

The Identification, Conservation, and Management of Estuarine and Marine Nurseries for Fish and Invertebrates

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Nearshore estuarine and marine ecosystems—e.g., seagrass meadows, marshes, and mangrove forests—serve many important functions in coastal waters. Most notably, they have extremely high primary and secondary productivity and support a great abundance and diversity of fish and invertebrates. Because of their effects on the diversity and productivity of macrofauna, these estuarine and marine ecosystems are often referred to as nurseries in numerous papers, textbooks, and government-sponsored reports (Boesch and Turner 1984, NRC 1995, Butler and Jernekoff 1999). Indeed, the role of these nearshore ecosystems as nurseries is an established ecological concept accepted by scientists, conservation groups, managers, and the public

A BETTER UNDERSTANDING OF THE HABITATS THAT SERVE AS NURSERIES FOR MARINE SPECIES AND THE FACTORS THAT CREATE SITE-SPECIFIC VARIABILITY IN NURSERY QUALITY WILL IMPROVE CONSERVATION AND MANAGEMENT OF THESE AREAS

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and cited as justification for the protection and conservation of these areas. Nonetheless, the nursery-role concept has rarely been stated clearly, even in papers that purport to test it. This ambiguity hinders the effectiveness of the nursery-role concept as a tool for conservation and management. We seek to redress that ambiguity by briefly tracing the history of the concept, developing a clear hypothesis with testable predictions, and discussing how this work can focus efforts in research, conservation, restoration, and management.

History of the nursery-role concept

The nursery-role concept was first applied nearly a century ago to motile invertebrates and fishes with complex life cycles, in which larvae are transported to estuaries, metamorphose, grow to subadult stages, and then move to adult habitats offshore. Gunter (1967) traces this idea to work on blue crabs on the Atlantic coast of the United States (Hay 1905), penaeid shrimp on the Gulf of Mexico coast, and finfish on both of these coasts (Hildebrand and Schroeder 1928). The concept became so pervasive that it has been termed a "law" (Gunter 1967). For example, Deegan (1993, p. 74) states that "estuarine fish faunas around the world are dominated in numbers and abundance by species which move into the estuary as larvae, accumulate biomass, and then move offshore."

In early papers the estuary as a whole was considered to be the nursery. In subsequent works, however, the focus shifted to specific areas within estuaries as nurseries, especially wetlands (herein marshes and mangrove forests) and seagrass meadows, because evidence suggested that they supported much greater densities of organisms than adjacent unvegetated (i.e., without macrophytes) substrates (Williams 1955, Hutchings and Recher 1974, Turner 1977, Orth et al. 1984, Minello 1999). We concentrate on seagrass meadows and wetlands because most research to date has addressed their potential to serve as nurseries. Examples are drawn from other ecosystems when possible and we note that the potential nursery value of some of them, for example oyster reefs, has not received due recognition. Throughout the paper, the term *ecosystem* is used to identify characteristic assemblages of plants and animals (e.g., marshes or oyster reefs). The term *habitat* refers to the area used by a species, with modifiers added to identify the particular habitats used by an animal. For example, the blue crab, *Callinectes sapidus*, has a seagrass habitat and a marsh habitat, which refer to particular portions of seagrass and marsh ecosystems, respectively, used by the crab.

We also focus on the direct effects of ecosystems on the productivity of individual species as opposed to their contributions to the productivity of coastal oceans. Seagrass meadows and wetlands have been identified as nurseries in part because they export vast quantities of carbon, nitrogen, and phosphorus to coastal food webs. This export may occur through the direct transfer of animal biomass via movement of individuals, predation, or outwelling of dissolved and particulate organic matter (Teal 1962, Nixon 1980, Deegan 1993, Lee 1995,

Childers et al. 2000). This transfer of productivity from coastal ecosystems to food webs is undoubtedly important. Nonetheless, there is a separation in the conceptual underpinnings and testing of hypotheses about the effects of ecosystems on the productivity of individual species versus their effects on the productivity of estuaries and coastal oceans in general. An analysis of these effects is beyond the scope of this paper, but they will be addressed in a future work.

Most studies of the nursery-role concept have examined the effects of seagrass meadows or wetlands on either the density, survival, or growth of juveniles on the species' movement to adult habitats (Figure 1; Heck et al. 1997, Butler and Jerinakoff 1999, Minello 1999). Some studies make direct comparisons of these parameters among the habitats used by a species (Weinstein and Brooks 1983, Sheridan 1992, Jenkins and Wheatley 1998), but such comparisons are often limited to vegetated versus unvegetated habitats (Edgar and Shaw 1995, Gray et al. 1996). Generally, an area has been called a nursery if a juvenile fish or invertebrate species occurs at higher densities, avoids predation more successfully, or grows faster there than in a different habitat.

