Aquat Ecol (2007) 41:25–45
DOI 10.1007/s10452-006-9052-4

ORIGINAL PAPER

Spatial and temporal habitat use patterns for salt marsh nekton: implications for ecological functions

Rodney A. Rountree · **Kenneth W. Able**

Received: 28 June 2005 / Accepted: 3 May 2006 / Published online: 12 July 2006

Abstract We synthesized information on temporal and spatial patterns of salt marsh habitat use by nekton in order to infer the importance of five main types of marsh function: reproduction, foraging, refuge from predation, refuge from stressful environmental conditions and environmental enhancement of physiology. We then extended the concept that intertidal gradients regulate habitat use patterns of nekton to a more universal concept that applies to all salt marsh habitats. We contend that all marsh habitats are linked to each other and to adjacent estuarine habitats along a depth gradient that mediates gradients in abiotic and biotic conditions. Tidal, diel and seasonal shifts in the magnitude and direction of these gradients result in gradients in tidal, diel and seasonal variation in biotic and abiotic conditions within the salt marsh. Collectively these gradients form the 'marsh gradient'. We propose that patterns of marsh use and ecological function for nekton result primarily from physiological and behavioral responses to this marsh gradient. A comparison of habitat use patterns in the context of the marsh gradient is an important – and underutilized – method to study marsh function and essential fish habitat. We note that our limited insight into the function of the marsh habitat results from a significant lack of information on the occurrence and causes of tidal, diel and ontogenetic marsh use patterns by nekton; this is particularly relevant with respect to data on the variation in environmental conditions along marsh gradients over tidal, diel and seasonal cycles and on how environmental variation on these scales influences nekton behavior, growth and survival.

Keywords Environmental gradients · Habitat requirements · Nekton · Salt marsh function · Spatial zonation

Introduction

Part of the lore – and some of the data – on salt marshes suggest that they function as sites for reproduction, food and predator refuge in support of nektonic resources (Thayer et al. 1978; Boesch

---

R. A. Rountree
School for Marine Science and Technology,
University of Massachusetts at Dartmouth, 706 S.
Rodney French Blvd., New Bedford, MA 02744-1221,
USA

K. W. Able
Marine Field Station, Institute of Marine and Coastal
Sciences, Rutgers University, 800 c/o 132 Great Bay
Boulevard, Tuckerton, NJ 08087-2004, USA

R. A. Rountree (✉)
(RAR) Marine Ecology and Technology
Applications, Inc., 23 Joshua Ln, Waquoit, MA 02536,
USA
e-mail: rrountree@fishecology.org

and Turner 1984; Kneib 1987, 1997a). To this we will add the concepts of environmental refuge and environmental enhancement functions, where nekton obtain shelter from stressful environmental conditions or gain improved conditions for physiological processes such as growth (Deegan et al. 2000). Unfortunately, even the structure (temporal and spatial pattern) of nektonic marsh assemblages is often inadequately understood and seldom quantified. As a result, even less is known of salt marsh habitat function.

The purpose of this paper is to synthesize information on our understanding of the structure and function of salt marsh nekton assemblages and to suggest, where possible, approaches to fill the gaps. This discussion is not meant to provide an exhaustive review of the available literature on this subject, but rather to present a picture of what is known about how marshes function as a habitat for nekton and the processes that regulate habitat selection and movements by salt marsh nekton. Further, we admit to a bias towards fishes in our consideration of marsh use and functions, but stress that much of our discussion applies to invertebrate nekton as well. Because structure and function are closely intertwined, it is difficult to discuss one without the other. In the following we will first point out how little is known of marsh functions for nekton, and then we will present a more detailed discussion of marsh structure, including inferences about function that can be drawn from structure.

Before we can begin our discussion of marsh function, it is necessary to carefully define some ecological terms (Table 1). In recent years, numerous investigators have discussed the proper use of the ecological term ‘habitat’ (e.g. Hall et al. 1997; Morrison 2001; Franklin et al. 2002; Mitchell 2005). Hall et al. (1997) define habitat as: “the resources and conditions present in an area that produce occupancy – including survival and reproduction – by a given organism”. However, even this definition is somewhat ambiguous and open to interpretation. A review of the literature revealed that some of the confusion on the use of this term arises from the greatly differing perspectives of scientists interested in either the ‘habitat’ or the ‘organism’. Many ecologists approach the study from the point of view of determining the value of specific ‘habitat types’, such as coral reefs, mud flats, eelgrass beds and salt marshes. Some recent work, for example, has been to describe the nekton assemblages associated with marsh creeks (Rountree and Able 1992a) and marsh pools (Smith and Able 2003; Hampel et al. 2004; Able et al. 2005). Minello et al. (2003) reviewed the literature on nekton association with habitat types based on density, growth and survival. This type of work does not fit the definition of habitat presented by Hall et al. (1997) and others, but rather defines habitat based on the human perspective of a defining geology, community or place. Other researchers approach the study from the point of view of defining the resource requirements of specific species, in which case the definition used by Hall et al. (1997) would apply. We feel that both approaches are useful and that habitat terms and definitions are needed to distinguish them. We, therefore, define the term ‘Ecological Habitat Type’ to be used when studying the habitats themselves, and offer the definition: ‘the space potentially used by an organism, population, species or community of organisms that provides resources necessary for survival, growth, and/or reproduction that is defined based on perceived dominant physical or biological characteristics’ (e.g. salt marsh, coral reef, marsh creek, etc.). We also suggest that the term ‘Organismal Habitat’ be used when adopting Hall et al.’s (1997) definition for habitat after modifying it to account for the biological scale (see Table 1).

We recognize that additional confusion in the use of the term habitat arises from applications of the term on different biological scales, from the individual to the community, and suggest that researchers indicate the biological scale when using the organismal habitat definition (Table 1). We illustrate how organismal habitat can be applied on these different scales – from both ecological and organism perspectives (Fig. 1). Ecological habitat types are often defined based on some perceived dominating characteristic, such as location, sediment type, depth, dominant vegetation or animal, or on the community assemblage. Organismal habitat types can be applied on the scale of the individual (basically the home range), local population (aggregation of the

Table 1 Terms and definitions[a] used to describe habitat functions in this synthesis

Term	Definition
Ecological habitat type	The space potentially used by an organism, population, species or community of organisms that provides resources necessary for survival, growth, and/or reproduction that is defined based on perceived dominant physical or biological characteristics'' (e.g., salt marsh, coral reef, marsh creek, etc.). May be defined on either macro (intertidal, estuarine) or micro (marsh pool) scales.
Organismal habitat	A habitat defined based on organism use: the resources and conditions present in an area that produce occupancy, including survival and reproduction, by a given individual organism, population, species or community.
Individual habitat	The habitat used by an individual organism.
Population habitat	The aggregate habitat used by a local population of individuals.
Species habitat	The aggregate habitat used by all populations of a species.
Community habitat	The aggregate habitat used by all individuals in the local populations of a spatially overlapping group of species (e.g. a community of species A and B would use portions of ecological habitats A through C in Fig. 1).
Assemblage	A group of individuals, populations or species that use one ecological habitat type.
Functional habitat	Any habitat that contributes to the reproduction, feeding, growth or survival of an individual, population or species during some portion of its life history on any temporal scale.
Habitat function	We define habitat function as the manner in which a habitat contributes to the survival, growth or reproduction of an individual, population or species. We recognize five major categories of habitat function: reproduction, foraging, predator refuge, environmental refuge and environmental enhancement of physiological processes.
Habitat quality	The ability of the habitat to provide conditions appropriate for individual, population or species persistence (modified from Hall et al. 1997).
Habitat suitability	The relative quality of functional habitats used by an individual, population or species.
Habitat transient	Individual, population or species that occurs temporarily in a given habitat. Can be applied to different temporal scales.
Habitat resident	Individual, population or species that remains within a given habitat. Can be applied to different temporal scales such as life span, life history stage, season, diel stage or tidal stage. Use of either transient or resident depends on the temporal scale being discussed; for example, a tidal transient may be a low tide resident.
Ontogenetic migrant	Migration between/among habitats at different sizes, life history stages or ages.
Cyclic migrant	Migration between/among habitats on tidal, diel, seasonal or other repeated cycles.
Seasonal ontogenetic migrant	Ontogenetic migration corresponding to a seasonal environmental or biological trigger; for example, the onset of cold temperatures and decreasing photoperiod in the fall might trigger some species to immigrate from the salt marsh in the fall.
Non-seasonal ontogenetic migrant	Ontogenetic migration resulting from physiological and/or behavioral changes in habitat requirements associated with growth that may or may not correspond to seasons.
Marsh gradient	A gradient of abiotic and biotic conditions formed along a depth or elevation transect within the marsh. It can occur on scales of meters to kilometers.
Marsh habitat gradient	A gradient of ecological habitats occurring along a given marsh gradient.
Salt marsh	A complex of vegetated and nonvegetated ecological habitats that includes the intertidal vegetated marsh surface, marsh pools and ponds, intertidal creeks, subtidal creeks, marsh coves and the marsh-bay fringe (adapted from Minello et al. 2003). In tidal systems, ecological habitats may also be defined on frequency of flooding, such as the high marsh (irregularly flooded), low marsh (regularly flooded), intertidal creeks and subtidal creeks.

