

Bioenergetic and landscape considerations for scaling expectations of nekton production from intertidal marshes

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ABSTRACT: The connection between fishery production and vegetated intertidal habitats is often a key consideration in the rationale for protecting and restoring estuarine salt marshes. Evaluating the contribution of marsh habitats to estuarine nekton production requires an understanding of the mechanisms and constraints controlling production flows to nekton populations; this is especially important for setting and judging success criteria associated with restoration projects. This contribution considers both bioenergetic and landscape constraints on direct flows of marsh-derived production to populations of resident and migrant nekton. Nekton access to marsh resources is defined in terms of trophic (bioenergetic) and physical (landscape) constraints that determine the amount of nekton production that can be expected. Production to biomass (P:B) ratios applied to measurements of nekton standing stock from multiple marsh sites around Sapelo Island, Georgia, USA provided an example of the spatial variation in nekton production that can be expected from natural marshes. When P:B ratios of 2, 5, and 3 were applied to standing stocks of fishes, caridean shrimps and penaeid shrimps, respectively, annual net production of nekton from 12 intertidal marsh sites ranged from 0.12 to 2.88 g dry weight (dw) m⁻² and averaged ca. 1.50 g dw m⁻²; other scenarios using different sets of P:B ratios yielded production ranges of 0.11 to 2.25 and 0.17 to 4.57 g dw m⁻². There was a strong sigmoid relationship between nekton production and the amount of intertidal marsh/creek edge within a 200 m radius of a site for both resident and migrant species. Production was lowest at sites with relatively little marsh/creek edge, and increased rapidly with increasing drainage density until reaching an asymptote, after which even large changes in the amount of marsh/creek edge had no effect on nekton production. The findings suggest that bioenergetic constraints determine the ultimate capacity of intertidal marsh systems to produce nekton, but nekton production may be enhanced by relatively small additions of marsh/creek edge up to a threshold level above which no additional enhancement should be expected. Site-specific bioenergetic and landscape constraints should be considered when developing realistic expectations and success criteria for marsh restoration efforts aimed at enhancing estuarine nekton production.

KEY WORDS: Estuaries · *Fundulus* · P:B ratio · Salt marsh · *Palaemonetes* · *Litopenaeus*

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INTRODUCTION

Tidal marshes along the Atlantic and Gulf coasts of the US can produce up to 8 kg m⁻² yr⁻¹ of plant material, inclusive of vascular plants, benthic algae and phytoplankton (Mitsch & Gosselink 1993). The quantity of organic material annually generated in these habitats clearly suggests their potential for supporting

organisms at higher trophic levels. While most of the production from intertidal wetlands is used *in situ*, some is exported to adjacent estuarine and coastal habitats (Odum 2000, Teal & Howes 2000). There is no clear consensus regarding the magnitude of those exports or the mechanisms involved (e.g. passive movement of organic material or directional migration of animals). However, local and regional variation in

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tidal regimes, edaphic and climatic factors, together with geomorphic characteristics of the landscape (both natural and anthropogenic) may affect variation in primary production (Mendelssohn & Morris 2000) as well as material and energy fluxes between the intertidal and subtidal components of estuaries (Mitsch & Gosselink 1993).

Intertidal vegetation contributes not only to the foundation of many estuarine food webs but also to the maintenance of structural complexity at multiple spatial scales in the coastal landscape (Kneib 1994, 1997). Trophic support and refuge values have been the basis of a long-standing rationale within the scientific community for the importance of intertidal wetlands in maintaining coastal productivity (e.g. Teal 1962, Boesch & Turner 1984). Positive statistical relationships between fishery yields and either the area of vegetated intertidal habitat (e.g. Turner 1977, Zimmerman et al. 2000) or the amount of intertidal edge associated with such habitats (e.g. Teal & Howes 2000, Minello & Rozas 2002) can be found at multiple spatial scales (Webb & Kneib 2002), adding credence to the original tenet (*sensu* Teal 1962) that these habitats are net exporters of secondary production and highlighting the importance of transitional areas that promote the movements of organisms and materials among habitats (e.g. vegetated intertidal and subtidal estuary).

Recognition of the importance of intertidal wetlands in the support of estuarine and nearshore coastal secondary production has led to their designation as 'essential fish habitat' (e.g. see Benaka 1999), and promoted interest in the restoration and creation of intertidal wetlands as a management tool for enhancing ecosystem services, including fisheries production, in estuaries (e.g. Lewis 1992, Kruczynski 1999). The amount of nekton production annually attributable to a given area of vegetated intertidal habitat is a long-standing and crucial question from the perspectives of both basic science and applied management. It must encompass an understanding of what species and life stages are dependent upon the resources available in intertidal vegetated habitats, including accurate measures of densities and standing-stock biomass and how these vary in time and space. For some species, intertidal wetlands may be essential for survival, while for others their presence may simply improve survival and growth, contributing to an enhancement of production.

Marshes are only periodically available to fully aquatic organisms and the boundaries of the aquatic and terrestrial portions of the environment continuously change with the ebb and flow of the tides. Consequently, most nekton associated with intertidal vegetated environments do not permanently reside there, and exhibit a range of life-history strategies involving ontogenetic shifts in habitat use as well as

tidal, seasonal and annual migration patterns that vary across a range of spatial scales (Kneib 1994, 1997). The open nature of intertidal habitats has presented a unique challenge to researchers attempting quantitative studies of the dynamics of mobile populations, and consequently, actual estimates of production by nekton populations within tidal wetlands are uncommon.

Most estuarine species rely on the resources of many habitats during their life histories and so it is difficult to quantify the fraction of a population's total annual production that can be attributed to a specific environment (e.g. intertidal marsh, subtidal seagrass bed, etc.). Also, one must recognize that there is variation both among and within habitat types in regard to potential for contributing to production of estuarine nekton. The secondary production attributable to intertidal wetlands depends on the amount of primary production entering the base of the food web, and its accessibility to consumers. Accessibility is used here in a very general sense that encompasses *physical access* to intertidal production, which is controlled by the frequency and duration of tidal inundation as well as structural features of the landscape (e.g. tidal channels, levees, impoundments, etc.), and *trophic access*, which controls the efficiency of production transfers within the system (i.e. the number of trophic links and the amount of production lost at each link). There is substantial variation in primary production not only at the global and regional level but also within wetland ecosystems (Mitsch & Gosselink 1993, Mendelssohn & Morris 2000), and one might expect a similar degree of variation in the secondary production attributable to different intertidal wetland sites.

Here I describe constraints on nekton production from bioenergetic and structural landscape perspectives that should be considered in scaling the contributions of frequently flooded natural and restored intertidal marshes to estuarine fisheries production. The bioenergetic component focuses on availability of primary production to consumers and trophic transfer efficiency as reflected in annual production to biomass (P:B) ratios, while the landscape component considers the effect of marsh channel complexity (i.e. tidal drainage density) on habitat use, standing-stock biomass and production of nekton. The concepts are applied to data collected from Sapelo Island, Georgia, USA, to demonstrate expected levels of spatial variation (10 m to 10 km) in nekton production derived from undisturbed intertidal marshes where *Spartina alterniflora* is the characteristic emergent vegetation. This is intended to provide an empirical framework for the development of realistic targets and expectations in connection with marsh restoration projects aimed at enhancing estuarine nekton production.

Nekton assemblages of tidal marshes

Nekton assemblages of intertidal wetlands are not easy to define because there is not a universally recognized seaward boundary for these systems. Historically, tidal marshes have been characterized by the presence of certain vegetation types found primarily at intertidal elevations between mean sea level and the highest spring-tide line (Chapman 1960). If either vegetation type or some tidal elevation above mean low water defines the boundary of the system, then subtidal waters are not—strictly-speaking—components of these habitats (e.g. Kneib 1997). From this perspective, intertidal creeks, ponds, pannes and impoundments within the vegetated matrix may be considered elements embedded within the marsh habitat, but subtidal creeks that maintain a continuous aquatic connection with the sea at low tide are transitional habitats between the marsh proper and the broader open water estuarine system.

A popular alternative perspective among estuarine fisheries researchers extends the tidal marsh to include the adjacent shallow subtidal creek system into which intertidal creeks drain (see Rountree & Able 1992 or Deegan et al. 2000). The problem with this perspective is that the boundary between the open estuary and the intertidal wetlands becomes very subjective. How far into the open estuary or coastal ocean does a tidal marsh extend? Note that this question does not refer to the influence of the intertidal vegetated habitat, but the seaward boundary of the marsh habitat. It also has important implications for the measurement of nekton secondary production from marshes. What is the relationship between distance from the intertidal habitat and the amount of estuarine secondary production supported by marshes?