Of all the studies on the nursery-role concept, most have focused on the effects of seagrass meadows or wetlands on an animal's density. The evidence usually indicates that the density of fish and invertebrates is higher in vegetated than in unvegetated habitats (for reviews see Orth et al. 1984, Heck et al. 1997, Able 1999, Minello 1999). Direct comparisons of an animal's abundance between mangrove forests and other habitats are rare (Sheridan 1992). There are also difficulties with these comparisons, because different sampling methods usually are used to estimate densities inside and outside of mangrove forests and frequently samples are only collected in areas adjacent to mangrove forests rather than directly within the flooded forest.

The few studies that have focused on differences in juvenile survival among wetlands, seagrass meadows, and other areas indicate that survival of a species is generally greater in vegetated than in unvegetated habitats (Orth et al. 1984, Heck and Crowder 1991, Able 1999). Even fewer studies have focused on the effects of wetlands and seagrass meadows on the growth of fish and invertebrates (Heck et al. 1997, Phelan et al. 2000). In seagrass meadows, evidence regarding growth is, surprisingly, equivocal. Only about half of the studies report that the growth rate of individuals is higher in seagrass habitats than in adjacent habitats (Heck et al. 1997).

Finally, only a handful of studies have attempted to determine whether the juveniles of a species move successfully from putative nursery habitats to adult habitats (Costello and Allen 1964, Deegan 1993, Gillanders and Kingsford 1996, Gillanders 1997, Fry et al. 1999). The evidence that supports successful movement of seagrass- or wetland-associated juveniles to adult habitats is largely indirect (Eggleston 1995), both because movement data are difficult to obtain and because there has been a dearth of communication between benthic ecologists and fisheries biologists.



Figure 1. Examples of field experiments and observations used to assess whether some habitats serve as nurseries. (a) A drop trap used to compare density between marsh and nearby unvegetated habitats. (b) A tethered shrimp used to assess differences in survival between sand, seagrass, and marsh habitats. (c) Cages used to examine shrimp growth between marsh and unvegetated habitats. (d) A juvenile summer flounder, *Paralichthys dentatus*, being injected subcutaneously with a nontoxic acrylic paint marker to examine movement patterns.

There is growing recognition that there are exceptions to the nursery-role concept. For example, few commercially important species of fish and invertebrates appear to rely exclusively on seagrass meadows in coastal waters of Massachusetts (Heck et al. 1995) or New Jersey (Able and Fahay 1998). Instead, most of these species use seagrass meadows opportunistically but can survive well in unvegetated areas. Edgar and Shaw (1995) reported that seagrass beds in southern Australia were not always better nurseries than nearby unvegetated substrates. A study on the labrid Australian blue groper, *Achoerodus viridis*, indicated that recruits to the offshore adult population came primarily from young that settled in offshore rocky reefs, not from the abundant young in inshore seagrass beds (Gillanders and Kingsford 1996). A recent planning document produced for the Australian Fisheries Research Development Corporation concluded that there was very little strong evidence that Australian seagrass provided critical nursery habitat for the majority of Australian finfish species (Butler and Jernakoff 1999).

That the evidence about the role of certain ecosystems as nurseries is sometimes contradictory is not surprising—there are exceptions to any broad ecological concept. However, much of the disagreement about evidence that sup-

ports or refutes the nursery-role concept is exacerbated by the fact that the nursery-role concept does not have a clearly defined hypothesis, and therefore it has been difficult to test directly (Edgar and Shaw 1995, Gillanders 1997).

A nursery-role hypothesis

The underlying premise of most studies that examine nursery-role concepts is that some nearshore, juvenile habitats contribute disproportionately to the production of individuals that recruit to adult populations. From this premise, we have developed a hypothesis from which clear and testable predictions can be made: A habitat is a nursery for juveniles of a particular species if its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur.

The ecological processes operating in nursery habitats, as compared with other habitats, must support greater contributions to adult recruitment from any combination of four factors: (1) density, (2) growth, (3) survival of juveniles, and (4) movement to adult habitats (Figure 2). A general null hypothesis is that there is no difference in the nursery value (i.e., production of individuals that recruit to adult populations per

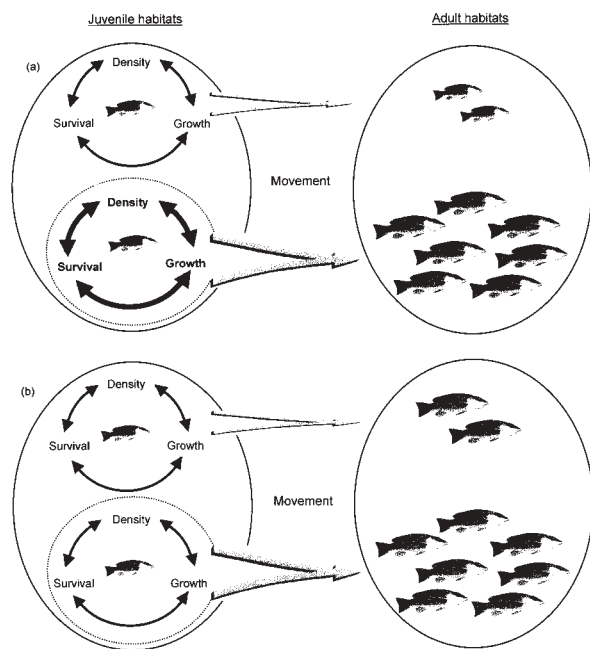


Figure 2. A representation of the factors operating in juvenile and nursery habitats. The thickness of the arrows indicates the relative contribution from each factor to the recruitment of adults. A nursery habitat (dashed oval) supports a greater than average combination of increased density, survival, and growth of juveniles and movement to adult habitats. (a) All four factors are greater in the nursery versus other juvenile habitats. (b) Only one of the four factors, in this case movement, is greater in the nursery versus other juvenile habitats.

