Vol. 312: 291–295, 2006 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published April 24

NOTE

Marine nurseries and effective juvenile habitats: concepts and applications

Craig P. Dahlgren[1,*], G. Todd Kellison[2,10], Aaron J. Adams[3], Bronwyn M. Gillanders[4], Matthew S. Kendall[5], Craig A. Layman[6], Janet A. Ley[7], Ivan Nagelkerken[8], Joseph E. Serafy[9]

[1]Perry Institute for Marine Science, 100 N. US Highway 1, Suite 202, Jupiter, Florida 33477, USA

[2]Biscayne National Park, 9700 SW 328th Street, Homestead, Florida 33033, USA

[3]Mote Marine Lab, Charlotte Harbor Field Station, PO Box 2197, Pineland, Florida 33945, USA

[4]Southern Seas Ecology Laboratories, Darling Building, School of Earth and Environmental Sciences, University of Adelaide, South Australia 5005, Australia

[5]NOAA Biogeography Team, 1305 East West Highway, Silver Spring, Maryland 20910, USA

[6]Department of Ecology and Evolutionary Biology, Yale University, PO Box 208106, New Haven, Connecticut 06520-8106, USA

[7]Australian Maritime College, PO Box 21, Beauty Point, Tasmania 7270, Australia

[8]Department of Animal Ecology and Ecophysiology, Institute for Water and Wetland Research, Radboud University Nijmegen, Toernooiveld 1, 6525 ED, Nijmegen, The Netherlands

[9]National Marine Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, Florida 33149, USA

[10]*Present address:* National Marine Fischeries Service, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, Florida 33149, USA

ABSTRACT: Much recent attention has been focused on juvenile fish and invertebrate habitat use, particularly defining and identifying marine nurseries. The most significant advancement in this area has been the development of a standardized framework for assessing the relative importance of juvenile habitats and classifying the most productive as nurseries. Within this framework, a marine nursery is defined as a juvenile habitat for a particular species that contributes a greater than average number of individuals to the adult population on a per-unit-area basis, as compared to other habitats used by juveniles. While the nursery definition and framework provides a powerful approach to identifying habitats for conservation and restoration efforts, it can omit habitats that have a small per-unit-area contribution to adult populations, but may be essential for sustaining adult populations. Here we build on the nursery concept by developing a framework for evaluating juvenile habitats based on their overall contribution to adult populations, and introduce the concept of Effective Juvenile Habitat (EJH) to refer to habitats that make a greater than average overall contribution to adult populations.

KEY WORDS: Habitat · Juvenile · Nursery · Nearshore

INTRODUCTION

Marine ecologists have long recognized that nearshore habitats often support a high abundance of juvenile fishes and invertebrates, many of which utilize different habitats as adults (e.g. Gunter 1967, Lenanton 1982, Blaber et al. 1989, Appeldoorn et al. 1997, Nagelkerken et al. 2000b,c). These juvenile habitats tend to be found in shallow waters, and are assumed to have higher food abundance (Orth et al. 1984, Nagelkerken et al. 2000a) or lower predation risk (Shulman 1985) compared to adult habitats. Habitats that support high juvenile densities, and may contribute juveniles or sub-adults to adult popu-

*Email: cdahlgren@perryinstitute.org

lations, have historically been referred to as nurseries (reviewed in Beck et al. 2001). Until recently, however, the concept of marine nurseries was poorly defined and was used to refer to any general area (e.g. estuaries) or specific habitat type (e.g. seagrass beds) where juveniles of a species were present, or occurred in relatively high density (e.g. Nagelkerken et al. 2000b, Adams & Ebersole 2002, Cocheret de la Morinière et al. 2002). This broad use of the term nursery, with no criteria for evaluating the relative importance for supporting populations, limited its utility for researchers and managers and contributed to the failure of marine fisheries managers to give adequate consideration to the importance of juvenile production (and thus juvenile habitats) in management strategies (Beck et al. 2001, 2003).

Beck et al. (2001) provided a much needed refinement to the term 'nursery habitat' by defining it as a habitat for a particular species that contributes a greater than average number of individuals to the adult population on a per-unit-area basis in comparison to other habitats used by juveniles. In this article we refer to this definition of 'nursery'. According to this definition, not all habitats used by juveniles are nurseries, including some habitats that contain high densities of juveniles, because of their below average contribution to adult populations. Thus, whether a habitat is a nursery or not depends on its juvenile contribution function. The refined definition of nursery habitats by Beck et al. (2001) has greatly facilitated research and management of marine nurseries, has improved evaluation of the nursery value of marine habitats (e.g. Beck et al. 2003, Heck et al. 2003, Sheridan & Hays 2003, Adams et al. in press), and has focused the use of techniques for assessing the juvenile contribution function of marine nurseries (e.g. Gillanders et al. 2003), to improve management (Beck et al. 2003).