Regardless of the perspective in defining the system, it is clear that as one proceeds from the open embayments and large tidal channels of the estuary into the smaller creek channels, and ultimately onto the intertidal plain of the vegetated marsh proper, the nekton assemblage becomes a smaller subset of the total estuarine nekton community. More species and higher densities of nekton usually occur at the seaward edge of intertidal vegetation than in the interior of the vegetated marsh plain (Kneib 1997, Kruczynski & Ruth 1997, Minello 1999, Rozas & Zimmerman 2000). Densities of nekton also often decline with increasing water depth and distance seaward of intertidal edge habitats (Ruiz et al. 1993, Kurz et al. 1998).

Species vary considerably in their degree of association with intertidal vegetated habitats. Some, such as the mummichog *Fundulus heteroclitus* and other killifishes, range widely throughout the habitat whenever it is tidally inundated (Kneib 2000), while others, such

as spotted seatrout *Cynoscion nebulosus* or red drum *Sciaenops ocellatus*, are found primarily at the estuarine edge of intertidal vegetated habitat (Minello 1999) and only occasionally forage across the marsh plain (see Montague & Wiegert 1990, p. 507). Detailed knowledge of how nekton species (much less their various life stages) use intertidal habitats is far from complete, but different species and size classes clearly have affinities for different portions of vegetated intertidal habitats (Hettler 1989, Montague & Wiegert 1990, Whitman & Gilmore 1993, Kneib & Wagner 1994, Minello 1999, Kneib 2000, Rozas & Zimmerman 2000). Although the estuarine nekton community comprises mostly migrant or transient species that usually spend only a portion of their life history (usually juvenile stages) in the estuary, nekton assemblages most closely associated with intertidal vegetation are dominated by resident species—those that can complete their life cycles within the shallow subtidal or even intertidal portions of the estuary (Kneib 1997). Even when maximally accessible to all estuarine nekton (e.g. at high-amplitude spring tides), interior portions of vegetated intertidal wetlands are frequented primarily by small (<10 cm) resident species (Peterson & Turner 1994, McIvor & Rozas 1996, Kneib 1997). Along the Atlantic and Gulf coasts of the southeastern US, these generally include killifishes (e.g. *Fundulus heteroclitus* on the Atlantic coast, *F. grandis* on the Gulf coast), live-bearers (e.g. *Poecilia latipinna* and *Gambusia holbrooki*) and grass shrimps (*Palaemonetes* spp.). All serve as important prey resources for juveniles of piscivorous species such as snook (Gilmore et al. 1983), red drum (Reagan 1985) and a variety of other estuarine predators (Abraham 1985) which compose the migrant or transient components of estuarine nekton assemblages.

NEKTON ACCESS TO MARSH RESOURCES

Trophic access

Primary production in intertidal marshes has 2 principal sources: vascular plants and benthic algae. Vascular plants are the most conspicuous and defining elements of marsh systems, but there has been considerable debate over their relative contribution to marsh food webs. Estimates of annual production from benthic algae in tidal marshes of the southeastern USA range from about 140 to 470 g dry weight (dw) m⁻² (converted from g C m⁻² yr⁻¹ given in Table 2 of Sullivan & Currin 2000—assuming 1 g C = 2 g dw), while estimates of net annual above-ground production of *Spartina alterniflora* (hereafter referred to as *Spartina*) in marshes within the same region range from 130 to

3700 g dw m⁻² (Table 8–7 in Mitsch & Gosselink 1993), with the lower values associated with marshes in northwestern Florida (Kruczynski et al. 1978). Algal production is generally grazed as live biomass by intertidal consumers, but relatively little (ca. 10%) of the vascular plant material produced annually in these systems is consumed live (Montague & Wiegert 1990). Instead, it enters a detritus-based food-web driven by fungi and bacteria, with a substantial loss of production to respiration of the microbial community.

In salt marshes, decomposition of *Spartina* leaves begins while the plant material is still in the standing state and fungi play a key role in the process. Recent estimates of conversion efficiency of dead *Spartina* biomass to fungi are in the range of 50 to 60% (Newell & Porter 2000). Fungi can be an important food source for a variety of invertebrate marsh consumers, including gastropods and amphipods (Kneib et al. 1997, Newell & Porter 2000). Nekton that feed on these potential prey can more efficiently capture marsh production derived from vascular plants before it enters the next phase of the decomposition process within the sediments, where bacterial communities can rapidly respire much of what remains to the atmosphere, and in the process re-mineralize nutrients that may become available to estuarine phytoplankton or benthic algal communities in adjacent habitats (e.g. unvegetated mudflat or open water column).

Diets of typical marsh resident species (e.g. killifishes) tend to include a variety of small intertidal invertebrates, such as copepods, amphipods, polychaetes, gastropods and insects (Kneib 1978, 1986). Even resident fishes with diets composed largely of algae (e.g. *Cyprinodon variegatus* or *Poecilia latipinna*) will feed opportunistically on animal prey (Harrington & Harrington 1961, 1982). Diets of common nektonic decapods (e.g. caridean and penaeid shrimps) similarly include a mixture of plant and animal food sources (e.g. Sikora 1977, Morgan 1980, Gleason & Wellington 1988, McTigue & Zimmerman 1991). Although evidence from analyses of stable isotopes (carbon, nitrogen and sulfur) in tissues of estuarine nekton has consistently demonstrated links to tidal marsh-derived organic matter (e.g. Deegan & Garritt 1997, Weinstein & Litvin 2000), the relative importance of algae and vascular plant detritus in support of estuarine nekton production is an issue that remains unresolved (Deegan et al. 2000).

Marsh systems contain an abundance of plant material in various stages of decomposition, and it is not surprising that detritus is commonly found in the gut contents of virtually all common aquatic organisms associated with these habitats, leading many investigators to identify this material as an important food source for nekton (e.g. Darnell 1967, Odum & Heald

1972, Welsh 1975). Although a few fish and shrimp species are capable of assimilating some components of plant detritus (e.g. Condrey et al. 1972, Deegan et al. 1990) and results of stable isotope studies suggest that detritus plays a role in supporting marsh food webs (e.g. Currin et al. 1995), other empirical studies have shown that plant detritus is of questionable direct nutritional value to some of the most common marsh nekton, including killifishes (Prinslow et al. 1974, D'Avanzo & Valeila 1990). In contrast, detrital diets have been shown to support not only growth, but also reproduction of smaller invertebrate prey populations such as amphipods (Kneib et al. 1997). The indirect pathway from microbial decomposers of detritus to small invertebrate prey populations and ultimately marsh nekton seems the most likely principal pathway by which detrital material contributes to nekton production.

Physical access to intertidal resources

Intertidal plant production, regardless of quantity or quality, cannot contribute to the production of estuarine nekton unless it is accessible. The previous section considered accessibility in terms of trophic pathways, but the physical structure of the landscape (e.g. McIvor & Rozas 1996, Kneib 1997, 2000) and the tidal regime (e.g. Rozas 1995, Kneib 2000) also define accessibility through effects on movements of nekton and food sources between the intertidal and subtidal portions of the estuarine environment. Experimental evidence for the importance of access to the intertidal marsh surface in the maintenance of estuarine nekton populations is rare. One study conducted by Weisberg & Lotrich (1982) used field enclosures to demonstrate that access to food resources available on the intertidal marsh was essential to support observed growth rates and population densities of the killifish *Fundulus heteroclitus* in Canary Creek, Delaware.

Current conceptual models of the transfer of production from intertidal to subtidal estuarine environments have been focusing on predator-prey interactions and ontogenetic shifts in the use of estuarine habitats by different species of resident and migrant nekton. Movements of production across the estuarine landscape via nekton populations have been referred to as a 'trophic relay' (Kneib 1997, 2000, Deegan et al. 2000). Vegetated intertidal habitats that are impounded or otherwise disconnected from direct communication with the open estuary obviously interfere with such transfers. This is evident in the species compositions and densities of nekton in closed and open impoundments examined in Florida wetlands (e.g. Gilmore et al. 1982, Rey et al. 1990, Vose & Bell 1994). These

studies have shown that closed impoundments, while dominated by small resident nekton, rarely contain estuarine transient species, but when these impoundments are open, usage by transient species increases while densities of residents may decline. Given that many transient species are predators, these observations imply that production accumulated in the biomass of resident species is quickly passed on to the transients when the system is physically accessible.