unit area of juvenile habitat) of different juvenile habitats for a given species.

Considerations for tests of the nursery-role hypothesis

There are a number of key considerations on the species, habitats, and variables that should be accounted for when testing the nursery-role hypothesis. These considerations have frequently been overlooked in the past.

The nursery-role hypothesis focuses on a particular set of life history strategies—that is, on those strategies where there is a separation between juvenile and adult habitats (Figure 3). The original literature on nurseries focused on an idealized or classic life history strategy: Juveniles grew up in nearshore or estuarine habitats and then undertook rapid, directional movement to completely different offshore adult habitats (Figure 3a). The gag grouper (*Mycteroperca microlepis*), for example, fit this classic life history strategy (Koenig and Coleman 1998). However, many other species with substantial overlap in juvenile and adult habitats have historically been thought to use nurseries. In blue crabs, for example, juveniles and adults often occupy the same habitats, but females make a directed movement (usually to the

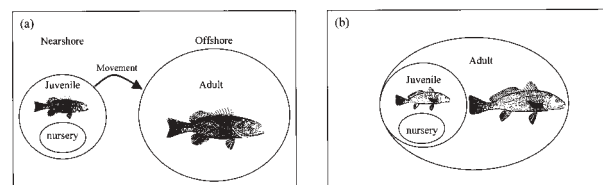


Figure 3. Relationship between juvenile, nursery, and adult habitats. The square represents all habitats. The ovals represent the portions of habitats used during juvenile and adult stages. Nursery habitats are a subset of juvenile habitats. (a) Classic concept of species that have nursery habitats. (b) General concept of species that have nursery habitats. There can be overlap in the habitats that juveniles and adults use, but there must be some movement to nonjuvenile habitats for a species to be considered to have a nursery habitat. This movement is often associated with reproduction or an ontogenetic habitat shift.

mouths of estuaries) to nonjuvenile habitats to release eggs (Orth and van Montfrans 1990). Some species do not move directly from juvenile to adult habitats but move gradually between them (e.g., spiny lobsters), and they also are considered to have nursery habitats.

We suggest that species must have at least some disjunction between juvenile and adult habitats to be considered to have nursery habitats (Figure 3b), and in most of these species, movement to nonjuvenile habitat is associated with reproduction. There are many other life history strategies, of course—this hypothesis does not imply that seagrass meadows, for example, do not have important effects on species that spend their entire life there. These other life history strategies, however, do not fit the nursery-role hypothesis. Based on our definition, taxa that do not have nurseries per se include, for example, bay scallops (*Argopecten irradians*), killifish (*Fundulus*), bay anchovy (*Anchoa mitchilli*), and amphipods. Examples of taxa that do have nurseries are clawed lobster (*Homarus americanus*), eels (*Anguilla*), red drum (*Sciaenops ocellatus*), gag grouper, blue groper, pink snapper (*Pagrus auratus*), luderick (*Girella tricuspidata*), tarwhine (*Rhabdosargus sarba*), blue crabs, brown shrimp (*Farfantepenaeus aztecus*), flounder (*Paralichthys* spp.), pinfish (*Lagodon rhomboides*), striped mullet (*Mugil cephalus*), and gray snapper (*Lutjanus griseus*).

The nursery role of habitats must be compared on a unit-area basis. Even if a habitat is small in area, it is an important nursery habitat if it produces relatively more adult recruits per unit of area than other juvenile habitats used by a species. This distinction is important in conservation and management, where priorities must be set for limited funding and effort. It is more important to conserve, abate the loss, restore, or otherwise manage habitats that contribute disproportionately to the production of adults. This need is even more pressing if these habitats are relatively uncommon.

It is possible that common habitats may make important contributions to the recruitment of adults even if the density of individuals per area is low, simply because the habitats are widespread. We predict, however, that there will be few cases where habitats that have lower densities and often lower survival and growth rates of individuals will make significant contributions to adult recruitment simply because they are widespread. And if these habitats do make significant contributions solely because of their large areal coverage, they will be important juvenile habitats, but not nurseries per se.

