks in North Carolina. Our motivation was two-fold: (1) demonstrate a technique whereby natural resource planners could combine estimates of areal production with historical imagery to calculate long-term changes in production due to coastal development and (2) give natural resource planners insight into the magnitude of the effects of coastal development that could potentially be extrapolated to a larger (region-wide) area of lost habitat. This study provides guidance to planners on reductions in secondary production that can be expected for a species that inhabits tidal creeks that are being developed along the southeastern U.S. coast.

METHODS

Study areas.— We examined the area of salt-marsh loss in two second-order polyhaline estuarine systems, Spooners and Pelletier creeks, located in Morehead City, North Carolina, USA. The intertidal area of each creek is almost exclusively composed of salt-marsh cordgrass *Spartina alterniflora* with minor coverage of black needlerush *Juncus roemerianus*. Each creek has experienced a range of types and intensities of development in its main stem and first-order prongs. The types of development within the high-tide wetted area of each creek include constructing shoreline armoring (mainly concrete and wooden bulk heading), dredging intertidal area for boat use, and constructing culverts (one in Spooners Creek and three in Pelletier Creek) that have fragmented formerly contiguous salt-marsh habitats.

Spatial analyses.— All of the spatial analyses that were used to determine the intertidal areas were performed by using ArcMap version 10.7.1 (ESRI 2019). Historical aerial imagery taken at a scale of 1:38,265 in 1939 by the U.S. Department of Agriculture (SANC 2020) was georeferenced by establishing five control points at known road crossings that could be located in both the historical imagery and the (contemporary [2019]) ESRI basemap. One historical aerial image that was taken over a portion of Carteret County, North Carolina, that borders Bogue Sound covered both study creeks (map BUS-105-3; SANC 2020; Figure 1). The root mean square error (RMSE), a measure of accuracy in the georeferencing process, was 15.7 m^2. This is within the range of acceptable RMSE