If there are no physical obstructions between the open estuary and intertidal wetlands, the tidal regime of a region determines the potential level of opportunity for direct use of the habitat by nekton (e.g. Rozas 1995, McIvor & Rozas 1996). The frequency and duration of tidal inundation control the amount of time that intertidal habitat is available to nekton, while tidal amplitude influences the areal extent of the habitat. Species-specific life histories, behavior and size-specific swimming ability then determine the actual level of direct use of intertidal habitats by nekton (see Kneib 1995). For example, resident nekton (e.g. killifishes such as *Fundulus* spp.) use intertidal creeks and pools as low-tide staging areas from which they have immediate access to all areas of the marsh that are tidally inundated, while some migrant species (e.g. juvenile white shrimp *Litopenaeus setiferus*) may not appear on the vegetated marsh until it has been inundated for a longer period of time (see Fig. 1 in Kneib 2000). The extent of movement by nekton across the marsh plain in response to tidal stages (i.e. flooding vs ebbing flows) varies with species and size (Kneib & Wagner 1994), and relates in part to the swimming capacity and the degree of aversion to intertidal stranding exhibited by different organisms. In general, resident species are least averse to stranding and thus tend to be the first to enter and the last to leave the marsh, thus maximizing their time directly using the resources of the tidal marsh. Transient species tend to arrive later on flood tides and leave the marsh earlier on ebbing tides than resident nekton (Kneib & Wagner 1994).

Edges defining the border between the vegetated intertidal and adjacent water bodies (embayments, tidal creeks, canals, etc.) can be described as 'critical transition zones' (Levin et al. 2001). These are areas of potentially intense biological activity and often exhibit the highest densities of nekton associated with intertidal wetlands, particularly in microtidal environments associated with marshes along the northern shoreline of the Gulf of Mexico (e.g. Minello 1999, Rozas & Zimmerman 2000). The attraction of nekton to structural edges has prompted the application of manipulative management techniques designed to enhance the amount of edge habitat as a means of increasing fish production, particularly in shallow open water habitats (e.g. Rozas & Minello 2001). A narrow (a few meters)

vegetated intertidal edge can provide a structural refuge for prey or a habitat from which predators can ambush prey organisms (Thayer et al. 1987, Whitman & Gilmore 1993), but this relatively small area of marsh habitat is unlikely to have the capacity to satisfy the nutritional requirements of the high densities of nekton often found there, unless there is additional trophic support from adjacent portions of the estuary (e.g. interior marsh, mudflat or subtidal aquatic/benthic habitats). In most estuarine marshes, tidal channels and their associated edges function to increase accessibility of intertidal resources to both resident and migrant nekton. Higher densities of nekton occur in the interior of tidal marshes associated with complex drainage networks compared to marshes drained by only a few simple tidal channels (e.g. see Fig. 6 in Kneib 1994).

NEKTON PRODUCTION

Bottom-up estimate of nekton production from tidal marshes

From the background information on plant production, food sources and trophic links involved in the production of nekton from intertidal habitats (previous section on *Trophic access*), together with a basic understanding of ecological energetics, one can roughly estimate the amount of net production of nekton expected from an area of *Spartina* marsh with an intermediate rate of annual plant production totaling 1250 g dw m⁻² (Fig. 1). For purposes of illustration, I have assumed above-ground net primary production that includes 1000 g from *Spartina alterniflora* and 250 g from benthic algae. Trophic transfer efficiencies of 10% (Pauly & Christensen 1995) were applied in all cases, except for conversion of detritus to fungi, which is more efficient and was assigned a value of 55% (Newell & Porter 2000). Neither dissolved organic carbon (DOC) nor below-ground production from *Spartina* were included here because there is currently little evidence linking these sources directly to food webs that support the production of nekton from marshes. Foliar release of DOC from *Spartina* is quickly taken up by bacteria (Hullar et al. 1996) and respired into the atmosphere, while most of the below-ground plant production—the source of which of course is aerial production—is readily translocated among living roots, rhizomes and above-ground shoots (Dai & Wiegert 1996). Thus, above-ground growth of *Spartina* in the spring depends on winter reserves stored in the below-ground rhizomes and roots. However, the current model (Fig. 1) should be viewed as an underestimate if some nekton production derives from these sources either directly or indirectly.

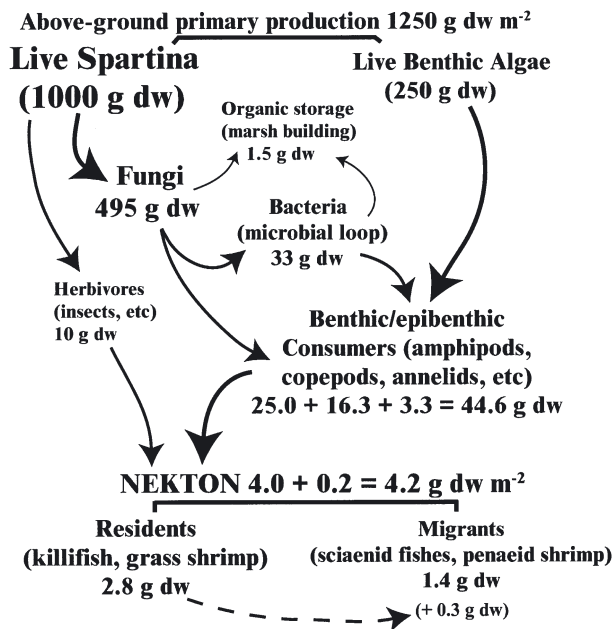


Fig. 1. Production flows to nekton populations from a hypothetical 1250 g dry weight (dw) m⁻² of annual primary production from an intertidal salt marsh. Size of arrows indicates relative importance of flows to nekton populations, not necessarily total magnitude of material or energy pathway. Ecological efficiencies were assumed to be 10% except for conversion of *Spartina alterniflora* to fungi, which was 55% (see section 'Bottom-up estimate of nekton production from tidal marshes' for additional constraints). It was further assumed that most of the production of herbivores (10 g dw) from live *Spartina* contributed to a terrestrial food web (i.e. spiders and birds), and only 20% was available to nekton

In the present scenario, 10% of the *Spartina* production is consumed live by insects and other herbivores (Montague & Wiegert 1990), and most of that pathway would likely contribute to a terrestrial food web (e.g. spiders and birds). Nonetheless, I presumed that 20% of that production or 2 g of insects (100 g × 0.1 × 0.2) would be available to aquatic predators and thus would yield 0.2 g of nekton (2 g × 0.1). Most of the *Spartina* production (900 g) enters a detrital pathway beginning with fungi, which yields 495 g dw m⁻² (900 × 0.55 efficiency of conversion to fungi) potentially available to benthic/epibenthic invertebrate consumers. Assuming further that invertebrate consumers (amphipods, annelids, insect larvae, etc.) could capture 1/3 of that material before it entered the next phase of decomposition involving bacterial communities, the available material could yield 16.3 g dw m⁻² (495 × 0.33 × 0.1) of invertebrate prey organisms.

The balance of detrital production which passes through the fungal component and on to bacterial communities (495 × 0.67 × 0.1 = 33 g dw) also could contribute 3.3 g dw m⁻² (33 × 0.1) to the invertebrate prey

assemblage through a weaker link to the microbial loop. If most of the primary production from benthic algae is readily and directly available for consumption, it would yield an additional 25.0 g dw m⁻² (250 × 0.1) of potential invertebrate prey, providing a potential food reservoir for nekton of 44.6 g dw m⁻², not all of which would be available to aquatic predators. Some molluscs (e.g. periwinkle snails and mussels) and larger crustaceans (e.g. fiddler crabs and mud crabs) may be relatively long-lived and ultimately consumed by terrestrial predators (Carlton & Hodder 2003). However, here I have assumed that a substantial majority (90%) of invertebrate prey production is available and turns over rapidly, so could yield 4.0 g dw m⁻² (44.6 × 0.9 × 0.1) of nekton. Combined with the 0.2 g from the consumer pathway linked to live *Spartina* production, this yields a grand total of 4.2 g dw m⁻² of fishes, shrimps and crabs supported on 1250 g dw m⁻² of above-ground tidal marsh primary production.