A definitive test of the nursery-role hypothesis requires a comparison among all habitats that juveniles use (Figure 4). Comparisons among putative nursery habitats have usually involved only vegetated and unvegetated habitats, even though individual species may use many different habitats (Minello 1999). Thus, seagrasses or wetlands may seem less important as nurseries in regions where alternative habitats are used successfully. For example, in bays in southern Australia and in the northeastern United States, a species may be found in many habitats (e.g., cobble, rocky reef, oyster reef, kelp, sandy or muddy bottom) in addition to its marsh and seagrass habitats (Ward et al. 1999). To determine which, if any, habitats serve as nurseries, all of a species' juvenile habitats should be surveyed.

Nursery habitats are a subset of juvenile habitats.

Any habitat that makes a greater than average contribution to the recruitment of adults should be considered a nursery habitat. Thus, some portions of juvenile habitats will be nurseries, but not all juvenile habitats can be nurseries (Figure 3). Previously, there has been little discussion of the quantitative contribution that a habitat must make before it is considered a nursery. In most tests, however, a habitat was considered a nursery if some parameter (usually density) was statistically significantly greater in that habitat than in another. This usage implies that any habitat with a greater than average contribution to adult recruitment should be considered a nursery. Juvenile habitats that are found not to be nurseries can and often do contribute individuals to adult populations, but they make a less than average contribution when compared with other habitats (Figure 4). If many habitats are examined, it should be possible to identify and focus on those that make the greatest contribution to adult recruitment, that is, the best nursery habitats.

The movement of individuals from juvenile to adult habitats must be measured. There are very few studies on movement patterns, and this is a vital missing link in our understanding of nurseries. Movement of individuals is one of the most difficult variables to measure in ecology. Fortunately, vast improvements in technology—archival data loggers, stable isotopes, genetic markers, and otolith microchemistry—allow researchers to track and infer movements (Gillanders and Kingsford 1996, Thorrold et al. 1998, Fry et al. 1999).

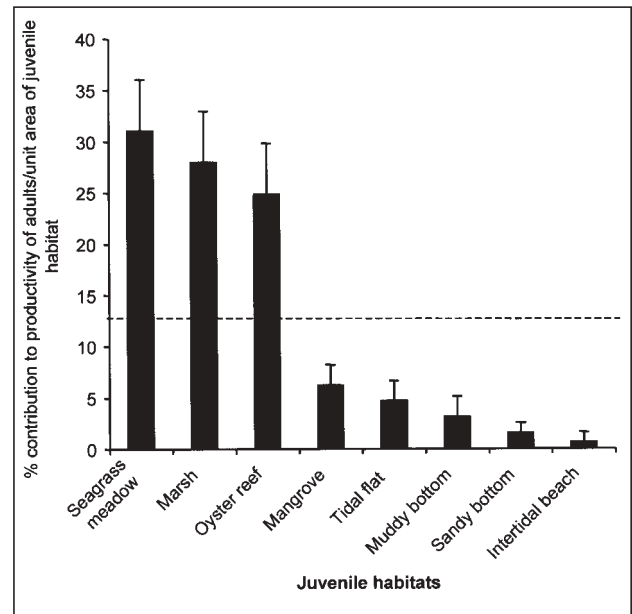


Figure 4. A hypothetical comparison of the nursery value of several different habitats. The dashed line represents the average percentage productivity of adults per unit area from all the juvenile habitats. In this example seagrass meadows, marshes, and oyster reefs are nursery habitats.

The total biomass of individuals recruiting to adult populations is the best single measure of the contribution from juvenile habitats. The nursery habitats for a species are those that are the most likely to contribute to future populations. This contribution should be a function of both the size and number of individuals that recruit to adult populations, because these variables affect survival, growth, and reproductive success in the adult habitats. Total biomass (i.e., production) of individuals recruiting to adult populations should be the best integrative measure of this potential contribution from juvenile habitats to future generations.

Examinations of the density of juveniles among habitats do not provide a conclusive test of the nursery-role hypothesis. In the overwhelming majority of studies, a habitat is suggested to be a nursery largely because it supports high densities of juveniles relative to another habitat. It is assumed that higher juvenile densities will lead to a greater recruitment to adult populations. Although a habitat may support high densities of juveniles, if these individuals never reach adult populations, then that habitat does not function as a productive nursery. In most studies the unstated premise has been that, all else being equal, habitats with higher densities of juveniles are likely to make a greater contribution to the production of adults than habitats with lower densities of juveniles. This correlation, which is rarely tested, may hold in many cases, but there are likely to be important exceptions. For example, some sites may be well

placed to receive larval influx, but these could be sites where juveniles grow slowly or where movement to adult habitats is risky or difficult (e.g., there are no adult habitats nearby or there is particularly intense predation; Lipcius et al. 1997, McBride and Able 1998). Density is only one of four factors that must be considered to determine whether a habitat serves as a nursery.

It also is not sufficient to measure how long individuals spend in nursery habitats to determine whether that habitat is a nursery. That is, the duration of occupancy is important only inasmuch as it contributes to a greater combination of survival and growth of the individuals that leave the nursery habitat.