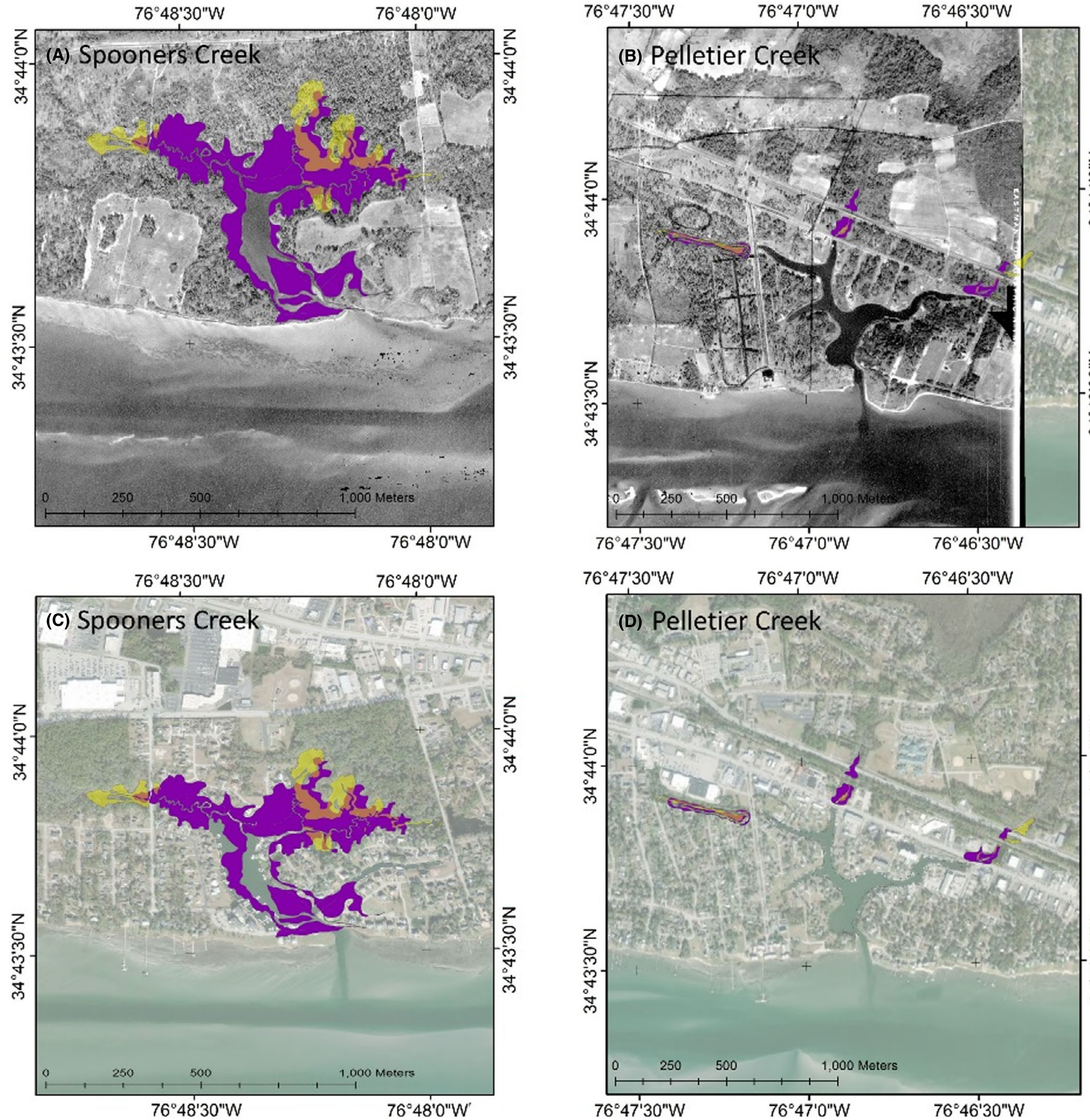

FIGURE 1. Intertidal area of Spooners Creek and Pelletier Creek in Morehead City, North Carolina, USA. Each panel displays the intertidal area that was estimated by using orthoimagery in 1939 (purple shading) overlaid with the estimated intertidal area in 2019. The semitransparent yellow shading shows areas with no overlap in intertidal coverage between periods, and the orange shading indicates areas with overlap in intertidal coverage between periods. The upper panels display background imagery from **(A)** Spooners Creek and **(B)** Pelletier Creek from 1939, and the lower panels display satellite imagery from **(C)** Spooners Creek and **(D)** Pelletier Creek from 2019.

values for a contemporary analysis of georeferencing methodologies (Wernette et al. 2017).

Following georeferencing, each creek's area was digitized as polygon feature-classes. Respective shapefiles represented low- and high-tide areas within each period (1939 and 2019). This was accomplished by tracing the outlines of prominent low-tide features (vegetated and nonvegetated edges of subtidal creek channels) and high-tide features (high tide/upland edge) in the historical and contemporary imagery. The intertidal area of each creek and period was found by subtracting the low-tide from the high-tide area, and shapefiles were created by using the "Erase" tool. For each of these shapefiles, a new field was added to the attribute table to calculate intertidal area (m^2) using the "Calculate Geometry" tool for the newly created area field. We assumed for each period that the intertidal area was comprised of salt-marsh cordgrass, where production by larval/juvenile Mummichog does occur, rather than nonvegetated mud, where production by this species' early life stages does not occur (Kneib 1984; Talbot and Able 1984; Teo and Able 2003b), or other types of other intertidal vegetation. This assumption that salt-marsh cordgrass covered the overwhelming majority of intertidal area was supported by an inspection of the historical image and ground-truthing the intertidal area that appeared in the contemporary imagery. Finally, lost intertidal area and linear distance of the salt-marsh interface for each creek was computed as its difference between periods.

Estimating lost Mummichog production.— Secondary production represents the accretion of animal tissues per unit area and time. We used creek-specific published estimates of production of larval/juvenile Mummichog ($g_{dry\ weight}/m^2/d$) within the salt-marsh habitats (Rudershausen and Buckel 2020) to determine creekwide daily losses due to development. We studied Mummichog because it is an indicator species for examining environmental impacts to salt marshes given its abundance and role in salt-marsh trophic dynamics (Kneib 1986, 1997b), small home range, localized recruitment, and site fidelity (Lotrich 1975; Sweeny et al. 1998; Skinner et al. 2005; Able et al. 2012). Furthermore, Mummichog uses these estuaries and associated salt-marsh habitats throughout its life cycle for foraging, refuge, reproduction, and nursery (Kneib 1986, 1997b).

Production estimates for Spooners and Pelletier creeks were computed via a production estimation technique whereby each specific cohort is identified (cohort-specific method; Ricker 1946). The data that were used to estimate production were collected from the western first-order prong of Spooners Creek (Spooners West) and from two first-order prongs of Pelletier Creek: Pelletier East (northeastern prong) and Pelletier West Creek (western prong). Only production of age-0 larval and juvenile Mummichog was calculated because this age-class and these life stages are major contributors to production among populations of this species (Meredith and Lotrich 1979; Teo and Able 2003b; Hagan et al. 2007). These are also life stages that remain on the vegetated marsh surface across tidal periods (Kneib 1984, 1997a; Teo and Able 2003a). Thus, corrections to the estimates of developed area that may influence the production of these life stages are not needed because they are unlikely to use other habitats (such as nonvegetated channels) within tidal creeks. Our approach assumes that changes in production are linearly related to creekwide changes in salt-marsh coverage, with any density-dependent biological effects remaining constant during creekwide fluxes in salt-marsh coverage. The approach we take also assumes that changes in production are independent of temporal changes in other factors that may influence Mummichog such as eutrophication, contamination from toxins, or changes in predator abundance. We are not aware of scientific data collection over this period that has documented acute or chronic changes in nutrients, contaminants, or predators in these study creeks.