If 2/3 of this total represents resident species with the balance in migrants, and the residents are an important source of prey for other estuarine migrant species (e.g. drums, flatfishes and other predatory species), a total of 1250 g dw m⁻² of primary production from a marsh could contribute 1.7 g dw m⁻² of migrant nekton to the estuary (4.2 × 0.33 = 1.4 g produced directly by the marsh and another 4.2 × 0.67 × 0.1 = 0.3 g produced as a result of migrant predators feeding on resident prey species). The estimate of 4.2 g dw m⁻² of total nekton production from this hypothetical marsh system provides a 'ball park' value that may not adequately account for all potential pathways by which marsh production contributes to the trophic support of adjacent estuarine and terrestrial ecosystems, including consumption by birds or other non-aquatic predators (Carlton & Hodder 2003). Neither does it account for the biomass stored in long-lived potential prey species such as marsh periwinkles *Littoraria irrorata* or ribbed mussels *Geukensia demissa*, both of which have lifespans ranging from 10 to 20 yr (Stiven & Hunter 1976, Franz 2001). However, it provides a point of reference from which to compare estimates from an alternative empirical method described in subsequent sections.

Production:biomass ratios

Production (P) during short time intervals can be estimated from a single measure of biomass (B) if there is some prior knowledge of both growth (G) and mortality (Z) rates, as these vital rates can be related to production as follows: $P = GB [(e^{G-Z} - 1)/(G - Z)]$. Annual production is then calculated by summing the production over all short time intervals. Of course, this assumes that growth and mortality schedules are accu-

rately known for a sufficient number of short time intervals to define the annual pattern. Chapman (1978) pointed out that while growth rates can usually be estimated with reasonable certainty, mortality rates can be notoriously inaccurate, not to mention difficult and time-consuming to obtain. If one can assume an empirical relationship between production and biomass (i.e. $\bar{P} = c\bar{B}$, where c is a constant for a given species and set of conditions) on an annual basis, a reasonable estimate of one variable can be made from an accurate estimate of the other; this concept is supported by a substantial literature that has developed for some aquatic systems.

Fishes

Production is strongly correlated with standing-stock biomass for fishes in freshwater lakes and stream systems. Several researchers (e.g. Chapman 1978, Banse & Mosher 1980, Downing & Plante 1993) have compiled lists of P:B ratios for freshwater fishes and observed that the ratio also varies consistently with species size and with regional climatic temperature regimes. Values of P:B ratios are inversely related to adult or maximum body mass (Banse & Mosher 1980), mostly because smaller species tend to exhibit more rapid growth rates and exhibit shorter generation times than large species. P:B ratios of the 11 species listed by Banse & Mosher (1980) ranged from 0.4 to 2.82 and averaged 1.78; those listed in Chapman (1978) ranged from 0.44 to 5.0 and averaged 1.69. A larger survey of 100 fish populations by Downing & Plante (1993) indicated a range of P:B values between 0.2 and 5.0, with an average value of 0.93 (Fig. 2).

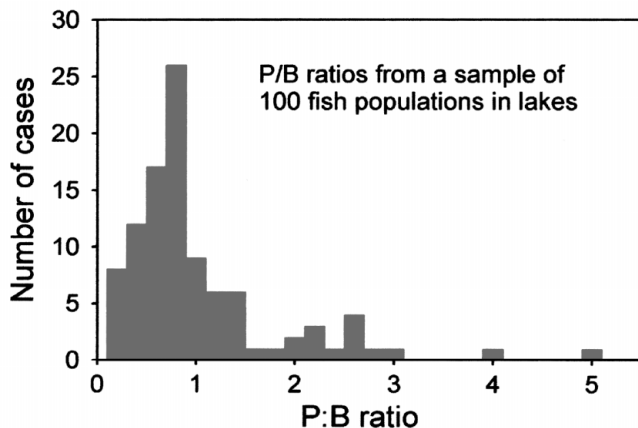


Fig. 2. Distribution of production to biomass (P:B) ratios from 100 populations of fishes. Data came from Downing & Plante (1993)

Note that there is a primary mode around a P:B ratio of 1 and another between 2 and 3. The higher P:B values are associated with smaller fish species. This is an important consideration for nekton assemblages in tidal marshes because they are characterized by species or size classes that are relatively small, averaging <10 cm in length (Kneib 1997). A survey of the few studies of fish production available from tidal marshes reveals a range of P:B ratios similar to those reported for freshwater fishes (Table 1). Mean values of P:B ratios from the few studies of marsh fishes that provided sufficient information to permit an estimate, ranged from 0.81 to 4.48, with an average value pooled across all studies of 2.41.

The P:B ratios from studies based on mark-recapture data, which should provide the most accurate estimates of population size (i.e. standing stocks) and mortality rates, yielded values around 1 (e.g. Valiela et al. 1977, Weinstein & Walters 1981). The higher values presented in some studies (e.g. Warburton 1979, Allen 1982) were based on variable intervals during which species were present in the system, and may not represent expected values on an annual basis. Consequently, a P:B ratio of 2 for marsh fishes is a reasonable compromise, given the lower values (Fig. 2) representing freshwater fishes and the paucity of information on estuarine species.

Many of the literature estimates reported for fishes from both freshwater and marine environments may not include the earliest life stages within Age 0, which often account for most of the production in a population. For example, Wang & Houde (1995) estimated production of bay anchovy in Chesapeake Bay from acoustic-calibrated data and found that young-of-the-year accounted for 92.6% of the annual production in the population; they reported a P:B ratio of 0.97 (very similar to the value for fish in lakes) when larvae and early juveniles were excluded, but when these earliest life stages were factored in, the P:B ratio jumped to 7.08 (note: incorrectly reported in the paper as 8.07). Similarly, Allen (1982) observed that the P:B ratio for young-of-the-year atherinids from the littoral zone of a California wetland system was substantially higher (7.55) than that of adults (1.27).

The high P:B values resulting from the production of the very earliest life stages in tidal wetlands are not considered further here for 2 reasons: (1) Much of the mortality in the youngest age classes of resident species has been connected to consumption by adult residents (Kneib 1987, 1993), essentially forming a closed trophic loop (i.e. early larval production is used in situ) and so is unavailable for direct export from the intertidal to the open estuary; (2) Migrant species found in tidal marshes arrive as juveniles because the early stages are generally produced elsewhere (spawned in

Table 1. Summary of annual production and production to biomass (P:B) estimates for nekton (fishes and decapod crustaceans) from tidal wetlands. Values are converted to g dry weight (g dw) m⁻² from units used in the original papers (conversion factors: dry wt = 0.22 × wet wt; 1 g dry wt = 4.7 kcal; 1 kcal = 4.2 kJ). YOY: young of year

Species	Location	Production (g dw m ⁻² yr ⁻¹)	P:B	Source
Fishes				
<i>Fundulus heteroclitus</i>	Great Sippewissett Marsh, MA	1.6 ^a	0.81	Valiela et al. (1977)
<i>Fundulus heteroclitus</i>	Canary Creek, DE	8.8 (78% from YOY) for creek only		Meredith & Lotrich (1979)
<i>Fundulus parvipinnis</i>	Ojo de Liebre Lagoon, Mexico	0.32 (for lagoon only)	2.1	Pérez-España et al. (1998)
<i>Leiostomus xanthurus</i>	Creeks on Cape Fear River, NC	0.26 (creek only, YOY)	1.06	Weinstein & Walters (1981)
<i>Leiostomus xanthurus</i>	2 tidal creeks in York River, VA	4.2–4.6 in creeks only; corrected for marsh drainage area, value is 0.38		Weinstein (1983), Weinstein et al. (1984)
All fishes	Mesohaline impounded salt marsh, FL	9.6–14.0 (not inclusive of surrounding marsh drainage)		Schooley (1981)
<i>Atherinops affinis</i> : Adults	Littoral zone of tidal marsh, Upper Newport Bay, CA (not inclusive of entire intertidal); only species present in more than 1 mo are included here	0.13	1.27	} Allen (1982)
YOY		7.96	7.55	
9 other spp.		<0.01 to 0.46 (mean: 0.16)	0.54–10.59 (mean: 3.42)	
<i>Mugil curema</i>	Caimanero Lagoon, Mexico (subtidal area only)	2.7	3.25–8.44	} Warburton (1979)
<i>Anchoa panamensis</i>		2.7	(mean: 4.48)	
<i>Galeichthys caerulescens</i>		1.8		
All other spp.		All others 2.8 (average)		
Decapod crustaceans				
<i>Palaemonetes pugio</i>	Killer Creek, SC	10.8 for creekbank area only, and 0.67 when adjusted for marsh drainage area	5.06	Sikora (1977)
<i>Palaemonetes pugio</i>	Bissel Cove, RI	6.8 (embayment only, not corrected for surrounding marsh drainage)	2.34	Nixon & Oviatt (1973), Welsh (1975)

^aAnnual production value reported in Valiela et al. (1977) was 16.0 g dw m⁻², but length-weight equations used in calculations over-estimated dry mass of individuals by an order of magnitude, thus the annual production value was reduced proportionally for this table

the coastal ocean or open estuary) and so the earliest production cannot be associated directly with the marshes.