Factors that contribute to site-specific variation in nursery value

The nursery value of seagrass meadows, wetlands, and other ecosystems may vary geographically. For example, recent analyses suggest that seagrass meadows in the tropical Caribbean are more important as nurseries than they are in the Indo-Pacific region (Williams 1991); other analyses have found seagrass meadows more important as nurseries in the United States than in Australia (Edgar and Shaw 1995, Butler and Jernakoff 1999, Ward et al. 1999). Within the United States, seagrass meadows in warm temperate regions may serve as better nurseries than those in cool temperate regions (Orth and van Montfrans 1990, but see Grant and Brown 1998). Marshes in the Gulf of Mexico are suggested to be more important as nurseries than marshes in the US South Atlantic (Minello 1999).

This potential geographic variation is a source of contention about the importance of nurseries in general. Much of the apparent discrepancy in the importance of nurseries in different regions could be understood, however, by examining factors that contribute to local variation (e.g., within estuaries) in nursery value. For example, even within an estuary there is variation in the nursery value of different seagrass meadows for a species. Factors that can create this site-specific variation in the nursery value of habitats can be grouped into three broad categories: biotic, abiotic, and landscape (Table 1).

Many biotic and abiotic factors can influence the nursery value of habitats for a species (Table 1). For example, Heck and Crowder (1991) found that predation on target species in seagrass beds was lower in more structurally complex beds, which suggests that more complex beds may serve as better nurseries for many species because they increase survivorship. Salinity also appears to have important effects on site-specific variation in the nursery value of habitats. For example, the densities of many species within marshes are highly dependent on salinity (Minello 1999). Larval supply and presettlement processes also can affect the initial density and condition (e.g., size) of juveniles within a habitat (Grimes and Kingsford 1996, Roy 1998). In general, presettlement processes are rarely considered when evaluating how well habitats function

as nurseries; greater attention needs to be paid to their interaction with postsettlement processes.

Landscape-level factors also can affect the nursery value of sites within habitats (Table 1). For example, the relative location of seagrass beds in an estuary can affect the density of fish species; some seagrass beds near the site where larvae enter estuaries have higher densities of fish than similar beds farther up the estuary (Bell et al. 1988). Lipcius and colleagues (1997) suggested that proximity—i.e., relative location of nursery and adult habitats in the Exuma Sound, Bahamas seascape—affects the abundance of adult lobsters by affecting the success of movement between habitats. Relative location, with respect to large water movements such as upwelling or retention zones, has also been shown to strongly influence larval delivery (Roy 1998), thus playing a crucial role in setting initial juvenile densities within a habitat. Irlandi and Crawford (1997) concluded that for pinfish the nursery value of salt marshes was affected by their location relative to seagrass beds: Both the density and growth of pinfish were higher in marshes adjacent to seagrass beds than in marshes adjacent to unvegetated bottom. Several good landscape-scale studies document phenomena that are likely to create variation in the value of nursery habitats, even though they do not specifically address the nursery-role hypothesis. For example, Irlandi (1994) found that rates of predation on clams were higher in more fragmented seagrass beds. Micheli and Peterson (1999) found that densities of macroinvertebrates on oyster reefs were lower where the reefs were next to salt marshes, which harbored blue crab predators. The importance of these factors (Table 1) needs to be better examined, because much of the apparent discrepancy in nursery roles in different regions (across latitudinal gradients or between continents) very likely can be attributed to one or several of these factors operating locally (e.g., within estuaries).

Implications for research, conservation, restoration, and management of nurseries

Throughout the world, the degradation of coastal ecosystems continues at an alarming rate (Hinrichsen 1998). Estuaries may be some of the most degraded environments on

Table 1: Factors that create site-specific variation in nursery value

Biotic	Abiotic	Landscape
Larval supply	Water depth	Spatial pattern
Structural complexity	Physico-chemical	(e.g., size,
Predation	(dissolved O ₂ ,	shape,
Competition	salinity)	fragmentation,
Food availability	Disturbance regime	connectivity)
	Tidal regime	Relative location
		(e.g., to larval
		supply, other
		juvenile habi-
		tats, adult habi-
		tats)

earth, because they have been focal points for human colonization for centuries (Edgar et al. 2000). Interest in conserving and managing coastal waters is intense and widespread, but funds are limited and must be targeted judiciously. Development of a better nursery-role hypothesis may help researchers identify the habitats and, even more important, the sites within habitats that serve as nurseries for a species, thus focusing efforts in research, conservation, restoration, and management. However, it is not useful to wait for irrefutable evidence of a given area's function as a nursery before action is taken to conserve, manage, or restore it. Rather, it is necessary to err on the side of caution and to act on current knowledge of the potential for a given area to serve as a nursery for some species.