[a] These extrapolations are based in part on the definition of habitat by Hall et al. (1997): ''The resources and conditions present in an area that produce occupancy, including survival and reproduction, by a given organism''

home ranges of all local individuals) and species (aggregation over all populations) scales. Note that the organismal habitats do not necessarily correspond to the ecological habitat types, thereby resulting in some of the confusion over the use of the term habitat in the literature. For

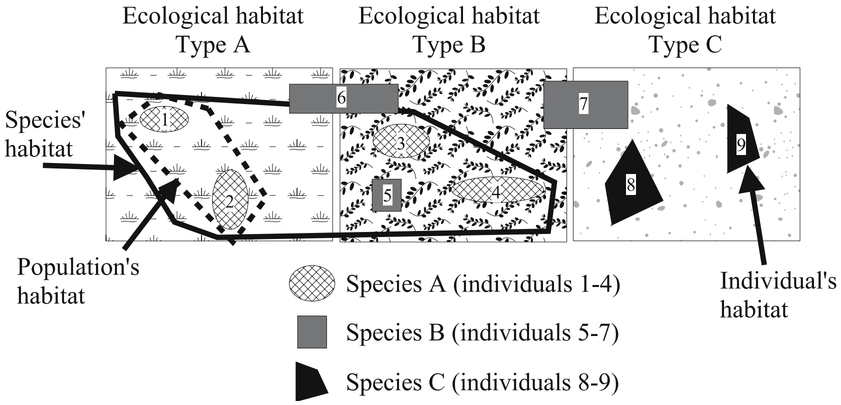

Fig. 1 Illustration of the concept of ecological habitat types and organismal habitat types based on individual organisms, local populations, species and community scales. Definitions of terms are found in Table 1. Ecological habitat types are defined based on human-perceived factors such as geology, geography, dominant species and species assemblages. The area used by individual organism (*1–9*) corresponds to the individual's habitat. The habitat occupied by local populations represents the population habitat, while that occupied by all populations is the species habitat. Organismal habitats do not necessarily correspond to ecological habitats, as indicated by the individual habitats for individuals 6 and 7, and others which cross habitat types

example, species B individuals nos. 6 and 7 in Fig. 1 use two different ecological habitat types each. Similarly, the local populations of species A (individuals 1 and 2, and 3 and 4, respectively; Fig. 1) each use different habitat types; therefore, the 'habitat' for the species encompasses two ecological habitats. We additionally define a 'community habitat' as the aggregate habitats required for a community of species. A species assemblage is defined as the aggregate species that use an ecological habitat type. For example, ecological habitat type A in Fig. 1 would be used by an assemblage of species A and C. In contrast, the 'local community' composed of species A and C uses both ecological habitat type A and B.

We believe that another major cause for confusion in the use of habitat terms results from the failure to define temporal scales. The classic definitions referred to above, as well as the ecological and organismal habitat definitions we set forth, implicitly assume that the habitat is used throughout the life of the organism. However, many researchers routinely speak of habitat use at different life stages, at different seasons and, indeed, on different daily and tidal cycles (this usage arises partly from the common use of ecological habitat type rather than organismal habitat definitions). Defining habitats based solely on the total area used is problematic and can trivialize habitat descriptions because the highly mobile nekton can cover long distances over short time periods (e.g. the species habitat of the Atlantic silverside, *Menidia menidia*, would be all inshore continental shelf and estuarine waters because the species is widely distributed and makes extensive movements over daily, tidal, ontogenetic and seasonal scales; Able and Fahay 1998). Therefore, a way to define the sub-habitats that impact on individual, population and species scales is needed. Herein, we adopt a modification of the classic definition of habitats that will allow researchers to define habitats that contribute to the survival, growth or reproduction of an individual, population or species for at least part of the life of the organism. Thus, on a tidal scale we would refer to low and high tide habitats; on a diel scale we would refer to day and night habitats, on a seasonal scale we would refer to spring, summer, fall and winter habitats and on an ontogenetic scale we would refer to egg, larval, juvenile and adult habitats (or variously by age, size class, etc.).

To further clarify the scope of this discussion, we adopt a modified version of the Minello et al. (2003) definition of a salt marsh: "A complex of vegetated and nonvegetated habitat types that includes the intertidal vegetated marsh surface, marsh pools and ponds, and intertidal and subtidal creeks." We recognize a number of important ecological habitat types within the salt marsh as shown in Fig. 2: (1) the marsh surface, including the high marsh (flooded only during spring and storm tides, or the emergent marsh in non-tidal system), and the low marsh (regularly flooded, or submergent marsh in non-tidal systems); (2) intertidal marsh creeks; (3) subtidal marsh creeks (sensu Hackney et al. 1976; Hackney 1977); (4) bay-marsh fringe subtidal zones. The high and low marsh can also include irregularly flooded (high marsh) and regularly flooded (low marsh) marsh pools, and the bay-marsh fringe may include tidal coves. Many other ecological types of sub-habitats can also be defined based on other attributes such as emergent vegetation type (*Juncus*, *Spartina*, etc.), sediment type or presence of submerged vegetation. However, as Fig. 2 illustrates, all of these habitat types are either completely contained within the salt marsh landscape, or they constitute the border with the adjacent estuary. Indeed, despite this somewhat artificial separation of salt marshes from the rest of the estuary, we recognize that they are part of a continuum that are joined to coastal landscapes by the life histories and migrations of the nekton.

Marsh functions for nekton

We believe that a general review of the literature suggests that salt marshes function as sites for reproduction, enhanced feeding, predator refuge, environmental refuge and environmental enhancement of physiological processes. We define habitat function as the manner in which a habitat contributes to the survival, growth or reproduction of an individual, population or species. Unfortunately, the data to support these presumed functions are seldom available. The following are brief treatments of each of these hypothetical functions for nekton using salt marsh habitats.

Reproduction

Reproduction in marshes is largely limited to several families of fishes (for galaxids, fundulids, cyprinodontids, poeciliids, atherinids, gasterosteids, gobiids; see review in Kneib 1997a; for belonidae, see Breder 1959) and crustaceans (palaemonid shrimps, and xanthid, grapsid and ocypodid crabs (Williams 1984); however, most of

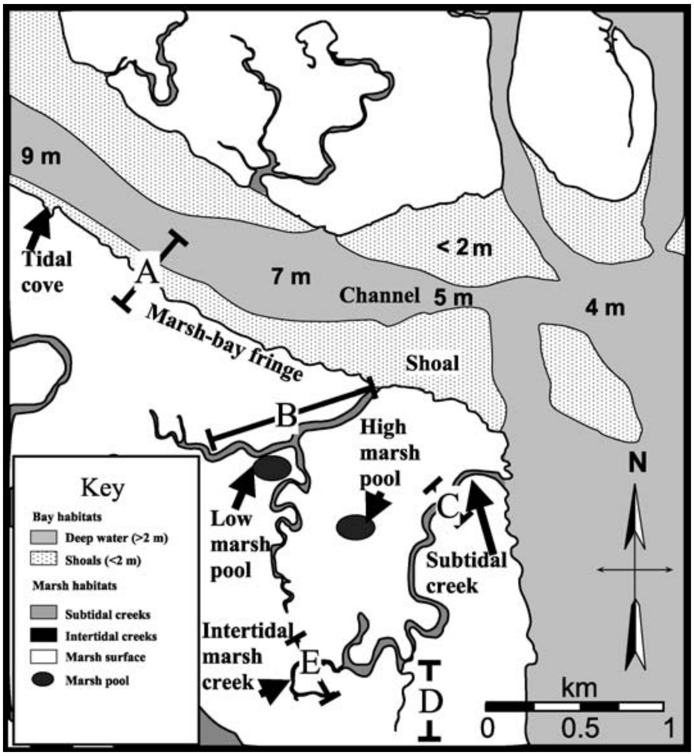

Fig. 2 Illustration of salt marsh habitat types and gradients described in the text. Gradients include: *A* the marsh-bay fringe gradient, *B* subtidal marsh creek gradient, *C* a cross-section of a subtidal marsh creek, *D* intertidal marsh creek gradient, *E* cross-section of an intertidal marsh creek

these taxa also reproduce in other habitats, with the exception of some species of fundulids, cyprinodontids and atherinids.

It is interesting to note that so few species reproduce in marshes. Perhaps this rigorous environment, with its fluctuating tides, temperatures, salinities and dissolved oxygen, presents too many obstacles for successful reproduction. The salt marsh resident fundulids and cyprinodontids have adapted for reproduction in salt marshes despite these environmental conditions, although they also are not immune to extreme physiological constraints such as the detrimental effects of varying salinity that appears to negatively influence fertilization success (Palmer and Able 1987; Able and Palmer 1988). The daily flooding of the vegetated marsh may make it difficult for species with pelagic eggs to reproduce in the marsh because they would risk stranding the eggs on the marsh surface at low tide; this may partially explain why most salt marsh and estuarine fishes have demersal eggs (Able and Fahay 1998). Among salt marsh transient species that spawn in the marsh, such as *Menidia menidia*, the low dissolved oxygen in marsh surface pools that typically occurs at night may limit these areas as locations for reproduction because of subsequent mortality for young-of-the-year (Smith and Able 2003).

While reproduction in the marsh may appear limited to a few species of nekton, the contribution of the latter to estuarine and coastal assemblages is often dramatic because of their large populations (Meredith and Lotrich 1979; Haedrich 1983; Able et al. 1996) and their occurrence through much of the year (see Able and Fahay 1998 for examples). We know of no published study aimed at synthesizing patterns of use in salt marshes for fish reproduction on a continental or global scale (although Kneib 1997a provides some review and discussion). Such an examination of the diversity of fauna reproducing in salt marshes is needed to shed some light on why salt marshes appear to be poorly suited to reproduction.

Foraging

Probably because of an awareness of the high primary production available in salt marshes relative to other coastal marine habitats (Deegan et al. 2000; Minello et al. 2003), an enhanced foraging function relative to other parts of the estuary and the ocean has often been assumed (Boesch and Turner 1984). In the last two decades there has been a surge of interest in determining the source of carbon and nitrogen for fishes utilizing the marsh (see review by Deegan et al. 2000). However, demonstrating foraging on marsh-derived primary, and even secondary, production does not demonstrate that foraging is the causative, or contributing, function of nekton use of the marsh. It must also be demonstrated that other habitats (i.e. other portions of the estuary and ocean) potentially utilized by the fauna are less suitable for foraging. Similarly, to demonstrate a foraging function of a specific habitat within the marsh, one must demonstrate that other habitats are less suitable. Some attempts have been made to address this by comparing gut contents of fishes captured entering and exiting marsh habitats or along marsh elevations (e.g. Baker-Dittus 1978; Kleypas and Dean 1983; Archambault 1987; Rozas and LaSalle 1990; Rountree and Able 1992b; Miltner et al. 1995; Hampel and Cattrijsse 2004; Nemerson and Able 2004; Baker and Sheaves 2005; Hampel et al. 2005). There is a strong need for more research to be directed at this issue, and until this research is completed we can not assume that an enhanced foraging function of the salt marsh for nekton is accurate.