Fish production is strongly influenced by the effect of temperature on growth rates (Downing & Plante 1993) and the P:B ratios of fish populations in tropical areas are expected to be greater than in temperate areas. Chapman (1978) suggested a P:B value of 1.5 as an estimator for cold-water habitats and 1.7 to 2.0 for warmer waters for fishes in freshwater streams. However, a survey of P:B values associated with tropical fish species worldwide does not differ dramatically from those in temperate waters. For example, Lowe-McConnell (1987) reported P:B values for tropical fishes ranging from 0.68 to 3.77 and averaging 1.8. Agostinho & Penczak (1995) reported mean values of 0.79 and 0.90 for 2 small tributaries of the Paraná River in Brazil; the range for individual species at the 11 sites examined ranged from 0.51 to 1.35.

Decapods

P:B ratios for decapod crustaceans in tidal marshes are even less common than those for fishes. The 2 studies of grass shrimp production cited in Table 1 yield an average value of 3.70, which is substantially higher than that for fishes. Grass shrimp reach maturity at a size of 20 to 25 mm, produce multiple generations annually (Sikora 1977), and serve as important forage species for many other estuarine nekton, including marsh resident fishes. The 2 studies of grass shrimp production shown in Table 1 are from different latitudes, and thus very different climatic regimes. The higher value (5.06) reported from South Carolina compared to Rhode Island (2.34) most likely reflects latitudinal differences in mean annual temperatures and length of the growing season. The value from Sikora (1977) should be more representative of warm temperate and sub-tropical conditions in the southeastern USA.

Estimates of production from commercially harvested decapod species focus on mariculture and yields to the fishery rather than on net production from natural populations. Herke et al. (1992) reported on the net export of nekton, including penaeid shrimps, from a pair of 35 ha impoundments in a Louisiana marsh. Each impoundment enclosed ca. 26.5 ha of open water and ca. 8.7 ha of *Spartina patens* marsh (ca. 75% open water, 25% marsh); one included a fixed-crest weir across the channel connecting the impoundment to the estuary and the other had no weir. Sampling was conducted for 2 consecutive years and the average net annual export (yield) of penaeid shrimp was 4.5 g wet weight (ww) m⁻² (0.99 g dw) in the absence of a weir and 1.8 g ww m⁻² (0.4 g dw) when a weir was present, but no estimate of standing-stock biomass in the ponds was provided. Consequently, I used data from Rozas & Minello (2001) on penaeid shrimp density expressed in biomass from a reference marsh (18 g ww m⁻² or 4.0 g dw) and reference pond (1 g ww m⁻² or 0.22 g dw) in Louisiana to provide an expected value of penaeid standing stocks that reflected the vegetated condition of impoundments in Herke et al. (1992).

Data in Rozas & Minello (2001) were taken to represent conditions from spring through autumn; penaeids were assumed to be absent from these shallow marsh habitats in winter, so the values for annual standing stocks had to be adjusted (reduced to 75% of the spring to autumn average) for this seasonal effect. Thus, the annual standing stock of penaeids in the 25% of the impoundment area that was vegetated was taken to be 3.0 g dw m⁻² (4 × 0.75) and 0.16 g dw m⁻² (0.22 × 0.75) in the 75% that was open water. This gives an overall average annual standing-stock biomass estimate for the impoundments of ca. 0.9 g dw m⁻² (3.0 × 0.25 marsh area + 0.16 × 0.75 open water area).

If the exported biomass is considered the total net production, then the P:B ratio for penaeid shrimp in the unobstructed impoundment studied by Herke et al. (1992) would be 1.1 (0.99:0.90). However, this does not account for losses to predators such as red drum and other sciaenids, which were abundant in the impoundment. Knudsen et al. (1989) had earlier estimated mortality rates of brown shrimp in these same impoundments and, in the situation without weirs, estimated mean monthly instantaneous mortality rates of between 0.877 and 1.27. Assuming an average mortality rate of 1.07, net production would have to account for at least 2.9 times (e^{1.07}) the standing stock to maintain a constant value for shrimp biomass in the ponds. If this rate is used as a multiplier, the estimated P:B ratio for penaeids is then 3.2 (1.1 × 2.9). Given that penaeid shrimp are larger than grass shrimp and decapods

generally exhibit growth rates greater than most fishes, a P:B value that falls between grass shrimp and fishes seems reasonable for penaeids.

SPATIAL VARIATION IN NEKTON PRODUCTION—AN EXAMPLE

Field collections

In order to provide an estimate of the expected spatial variation in standing-stock biomass and production of nekton from a warm-temperate/subtropical tidal marsh, samples were collected at 2 wk intervals from 6 intertidal marsh sites on Sapelo Island, Georgia (Fig. 3) using flume weirs (see Kneib 1991 for details). The flume weir was designed for the quantitative collection of nekton (>20 mm in length) from 100 m² sampling areas of tidally inundated vegetated marsh surface.

Two sampling sites were selected in each of the lower, middle and upper reaches of the Duplin River (designated LD, MD, UD, respectively) to represent relatively simple and complex (designated 1 and 2,

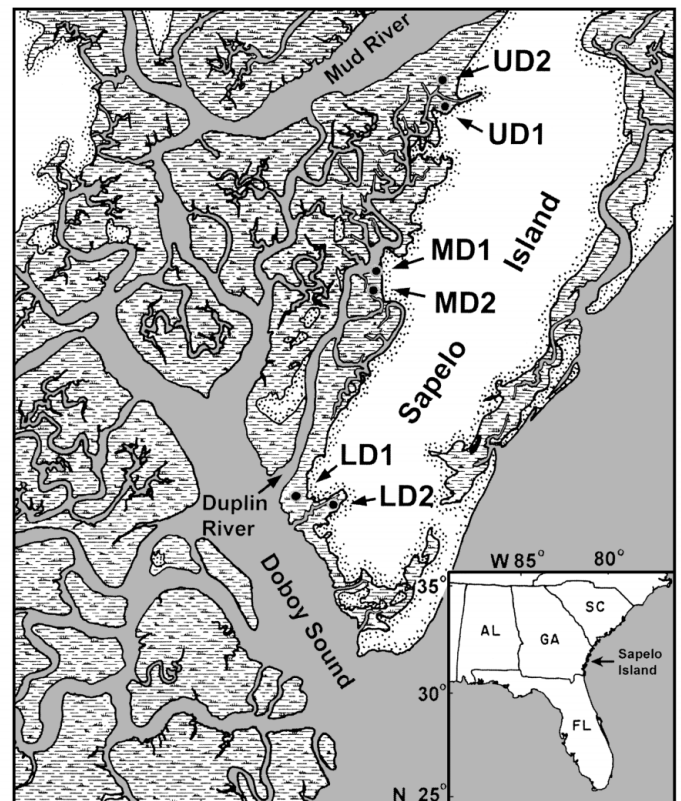


Fig. 3. Sapelo Island, Georgia, USA showing locations of the 6 principal sampling sites (lower, middle and upper reaches of the Duplin River, designated LD, MD, UD, respectively, representing relatively simple and complex tidal drainage networks, designated 1 and 2, respectively: LD1, LD2, MD1, MD2, UD1 and UD2) for nekton in marshes along the Duplin River

Table 2. Summary of physical characteristics at each of 12 sampling sites in marshes on the Duplin River, Sapelo Island, Georgia. Abbreviations represent lower, middle and upper reaches of the Duplin River, designated LD, MD, UD, respectively, representing relatively simple and complex tidal drainage networks, designated 1 and 2, respectively: LD1, LD2, MD1, MD2, UD1 and UD2. At each site, a flume weir was located at each of 2 distances (6 to 20 and 28 to 85 m) from the nearest tidal channel (designated -L and -H, respectively). +MLW: above mean low water

Physical feature	LD1-L	LD1-H	LD2-L	LD2-H	MD1-L	MD1-H	MD2-L	MD2-H	UD1-L	UD1-H	UD2-L	UD2-H
Elevation (+MLW, cm)	221.2	225.4	194.2	197.1	178.2	200.8	153.9	179.4	199.9	216.3	154.7	189.2
Meters to intertidal creek	12	85	20	44	16	49	16	28	6	44	10	73
Meters to subtidal zone	178	278	89	142	97	181	168	171	276	321	149	265
Intertidal edge within 200 m radius (m)	1935	1103	2269	2472	2267	2024	5723	5660	2998	1971	5201	2781
Subtidal edge within 200 m radius (m)	326	0	805	628	436	341	164	68	0	0	132	0

respectively) tidal drainage networks. At each site, a flume weir was located at each of 2 distances (6 to 20 and 28 to 85 m) from the nearest tidal channel (designated -L and -H, respectively). For example, the sampling location designated 'LD1-L' was the flume weir nearest the creek in a relatively simple drainage system within the lower reaches of the Duplin River (Fig. 3). Nekton samples were collected from each flume weir at or very near slack high tide approximately twice monthly during 1999.