Seagrasses and wetlands have been the focus of most work on nurseries, and in many cases this emphasis is justified. However, improved tests of predictions from the nursery-role hypothesis may show that previously ignored areas also serve as nurseries and therefore should be better conserved and managed (Gray et al. 1996). The question this article addresses is not "Are wetlands and seagrasses important?" There is undeniable evidence of their importance, aside from their potential as nurseries, at many sites. They provide many ecosystem services and serve many important functions (Costanza et al. 1997), stabilizing shorelines, reducing wave impacts, removing suspended solids, recycling nutrients, and adding oxygen to surrounding waters (Short and Wyllie-Echeverria 1996, Costanza et al. 1997, Gosselink et al. 1999). Seagrasses and wetlands are highly productive, and this production enters coastal food webs through many different pathways, not just as fish moving to adult habitats.

The development of the nursery-role concept is similar in some respects to the development of the keystone species concept. There are few rigorous tests of predictions developed from the keystone species concept, and it is difficult to conduct all the experiments that would be necessary to show unequivocally that a keystone species exists (Power et al. 1996). Nonetheless, it would be useful to know what a definitive test would encompass, so that researchers could arrive at the best approximation of it. Although there is no unequivocal test of the keystone species concept, sufficient evidence exists to indicate that some species are likely to be keystone species (Estes and Duggins 1995) and others are not (Elner and Vadas 1990). The situation is much the same for nursery habitats. For example, substantial evidence supports the contention that some seagrasses and wetlands are likely to serve as nurseries (Heck et al. 1997, Butler and Jernakoff 1999, Minello 1999) even if there is no definitive test.

Many practical considerations can help in the testing of predictions from the nursery-role hypothesis. First, more than one factor must be considered. Ideally, all four factors—density, growth, survival, and movement—would be examined in a study of putative nursery habitats, but doing so may be difficult. Nonetheless, researchers cannot continue to be satisfied with single-factor studies in this field. Multifactor ex-

periments are preferred also because they often lead to useful insights about factor interaction.

Second, researchers must consider multiple habitats. Although most species are found in more than one or two habitats, surprisingly few studies make comparisons among more than two potential nursery habitats.

Third, we must attempt to better quantify the movement of individuals between juvenile and adult habitats with all available tools. Refinements in tagging and chemistry will help substantially to identify the sources of individuals that recruit to adult habitats, yet these techniques can be labor intensive and expensive; moreover, they involve more laboratory than field work, which would require a major shift in many research programs. Nonetheless, it should be possible to design simple but elegant field studies to examine the movement of juveniles. It is surprising, for example, that so few studies examine season- and size-specific movements of juveniles out of the mouths of estuaries towards adult habitats (Deegan 1993).

Fourth, although we have focused on direct methods of study in this article, correlative and case study analyses can yield many useful insights. For example, Butler and Jernakoff (1999) reviewed many studies that looked for correlations between inshore habitat loss and offshore fisheries production. These correlative analyses cannot provide strong inference for the existence of nursery habitats, but they do provide relevant observations on potential nurseries at scales that are ecologically and economically important.

Better and more consistent tests of the nursery-role hypothesis will identify nursery habitats. More important, they will reveal which factors create site-specific variation within habitats in the production of juveniles that recruit to adult populations. These tests should also provide a better indication of the species that depend on particular nursery habitats. Conservation and management organizations now commonly consider all seagrasses and wetlands as nurseries. These broad declarations may be useful for generating public interest, but they hinder the actual work that needs to be accomplished by these groups because the statements lack focus. A clearer understanding of the habitats that serve as nurseries for species, and the factors that make some sites more valuable as nurseries, will allow more efficient use of limited money, time, and effort in conservation and management. Not all oyster reefs, cobble, or wetlands are created equal. If it were known, for example, that for some species the best seagrass, marsh, or mangrove nurseries were large areas near sources of larval influx and in close proximity to adult habitats, then efforts in habitat conservation and management aimed at preserving or restoring nurseries could be more judiciously invested in those types of sites.

Some of this information is or should be available, but it has not been applied specifically to the identification of the habitats and the sites within habitats that serve as nurseries. A better understanding and testing of predictions of the nursery-role hypothesis should enable scientists and funding agencies to fill the gaps in our knowledge, help nongovern-

mental organizations better target their conservation efforts to protect the diversity of species and natural resources, and allow state and federal agencies and fishery management councils to make better regulatory decisions for fisheries management, habitat conservation, habitat restoration, and mitigation.