Creek-specific values for areal production were used to estimate lost daily production (g dry weight) on a creekwide basis for each study system. Estimated lost production of Mummichog in each creek was then computed by multiplying interdecadal lost intertidal area in each study creek by each cohort/creek-specific published value for daily production (Rudershausen and Buckel 2020); lost production was also calculated for the entire 7-month (210-d) growing season. We specified a 7-month growing season because this is the approximate duration of Mummichog growth in this region (Rudershausen et al. 2019). Calculating lost creekwide production due to development in this manner accounts only for variability around estimates of production rather than that from error that is related to our estimates of the lost intertidal area between the historic and contemporary points. Using the average sizes and areal production estimates for each creek (Rudershausen et al. 2019), we calculated the number from a single cohort of age-0 Mummichog that has been lost as a result of reduction of salt-marsh coverage between 1939 and 2019.

RESULTS

Intertidal area was lost in both Spooners (72% loss) and Pelletier creeks (47% loss) over the 80-year period between 1939 and 2019 (Figures 1 and 2). While the extent of loss via our analysis was greater in Spooners Creek, there was evidence from the historic image that some intertidal area in Pelletier Creek had already been eliminated before 1939. The amount of intertidal/subtidal vegetated edge also decreased in Spooners Creek (54% reduction) and Pelletier Creek (4% reduction) between 1939 and 2019.

Estimated inter-decadal reductions in dry-weight, creekwide production of Mummichog differed between creeks (Table 1). This was because a larger intertidal area has been developed in Spooners Creek than in Pelletier Creek, even though the rates of areal production were lower in Spooners Creek ($0.0015\ g/m^2/d$) than in Pelletier Creek ($0.0031\ g/m^2/d$). These daily losses translated into mean

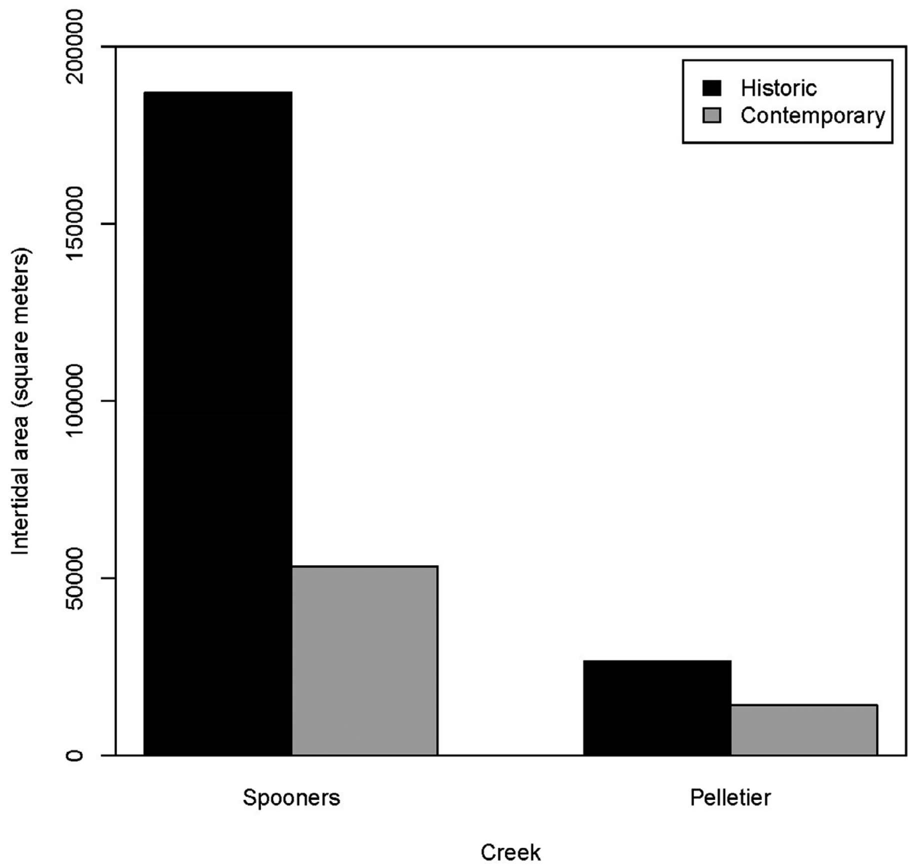

FIGURE 2. Estimates of intertidal salt-marsh area (y-axis: m^2) in Spooners and Pelletier creeks, North Carolina, USA, in historic (1939: black bars) and contemporary periods (2019: gray bars).

annual losses in dry weight production of 43,659 and 8,169 g in each of the respective creeks over the course of a 7-month (210-d) growing season (Figure 3). At the average sizes that are used to estimate production, this is an estimated annual loss for a single cohort of Mummichog of 695,207 age-0 fish in Spooners Creek and 186,507 fish in Pelletier Creek.