Predator refuge

Numerous authors have suggested that predator refuge is an important function of the salt marsh; however, this hypothesis has rarely been formally addressed (see reviews in Kneib 1997a; Able and Fahay 1998; Deegan et al. 2000; Sheaves 2001; Baker and Sheaves 2005). There are some data to support the idea that species that occur abundantly in salt marshes may be important predators on nekton (Kneib 1982; Rountree and Able 1992b; Witting and Able 1993, 1995; Rountree and Able 1996, 1997, Nemerson and Able 2004) and, consequently, the refuge value of salt marshes is still an open question. There are only a few ways to address the question of predator refuge: (1) infer low predation in one habitat versus another based on lower mortality; (2) direct field experiments on survival in various habitats (e.g. tethering, laboratory experiments on the influence of structure on predator success; Minello 1993); (3) a comparison of the food webs in each habitat. Only the second method has been attempted in the salt marsh (see review in Kneib 1997a). Unbiased estimates of mortality in salt marsh habitats (as well as most other habitats) are very difficult to obtain due to the difficulty of measuring density and to the high mobility of the fauna. This is evident in the literature where values assumed to be 'mortality' are actually 'loss' based on natural mortality and emigration (see Able and Fahay 1998; Deegan et al. 2000).

In many ways, the analysis of food webs in marsh habitats based on stomach contents is the easiest – and most direct – method to assess the relative magnitude of predation in each habitat. If the densities of both predators and prey are known, then predator consumption rates of the prey and prey mortality due to predation (excluding other sources of natural mortality) can be determined. However, as with other sources of mortality, quantification of mortality due to predation in each habitat is also hampered by the difficulty of quantifying predator and prey densities. If density data are not available, then at least relative predation levels can be inferred from relative catch abundances. We do not know of any published study specifically designed to quantitatively compare food webs in marsh habitats in order to address the question of a predator refuge function. To use this approach to determine whether marsh habitats differ in their roles as predator refugia for a given species, one must identify a suite of potential predators in each habitat under consideration and examine their food habits. This provides direct evidence of the relative predation risk in each habitat, which is biased mainly by how comprehensive the suite of predators examined is. As in other assumptions about marsh function, more detailed studies are needed, especially those relative to nekton movements among habitat types, before we can confidently assume these habitats provide a real refuge to nekton.

Environmental refuge and enhancement of physiological processes

Salt marshes, and specific habitats within salt marshes, may function as environmental refugia for nekton, or they may function to enhance physiological processes such as growth by providing optimum environmental conditions relative to other habitats. For example, Deegan (1990) hypothesized that larvae and juveniles of gulf menhaden (*Brevoortia patronus*) use salt marshes as a late winter and spring habitat to take advantage of warmer temperatures relative to other estuarine and continental shelf habitats. The idea of an environmental refuge is often implicitly assumed for seasonal migrations in northern latitudes, where most nekton typically move into marshes in the spring and summer when temperatures are warmer and abandon marshes in the fall and winter as temperatures decline. Here the ocean serves as an environmental refuge, while the marsh may serve as an enhanced environment conducive to rapid growth [see Deegan et al. (2000) for a more detailed discussion of environmental enhancement for nekton growth]. The environmental functions of specific habitats within the marsh may be markedly different due to differences in environmental conditions. For example, marsh pools may provide a thermal refuge for some fundulids during the winter (Smith and Able 1994), and subtidal marsh creek and marsh fringe habitats may provide a low tide refuge for most nekton utilizing the marsh (e.g. Able et al. 1996).

Structure of marsh nekton

In the following sections, we attempt to draw attention to gaps in our understanding of the structure of marsh nekton and how this structure can be useful in revealing how marshes function for nekton. We attempt to isolate temporal and spatial patterns for purposes of discussion, while being fully aware that this is an artificial designation because they are closely intertwined.

Spatial patterns of marsh use by nekton

In this section we consider how two broad types of spatial patterns – ecological habitat types and ecological habitat gradients – can be used to elucidate the structure of marsh nekton and contribute to our understanding of marsh function.

Ecological habitat types

While much effort has been expended towards quantification of the abundance of nekton in selected salt marsh ecological habitats, there has been a tendency to emphasize a single habitat for the practical reason that sampling methods are often suitable for only one type of habitat. Many different gear types and sampling methods are necessary to sample in more than one ecological habitat at the same time, and results obtained with different gears are usually not directly comparable (see reviews by Rozas and Minello 1997; Kneib 1997a; Minello et al. 2003). Because nekton are highly mobile and move freely among marsh habitats, studies of single ecological habitats usually fail to define spatial patterns of habitat use by nekton and, hence, provide limited insight into habitat ecological functions.

It seems intuitive that different ecological habitats can exhibit different habitat quality and that nekton should select the highest quality habitat available. Thus, many studies have been carried out that seek to compare the relative importance of different ecological habitats in support of estuarine nekton (reviewed by Minello et al. 2003). But what happens when the quality of a habitat exhibits temporal shifts – for example, when tidal, diel or seasonal cycles in conditions occur? We suggest that under those conditions, nekton have either evolved to remain resident within the habitats and consequently adapted to the temporary and cyclic shifts in habitat quality, or that they have evolved to migrate between habitats to maintain optimum conditions (Fig. 3). For example, in Fig. 3 we consider the affect of diel shifts in the relative quality of two habitats as indicated by three types of habitat function: predation risk, food availability and environmental conditions. Night conditions are optimal in Habitat A, but increased predation risk during the day causes a migration to Habitat B. Diel residency is not established in Habitat B because a decline in environmental conditions at night forces migration back to Habitat A. We argue that the causes for migration and habitat use patterns can not be fully understood by examining either a single habitat function or all functions in only one habitat. In order to understand habitat use patterns one must examine the relative quality of each habitat in terms of all habitat functions over the appropriate temporal scales (tidal, diel and seasonal).

Ecological habitat gradients

Rather than attempt to study the significance of specific ecological habitats in isolation, we suggest that it may be appropriate to identify ecological habitat gradients based on environmental attributes. Ecological habitat gradients can occur on latitudinal and estuarine (i.e. upper, middle,

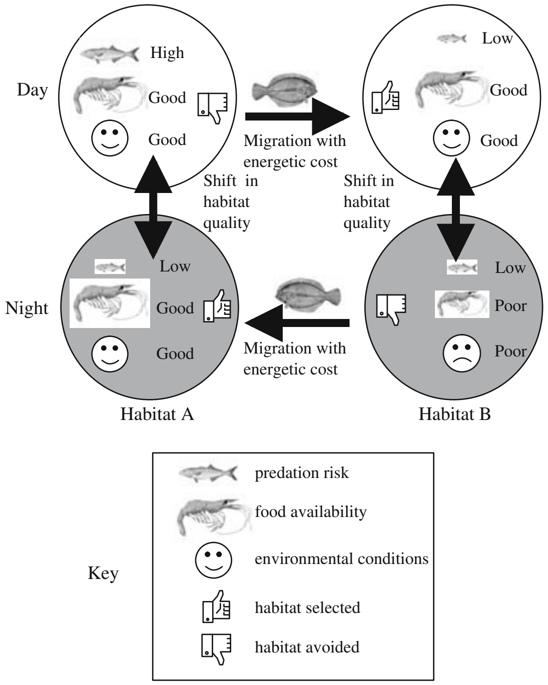

Fig. 3 Illustration of how cyclic variation in habitat quality, as measured by the level of habitat functions (predation refuge, food availability and environmental refuge/enhancement) that are provided, influences habitat selection and cyclic migration patterns. During the day Habitat B is selected because conditions are optimal (low predation, high food availability and favorable environmental conditions), but a shift in habitat function (decline in environmental conditions) at night results in migration to the more favorable Habitat A at night

lower) scales or on local scales. For example, on a local scale ecological habitats located along a tidal gradient may be appropriately studied together, rather than separately, to understand the influence of the tidal gradient on habitat use. Researchers wishing to examine marsh use by fishes, for example, might design their study to sample points along the tidal elevation gradient from the high marsh to the adjacent subtidal marsh rather than simply sampling on the marsh surface. This may foster a better understanding of the dynamics of habitat use as opposed to attempting to partition out ecological habitats used by mobile fauna. We recognize, of course, that the design of sampling, and other logistics, make this difficult.

One of the most important ideas we wish to present is that many estuarine and salt marsh habitats serve similar ecological functions for nekton because they all exhibit similar underlying environmental gradients (Figs. 2, 4). Let us consider the transects along a depth or elevation gradient in several different marsh ecological habitats. A transect from the marsh surface across the marsh-bay fringe into the open bay (A in Fig. 2) shares many similarities with transects taken along a subtidal creek axis (B), across a subtidal creek (C), along an intertidal creek axis (D) and across an intertidal creek (E). Each of the resulting habitat gradients share many similarities which are illustrated in a composite 'marsh gradient' in Fig. 4. The different ecological habitat gradients are distinguished primarily by the spatial extent of ecological habitats within the habitat gradient (from meters to kilometers), which in turn results from differences in the shape of the elevation profile under a particular tidal regime. For example, intertidal creeks share many similarities with the upper portion of subtidal creeks (Rountree and Able in review).