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References cited

- Able KW. 1999. Measures of juvenile fish habitat quality: Examples from a national estuarine research reserve. Pages 134–147 in Benaka LR, ed. *Fish Habitat: Essential Fish Habitat and Rehabilitation*. Bethesda (MD): American Fisheries Society.
- Able KW, Fahay MP. 1998. *The First Year in the Life of Estuarine Fishes in the Middle Atlantic Bight*. New Brunswick (NJ): Rutgers University Press.
- Bell JD, Steffe AS, Westoby M. 1988. Location of seagrass beds in estuaries: Effects on associated fish and decapods. *Journal of Experimental Marine Biology* 122: 127–146.
- Boesch DF, Turner RE. 1984. Dependence of fishery species on salt marshes: The role of food and refuge. *Estuaries* 7: 460–468.
- Butler AJ, Jernakoff P. 1999. *Seagrass in Australia: Strategic Review and Development of an R&D Plan*. Collingwood (Australia): CSIRO Publishing.
- Childers DL, Day JW Jr, McKellar HN Jr. 2000. Twenty more years of marsh and estuarine flux studies: Revisiting Nixon (1980). Pages 391–424 in Weinstein MP, Kreeger DA, eds. *Concepts and Controversies in Tidal Marsh Ecology*. Dordrecht (Netherlands): Kluwer Academic.
- Costello T, Allen D. 1964. Migrations and geographic distribution of pink shrimp, *Penaeus duorarum*, of the Tortugas and Sanibel Grounds Florida. *Fishery Bulletin* 65: 449–459.
- Costanza R, et al. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387: 253–260.
- Deegan LA. 1993. Nutrient and energy transport between estuaries and coastal marine ecosystems by fish migration. *Canadian Journal of Fisheries and Aquatic Science* 50: 74–79.
- Edgar GJ, Shaw C. 1995. The production and trophic ecology of shallow-water fish assemblages in southern Australia. I: Species richness, size structure and production of fishes in Western Port, Victoria. *Journal of Experimental Marine Biology and Ecology* 194: 53–81.
- Edgar GJ, Barrett NS, Graddon DJ, Last PR. 2000. The conservation significance of estuaries: A classification of Tasmanian estuaries using ecological, physical and demographic attributes as a case study. *Biological Conservation* 92: 383–397.
- Eggleston DB. 1995. Recruitment in Nassau grouper, *Epinephelus striatus*: Post-settlement abundance, microhabitat features, and ontogenetic habitat shifts. *Marine Ecology Progress Series* 124: 9–22.
- Elnor RW, Vadas RL Sr. 1990. Inference in ecology: The sea urchin phenomenon in the northwestern Atlantic. *American Naturalist* 136: 108–125.
- Estes JA, Duggins DO. 1995. Sea otters and kelp forests in Alaska: Generality and variation in a community ecological paradigm. *Ecological Monographs* 65: 75–100.
- Fry B, Mumford PL, Robblee MB. 1999. Stable isotope studies of pink shrimp (*Farfantepenaeus duorarum* Burkenroad) migrations on the southwestern Florida shelf. *Bulletin of Marine Science* 65: 419–430.
- Gillanders BM. 1997. Patterns in abundance and size structure in the blue groper, *Achoerodus viridis* (Pisces, Labridae): Evidence of links between estuaries and coastal reefs. *Environmental Biology of Fishes* 49: 153–173.
- Gillanders BM, Kingsford MJ. 1996. Elements in otoliths may elucidate the contribution of estuarine recruitment to sustaining coastal reef populations of a temperate reef fish. *Marine Ecology Progress Series* 141: 13–20.
- Gosselink JG, Coleman JM, Stewart RE Jr. 1999. Coastal Louisiana. Pages 385–436 in Mac MJ, Opler PA, Puckett Haecker CE, Doran PD, eds. *Status and Trends of the Nation's Biological Resources*. Vol. 1. Reston (VA): US Department of the Interior, US Geological Survey.
- Grant SM, Brown JA. 1998. Nearshore settlement and localized populations of age-0 Atlantic cod (*Gadus morhus*) in shallow coastal waters of Newfoundland. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 1317–1327.
- Gray CA, McElligott DJ, Chick RC. 1996. Intra- and inter-estuary differences in assemblages of fishes associated with shallow seagrass and bare sand. *Marine and Freshwater Research* 47: 723–735.
- Grimes CB, Kingsford MJ. 1996. How do riverine plumes of different sizes influence fish larvae: Do they enhance recruitment? *Marine and Freshwater Research* 47: 191–208.
- Gunter G. 1967. Some relationships of estuaries to the fisheries of the Gulf of Mexico. Pages 621–638 in Lauff GH, ed. *Estuaries*. Washington (DC): American Association for the Advancement of Science.
- Hay WP. 1905. *The Life History of the Blue Crab, Callinectes sapidus*. Washington (DC): US Bureau of Fisheries.
- Heck KL Jr, Crowder LB. 1991. Habitat structure and predator–prey interactions in vegetated aquatic systems. Pages 282–299 in Bell SS, McCoy ED, Mushinsky HR, eds. *Habitat structure: The physical arrangement of objects in space*. New York: Chapman and Hall.
- Heck KL Jr, Able KW, Roman CT, Fahay MP. 1995. Composition, abundance, biomass, and production of macrofauna in a New England estuary: Comparisons among eelgrass meadows and other nursery habitats. *Estuaries* 18: 379–389.
- Heck KL Jr, Nadeau DA, Thomas R. 1997. The nursery role of seagrass beds. *Gulf of Mexico Science* 1997(1): 50–54.
- Hildebrand SF, Schroeder WC. 1928. *Fishes of Chesapeake Bay*. 33(1).
- Hinrichsen D. 1998. *Coastal waters of the world: Trends, threats, and strategies*. Washington (DC): Island Press.
- Hutchings PA, Recher HF. 1974. The fauna of Careel Bay with comments on the ecology of mangrove and sea-grass communities. *Australian Zoologist* 18: 99–128.
- Irlandi EA. 1994. Large- and small-scale effects of habitat structure on rates of predation: How percent coverage of seagrass affects rates of predation and siphon nipping on an infaunal bivalve. *Oecologia* 98: 176–183.
- Irlandi EA, Crawford MK. 1997. Habitat linkages: The effect of intertidal salt-marshes and adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish. *Oecologia* 110: 222–230.
- Jenkins GP, Wheatley MJ. 1998. The influence of habitat structure on nearshore fish assemblages in a southern Australian embayment: Comparison of shallow seagrass, reef-algal and unvegetated sand habitats, with an emphasis on their importance to recruitment. *Journal of Experimental Marine Biology and Ecology* 221: 147–172.
- Koenig CC, Coleman FC. 1998. Absolute abundance and survival of juvenile gags in sea grass beds in the northeastern Gulf of Mexico. *Transactions of the American Fisheries Society* 127: 44–55.
- Lee SY. 1995. Mangrove outwelling: A review. *Hydrobiologia* 295: 203–212.
- Lipcius RN, Stockhausen WT, Eggleston DB, Marshall LS Jr, Hickey B. 1997. Hydrodynamic decoupling of recruitment, habitat quality and adult abundance in the Caribbean spiny lobster: Source-sink dynamics. *Marine and Freshwater Research* 48: 807–815.
- McBride RS, Able KW. 1998. Ecology and fate of butterfly fishes, *Chaetodon* spp., in the temperate, western north Atlantic. *Bulletin of Marine Science* 63: 401–416.
- Micheli F, Peterson CH. 1999. Estuarine vegetated habitats as corridors for predator movements. *Conservation Biology* 13: 869–881.
- Minello T. 1999. Nekton densities in shallow estuarine habitats of Texas and Louisiana and the identification of essential fish habitat. Pages 43–75 in Benaka LR, ed. *Fish Habitat: Essential Fish Habitat and Rehabilitation*. Bethesda (MD): American Fisheries Society.