Landscape complexity

Some physical characteristics of each of the 12 flume weir locations are given in Table 2. Included is a measure of tidal creek complexity, expressed as the linear amount of intertidal and subtidal channel edge within a 200 m radius of each flume weir location. Channel edge data were collected from digitized black & white negatives (1:16000 scale) recorded during an aerial photographic survey conducted in December 1989. A scaled circle of 200 m radius, centered on the location of each flume weir, was superimposed on the photographs (23 by 23 cm) and the combined images were enlarged to 9.5 times their original size. Outlines of the intertidal and subtidal creeks located within the circle were traced and measured using Sigma Scan Pro® (Version 4.0, SPSS) software on a Dell® Optiplex XMT 5100 desktop computer.

Results of nekton sampling

A total of 94 827 individuals (>20 mm in total length) distributed among 33 species of nekton was collected. As is typical of estuarine nekton samples, most of the individuals were represented by only a

few species. In this case, 11 species of fishes and decapod crustaceans accounted for >99% of the individual organisms in the samples (Table 3). Three species, the caridean shrimp *Palaemonetes pugio* (49.1%), the killifish *Fundulus heteroclitus* (30.2%), and juveniles of the white shrimp *Litopenaeus setiferus* (10.8%), accounted for >80% of all the nekton. Overall, resident species composed ca. 85% of the assemblage, with the remainder (15%) considered migrants. Densities within each group were averaged across all samples to provide a mean annual density for each flume weir site (Table 4).

A substantial amount of spatial variation was evident across sites, with the maximum mean annual density of ca. 7.0 ind. m⁻² at the MD2-H site being >17 times greater than the minimum density of 0.4 ind. m⁻² at the LD1-H site. In general, densities were similar to those reported from other marshes on the east and west coasts of the USA, but were substantially lower than those reported from many sites in the Gulf of Mexico (Table 5). Resident and migrant species both were more abundant at lower intertidal elevations (Fig. 4a); slopes of regression lines relating nekton densities to elevations were significantly different from zero ($p = 0.004$ for residents and migrants). Weaker relationships seemed to exist between nekton abundance and proximity to the marsh edge (Fig. 4b), but these regressions were not statistically significant ($p = 0.09$ for residents and $p = 0.116$ for migrants). Observations of decreasing nekton densities with increasing distance landward of the marsh/estuary edge are common elsewhere (Table 5).

Individual fishes and shrimps from each sample were measured (total length to the nearest mm) and biomass (mg dw) was determined from a set of empirically derived length-weight equations for each species (Table 3). The annual mean standing-stock biomass (g dw m⁻²) at each site (Table 4) was determined by

Table 3. Length-weight equations used to calculate dry weight (DW; mg) of individuals for each of the 11 most common species captured on the marsh surface, Sapelo Island, Georgia, USA. n = number of individuals measured and weighed; TL = total length in mm; for shrimp, TL is from the tip of the rostrum to the tip of the telson. Wet weight (WW; mg) can be estimated by applying the following: $WW = DW/0.22$; resident and migrant species are identified as R and M, respectively

Species	n	Equation	Regression r^2
Fishes			
<i>Fundulus heteroclitus</i> (R)	1744	$DW = 0.0005616(TL)^{3.485}$	0.987
<i>Fundulus luciae</i> (R)	742	$DW = 0.0007498(TL)^{3.327}$	0.935
<i>Cyprinodon variegatus</i> (R)	351	$DW = 0.0005207(TL)^{3.620}$	0.961
<i>Poecilia latipinna</i> (R)	317	$DW = 0.000740(TL)^{3.428}$	0.973
<i>Gobionellus smaragdus</i> (R)	177	$DW = 0.002117(TL)^{2.854}$	0.984
<i>Leiostomus xanthurus</i> (M)	556	$DW = 0.0005674(TL)^{3.323}$	0.987
<i>Mugil cephalus</i> (M)	123	$DW = 0.0006724(TL)^{3.321}$	0.980
<i>Mugil curema</i> (M)	121	$DW = 0.0008644(TL)^{3.248}$	0.989
<i>Menidia menidia</i> (M)	230	$DW = 0.0005886(TL)^{3.218}$	0.991
Decapod crustaceans			
<i>Palaemonetes pugio</i> (R)	1385	$DW = 0.0007118(TL)^{3.291}$	0.873
<i>Litopenaeus setiferus</i> (M)	286	$DW = 0.0008046(TL)^{3.067}$	0.982

applying the length-weight relationships to the size distributions of each species, and averaging across the 24 sampling dates at each site. Standing stocks varied by more than an order of magnitude across sites, ranging from a maximum of 1.13 g dw m^{-2} at UD1-L to a minimum of 0.05 g dw $\times m^{-2}$ at LD1-H. In general, annual standing stocks were greater toward the upper reaches and least in the lower reaches of the Duplin River system. With respect to seasonal variation, standing stocks were greatest in the summer and autumn (July to November) and lowest during the winter (December to February).

Estimates of nekton production based on P:B ratios

Using the annual standing-stock biomass estimates from Table 4, and applying the appropriate set of P:B ratios, one can calculate an estimated range for ex-

pected annual secondary production of estuarine nekton from intertidal marsh sites around Sapelo Island, Georgia, USA.

Three scenarios were generated from different combinations of P:B ratios to estimate a range of production values (Table 6). Scenario 1 was the least complicated and most conservative. It applied a P:B ratio of 2 as a multiplier on the standing stocks of all species to provide an average production estimate of ca. 1.2 g dw m^{-2} for all nekton that use intertidal marsh as habitat. In Scenario 2, production of fish was estimated by multiplying their mean annual standing-stock biomass by a P:B ratio of 2, while a multiplier of 5 was applied to grass shrimp (the most abundant of the resident nekton), and an intermediate value of 3 was used for juvenile white shrimp; this gave an annual production

estimate of ca. 1.5 g dw m^{-2} , and is considered the most likely and defensible scenario based on current knowledge. Scenario 3 was the least conservative and applied a relatively high P:B value of 3 to fishes and 5 to all shrimp species (caridean and penaeid shrimp), resulting in a production estimate of 2.2 g dw m^{-2} .

Much of the considerable spatial variation in production from the intertidal marsh in this example is associated with the amount of intertidal creek edge within 200 m of each sampling site (Fig. 5). The production data for both resident and migrant species were fitted to non-linear relationships using the regression wizard in SigmaPlot® Version 8 (SPSS) and both exhibited similar sigmoidal shapes, with production increasing sharply above 2000 m of edge before reaching an asymptotic limit at or above 3000 m in a radius within 200 m of the sampling sites. The fitted equations for resident and migrant species respectively were as follows:

Table 4. Summary of mean annual densities (ind. m^{-2}) and standing-stock biomass (g dry weight m^{-2}) of resident and migrant nekton collected by flume-weir at slack high-tide from 12 sampling sites in marshes on the Duplin River, Sapelo Island, Georgia; N = 24 collections site⁻¹ during January to December 1999. See Table 2 for site abbreviations

	LD1-L	LD1-H	LD2-L	LD2-H	MD1-L	MD1-H	MD2-L	MD2-H	UD1-L	UD1-H	UD2-L	UD2-H
Mean annual density												
Resident species	1.00	0.39	1.96	2.89	1.46	0.88	6.28	6.30	4.69	0.94	5.12	2.00
Migrant species	0.002	0.001	0.01	0.06	1.59	0.004	0.71	0.71	0.56	0.03	1.81	0.41
Total nekton	1.00	0.39	1.97	2.95	3.05	0.88	6.99	7.01	5.25	0.97	6.93	2.41
Mean annual biomass												
Resident species	0.135	0.053	0.558	0.534	0.375	0.231	0.565	0.809	0.941	0.196	0.412	0.500
Migrant species	<0.001	<0.001	0.004	0.016	0.707	0.025	0.310	0.139	0.185	0.006	0.532	0.092
Total nekton	0.135	0.053	0.562	0.550	1.082	0.256	0.876	0.948	1.126	0.202	0.944	0.593