In the following, we discuss how abiotic and biotic gradients forming along a marsh gradient can regulate the pattern of marsh use by nekton as well as help elucidate marsh function. As depicted in Figs. 4 and 5, gradients in physical conditions can form along a marsh gradient (such as a creek gradient) as a result of interactions between the influences of the adjacent estuarine waters, atmospheric conditions and terrestrial conditions (Dewitt and Daiber 1973; Hackney et al. 1976; Daiber 1977, 1982). However, similar intertidal gradients described along a creek cross-section have been more extensively studied (Kneib 1984). Herein, we illustrate how the gra-

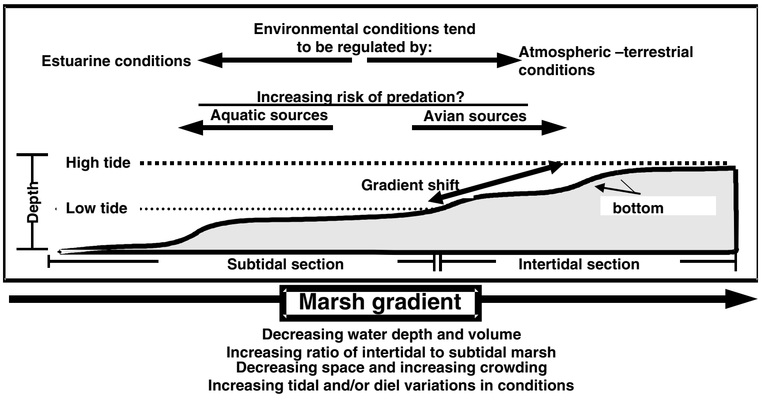

Fig. 4 Schematic of selected hypothetical gradients in physical and biological conditions along a marsh habitat gradient. These gradients occur to varying degrees in intertidal and subtidal creeks, intertidal marsh surface, marsh-bay fringe and other marsh habitats. The marsh habitat gradient in depth, water volume and ratio of intertidal to subtidal marsh areas would result in the development of weak to strong horizontal stratification of one or more physical factors (e.g. water temperature, dissolved oxygen concentration, turbidity, light intensity, salinity) and biological factors (predation, food availability, crowding, competition, etc.) at any given time. However, the habitat gradient in these physical and biological conditions would also vary over the diel cycle in non-tidal systems, resulting in a habitat gradient in diel variations in one or more of these factors. Biotic factors, such as risk of predation and stress due to crowding, would also form along the habitat gradient

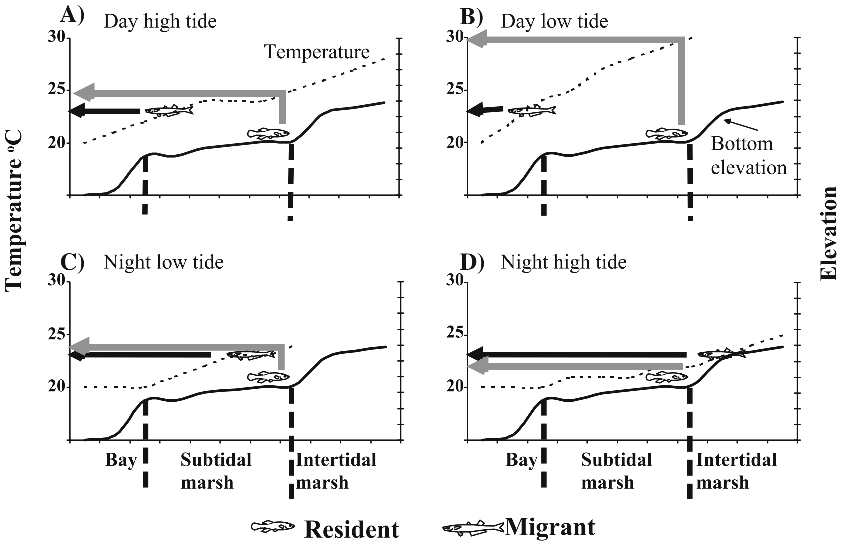

Fig. 5 Schematic illustrating how the marsh gradient can mediate the environmental gradients and their tidal and diel cycles, which in turn can regulate nekton distribution and migration behaviors. The temperature gradients depicted are based on realistic values observed in subtidal marsh creeks (Rountree 1992; Rountree and Able in review). Because the creek is inundated with adjacent estuarine water during flood tides, physical conditions along the creek gradient, here represented by water temperature, tend to be re-set to conditions present in the adjacent estuary regardless of time of day. In contrast, strong horizontal stratification can be set up at low tide. Therefore, the gradient fluctuates on tidal, diel and seasonal scales, creating a resultant gradient of environmental variability. These environmental gradients, as well as biological gradients (see Fig. 4), regulate species distributions and movements in the marsh. Residents that remain at a given location along the gradient must be able to physiologically accommodate tidal, diel and seasonal fluctuations in the conditions, while migrant species maintain relatively homogenous environmental/physiological conditions by moving up and down the gradient on tidal, diel and seasonal scales

dient concept can be applied to many marsh habitats.

Generally, at any given point in time, because of the decreasing depth and water volume and increasing distance from the adjacent estuary, physical conditions are increasingly influenced by atmospheric and land conditions moving up the marsh gradient, while adjacent estuarine conditions have an increasing influence moving down the gradient (Fig. 4). For example, if the atmospheric temperature is significantly different than the adjacent estuarine water temperature, then a horizontal stratification in water temperature along the marsh is likely to develop (Fig. 5). When the atmosphere is warmer than the adjacent estuary, then temperature increases moving up the marsh gradient. In contrast, when the atmosphere is colder than the adjacent estuary, then water temperature decreases moving up the marsh gradient. Of course, whether horizontal temperature gradients are established, and how steep they become, are dependent on the length of the marsh gradient and local atmospheric and hydrodynamic conditions.

In addition to temperature, other abiotic factors that may exhibit horizontal stratification with depth include dissolved oxygen concentration, turbidity, light penetration, exposure to ultraviolet light and the ratio of intertidal to subtidal marsh area (Fig. 4). In tidal systems, the tidal exchange volume (ratio of intertidal to subtidal volume) can also form a gradient – i.e., increasing while moving up the gradient until the marsh becomes intertidal. Dissolved oxygen concentration is likely to be one of the most important environmental regulators of habitat use by nekton in marsh habitats (Rakocinski et al. 1992), but it has rarely been studied on this scale. Dissolved oxygen concentrations tend to increase moving up the marsh gradient during day low tides because of high oxygen production by benthic microalgae and macroalgae (often reaching supersaturation conditions in the upper reaches of creeks; Rountree and Able unpublished data). This pattern often reverses at night, however, because of high respiration rates and a lack of photosynthesis, with concentrations of less than 2 ppm common in the upper reaches of subtidal creeks (Rountree and Able unpublished data). Turbidity can also increase sharply moving up the marsh gradient, resulting in declining light intensity. However, turbidity, light penetration, and depth can interact in complex ways so that light intensities can sometimes increase along the marsh gradient, especially at low tide (personal observations). The ecological implications of a gradient in light intensities, especially ultraviolet light intensities, is unknown.

An example of how the marsh gradient can mediate the environmental gradients and their tidal and diel cycles, which in turn can regulate nekton distribution and migration behaviors, is illustrated in Fig. 5. Because the creek is inundated with adjacent estuarine water during flood tides, physical conditions along the creek gradient, here represented by water temperature, tend to be re-set to conditions present in the adjacent estuary regardless of the time of day the flood occurs. At low tide, conditions along the creek gradient are strongly influenced by current atmospheric and terrestrial conditions, which can result in strong horizontal gradients in environmental conditions. In the case of water temperature, the horizontal gradient is likely to be stronger during the day when atmospheric conditions are typically warmer (but this pattern can reverse seasonally). Residents that remain at a given location (ecological habitat) along the gradient must be able to physiologically accommodate tidal, diel and seasonal fluctuations in the conditions, while migrant species can maintain relatively homogenous environmental/physiological conditions by moving up and down the gradient on tidal, diel and seasonal scales (Fig. 5).

Because flood tides bring adjacent estuarine waters into the marsh and tend to homogenize conditions, predators acclimated to adjacent estuary water conditions could then invade the creek along its full length, thereby gaining potential access to prey species. Such a mechanism might explain observations that larger 'predator' species tend to be tidal migrants in the marsh (Rountree and Able 1993, 1997, in review). Faunal distributions of both predator and prey along the creek gradient could then be affected by their physiological tolerance to the temperature, or to the diel and/or tidal rate of change in temperature or to other environmental conditions along the gradient. However, we suggest that behavioral responses to the physiological costs of acclimating to temperature, or the rate of change of temperature, may also be just as important as physiological limits. For example, although nekton may be capable of acclimating to the gradually changing conditions moving up the marsh gradient, the extent of their movements may be controlled by the energetic cost of the acclimation. Similarly, the energetic cost of acclimating to the rate of change in conditions over the diel and/or tidal cycles may also limit nekton distribution.

Biological interactions may also form gradients across the marsh (Fig. 5). Predation pressure from aquatic sources may increase moving down the gradient (Kneib 1997a; Rountree and Able 1997), while in some systems, predation pressures from avian and terrestrial sources may increase moving up the gradient (Kneib 1982, 1997a, b). A strong negative relationship between fish size and water depth, resulting from an increased risk of avian predation is well known for freshwater stream systems (Power 1987), but the importance of avian predation in structuring nekton use of salt marshes has received very little attention (except for Kneib 1982). Additionally, because of the increasing ratio of marsh surface to subtidal volume, marsh nekton tend to become increasingly concentrated at low tide moving up the gradient, resulting in crowding.

In a few studies, the importance of environmental gradients in marshes is suggested by evidence of assemblage differences among marsh habitat types (e.g. subtidal creek, intertidal marsh surface and marsh pond; Subrahmanyam and Drake 1975; Subrahmanyam and Coultas 1980; Werme 1981; McIvor and Odum 1988; Rakocinski et al. 1992; Able et al. 1996; Hampel et al. 2004) or by evidence of assemblage changes between locations within subtidal creeks (Hackney et al. 1976; Weinstein 1979; Weinstein and Brooks 1983; Rozas and Hackney 1984; Smith et al. 1984; Rozas and Odum 1987; McIvor and Odum 1988; Hettler 1989). The influence of location within a creek on assemblage structure has variously been described as occurring along a mouth-to-headwater creek gradient (Hackney et al. 1976), along a marsh creek coenocline (Weinstein 1979; Weinstein and Brooks 1983; Smith et al. 1984) or along a marsh creek order gradient (Rozas and Odum 1987; Hettler 1989).

In a study of intertidal and subtidal marsh creeks in New Jersey, we similarly found different faunal assemblages between upper and lower regions of the creeks, which we suggest resulted partly from an environmental gradient along the creek axis (Rountree 1992; Rountree and Able in review). We observed strong gradients in dissolved oxygen concentration (DO), turbidity and temperature as well as in the magnitude of diel variation in DO, turbidity and water temperature. However, these gradients were highly seasonal (Rountree and Able unpublished data).

Temporal patterns of marsh use by nekton

We recognize six basic temporal types of ecological habitat use patterns by marsh nekton (Fig. 6). It is also apparent that irregular, episodic movements among ecological habitats also occur as a result of episodic abiotic (e.g. storms, anoxia) and biotic (e.g. sudden predator or prey population changes) conditions. A careful study of episodic conditions can provide valuable insight into marsh ecological function but, because of the uniqueness of such events, can only be considered on a case-by-case basis and thus is beyond the scope of this discussion. Instead we are interested in what regularly repeating temporal patterns can reveal about marsh function.