The refined nursery definition was developed with a conservation framework in mind, and greatly improves our ability to evaluate juvenile habitat productivity for use in habitat conservation, restoration, and management decisions, where priorities must be set for limited resources (Beck et al. 2001). However, under some scenarios this definition excludes habitats that may be critical to sustaining adult populations. Moreover, despite their high per-unit-area contributions, some high quality but small habitats that meet the nursery habitat definition may actually contribute little to supporting adult populations. Here we expand on the Beck et al. (2001) nursery concept to provide a broader framework for evaluating juvenile habitats, with the goal of improving the ability of researchers and managers to identify and evaluate all habitats that are critical to sustaining populations of target species.

BUILDING ON THE NURSERY CONCEPT

Following the Beck et al. (2001) definition, only habitats that contribute the greatest number of individuals to the adult population on a per-unit-area basis are considered nurseries, regardless of the overall contribution that a juvenile habitat makes to the adult population. Habitats contributing fewer individuals per-unit-area, but perhaps contributing a majority of individuals to the adult population, are not considered nurseries. Consider a simple case where juveniles use 2 habitats, one of which covers 90 % of a particular system and contributes 85 % of the juveniles that enter the adult population, and one which comprises 10 % of the system and contributes 15 % of juveniles entering the adult population. In this case the second habitat would be classified as nursery habitat (per-unit-area contribution = 1.5) but not the first (per-unit-area contribution = 0.94), even though the first habitat contributes more than 5 times as many individuals to the adult population.

While the larger habitat in the preceding example falls outside the Beck et al. (2001) definition of a nursery, it is clearly important to maintaining the adult population. Such larger-area habitats that fall outside the nursery habitat definition, but contribute significantly to the adult population, must be considered of equal, or even greater, importance for supporting viable populations (necessary for sustainability of the species) than smaller habitats that meet the nursery criteria. Nonetheless, there is no terminology or conceptual framework for describing habitats making the greatest contribution to the adult population, or for assessing the relative importance of habitats based on their overall contribution to the adult population. Thus, such habitats are at risk of being classified as juvenile habitats of low importance by researchers and marine resource managers.

We propose the term Effective Juvenile Habitat (EJH) to describe juvenile habitats that, in terms of their overall contribution, are most important for maintaining adult populations. We define an EJH as a habitat for a particular species that contributes a greater proportion of individuals to the adult population than the mean level contributed by all habitats used by juveniles, regardless of area coverage. This definition is similar to that of nursery habitat used by Beck et al. (2001) with the key difference being that, for EJH, the contribution of individuals from juvenile habitats to the adult population is based on comparisons of the *overall* contribution that the habitat makes rather than the per-unit-area comparisons required for nursery habitats. Importantly, because comparisons are not being made on a per-unit-area basis, the areal coverages of habitats are not considered (nor need to be known) in the EJH classification scheme.

Evaluations of the importance of juvenile habitats using the 2 classification schemes can result in considerable differences. Consider a hypothetical situation in which a nearshore marine system encompasses 7 general habitats used by juveniles of a particular species (Table 1). Research and habitat mapping provide estimates of the habitat-specific contribution of juveniles to the adult population of a particular species, as well as the area that each habitat type comprises (expressed as a percentage of the cumulative area of the 7 habitats). In this example, 3 habitats meet the criteria of nursery habitats and 3 are classified as EJH, while only patch reefs are classified as both EJH and nursery habitat. Because algae and artificial habitat each only represent 1% of the total area, their per-unit-area contribution to the adult population is above average (4.3% contribution/area), making them nursery habitats. However, algae and artificial habitats contribute only 10 and 5% of individuals to the adult population, respectively, and thus fail to meet the criteria of EJH (at least 14.3% contribution required in this example). In contrast, the overall contribution of seagrass and mangroves is above average (30 and 20%, respectively), in spite of their relatively low contribution on a per-unit-area basis, because they cover large areas. Thus, both seagrass and mangroves are EJH, but not nursery habitats. Management focused on protecting nursery habitats in this hypothetical example would result in protecting only 45% of the juvenile contribution to adult populations, whereas protecting all effective juvenile habitats would result in protection of 80% of the juvenile contribution to adult populations.

Empirical studies have shown similar results. For example, Kraus & Secor (2005) examined a simple 2-habitat system and measured the contribution that freshwater (3.3 km^2) and brackish (34.1 km^2) habitats made to *Morone americana* adult populations in the Patuxent River estuary (Maryland, USA) for normal year classes (8 yr total), for year classes that are dominant in the population (3 highest yr), and for all year classes examined pooled together. Their data showed that the total contribution of brackish habitats greatly exceeds that of freshwater habitats under all circumstances (Table 2). Brackish habitats were also nursery habitats for dominant year classes. For normal year classes, however, freshwater rather than brackish habitats are considered nursery habitats, despite only contributing <15% of adults during those years. Clearly brackish habitats make the greatest contribution to sustaining adult populations, but would not be considered a nursery habitat during most years.