- [NRC] National Research Council. 1995. Understanding Marine Diversity: A Research Agenda for the Nation. Washington (DC): National Academy Press.
- Nixon SW. 1980. Between coastal marshes and coastal waters: A review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry. Pages 437–525 in Hamilton P, MacDonald KB, eds. Estuarine and Wetland Processes. New York: Plenum Press.
- Orth RJ, van Montfrans J. 1990. Utilization of marsh and seagrass habitats by early stages of *Callinectes sapidus*: A latitudinal perspective. Bulletin of Marine Science 46: 126–144.
- Orth RJ, Heck KL Jr, van Montfrans J. 1984. Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator–prey relationships. Estuaries 7: 339–350.
- Phelan BA, Goldberg R, Bejda AJ, Pereira J, Hagan S, Clark P, Studholme AL, Calabrese A, Able KW. 2000. Estuarine and habitat-related differences in growth rates of young-of-the-year winter flounder (*Pseudopleuronectes americanus*) and tautog (*Tautoga onitis*) in three northeastern U.S. estuaries. Journal of Experimental Marine Biology and Ecology 247: 1–28.
- Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT. 1996. Challenges in the quest for keystones. BioScience 46: 609–620.
- Roy C. 1998. An upwelling-induced retention area off Senegal: A mechanism to link upwelling and retention processes. South African Journal of Marine Science 19: 89–98.
- Sheridan PF. 1992. Comparative habitat utilization by estuarine macrofauna within the mangrove ecosystem of Rookery Bay, Florida. Bulletin of Marine Science 50: 21–39.
- Short FT, Wyllie-Echeverria S. 1996. Natural and human-induced disturbance of seagrasses. Environmental Conservation 23: 17–27.
- Teal JM. 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology 43: 614–624.
- Thorrold S, Jones C, Swart P, Targett T. 1998. Accurate classification of juvenile weakfish *Cynoscion regalis* to estuarine nursery areas based on chemical signatures in otoliths. Marine Ecology Progress Series 173: 253–265.
- Turner RE. 1977. Intertidal vegetation and commercial yields of penaeid shrimp. Transactions of the American Fisheries Society 106: 411–416.
- Ward TJ, Vanderklift MA, Nicholls AO, Kenchington RA. 1999. Selecting marine reserves using habitats and species assemblages as surrogates for biological diversity. Ecological Applications 9: 691–698.
- Weinstein MP, Brooks HA. 1983. Comparative ecology of nekton residing in a tidal creek and adjacent seagrass meadow: Community composition and structure. Marine Ecology Progress Series 12: 15–27.
- Williams AB. 1955. A survey of North Carolina shrimp nursery grounds. Journal of the Mitchell Society 71: 200–207.
- Williams DM. 1991. Patterns and processes in the distribution of coral reef fishes. Pages 437–474 in Sale P, ed. The Ecology of Fishes on Coral Reefs. New York: Academic Press.

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