Resident species spend their entire life cycle in the ecological habitat which meets all of their habitat needs (Fig. 6). All other temporal patterns involve shifts in nekton use between functional habitats within the marsh, or between the marsh and other estuarine or coastal habitats (see Able and Fahay 1998 for examples from the Middle Atlantic Bight). Non-seasonal ontogenetic migrations result when a species shifts habitats upon reaching a specific size, age or developmental stage regardless of season, while seasonal ontogenetic migrations can be size-independent (Rountree 1992; Rountree and Able 1993). Seasonal patterns can be cyclical (e.g. adults returning annually to a seasonal spawning habitat) or non-cyclical (e.g. in the case of seasonal ontogenetic migration where migration is one-way; Fig. 6). Cyclical seasonal patterns involve at least one full cycle of movement between habitats coinciding with the seasons (e.g. seasonal migration between spawning and foraging habitats), while seasonal ontogenetic movements involve shifting between habitats in one direction that coincides with the seasons (e.g. seasonal migrations of juvenile nekton out of the salt marsh and onto the continental shelf). Finally, tidal and diel movements result in cyclic migrations between habitats (Fig. 6). Each of these six

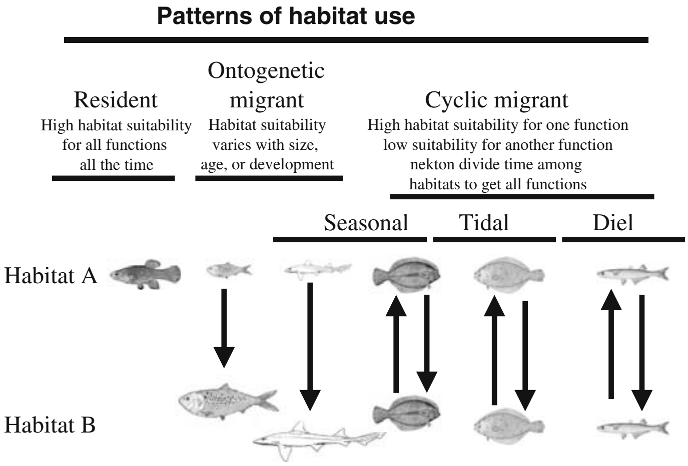

Fig. 6 Schematic illustrating six types of temporal distribution patterns of nekton among marsh habitats, resulting from different patterns of habitat function

temporal patterns are discussed in further detail in separate sections below.

We believe that research into the causes of these temporal patterns of habitat use is an important, and currently underutilized, way to elucidate how marshes and marsh habitats function. The function of marshes and marsh habitats to resident species is self-evident. For these species, the marsh fulfills all functional roles. Nekton exhibiting the other temporal patterns, however, are dependent on two or more ecological habitats over one or more temporal scales. We contend that for this behavior to be evolutionary stable, there must be opposing attraction and repulsion forces operating in each habitat to induce movement between the habitats despite the energetic cost – and increased risks – associated with migration (Fig. 3). Or put another way, fish should seek to remain in one ecological habitat unless changes in the biotic and abiotic environment force the fish to move.

Some factors which could contribute to periodic avoidance of a habitat include: food limitation, competitive exclusion, environmental/physiological stress, predation risk and poor reproductive success (itself due to many causes). Corollary factors causing periodic attraction to a habitat include: enhanced food availability, predator refuge, environmental refuge, competitive release and high reproductive success. We stress that to adequately understand the causes of each type of habitat shift, it is necessary to study both habitats. For example, high foraging success in one ecological habitat does not in itself prove a foraging function. It must also be demonstrated that foraging success is significantly less in one ecological habitat relative to the other. But even this does not explain the habitat shift, as there must be some factor operating to cause avoidance of the ecological habitat with high foraging success, otherwise migration would not occur because the fish would tend to remain in the ecological habitat with greater foraging success. It is only by studying the use patterns of both ecological habitats that we can understand habitat ecological function. We contend that cyclic movements require alternating attraction/repulsion conditions in each habitat (Fig. 3). Noncyclic ontogenetic movements require changes in habitat suitability (due to environmental or physiological changes) among ontogenetic stages (Fig. 6).

Residence

Relatively few species of nekton can be considered to be true salt marsh residents (e.g. some fundulids and cyprinodontids; see Kneib 1997a, b; Able and Fahay 1998) across all temporal scales (i.e. year-round and all life stages). Indeed, if subtidal creek and bay fringe habitats are excluded from one's definition of the marsh (e.g. Kneib 1997a), then most nekton traditionally considered residents are actually transients on one or more temporal scales. Even fewer species can be considered to be true residents within any specific salt marsh ecological habitat. Most species of nekton, even salt marsh residents, exhibit ecological habitat shifts on one or more temporal scales. The low diversity of salt marsh residents and the fact that it is difficult to find species restricted to specific ecological habitats are patterns that deserve closer attention. The low diversity of salt marsh residents suggests that the salt marsh ecosystem has some fundamental functional limitations that are difficult to overcome sufficiently to allow for residency. The lack of many highly specialized species that utilize specific ecological habitats suggests either that salt marsh residents are habitat generalists, or that marsh ecological habitats fulfill similar functions, or that marsh residents must use many different ecological habitats at different times in order to fulfill all the ecological functions necessary for residence within the salt marsh ecosystem.

Diel patterns

Although strong diel patterns in species abundances have been reported in the marsh (Shenker and Dean 1979; Reis and Dean 1981; Rozas and Hackney 1984; McIvor and Odum 1986; Middleton 1986; Rozas and Odum 1987; Rountree and Able 1993; Hampel et al. 2003, 2004), most studies of marsh use are based exclusively on day time sampling (see review in Rountree and Able 1993). In New Jersey marshes, night time abundances in subtidal creek seine and intertidal creek block net samples were two- to fourfold greater than day abundances, while abundances of tidal migrators captured in subtidal creek weirs were tenfold greater at night (Rountree and Able 1993). Together these observations suggest that studies based exclusively on day collections can greatly underestimate the use of salt marsh habitats by nekton.

Diel changes in physical conditions can lead to diel movement behavior (Rountree and Able 1993; Hampel et al. 2003). Strong diel changes in physical conditions have been noted in marsh creeks and other shallow subtidal estuarine habitats (Nixon and Oviatt 1973; Hackney et al. 1976; Breitburg 1988; Portnoy 1991; Rountree and Able 1993; Sogard and Able 1994). Some diel movements may occur in response to diel occurrences of stressful or even lethal conditions. However, animals may respond to sublethal conditions by moving to maintain preferred physiological conditions (Brett 1971; Beitinger et al. 1975; Beitinger 1976; Reynolds and Casterlin 1976; Major 1978; Clark and Green 1991) or to gain a metabolic advantage (McLaren 1963; McAllister 1969; Brett 1971; Stuntz and Magnuson 1976; Biette and Green 1980; Mauchline 1980; Wurtsbaugh and Neverman 1989; Abou-Seedo et al. 1990; Clark and Green 1991, see discussion in Rountree and Able 1993). It is thought that a metabolic advantage may be gained by foraging within an environmentally variable habitat, and then moving into a more stable (often colder) habitat to digest food.

There is a strong interaction between diel period and the horizontal stratification of environmental conditions along the marsh gradient we discussed above. The strength, and even the direction, of the marsh gradients in physical conditions can fluctuate with the diel cycle. For example, a horizontal temperature gradient might be stronger during the day than during the night because the atmosphere is generally warmer during the day and cooler during the night (Fig. 5). This is because shallow waters in the upper gradient are heated up during the day due to radiant heating. Similarly, as mentioned above, DO gradients can change, or even reverse over the diel cycle, with higher concentrations in shallower depths during the day and lower concentrations during the night. We wish to emphasize, therefore, that in addition to a gradient in physical conditions that can form along a marsh gradient at any given time, there can also be a gradient in the variability of conditions over the diel cycle. In general, we expect conditions to become increasingly variable (with greater maxima and minima values) moving up the marsh gradient and to become more stable moving down the gradient, being minimal in the adjacent estuary (Fig. 4). Horizontal stratification of nekton assemblages as well as diel migrations of nekton in and out of the marsh have been suggested to result from physiological responses of the nekton to diel variability in environmental gradients in subtidal marsh creeks (Hackney et al. 1976; Hackney 1977; Rountree and Able 1993, 1996, 1997). We propose that similar relationships are likely in other marsh ecological habitat gradients (Fig. 4).

Tidal patterns

Although the importance of tidal movement is well known in the intertidal salt marsh (see Kneib 1984), little is known of tidal movements in the subtidal marsh (Subrahmanyam and Drake 1975; Blaber 1986; Rountree 1992; Rountree and Able 1993, 1997; Hampel et al. 2004). Many species utilizing subtidal marsh creeks in New Jersey undergo some form of tidal movement. In fact, many species generally considered to use estuaries appear to exhibit tidal migrations into and out of subtidal creeks, including *Paralichthys dentatus*, *Pomatomus saltatrix* and *Leiostomus xanthurus* (Rountree 1992; Rountree and Able 1992b, 1993; Szedlmayer and Able 1993; Rountree and Able 1996, 1997, in review).

Although, the importance of tidal gradients in environmental conditions with respect to structuring intertidal communities is well known for rocky and sandy shores, having been the subject of more recent research in salt marshes (see reviews by Kneib 1984, 1997a; Gibson 1986), researchers have generally failed to recognize their role in the shallow subtidal marsh (with the exception of Hackney et al. 1976; Hackney 1977). Tidal migrations probably often result from physiological causes similar to those influencing diel movements (see above). In the extreme case, most nekton are forced to abandon intertidal areas at low tide to avoid desiccation but return on flood tides to obtain food or escape predation. In subtidal areas, tidal changes in physical conditions can also lead to similar movements (Rountree 1992; Rountree and Able in review).