DISCUSSION

This study demonstrates a method whereby an orthoimagery time series and contemporary estimates of production can be combined to document and quantify the cumulative effects of development on the production of important estuarine consumers. Cumulative effects have been noted as being important for managers to consider when they are making policies (Peterson and Lowe 2009). The use of aerial and satellite imagery to document cumulative changes in habitat coverage is common in terrestrial systems (e.g., Zahawi et al. 2015; Brambilla et al. 2017) and in aquatic systems that are emergent (oysters, Grizzle et al. 2002; salt marsh, Erwin et al. 2004) or submerged but visible (submerged aquatic vegetation, Ward et al. 2003; kelp, Butler et al. 2020). Most studies only document the change in habitats, though some have linked these changes to ecosystem services (Craft et al. 2009) or attractiveness to fish (Amorim et al. 2017). However, to the best of our knowledge, there are no studies that have linked cumulative changes in salt-marsh habitats to changes in secondary production. Other researchers could use the approach to better determine the value of lost habitat by linking it to biological metrics for aquatic fauna. The methodology can be used to approximate a total amount of lost production of Mummichog or other species in other systems. The data requirements for a coastwide estimate of changes in production would be an estimate of salt-marsh change (gain or loss) and estimates of areal production (g/m^2/d) where Mummichog (or another species of interest) is produced.

The changes in habitat and fish production across decades differed by creek. Over an 80-year period in one of the two creeks, we measured substantial loss of salt-marsh area and corresponding lost fish production. The study creeks possess a range of development types and intensities within their high-tide areas that are representative of the adverse effects of development in the types of systems

TABLE 1. Mean and standard deviation (SD) values for areal production ($g_{dry\ weight}/m^2/d$) and lost intertidal area (m^2) and mean and confidence intervals (CI) for daily and annual (210-d growing season) lost production (g) of Mummichog in Spooners and Pelletier creeks, North Carolina, over an 80-year period (1939–2019). See Rudershausen and Buckel (2020) for details on the methods that were used to estimate areal production of Mummichog.

Creek	Prong for areal production data	Production: mean	Production: SD	Lost intertidal area: total	Lost daily production: mean	Lost daily production: CI	Lost annual production: mean	Lost annual production: CI
Spooners	Spooners West	0.0015	0.0010	133,659	207.9	47.9–227.7	43,659	10,059–47,817
Pelletier	Pelletier West	0.0031	0.0029	12,448	38.9	15.1–62.6	8,169	3,171–13,146

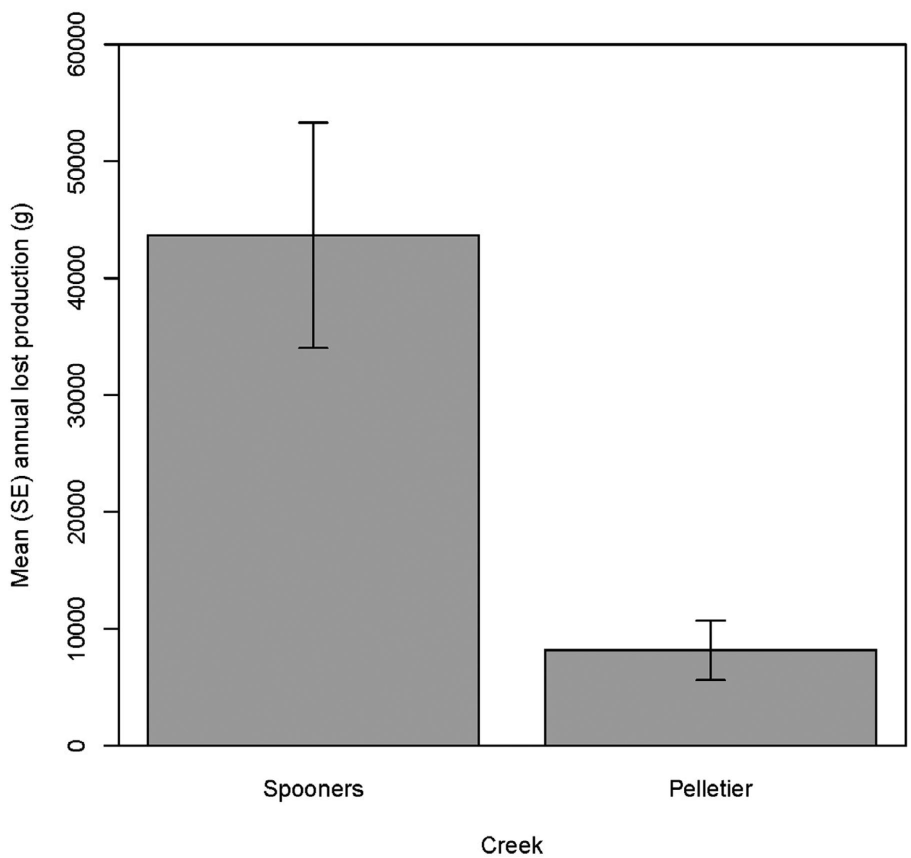

FIGURE 3. Estimates of mean (SE) annual lost production of a single cohort of Mummichog (g/m^2) over a 210-d growing season as a result of intertidal salt-marsh loss in Spooners and Pelletier creeks, North Carolina, USA, between 1939 and 2019.

that are found along the southeastern United States (Holland et al. 2004) and Gulf of Mexico (Krebs et al. 2014; Lowe and Peterson 2014). These prior studies have taken a contemporary cross-sectional approach by simultaneously comparing across marsh creeks that have different levels of anthropogenic influences. Our study is unique in that it takes a longitudinal approach within marsh creeks; we envision other natural resource professionals coupling secondary production estimates with historical salt-marsh imagery to estimate cumulative losses in production in other estuaries. Estimates of lost production such as these give coastal resource managers information on how development can cause reduced production in terms of either forgone tissue accretion by dominant species or reduced numbers of young that are hatched. These types of estimates are also a means of quantifying the lost ability of these systems to support the "trophic relay" of secondary production by resident species to higher-order consumers in open-water estuaries (Kneib 2000; Ziegler et al. 2019). We caution that applying this method to compute lost production would ideally be for an estuary where areal production estimates are available, owing to the variability in production that can arise among systems and regions.