Table 5. Survey of nekton densities (ind. m⁻²) mostly from *Spartina alterniflora* marshes identified as natural or reference sites compared to created or restored sites

Location	Natural/reference		Restored/created		Source
	Residents	Migrants	Residents	Migrants	
Harkers Island, NC,	4.2	9.2			Meyer et al. (1996)
Swansboro, NC,	1.4	17.8			
Sneads Ferry, NC	4.0	3.0			
Newport River, NC ^a	1.2	0.95			Hettler (1989)
Tampa Bay, FL ^b	1.4	0.1	0.77	0.49	Kurz et al. (1998)
Pascagoula, MS	2.0	0.7	7.9	2.1	LaSalle (1995)
Terrebonne-Timbalier, LA (2–22 m in from marsh edge)	7.9	3.0			Rozas (1992), Rozas & Reed (1993)
Calcasieu Lake, LA ^c (edge)	51.9	51.8	32.2	43.3	Rozas & Minello (2001)
Pooled sites in TX and LA (>5 m in from marsh edge)	13.4	3.9			Minello (1999)
East Matagorda, TX (edge)	32.5	15.4	14.3	6.2	Minello &
Chocolate Bay, TX (edge)	136.8	34.9	29.0	21.8	Zimmerman (1992)
Stedman Island, TX (edge)	73.4	15.2	9.2	10.2	
Galveston Bay, TX (1993)					Rozas & Zimmerman (2000)
(edge, 1–2 m from water)	50.8	40.4			
(interior, 5–6 m from edge)	12.4	4.3			
East Bay, TX (1994)					Williams & Zedler (1999)
(edge, 1–2 m from water)	50.8	38.0			
(interior, 5–6 m from edge)	18.4	13.8			
San Diego, CA	1.6	0.6	2.8	1.1	

^aFish only, no decapods; ^bno grass shrimp included; ^cassumes most unspecified fish species are migrant

$$y = 1.6431 \frac{1.6431}{1 + \left(\frac{x}{2196.2}\right)^{-9.393}} \quad (1)$$

and

$$y = 0.0172 \frac{0.8026}{1 + e^{-\left(\frac{x-2911.4}{137.8}\right)}} \quad (2)$$

where y = annual production (g dw m⁻²) and x = the amount of intertidal creek edge (m) within a 200 m radius of the sampling location. One data point shown as an open triangle in Fig. 5 was omitted from the analysis as an outlier. It was associated with migrant species (mostly the penaeid shrimp *Litopenaeus setiferus*) at the MD1-L, which was the only frequently flooded sampling site immediately adjacent to the main channel of the Duplin River in its middle reaches where transient species that grew in the upper reaches of the system would be subject to capture during their ontogenetic migrations into the open estuary.

DISCUSSION

Estimates of annual nekton production from the present study ranged from 0.11 to 4.57 g dw m⁻², depending

on location and the set of P:B ratios applied to the measured standing stocks. The range of values within any scenario demonstrated that one can expect substantial spatial variation in the amount of nekton production from intertidal marshes, even within a limited geographic region. The amount of material at the base of the food web (e.g. vascular plant detritus and benthic algae) that is ultimately available to nekton populations through trophic interactions sets the upper limit to the production that can be supported. An independent initial 'ball park' estimate of nekton production expected from 1250 g dw m⁻² of annual marsh primary production (4.7 g dw m⁻², Fig. 1), following the application of bioenergetic constraints within the food web, was consistent with the high end of the range of nekton production values estimated from P:B ratios applied to empirical nekton standing stocks from the flume weir samples.

Physical constraints (e.g. tidal frequency and duration of flooding) on accessibility of marsh resources also contribute to controlling the amount of intertidal production available to aquatic consumers. To some degree, these constraints are reflected in structure of the landscape as represented by the measure of creek drainage density (intertidal creek edge within 200 m of a site), which was a good predictor of nekton production (Fig. 5). This measure may have combined the

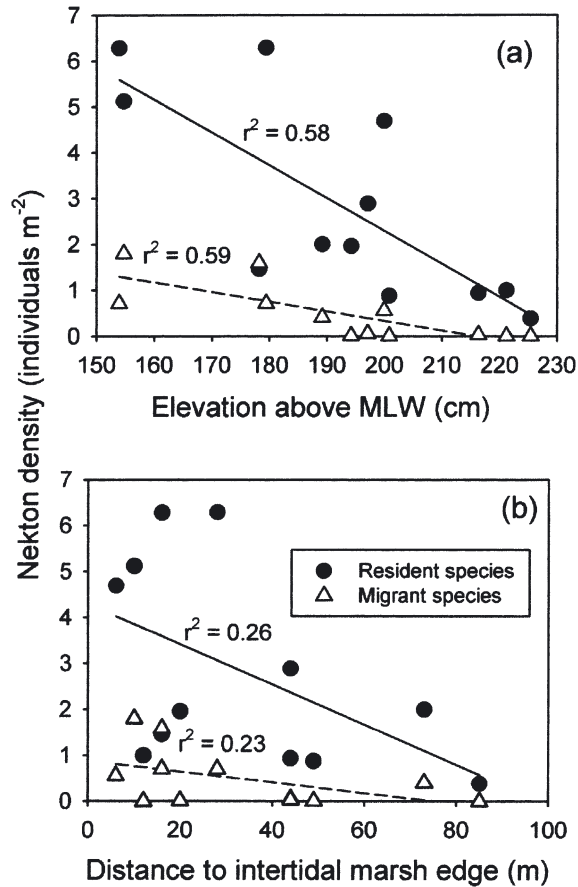


Fig. 4. Mean densities of resident and migrant nekton in relation to (a) intertidal elevation above mean low water (MLW); $p = 0.004$ for residents and migrants, and (b) distance from the vegetated marsh edge; $p = 0.09$ for residents and $p = 0.116$ for migrants

effects of intertidal elevation and proximity to tidal channel, which, when considered as independent factors, were weaker predictors of nekton abundance and, presumably, production (Fig. 4). More complex creek-drainage networks offer greater potential for low-tide aquatic refugia that may be used by nekton as staging areas between flood-tide forays on the vegetated marsh surface (Kneib 1995).

Estimates of nekton annual production from the preferred intermediate set of P:B ratios ranged from ca. 0.12 to 2.88 g dw m⁻² and were similar to values from other studies that used the total area of intertidal marsh as the basis for the estimate (Table 1). Considerably higher production estimates reported for some systems often included an inherent assumption that all of the nekton production originated from only a portion of the habitat adjacent to the marsh, such as a tidal creek or the vegetated marsh edge. Sufficient information to estimate production corrected for the entire area of vegetated intertidal marsh that may have contributed to the production of nekton was not always available. However, in the few cases where it was possible to correct for total area, one can see that values which initially appeared to differ substantially from those estimated from the Sapelo Island data are actually quite similar. For example, Weinstein et al. (1984) and Weinstein (1983) estimated the annual production of juvenile spot *Leiostomus xanthurus* from tidal creeks in Virginia to average ca. 4.4 g dw m⁻², but when extended to the entire area of tidal marsh, production of spot was 0.38 g dw m⁻². Similarly, production of grass shrimp in South Carolina was estimated by Sikora (1977) to be 10.8 g dw m⁻² of creekbank area,

Table 6. Summary of annual nekton production estimate (g dry weight m⁻²) scenarios at 6 tidal marsh sites on Sapelo Island, GA using the indicated production to biomass (P:B) ratio values. Overall average annual production includes all sites. See Table 2 for site abbreviations