There are strong interactions between environmental conditions along the marsh gradient and the tidal cycle. In tidal systems such as those prevalent along most of the east coast of the United States, the flood tide tends to break down any horizontal stratification that has built up during the day or night and 're-sets' the temperatures to conditions in the adjacent estuary (Fig. 5). Other environmental conditions (e.g. DO and salinity) can also be 're-set' with the flood tide to those more similar to the adjacent estuarine conditions. In contrast, at low tide, conditions tend to be controlled more by atmospheric conditions due to the decrease in water volume relative to the surface area of the water. Estuarine conditions have their greatest influence on marshes at high tide and atmospheric/land conditions at low tide due to changes in water volume (Hackney et al. 1976; Daiber 1977). Additionally, there is a strong interaction between tidal and diel cycles on the environmental gradients in the marsh (Rountree and Able 1993, unpublished). Tidal changes in temperature at the mouths of subtidal and intertidal marsh creeks in New Jersey were found to be negligible during the night, but averaged 4°C and 3 °C, respectively, with a maximum of 8 °C during the summer months (Rountree and Able 1993); these values correspond to tidal changes in temperature of 0.5–1.3°C h^{-1}. Although little is known of the behavioral responses of salt marsh nekton to rates of change of environmental conditions, rates as low as 1.0°C h^{-1} have been suggested to be physiologically important and capable of stimulating behavioral responses such as migrations (Miller and Dunn 1980).

Seasonal and ontogenetic patterns

Cyclic seasonal and non-cyclic seasonal ontogenetic shifts in ecological habitat use (Fig. 6) have been the most closely examined temporal patterns for salt marsh nekton. Most cyclic patterns have been attributed to reproductive migrations into the salt marsh to spawn (e.g. Gasterosteidae and Atherinidae; Able and Fahay 1998). *Menidia menidia* may undertake seasonal migrations out of the marsh to obtain an environmental refuge from winter temperatures (at least in northern estuaries), but they return in the spring to reproduce (Conover and Murawski 1982; Conover and Ross 1982). However, again, little effort has been expended towards understanding the causes of cyclic seasonal migrations in terms of its inferences for marsh ecological function (i.e. why do some nekton undergo regular, cyclic, seasonal migrations between the salt marsh and other habitats?).

By far the most effort has been directed towards understanding the causes of one-way, non-cyclic, seasonal ontogenetic migrations. This is exemplified by the migration of species that use the salt marsh during the early juvenile stages but move out of the marsh onto the continental shelf with the season. Examples of these species include *Menidia menidia*, *Strongylura marina*, *Gasterosteus aculeatus*, *Mustelus canis* and *Anchoa mitchilli* (Group II in Able and Fahay 1998). Less is known of seasonal ontogenetic movements on smaller scales, such as between estuarine areas, or between local marsh ecological habitats (but see Deegan 1990; Rountree 1992).

However, in some species, individuals appear to shift among ecological habitats during growth as they reach certain sizes independent of the seasons (non-seasonal ontogenetic migrations; Fig. 6). For example, successive intra-annual cohorts of *Menidia menidia* appear to emigrate from marsh creeks into the adjacent estuary at different times throughout the late summer and fall upon reaching 60 mm total length (TL) but later, in the fall, all individuals migrate regardless of size due to the onset of low temperatures (Rountree and Able 1993). Thus, this species exhibits both seasonal ontogenetic and non-seasonal ontogenetic migration behaviors. In many types of intertidal communities (e.g. rocky shore, sandy beach, mud flat and salt marsh), there is a tendency for intraspecific size stratification to occur along a habitat gradient where fish size increases with depth (Gibson 1973, 1986; Helfman 1978; Kneib 1984, 1997a, b), which suggests to us that non-seasonal ontogenetic migrations are common in these types of habitats. In fact, ontogenetic shifts in ecological habitats along a depth gradient is a very widespread phenomenon occurring in freshwater lakes and streams, seagrass beds, mangroves, coral reefs, sandy beaches and even in the deep ocean deep-scattering-layer (see reviews by Gibson 1973, 1986; Helfman 1978; Mauchline 1980; Kneib 1984, 1987, 1997a; Macpherson and Duarte 1991). This type of ontogenetic shift in ecological habitat use has rarely been studied in the salt marsh (see review in Kneib 1997a) but is critical to our understanding of ecological habitat use and of trophic relay of energy among ecological habitats connected along an environmental gradient (see review in Deegan et al. 2000).

Four main hypothetical causes of this size stratification have been suggested that may apply to salt marshes: (1) ontogenetic changes in predation pressures; (2) ontogenetic changes in food requirements/availability; (3) intraspecific competition for food and other resources; (4) ontogenetic changes in environmental tolerances (see reviews by Gibson 1973; Helfman 1978; Mauchline 1980; Kneib 1987; Macpherson and Duarte 1991; Ruiz et al. 1993). All of these hypotheses, except the last, require some mechanism for appropriate habitat – or depth – selection at a given size. The last hypothesis suggests both a functional cause and a mechanism for size stratification among habitats. In his study of the use of the intertidal zone by *Mugil cephalus*, Major (1978) suggests that its stratification among habitats with size results in reduced intraspecific competition for food and space in the shallow intertidal zone. More importantly, he presents evidence that the stratification is cued by ontogenetic changes in environmental tolerances. Pre-juveniles enter the estuary and select the shallowest intertidal habitats with near-lethal environmental conditions. As they grow, their tolerance to the absolute values of environmental conditions, and to the range in variation of these conditions, decreases so that they are forced to move into deeper water with more favorable and less variable conditions.

A number of fishes are thought to undergo ontogenetic changes in tolerances to environmental conditions. Estuarine species, in particular, are thought to become less tolerant of stress as they grow (Norris 1963; Wohlschlag and Cech 1970; Helfman 1978; Major 1978; Brett 1979; Miller and Dunn 1980). Therefore, stratification by size of fish along the creek gradient would be expected in response to physical gradients. Miller and Dunn (1980) discuss the importance of this type of environmental cue to inducing migrations and foraging movements of fishes in the estuary but predict that a range of environmental factors, rather than a single factor such as water temperature, operate as the cue. Our observations in New Jersey marsh creeks (Rountree and Able 1992b, 1993, 1996, 1997, in review) suggest that a gradient in overall environmental variability, over tidal, diel and seasonal scales, may function as the cue to ecological habitat selection along the creek gradient.

Seasonal interactions on diel and tidal variations in environmental gradients in the salt marsh have not been studied, but they may partially regulate seasonal patterns of habitat use by nekton. Seasonal changes in air temperature could result in changes in the direction of the temperature gradient. For example, in the winter, cold air temperatures may result in decreasing water temperature moving up the marsh gradient (negative temperature gradient), while during the summer warm, air temperatures result in increasing water temperature moving up the gradient (positive temperature gradient). Deegan (1990) hypothesized that larval and juvenile gulf menhaden (*Brevoortia patronus*) utilized subtidal marsh creeks as nursery habitat during the spring because warmer water temperature would enhance growth. We hypothesize that seasonal reverses in environmental gradients, especially temperature, may be important triggers for seasonal and ontogenetic migrations and merit future attention.

Regulation of the structure of marsh nekton

In the following, we summarize the ideas presented above to illustrate how spatial and temporal patterns can interact to regulate the structure of salt marsh nekton assemblages. We also suggest that these ideas may prove useful in the broader context of theories of community structure for other tidal ecosystems with a nektonic component (e.g. rocky intertidal shore, sandy beach and mud flats). Hypothetical species with spatial distributions among three ecological habitats within an ecological habitat gradient (e.g. the marsh gradient) are illustrated in Fig. 7. Species can respond to tidal, diel or seasonal changes in conditions in two ways: (1) they can establish permanent distributions within a habitat (species 1–3); (2) they can migrate up or down the marsh gradient as their habitat requirements shift among life history stages (species 4) or (3) they can migrate along the habitat gradient in response to cyclic (e.g. tidal, diel, and seasonal) gradient shifts in order to stay within suitable conditions (species 5). In all cases, the spatial distributions within specific habitats, as depicted by the shapes in Fig. 7, are ultimately regulated by tolerances to physical conditions and by biological interactions, as in classically studied rocky intertidal communities (Connell 1961). More complex mixed migration patterns are also possible. For example, species 6 in Fig. 7 is shown as migrating between intertidal and subtidal creek habitats at one life stage and then shifting down gradient to migrate between subtidal creek and bay habitats at a later life stage. One important implication of this model is that temporal partitioning of ecological habitat use by some species may allow the habitats to support more species than would otherwise be possible. It also illustrates a mechanism for energy exchange among habitats, where cyclic and ontogenetic movements provide trophic links among habitats connected along a habitat gradient (i.e. the chain of migration and trophic relay concepts; see review of Deegan et al. 2000).

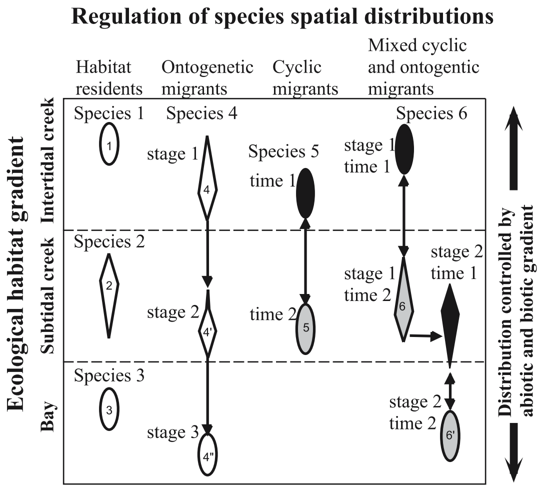

Fig. 7 Hypothetical species distributions among adjacent habitats within a ecological habitat gradient (e.g. the adjacent estuary, subtidal creek, and intertidal creek coenocline), under the influence of cyclical changes (e.g. tidal, diel, and seasonal) in conditions. Three basic types of distribution occur: (1) species are restricted within one habitat (*species 1–3*); (2) species migrate among habitats at different ontogenetic stages (*species 4*); (3) mobile species move between habitats in response to the cyclical changes in conditions between tidal, diel or seasonal stages (*species 5*). In addition, mixed cyclic and ontogenetic migrants alternate between different sets of habitats at different ontogenetic stages (*species 6*). The distribution of each species along the environmental and biological gradient within each habitat is regulated by the balances among physiological tolerances, competition and the threat of predation (see Fig. 4). Resident species must adapt to cope with cyclic variations in these gradients, while mobile species can move along gradient with the cycles to maintain preferred conditions (Fig. 5). *Arrows* indicate direction of migration: one way for ontogenetic migrants and two way for cyclic tidal, diel and seasonal migrants

The patterns illustrated herein suggest that each species has a basic distribution along the ecological habitat gradient resulting from its response to physical gradients. However, species interactions, such as competition, risk of predation, among others, may also influence their distributions (McIvor and Odum 1988; Shirley et al. 1990). Mechanisms regulating the distributions of nekton in tidal marsh ecological habitat gradients, therefore, parallel those regulating other intertidal habitats, being controlled by balances between physiological tolerances/preferences, predation pressures and competitive interactions (Connell 1961; Kneib 1984). However, the highly motile nektonic fauna of the salt marsh have the option of moving (actively or passively) between areas in response to changes in physical conditions, in contrast to sessile communities (Connell 1961). Therefore, distributions of some species may shift up and down the marsh gradient in response to cyclical tidal and diel changes in physical and biological gradients along the marsh habitat gradient.