Several factors potentially bias the estimates of the amount of biological production that has been lost in these two systems. It is likely that estimates into the magnitude of lost production represent minimums, as some development had already occurred within the high-tide area of each creek by the time that the historical (1939) photograph was taken. However, the complete extent of development prior to 1939 is uncertain. Maps of Carteret County from the late 19th and early 20th centuries do not provide sufficient resolution to be used to estimate lost salt-marsh coverage via maps rather than photographs (Bromberg and Bertness 2005). The lack of intertidal area in a substantial portion of Pelletier Creek in the 1939 imagery suggests that changes had already commenced there, given that wide intertidal zones are a prominent characteristic of tidal creeks along the southeastern U.S. coast (Blanton et al. 2006). There is also a possibility that historical relief and topography (e.g., sand dunes; Senter 2003) adjacent to Pelletier Creek resulted in less salt-marsh area in its high-tide wetted area relative to Spooners Creek, even before development occurred in this area. Our estimates of lost production are minimums because older (age 1+) and larger (those greater than ~40 mm total length) Mummichog were not used to calculate the production of this species in either study creek. Additionally, estimates in this study represent minimum lost numbers of age-0 Mummichog because the production estimate that was used for each creek was the average for a single cohort rather than a value that was summed cumulatively across multiple cohorts of age-0 fish. Given that Mummichog exhibits predominant spawns over full moons during the spring and summer months (Taylor et al. 1979) and that our estimates of lost numbers of age-0 fish apply from tracking an average single cohort in each creek, the true number of age-0 fish that have been lost could be roughly sixfold higher in each creek. There is evidence that its rate of production on an areal basis is reduced when creekwide salt-marsh coverage is lost (Rudershausen and Buckel 2020). This is a distinct possibility in the case of this study, given that some salt marsh had already been lost by the time that the historical image was taken. Other resident nekton species that use salt-marsh habitats were not factored into the estimates of lost production in the two study creeks. These species include the Sheepshead Minnow *Cyprinodon variegatus* and grass shrimps *Palaemonetes* spp., which can be abundant in flooded salt marshes in the southeastern USA and the Gulf of Mexico (Kneib 1997a; Rozas and Zimmerman 2000; Krebs et al. 2014; Rudershausen et al. 2016). We are not aware of any studies that have estimated areal production for these or other resident nekton species. The exercise that we performed to compute lost secondary production of a resident species could also be conducted for important transients, such as the Atlantic Silverside *Menidia menidia* or penaeid shrimps, which accrete tissues during parts of their life cycles in salt-marsh systems (Turner 1977; Conover and Ross 1982).

It is predicted that the global cumulative loss of salt marsh could exceed 90% by the year 2100 (Crosby et al. 2016). The rising sea level and shoreline armoring efforts, which are directed at ensuring the persistence of valuable coastal development, are likely to drive the restriction and reduction of salt-marsh habitat area (Reed and Cahoon 1992; Feagin et al. 2010), and this will affect the ecosystem services that are provided by tidal marsh (Craft et al. 2009). Shoreline armoring is of particular concern along the southeastern U.S. coastline, where the practice is most common (Gehman et al. 2018). In addition to anthropogenic loss of salt marsh, there are also naturally induced changes in salt-marsh areal coverage. For example, Hill et al. (2020) found storm effects on the shoot abundance of salt-marsh cordgrass that exacerbated stress from submergence due to sea level rise in the Gulf of Mexico. The approach taken in this study could be used to estimate a total amount of lost production of species that use salt marsh areas under different scenarios of habitat loss.

Given that areal production of Mummichog declines as creekwide salt-marsh coverage is eliminated (Rudershausen and Buckel 2020), there is a compounding effect of salt-marsh loss on this species; habitat where age-0 larval and juvenile production occur is eliminated, and the remaining salt-marsh habitat supports a reduced level of areal production. This compounding effect of reduced production may also hold for other nekton species that inhabit other salt marshes in North America or other continents. Future studies, similar to the one that was conducted here, will enable coastal planners and fisheries stakeholders to evaluate competing trade-offs between coastal development and salt-marsh conservation in terms of foregone production of estuarine species.

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REFERENCES

Able, K. W., D. N. Vivian, G. Petruzzelli, and S. M. Hagan. 2012. Connectivity among salt marsh subhabitats: residency and movements of the Mummichog (*Fundulus heteroclitus*). Estuaries and Coasts 35:743–753.