Nekton group	LD1-L	LD1-H	LD2-L	LD2-H	MD1-L	MD1-H	MD2-L	MD2-H	UD1-L	UD1-H	UD2-L	UD2-H	Mean
Scenario 1: P:B ratio = 2.0 for all species													
Residents	0.269	0.106	1.116	1.069	0.750	0.461	1.131	1.618	1.882	0.392	0.810	1.001	0.884
Migrants	<0.001	<0.001	0.008	0.032	1.477	0.050	0.617	0.278	0.369	0.013	1.051	0.185	0.340
Total	0.270	0.107	1.124	1.101	2.227	0.511	1.748	1.896	2.251	0.405	1.861	1.186	1.224
Scenario 2: P:B ratio = 2.0 for fishes, 5.0 for <i>Palaemonetes pugio</i>, 3.0 for <i>Litopenaeus setiferus</i> (recommended)^a													
Residents	0.326	0.115	1.207	1.239	0.814	0.525	1.558	2.081	1.955	0.409	1.232	1.064	1.044
Migrants	<0.001	<0.001	0.011	0.038	2.070	0.074	0.663	0.364	0.538	0.018	1.433	0.247	0.455
Total	0.327	0.116	1.218	1.277	2.884	0.599	2.221	2.445	2.493	0.427	2.665	1.311	1.499
Scenario 3: P:B ratio = 3.0 for fishes, 5.0 for <i>Palaemonetes pugio</i>, 5.0 for <i>Litopenaeus setiferus</i>													
Residents	0.442	0.165	1.735	1.716	1.168	0.734	1.981	2.736	2.872	0.599	1.496	1.543	1.432
Migrants	<0.001	<0.001	0.017	0.061	3.401	0.122	1.016	0.590	0.891	0.029	2.340	0.402	0.739
Total	0.443	0.166	1.752	1.777	4.569	0.856	2.997	3.326	3.763	0.628	3.836	1.945	2.171

^aThe preferred scenario uses P:B ratios that match most closely those from the literature for the small fishes and shrimp that predominated in samples from the intertidal marsh (see 'Production:biomass ratios')

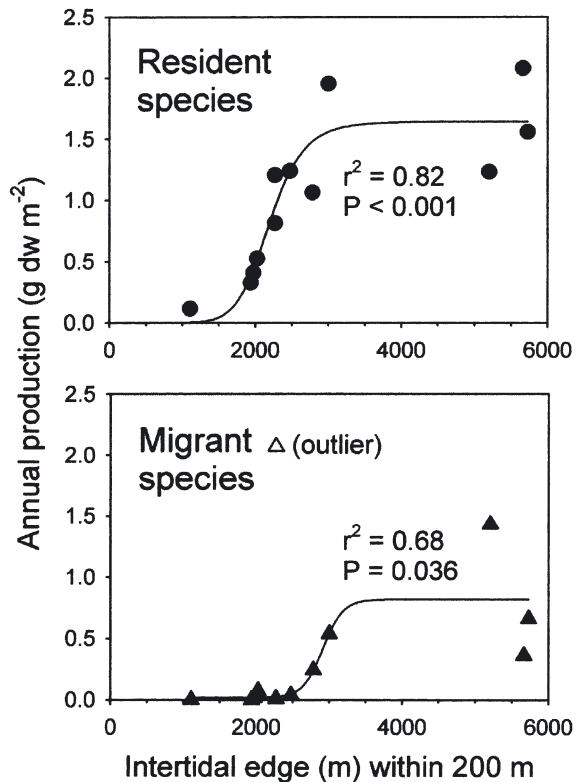


Fig. 5. Relationships between spatial variation in production of resident and migrant nekton estimated from production to biomass (P:B) ratios in Scenario 2 (see Table 6) and landscape complexity measured as the amount of intertidal marsh edge within a 200 m radius of the sampling site (see text for equations)

but was 0.67 g dw m⁻² when adjusted for the intertidal area drained by the marsh creek from which shrimp were sampled. If estuarine nekton production is attributed to intertidal production, then the standing-stock biomass must be calculated on the basis of the entire area providing the trophic support.

Nekton densities, standing stocks and production estimates from Sapelo Island were substantially lower than those reported from marshes in parts of the Gulf of Mexico. Most of the density estimates reported from Texas and Louisiana have been based on collections from 2.6 and 1 m² drop traps used at, or very near, the edges of marsh vegetation and do not account for standing stocks or production of nekton attributable to the interior intertidal marsh plain. In many cases, these marshes comprised a complex, reticulated pattern of vegetated patches (i.e. almost entirely edge) such that 'marsh edge' was assigned the status of a separate habitat (e.g. Minello et al. 2003). Because such marsh systems are surrounded by shallow subtidal water, and perhaps are adjacent to seagrass beds, it can be very difficult to determine their relative contribution to the production of estuarine nekton. It is also possible that

nekton production associated with some marshes in the Gulf of Mexico is substantially greater per unit area than in other regions because of substantial allochthonous nutrient inputs discharged from the Mississippi River (Chesney et al. 2000). In contrast, all samples collected by flume weirs in the present study would be classified as representing the marsh 'interior' by the definitions used in Minello (1999), Rozas & Zimmerman (2000) and Minello et al. (2003). The sites had neither a source of substantial allochthonous nutrient inputs nor areas of submerged aquatic vegetation as alternative sources of primary production to support nekton.

Deegan et al. (2000) recently considered the available evidence for the tenets that salt marsh habitats are associated with enhanced growth rates, reduced mortality rates and greater abundance of nekton compared to other estuarine environments. Their focus was on juveniles of migrant species, and also considered the potential mechanisms by which salt marsh food webs support nekton production. They concluded that there was no difference in growth rates of species associated with tidal marshes compared to other estuarine and coastal areas if one adjusted for effects of temperature. Higher temperatures were associated with shallow waters of the estuary and this factor alone could explain higher growth rates in juvenile nekton associated with intertidal wetlands. If growth rates per se are not enhanced by the presence of vegetated intertidal habitat, then the principal contribution of vegetated wetland habitat to estuarine nekton production might be through reduced mortality or greater trophic support for populations at higher densities. Evidence for the contention that mortality rates are generally lower in marshes compared to other estuarine environments was mixed, but Deegan et al. (2000) recognized that accurate measures of mortality rates are extremely difficult and there is a paucity of reliable estimates on which to base any general conclusions regarding the refuge value of tidal marshes. The strongest evidence connecting intertidal primary production to production of estuarine nekton remains in studies of diet and tissue analyses, which continue to link nekton production primarily to a mixture of detritus and benthic algae originating from tidal marshes.

There has been considerable debate over the issue of attaining habitat equivalency with respect to the restoration or creation of natural marsh functions. Whether engineered habitats can match the functioning of natural systems, and the length of time required to do so, seem to depend largely on what function is being considered (e.g. Simenstad & Thom 1996). The development of substrata containing a high organic content, and benthic assemblages that match those of natural marshes or reference sites, may require a considerable time (e.g. Moy & Levin 1991, Craft et al.

1999). However, as long as aquatic connections with the open estuary are maintained, marshes that have been created or restored are populated by nekton relatively quickly and early indications suggest that fishes do not discriminate between natural and excavated wetland channels (Whitman & Gilmore 1993, Zedler et al. 1997, Williams & Zedler 1999). Clearly, the immediate appearance of nekton at a new site is driven by immigration from elsewhere and not new production from the restored or created habitat. However, once a source of primary production is established and begins to be processed through detrital or herbivorous trophic pathways, it will lead to secondary production. Most estuarine nekton species are opportunistic and remarkably flexible in their dietary choices (Kneib 1997), and so will quickly begin to forage on whatever prey sources become established. Initial concerns about the development of a suitable prey base for nekton that forage in restored or created marshes (e.g. Moy & Levin 1991, Allen et al. 1994) seem to have given way to a recognition that vegetated intertidal habitats can rapidly (within 1 to 3 yr) develop prey resources useful to both resident and migrant nekton (Shreffler et al. 1992, Fell et al. 1998, James-Pirri et al. 2001). Assuming that restored or created tidal wetland develop a level of primary production typical of the region in which they are established, and the site is engineered in a way that allows access to nekton (i.e. adequate connection to the estuary and sufficient edge for the free flow of organisms and materials between intertidal and subtidal portions of the environment), then there should be every expectation that nekton production from the restored/created site has potential to rapidly match that of natural systems. In practice, many marsh restoration projects have taken considerably longer to achieve functional parity with natural systems, including the development of benthic prey communities (e.g. Craft et al. 1999), and may not meet the assumptions of appropriate site selection and engineering. Furthermore, the net enhancement of nekton production from a created or restored tidal marsh depends on the pre-project contribution of the candidate site to nekton production in the estuary. The conversion of a site that may already be contributing substantially to the trophic support of nekton populations (e.g. a productive mudflat with rich communities of benthic algae and associated invertebrate prey populations) will not provide the same net benefit as restoring a site that had previously been altered in a way that removed or reduced its communication with the estuary (e.g. impounded or diked marsh).

The findings presented here suggest that the amount of available primary production as modified by bioenergetic constraints operating through food web interactions will set the upper limit on the amount of nekton

production from marshes in a region, but that relatively small additions of marsh/creek edge may enhance nekton production up to a threshold level, above which no additional enhancement should be expected. Site-specific bioenergetic and landscape constraints should guide the development of realistic expectations and success criteria for marsh restoration efforts designed to enhance estuarine nekton production.

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