Summary and conclusions

It is apparent from our discussion that the functional significance of salt marsh ecological habitats can only be clarified by a greatly improved understanding of the spatial and temporal patterns of nekton use and environmental conditions within the salt marsh and by a comparison of reproduction, feeding, predation risk and environmental conditions across marsh ecological habitats as well as the adjacent estuary. We suggest that stratification of environmental conditions along marsh habitat gradients may play a large role in the regulation of nekton habitat use patterns. The strength, and even the direction, of the environmental stratification along the marsh gradient can undergo regular cyclic fluctuations on at least three different scales – tidal, diel and seasonal – resulting in a stratification of the variability of conditions along the marsh gradient over these scales. These spatial and temporal environmental patterns may in turn regulate tidal, diel and seasonal patterns in nekton use. Unfortunately, studies of the patterns of environmental conditions on diel, tidal and seasonal temporal scales and on habitat gradient spatial scales are difficult and, as a result, are often lacking. Additionally, studies of the influence of environmental conditions on nekton behavior, physiology, energetics, growth and mortality are critical in order to infer regulation of nekton ecological habitat use patterns from patterns of environmental conditions. Although some information on environmental tolerances (e.g. maximum and minimum temperature tolerances) is available for many species of marsh nekton, data on behavioral/energetic responses of nekton to the more subtle environmental conditions present on a marsh gradient spatial scale over tidal, diel and seasonal cycles are lacking. We suspect that the latter may be critically important to understanding nekton tidal and diel migration patterns in the marsh.

Conditions under which nekton are resident in salt marshes and those in which nekton reproduce in the salt marsh have received little attention and could provide valuable insight into the ecological function of marsh ecological habitats to nekton. Similarly, studies of nekton food webs across habitat gradients have rarely been undertaken (but see Nemerson and Able 2004), despite the fact that such studies are one of the best way to infer foraging enhancement and predator refuge functions.

Patterns of ontogenetic shifts in nekton ecological habitat use in the marsh are also poorly described, but they could provide valuable insight into how salt marsh ecological functions change with ontogeny as well as clarify patterns of emigration and immigration of transients from the marsh. Finally, studies on the magnitude and timing of seasonal ontogenetic shifts in ecological habitat use by nekton are needed to assess the importance of prey matching in nursery habitats (Beck et al. 2001) and, hence, foraging and predator ecological functions as well as to elucidate major temporal patterns for trophic relay.

Acknowledgements We benefitted from careful reviews of an early draft of this manuscript by M. Weinstein and R. Kneib. F. Juanes is thanked for his stimulating discussions on estuarine fish habitat use and behavior. This is an Institute of Marine and Coastal Sciences Contribution No. 2006-7 and School for Marine Science and Technology Contribution No. 06-05-02.

References

Able KW, Fahay MP (1998) The first year in the life of estuarine fishes in the Middle Atlantic Bight. Rutgers University Press, New Brunswick

Able KW, Palmer RE (1988) Salinity effects on fertilization success and larval mortality of *Fundulus heteroclitus*. Copeia 1988:345–350

Able KW, Witting DA, McBride RS, Rountree RA, Smith KJ (1996) Fishes of polyhaline estuarine shores in Great Bay-Little Egg Harbor, New Jersey: a case study of seasonal and habitat influences. In: Nordstrom KF, Roman CT (eds) Estuarine shore: evolution, environments and human alterations. John Wiley & Sons, New York

Able KW, Smith KJ, Hagan SM (2005) Fish composition and abundance in New Jersey salt marsh pools: sampling technique effects. Northeast Nat 12:479–495

Abou-Seedo F, Clayton DA, Wright JM (1990) Tidal and turbidity effects on the shallow-water fish assemblage of Kuwait Bay. Mar Ecol Prog Ser 65:213–223

Archambault JA (1987) Temporal patterns in gut fullness of juvenile spot, *Leiostomus xanthurus*, in North Inlet, South Carolina. MSc thesis, University of South Carolina, Columbia, S.C.

Baker R, Sheaves M (2005) Redefining the piscivore assemblage of shallow estuarine nursery habitats. Mar Ecol Prog Ser 291:197–213

Baker-Dittus AM (1978) Foraging patterns of three sympatric killifish. Copeia 1978:383–389

Beck MW, Heck KL Jr, Able KW, Childers DL, Eggleston DB, Gillandeers BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51:633–641

Beitinger TL (1976) Behavioral thermoregulation by bluegill exposed to various rates of temperature change. In: Esch GW, McFarlane RW (eds) Thermal Ecology II. Proc Symp. Technical Information Center, Energy Research and Development Administration, Augusta, Ga., pp 176–179

Beitinger TL, Magnuson JJ, Neill WH, Shaffer WR (1975) Behavioural thermoregulation and activity patterns in the green sunfish, *Lepomis cyanellus*. Anim Behav 23:222–229

Biette RM, Green GH (1980) Growth of underyearling salmon (*Oncorhynchus nerka*) under constant and cyclic temperatures in relation to live zooplankton ration size. Can J Fish Aquat Sci 37:203–210

Blaber SJM (1986) Feeding selectivity of a guild of piscivorous fish in mangrove areas of North-west Australia. Aust J Mar Freshw Res 37:329–336

Boesch DF, Turner RE (1984) Dependence of fishery species on salt marshes: the role of food and refuge. Estuaries 7:460–468

Breder CM Jr (1959) Observations on the spawning behavior and egg development of *Strongylura notata* (Poey). Zoologica 44:141–148

Breitburg DL (1988) Oxygen fluctuations and fish population dynamics in a Chesapeake Bay oyster bed. In: Understanding the estuary: advances in Chesapeake Bay research Proc Conf. Chesapeake Research Consortium Publication 129, CBP/TRS 24/88, pp 547–557

Brett JR (1971) Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). Am Zool 11:99–113

Brett JR (1979) Environmental factors and growth. In: Hoar WS, Randall DJ, Brett JR (eds) Fish physiology, vol 8. Bioenergetics and growth. Academic Press, New York, pp 599–675

Clark DS, Green JM (1991) Seasonal variation in temperature preference of juvenile Atlantic cod (*Gadus morhus*), with evidence supporting an energetic basis for their diel vertical migration. Can J Zool 69:1302–1307

Connell JH (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42:710–723

Conover DO, Murawski SA (1982) Offshore winter migration of the Atlantic silverside, *Menidia menidia*. Fish Bull 80:145–150

Conover DO, Ross MR (1982) Patterns in seasonal abundance, growth and biomass of the Atlantic silverside, *Menidia menidia*, in a New England estuary. Estuaries 5:275–286

Daiber FC (1977) Salt-marsh animals: distributions related to tidal flooding, salinity and vegetation. In: Chapman VJ (ed) Wet coastal ecosystems. Elsevier, Amsterdam, pp 79–108

Daiber FC (1982) Animals of the tidal marsh. Van Nostrand Reinhold, New York

Deegan LA (1990) Effects of estuarine environmental conditions on population dynamics of young-of-the-year gulf menhaden. Mar Ecol Prog Ser 68:195–205

Deegan LA, Hughes JE, Rountree RA (2000) Salt marsh ecosystem support of marine transient species. In: Weinstein MP, Kreeger DA (eds) Concepts and controversies in tidal marsh ecology. Kluwer, Dordrecht, pp 333–365

Dewitt P, Daiber FC (1973) The hydrography of the Broadkill River Estuary, Delaware. Ches Sci 14:28–40

Franklin AB, Noon BR, George TL (2002) What is habitat fragmentation? Stud Avian Biol 25:20–29

Gibson RN (1973) The intertidal movements and distribution of young fish on a sandy beach with special reference to the plaice (*Pleuronectes platessa* L.). J Exp Mar Bio Ecol 12:79–102

Gibson RN (1986) Intertidal teleosts: life in a fluctuating environment. In: Pitcher TJ (ed) The behavior of teleost fishes. The Johns Hopkins University Press, Baltimore, pp 388–408

Hackney CT (1977) Energy flux in a tidal creek draining an irregularly flooded *Juncus* marsh. PhD thesis, Mississippi State University. Mississippi

Hackney CT, Burbanck WD, Hackney OP (1976) Biological and physical dynamics of a Georgia tidal creek. Ches Sci 17:171–280

Haedrich RL (1983) Estuarine fishes. In: Ketchum BH (ed) Ecosystems of the world. Elsevier, Amsterdam,pp 183–207

Hall LS, Krausman PR, Morrison ML (1997) The habitat concept and a plea for standard terminology. Wildl Soc Bull 25:173–182

Hampel H, Cattrijsse A, Vincx M (2003) Tidal, diel and semilunar changes in the faunal assemblage of an intertidal salt marsh creek. Est Coast Shelf Sci 56:795–805

Hampel H, Cattrijsse A (2004) Temporal variation in feeding rhythms in a tidal marsh population of the common goby *Pomatoschistus microps* (Kroyer, 1838). Aquat Sci 66:315–326

Hampel H, Cattrijsse A, Mees J (2004) Changes in marsh nekton communities along the salinity gradient of the Schelde river, Belgium and The Netherlands. Hydrobiologia 515:137–145

Hampel H, Cattrijsse A, Elliott M (2005) Feeding habits of young predatory fishes in marsh creeks situated along the salinity gradient of the Schelde estuary, Belgium and The Netherlands. Helgol Mar Res 59:151–162

Helfman GS (1978) Patterns of community structure: summary and overview. Environ Biol Fish 3:129–148

Hettler WF Jr (1989) Nekton use of regularly-flooded salt marsh cordgrass habitat in North Carolina, USA. Mar Ecol Prog Ser 56:111–118