Amorim, E., S. Ramos, M. Elliott, A. Franco, and A. A. Bordalo. 2017. Habitat loss and gain: influence on habitat attractiveness for estuarine fish communities. Estuarine, Coastal and Shelf Science 197:244–257.

Bass, A. S., and R. E. Turner. 1997. Relationship between dredged canals and salt marsh loss in three Louisiana estuaries. Journal of Coastal Research 13:895–903.

Beach, D. 2002. Coastal sprawl: the effects of urban design on aquatic ecosystems in the United States. Pew Oceans Commission, Arlington, Virginia.

Bilkovic, D. M., and M. M. Roggero. 2008. Effects of coastal development on nearshore estuarine nekton communities. Marine Ecology Progress Series 358:27–39.

Blanton, J. P., F. Andraide, and M. A. Ferreira. 2006. The relationship of hydrodynamics and morphology in tidal-creek and salt marsh systems in South Carolina and Georgia. Pages 93–107 *in* G. Kleppel, R. DeVoe, and M. Rawson, editors. Changing land use patterns in the coastal zone: managing environmental quality in rapidly developing regions. Springer, New York.

Brambilla, M., M. Gustin, S. Vitulano, R. Falco, V. Bergero, I. Negri, G. Bogliani, and C. Celada. 2017. Sixty years of habitat decline: impact of land-cover changes in northern Italy on the decreasing ortolan bunting *Emberiza hortulana*. Regional Environmental Change 17:323–333.

Bretsch, K., and D. M. Allen. 2006. Tidal migrations of nekton in salt marsh intertidal creeks. Estuaries and Coasts 29:474–486.

Bromberg, K. D., and M. D. Bertness. 2005. Reconstructing New England salt marsh losses using historical maps. Estuaries 28:823–832.

Bromberg-Gedan, K., B. R. Silliman, and M. D. Bertness. 2009. Centuries of human-driven change in salt marsh ecosystems. Annual Review of Marine Science 1:117–141.

Butler, C. L., V. L. Lucieer, S. J. Wotherspoon, and C. R. Johnson. 2020. Multi-decadal decline in cover of giant kelp *Macrocystis pyrifera* at the southern limit of its Australian range. Marine Ecology Progress Series 653:1–18.

Conover, D. O., and M. R. Ross. 1982. Patterns in seasonal abundance, growth and biomass of the Atlantic Silverside, *Menidia menidia*, in a New England estuary. Estuaries 5:275–286.

Craft, C., J. Clough, J. Ehman, S. Joye, R. Park, S. Pennings, H. Guo, and M. Machmuller. 2009. Forecasting the effects of accelerated sea-level rise on tidal marsh ecosystem services. Frontiers in Ecology and the Environment 7:73–78.

Crosby, S. C., D. F. Sax, M. E. Palmer, H. S. Booth, L. A. Deegan, M. D. Bertness, and H. M. Leslie. 2016. Salt marsh persistence is threatened by predicted sea-level rise. Estuarine, Coastal and Shelf Science 181:93–99.

Dahl, T. E. 1990. Wetlands losses in the United States 1780s to 1980s, version 16JUL97. U.S. Fish and Wildlife Service, Washington, D.C. Available: http://www.npwrc.usgs.gov/resource/othrdata/wetloss/wetloss.htm. (February 2021).

Dame, R., M. Alber, D. Allen, A. Chalmers, R. Gardner, C. Gilman, B. Kjerfve, A. Lewitus, M. Mallin, C. Montague, J. Pinckney, and N. Smith. 2000. Estuaries of the south Atlantic coast of North America: their geographical signatures. Estuaries 23:793–819.

Eberhardt, A. L., D. M. Burdick, and M. Dionne. 2011. The effects of road culverts on nekton in New England salt marshes: implications for restoration. Restoration Ecology 19:776–785.

Erwin, M. P., G. M. Sanders, and D. J. Prosser. 2004. Changes in lagoonal marsh morphology at selected northeastern Atlantic coast sites of significance to migratory waterbirds. Wetlands 24:891–903.

ESRI (Environmental Systems Research Institute). 2019. ArcGIS desktop: release 10.7. ESRI, Redlands, California.

Feagin, R. A., M. L. Martinez, G. Mendoza-Gonzales, and R. Costanza. 2010. Salt marsh zonal migration and ecosystem service change in response to global sea level rise: a case study from an urban region. Ecology and Society [online serial] 15:14.

Gehman, A.-L.-M., N. A. McLenaghan, J. E. Byers, C. R. Alexander, S. C. Pennings, and M. Alber. 2018. Effects of small-scale armoring and residential development on the salt marsh-upland ecotone. Estuaries and Coasts 41:54–67.

Gittman, R. K., F. J. Fodrie, A. M. Popowich, D. A. Keller, J. F. Bruno, C. A. Currin, C. H. Peterson, and M. F. Piehler. 2015. Engineering away our natural defenses: an analysis of shoreline hardening in the US. Frontiers in Ecology and the Environment 13:301–307.

Grizzle, R. E., J. R. Adams, and L. J. Walters. 2002. Historical changes in intertidal oyster (*Crassostrea virginica*) reefs in a Florida lagoon potentially related to boating activities. Journal of Shellfish Research 21:749–756.

Hagan, S. M., S. A. Brown, and K. W. Able. 2007. Production of Mummichog (*Fundulus heteroclitus*): response in marshes treated for common reed (*Phragmites australis*) removal. Wetlands 27:54–67.

Hill, J. M., P. S. Petraitis, and K. L. Heck Jr. 2020. Submergence, nutrient enrichment, and tropical storm impacts on *Spartina alterniflora* in the microtidal northern Gulf of Mexico. Marine Ecology Progress Series 644:33–45.

Holland, A. F., D. M. Sanger, C. P. Gawle, S. B. Lerberg, M. S. Santiago, G. H. M. Riekerk, L. E. Zimmerman, and G. I. Scott. 2004. Linkages between tidal creek ecosystems and the landscape and demographic attributes of their watersheds. Journal of Experimental Marine Biology and Ecology 298:151–178.

Kennish, M. J. 2001. Coastal salt marsh systems in the U.S.: a review of anthropogenic impacts. Journal of Coastal Research 17:731–748.

Kneib, R. T. 1984. Patterns in the utilization of the intertidal salt marsh by larvae and juveniles of *Fundulus heteroclitus* (Linnaeus) and *Fundulus luciae* (Baird). Journal of Experimental Marine Biology and Ecology 83:41–51.

Kneib, R. T. 1986. The role of *Fundulus heteroclitus* in salt marsh trophic dynamics. American Zoologist 26:259–269.

Kneib, R. T. 1997a. Early life stages of resident nekton in intertidal marshes. Estuaries 20:214–230.

Kneib, R. T. 1997b. The role of tidal marshes in the ecology of estuarine nekton. Oceanography and Marine Biology: An Annual Review 35:163–220.

Kneib, R. T. 2000. Salt marsh ecoscapes and production transfers by estuarine nekton in the southeastern United States. Pages 267–291 *in* M. P. Weinstein and D. A. Kreeger, editors. Concepts and controversies in tidal marsh ecology. Kluwer Academic, Dordrecht, The Netherlands.

Krebs, J. M., C. C. McIvor, and S. S. Bell. 2014. Nekton community structure varies in response to coastal urbanization near mangrove tidal tributaries. Estuaries and Coasts 37:815–831.

Lotrich, V. A. 1975. Summer home range and movements of *Fundulus heteroclitus* (Pisces: Cyprinodontidae) in a tidal creek. Ecology 56:191–198.

Lowe, M. R., and M. S. Peterson. 2014. Effects of coastal urbanization on salt-marsh faunal assemblages in the northern Gulf of Mexico. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 6:89–107.

Mahood, S. P., C. M. Poole, J. E. M. Watson, R. A. MacKenizie, S. Sharma, and S. T. Garnett. 2020. Agricultural intensification is causing rapid habitat change in the Tonle Sap Floodplain, Cambodia. Wetlands Ecology and Management 28:713–726.

McIvor, C. C., and W. E. Odum. 1988. Food, predation risk and microhabitat selection in a marsh fish assemblage. Ecology 69:1341–1351.

Meredith, W. H., and V. A. Lotrich. 1979. Production dynamics of a tidal creek population of *Fundulus heteroclitus* (Linnaeus). Estuarine and Coastal Marine Science 8:99–118.

Minello, T. J. 1999. Nekton densities in shallow estuarine habitats of Texas and Louisiana and the identification of essential fish habitat. Pages 43–75 *in* L. Benaka, editor. Fish habitat: essential fish habitat and rehabilitation. American Fisheries Society, Symposium 22, Bethesda, Maryland.

Minello, T. J., K. W. Able, M. P. Weinstein, and C. G. Hays. 2003. Salt marshes as nurseries for nekton: testing hypotheses on density, growth, and survival through meta-analysis. Marine Ecology Progress Series 246:39–59.

Minello, T. J., R. J. Zimmerman, and R. Medina. 1994. The importance of edge for natant macrofauna in a created salt marsh. Wetlands 14:184–198.

Nixon, S. W., and C. A. Oviatt. 1973. Ecology of a New England salt marsh. Ecological Monographs 43:463–498.

Partyka, M. L., and M. S. Peterson. 2008. Habitat quality and salt-marsh species assemblages along an anthropogenic estuarine landscape. Journal of Coastal Research 24:1570–1581.

Peterson, G. W., and R. E. Turner. 1994. The value of salt marsh edge vs. interior as a habitat for fish and decapod crustaceans in a Louisiana tidal marsh. Estuaries 17:235–262.

Peterson, M. S., and M. R. Lowe. 2009. Implications of cumulative impacts to estuarine and marine habitat quality for fish and invertebrate resources. Reviews in Fisheries Science 17:505–523.

Reed, D. J., and D. R. Cahoon. 1992. The relationship between marsh surface topography, hydroperiod, and growth of *Spartina alterniflora* in a deteriorating Louisiana salt marsh. Journal of Coastal Research 8:77–87.

Ricker, W. E. 1946. Production and utilization of fish populations. Ecological Monographs 16:373–391.