Kleypas J, Dean JM (1983) Migration and feeding of the predator fish, *Bairdiella chrysoura* Lacepede, in an intertidal creek. J Mar Biol Ecol 72:199–209

Kneib RT (1982) The effects of predation by wading birds (Ardeidae) and blue crabs (*Callinectes sapidus*) on the population size structure of the common mummichog, *Fundulus heteroclitus*. Est Coast Shelf Sci 14:159–165

Kneib RT (1984) Patterns of invertebrate distribution and abundance in the intertidal salt marsh: causes and questions. Estuaries 7:392–412

Kneib RT (1987) Predation risk and use of intertidal habitats by young fishes and shrimp. Ecology 68:379–386

Kneib RT (1997a) The role of tidal marshes in the ecology of estuarine nekton. Oceanogr Mar Biol Annu Rev 35:163–220

Kneib RT (1997b) Early life stages of resident nekton in intertidal marshes. Estuaries 20:214–230

Macpherson E, Duarte CM (1991) Bathymetric trends in demersal fish size: is there a general relationship. Mar Ecol Prog Ser 71:103–116

Major PF (1978) Aspects of estuarine intertidal ecology of juvenile striped mullet, *Mugil cephalus*, in Hawaii. Fish Bull 76:299–314

Mauchline J (1980) The biology of mysids and euphausiids. Part 2. The biology of euphausids. Adv Mar Biol 18:372–623

McAllister CD (1969) Aspects of estimating zooplankton production from phytoplankton production. J Fish Res Bd Can 26:199–200

McIvor CC, Odum WE (1986) The flume net: a quantitative method for sampling fishes and macrocrustaceans on tidal marsh surfaces. Estuaries 9:219–224

McIvor CC, Odum WE (1988) Food, predation risk, and microhabitat selection in a marsh fish assemblage. Ecology 69:1341–1351

McLaren IA (1963) Effects of temperature on growth of zooplankton, and the adaptive value of vertical migration. J Fish Res Bd Can 20:685–727

Meredith WH, Lotrich VA (1979) Production dynamics of a tidal creek population of *Fundulus heteroclitus* (Linnaeus). Est Coast Shelf Sci 8:99–118

Middleton RW (1986) The seasonal and diel use by juvenile and adult finfishes of a mesohaline intertidal creek on the York River, Virginia. PhD thesis, The College of William and Mary, Virginia

Miller JM, Dunn ML (1980) Feeding strategies and patterns of movement in juvenile estuarine fishes. In: Kennedy VS (ed) Estuarine perspectives. Academic Press, New York, pp 437–448

Miltner RJ, Ross SW, Posey MH (1995) Influence of food and predation on the depth distribution of juvenile spot (*Leiostomus xanthurus*) in tidal nurseries. J Fish Aquat Sci 52:971–982

Minello TJ (1993) Chronographic tethering – a technique for measuring prey survival-time and testing predation pressure in aquatic habitats. Mar Ecol Prog Ser 101:99–104

Minello TJ, Able KW, Weinstein MP, Hays CG (2003) Salt marshes as nurseries for nekton: testing hypotheses on density, growth and survival through meta-analysis. Mar Ecol Prog Ser 246:39–59

Mitchell SC (2005) How useful is the concept of habitat? – a critique. Oikos 110:634–638

Morrison ML (2001) A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. J Wildl Manage 65:613–623

Nemerson DM, Able KW (2004) Spatial patterns in diet and distribution of juveniles of four fish species in Delaware Bay marsh creeks: factors influencing fish abundance. Mar Ecol Prog Ser 276:249–262

Nixon SW, Oviatt C (1973) Ecology of a New England salt marsh. Ecol Monogr 43:463–498

Norris KS (1963) The functions of temperature in the ecology of the percoid fish *Girella nigricans* (Ayers). Ecol Monogr 33:23–62

Palmer RW, Able KW(1987) Effect of acclimation salinity on fertilization success in the mummichog, *Fundulus heteroclitus*. Physiol Zool 60(5):614–621

Portnoy JW (1991) Summer oxygen depletion in a diked New England estuary. Estuaries 14:122–129

Power ME (1987) Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size.In: Kerfoot WC, Sih A (eds) Predation direct and indirect impacts on aquatic communities. University Press of New England, Hanover London, pp 333–351

Rakocinski CF, Baltz DM, Fleeger JW (1992) Correspondence between environmental gradients and the community structure of marsh-edge fishes in a Louisiana estuary. Mar Ecol Prog Ser 80:135–148

Reis RR, Dean JM (1981) Temporal variation in the utilization of an intertidal creek by the bay anchovy (*Anchoa mitchilli*). Estuaries 4:16–23

Reynolds WW, Casterlin ME (1976) Thermal preferenda and behavioral thermoregulation in three centrarchid fishes. In: Esch GW, McFarlane RW (eds) Thermal ecology II. Proc Symp. Technical Information Center, Energy Research and Development Administration, Augusta, Ga., pp 185–190

Rountree RA (1992) Fish and macroinvertebrate community structure and habitat use patterns in salt marsh creeks of southern New Jersey, with a discussion of marsh carbon export. PhD Thesis, Rutgers, The State University of New Jersey, New Brunswick, N.J.

Rountree RA, Able KW (1992a) Fauna of polyhaline subtidal marsh creeks in southern New Jersey: composition, abundance and biomass. Estuaries 15:171–185

Rountree RA, Able KW (1992b) Foraging habits, growth, and temporal patterns of salt marsh creek habitat use by juvenile summer flounder in New Jersey. Trans Am Fish Soc 121:765–776

Rountree RA, Able KW (1993) Diel variation in decapod crustacean and fish assemblages in New Jersey marsh creeks. Est Coast Shelf Sci 37:181–201

Rountree RA, Able KW (1996) Seasonal abundance, growth and foraging habits of juvenile smooth dogfish, *Mustelus canis*, in a New Jersey estuary. Fish Bull 96:522–534

Rountree RA, Able KW (1997) Nocturnal fish use of New Jersey marsh creek and adjacent bay habitats. Est Coast Shelf Sci 44:703–711

Rozas LP, Hackney CT (1984) Use of oligohaline marshes by fishes and macrofaunal crustaceans in North Carolina. Estuaries 7:213–224

Rozas LP, LaSalle MW (1990) A comparison of the diets of Gulf killifish *Fundulus grandis* Baird and Girard, entering and leaving a Mississippi brackish marsh. Estuaries 13:332–336

Rozas LP, Minello TJ (1997) Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. Estuaries 20:199–213

Rozas LP, Odum WE (1987) Use of tidal freshwater marshes by fishes and macrofaunal crustaceans along a marsh stream-order gradient. Estuaries 10:36–43

Ruiz GM, Hines AH, Posey MH (1993) Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. Mar Ecol Prog Ser 99:1–16

Sheaves M (2001) Are there really few piscivorous fishes in shallow estuarine habitats? Mar Ecol Prog Ser 222:279–290

Shenker JM, Dean JM (1979) The utilization of an intertidal salt marsh creek by larval and juvenile fishes: abundance, diversity and temporal variation. Estuaries 2:154–163

Shirley MA, Hines AH, Wolcott TG (1990) Adaptive significance of habitat selection by molting adult blue crabs *Callinectes sapidus* (Rathbun) within a subestuary of central Chesapeake Bay. J Exp Mar Biol Ecol 140:107–119

Smith KJ, Able KW (1994) Salt-marsh tide pools as winter refuges for the mummichog, *Fundulus heteroclitus*, in New Jersey. Estuaries 17:226–234

Smith KJ, Able KW (2003) Dissolved oxygen dynamics in salt marsh pools and their effects on the fish assemblages. Mar Ecol Prog Ser 258:223–232

Smith SM, Hoff JG, O'Neil SP, Weinstein MP (1984) Community and trophic organization of nekton utilizing shallow marsh habitats, York River, Virginia. Fish Bull 82:455–467

Sogard SM, Able KW (1994) Diel variation in immigration of fishes and decapod crustaceans to artificial seagrass habitat. Estuaries 17:622–630

Stuntz WE, Magnuson JJ (1976) Daily ration, temperature selection, and activity of bluegill. In: Esch GW, McFarlane RW (eds) Thermal ecology II. Proc Symp. Technical Information Center, Energy Research and Development Administration, Augusta, Ga., pp 180–184

Subrahmanyam CB, Coultas CL (1980) The animal communities in two north Florida, USA salt marshes: Part III. Seasonal fluctuations of fish and macroinvertebrates. Bull Mar Sci 30:790–818

Subrahmanyam CB, Drake SH (1975) Studies on the animal communities in two north Florida salt marshes. I. Fish communities. Bull Mar Sci 25:445–465

Szedlmayer ST, Able KW (1993) Ultrasonic telemetry of age-0 summer flounder, Paralichthys dentatus, movements in a southern New Jersey estuary. Copeia 1993:728–736

Thayer GW, Stuart HH, Kenworthy WJ, Ustach JF, Hall AB (1978) Habitat values of salt marshes, mangroves, and seagrasses for aquatic organisms. In: Greeson PE, Clark JR, Clark JW (eds) Wetland functions and values: The state of our understanding. Proc Natl Symp on Wetlands. Am Water Res Assoc, pp 235–247

Weinstein MP (1979) Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. Fish Bull 77:339–357

Weinstein MP, Brooks HA (1983) Comparative ecology of nekton residing in a tidal creek and adjacent seagrass meadow community composition and structure. Mar Ecol Prog Ser 12:15–28

Werme CE (1981) Resource partitioning in a salt marsh fish community. PhD thesis, Boston University, Boston, Mass.

Williams AB (1984) Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, D.C.

Witting DA, Able KW (1993) Effects of body size on probability of predation for juvenile summer and winter flounder based on laboratory experiments. Fish Bull 91:577–581

Witting DA, Able KW (1995) Predation by sevenspine bay shrimp, *Crangon septemspinosa*, on winter flounder, *Pleuronectes americanus*, during settlement: laboratory observations. Mar Ecol Prog Ser 123:23–31

Wohlschlag DE, Cech JJ Jr (1970) Size of pinfish in relation to thermal stress response. Contr Mar Sci 15:21–31

Wurtsbaugh WA, Neverman D (1989) Post-feeding thermotaxis and daily vertical migration in a larval fish. Nature 333:846–848