Rozas, L. P., and R. J. Zimmerman. 2000. Small-scale patterns of nekton use among marsh and adjacent shallow nonvegetated areas of the Galveston Bay Estuary, Texas (USA). Marine Ecology Progress Series 193:217–239.

Rudershausen, P. J., and J. A. Buckel. 2020. Urbanization impacts on production and recruitment of *Fundulus heteroclitus* in salt marsh creeks. Marine Ecology Progress Series 645:187–204.

Rudershausen, P. J., J. A. Buckel, M. A. Dueker, S. J. Poland, and E. Hain. 2016. Comparison of fish and invertebrate assemblages among variably altered tidal creeks in a coastal landscape. Marine Ecology Progress Series 544:15–35.

Rudershausen, P. J., J. E. Hightower, J. A. Buckel, M. O'Donnell, T. Dubreuil, and B. H. Letcher. 2019. Survival and density of a dominant fish species across a gradient of urbanization in North Carolina tidal creeks. Estuaries and Coasts 42:1632–1653.

Sahara, E. A., D. A. Sarr, R. W. Van Kirk, and E. S. Jules. 2015. Quantifying habitat loss: assessing tree encroachment into a serpentine savanna using dendroecology and remote sensing. Forest Ecology and Management 340:9–21.

SANC (State Archives of North Carolina). 2020. Carteret County, North Carolina [air photo; 1:200,000]. U.S. Department of Agriculture Photo BUS-105-3 (January 1939). Available: https://www.flickr.com/photos/north-carolina-state-archives/albums/72157708130088825/page 2. (December 2020).

Sanger, D. M., A. Blair, G. DiDonato, T. Washburn, S. Jones, G. Riekerk, E. Wirth, J. Stewart, D. White, L. Vandiver, and A. F. Holland. 2015. Impacts of coastal development on the ecology of tidal creek ecosystems of the US southeast including consequences to humans. Estuaries and Coasts 38:49–66.

Senter, J. 2003. Live dunes and ghost forests: stability and change in the history of North Carolina's maritime forests. The North Carolina Historical Review 80:334–371.

Skinner, M. C., S. C. Courtenay, W. E. Parker, and R. A. Curry. 2005. Site fidelity of Mummichogs (*Fundulus heteroclitus*) in an Atlantic Canadian estuary. Water Quality Research Journal of Canada 40:288–298.

Svensson, C. J., G. A. Hyndes, and P. S. Lavery. 2007. Food web analysis in two permanently open temperature estuaries: consequences of saltmarsh loss? Marine Environmental Research 64:286–305.

Sweeney, J., L. Deegan, and R. Garritt. 1998. Population size and sire fidelity of *Fundulus heteroclitus* in a macrotidal salt marsh creek. Biological Bulletin 195:238–239.

Talbot, C. W., and K. W. Able. 1984. Composition and distribution of larval fishes in New Jersey high marshes. Estuaries 7:434–443.

Taylor, M. H., G. J. Leach, L. DiMichele, W. M. Levitan, and W. F. Jacob. 1979. Lunar spawning cycle in the Mummichog, *Fundulus heteroclitus* (Pisces: Cyprinodontidae). Copeia 1979:291–297.

Teo, S. L. H., and K. W. Able. 2003a. Habitat use and movement of the Mummichog (*Fundulus heteroclitus*) in a restored salt marsh. Estuaries 26:720–730.

Teo, S. L. H., and K. W. Able. 2003b. Growth and production of the Mummichog (*Fundulus heteroclitus*) in a restored salt marsh. Estuaries 26:51–63.

Turner, R. E. 1977. Intertidal vegetation and commercial yields of penaeid shrimp. Transactions of the American Fisheries Society 106:111–116.

Valiela, I., D. Rutecki, and S. Fox. 2004. Salt marshes: biological controls of food webs in a diminishing environment. Journal of Experimental Marine Biology and Ecology 300:131–159.

Valiela, I., J. E. Wright, J. M. Teal, and S. B. Volkmann. 1977. Growth, production, and energy transformations in the salt marsh killifish *Fundulus heteroclitus*. Marine Biology 40:135–144.

Ward, D. M., A. Morton, T. L. Tibbitts, D. C. Douglas, and E. Carrera-González. 2003. Long-term change in eelgrass distribution at Bahia San Quintin, Baja California, Mexico, using satellite imagery. Estuaries 26:1529–1539.

Weinstein, M. P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. U.S. National Marine Fisheries Service Fishery Bulletin 77:339–357.

Wernette, P., A. Shortridge, D. P. Lusch, and A. F. Arborgast. 2017. Accounting for positional uncertainty in historical shoreline change analysis without ground reference information. International Journal of Remote Sensing 38:3906–3922.

Zahawi, R. A., G. Duran, and U. Kormann. 2015. Sixty-seven years of land-use change in southern Costa Rica. PLoS (Public Library of Science) ONE [online serial] 10(11):e0143554.

Ziegler, S. L., K. W. Able, and F. J. Fodrie. 2019. Dietary shifts across biogeographic scales alter spatial subsidy dynamics. Ecosphere [online serial] 10(12):e02980.