APPLICATION OF THE NURSERY AND EJH CONCEPTS

While assessments of EJH can use approaches similar to those used for assessing nursery habitats (Beck et al. 2001), a major advantage of the EJH classification

Table 1. Hypothetical example showing the difference between habitats classified as Effective Juvenile Habitat (EJH) and Nursery Habitat (NH; following the definition of Beck et al. 2001). EJH is determined from the overall contribution of each habitat. NH is calculated by dividing the overall contribution of each habitat by the area that the habitat comprises (on a measured area or percentage basis). EJH determines if the contribution of a habitat is greater than the average contribution of all habitats (14.3%); NH determines if contribution/area for a habitat is greater than the average contribution/area for all habitats (4.3)

Habitat	Contribution (%)	EJH	Area (% or km^2)	Contribution $area^{-1}$	NH
Sand	3.0	NO	40.0	<0.1	NO
Seagrass	30.0	YES	30.0	1.0	NO
Hardbottom	2.0	NO	20.0	0.1	NO
Mangrove	20.0	YES	5.0	4.0	NO
Patch reef	30.0	YES	3.0	10.0	YES
Algae	10.0	NO	1.0	10.0	YES
Artificial	5.0	NO	1.0	5.0	YES
Total	100.0		100.0	30.2	
Mean	14.3		14.3	4.3	

Table 2. Comparison of EJH and NH classification for the contribution of *Morone americana* from 2 juvenile habitat types to the adult population in the Patuxent River estuary, Maryland, USA (Kraus & Secor 2005). Data are presented for normal year classes, dominant year classes and for all year classes pooled together. Since this is a 2-habitat system, EJH classification requires a habitat to contribute greater than 50% of the adult population and NH is assigned to the habitat with a greater per-unit-area contribution

Habitat	Contribution (%)	EJH	Area (% or km^2)	Contribution $area^{-1}$	NH
Normal year classes					
Fresh	14.8	NO	3.3	4.48	YES
Brackish	85.2	YES	34.1	2.50	NO
Dominant year classes					
Fresh	7.4	NO	3.3	2.24	NO
Brackish	92.6	YES	34.1	2.72	YES
Pooled year classes					
Fresh	3.7	NO	3.3	1.12	NO
Brackish	96.3	YES	34.1	2.82	YES

scheme is that the area of each juvenile habitat does not need to be measured when the contribution of each habitat to adult populations is assessed directly. As Beck et al. (2001, 2003) and others (e.g. Gillanders et al. 2003, Adams et al. in press) assert, the most effective means of assessing the juvenile contribution of a habitat is to directly measure the movement of individuals from juvenile habitats to the adult population. The use of natural or artificial markers, which are unique to different juvenile habitats and are preserved as animals move to adult habitats, allows researchers to sample the adult population and identify the habitat type or area from which individuals originated (e.g. Gillanders & Kingsford 1996, Yamashita et al. 2000, Gillanders 2002, Chittaro et al. 2004, Kraus & Secor 2005; see review by Gillanders et al. 2003 for additional references). While this approach has been used to identify 'nurseries', the overall contribution to the adult population for each juvenile habitat is actually being measured and compared, so this approach provides a direct measure of EJH. Thus, using natural and artificial markers within the EJH approach allows a direct test of the null hypothesis that all habitats contribute equally to adult populations and will provide the ability to determine which habitats contribute more or less to the adult population. In contrast, using natural or artificial markers to identify the nursery value of juvenile habitats requires additional mapping of habitats to determine their area before calculating the per-unit-area contributions of juveniles that each habitat makes to the adult population. For many areas, particularly in developing countries, the additional effort of mapping habitats on relevant spatial scales may not be feasible due to the large amount of resources required. In such cases, the EJH evaluation not only provides an effective measure of the relative contribution of each juvenile habitat to adult populations, but also has the advantage of being easier to calculate than the nursery value of a habitat.

As caveats, both the nursery classification proposed by Beck et al. (2001) and the EJH classification presented here are based on comparisons of habitat-specific values to an 'average of all habitats' value. In such cases, the 'average of all habitats' value will be a function of the number and type of habitats considered in the analysis. Thus, researchers and managers must carefully consider what habitats to include before proceeding with analysis, as the inclusion, exclusion, or sub-categorization of habitats (e.g. seagrass as 1 habitat vs. seagrass species A, B, and C as separate habitats) has the potential to affect the 'average of all habitats' value, and thus whether or not habitats are classified as EJH or nurseries. Additionally, it is important that, as with nursery habitats, habitat-specific contributions to adult populations for defining EJH are averaged over time (i.e. multiple years), so temporal variation in settlement, and coinciding differences in habitat use, are incorporated (Adams & Ebersole 2004, Kraus & Secor 2005).

In conclusion, we believe that the Beck et al. (2001) nursery definition and framework is a powerful approach for identifying high quality habitats for conservation, restoration and management. Because the nursery framework is aimed at identifying high quality areas, it is particularly important for prioritizing spatially explicit management (e.g. establishment of marine protected areas) or restoration, when costs or other factors limit the amount of area that can be protected. Nevertheless, because marine resource managers must ensure that adult populations are sustainable, there is a need for a framework that identifies the most important habitats for supporting adult populations. Like the nursery framework, EJH will facilitate the identification of habitats for conservation, restoration, and management, but identification of EJH will be particularly important to focus marine resource management (e.g. habitat protection and protecting juveniles from threats, such as capture as bycatch or water quality issues) on the areas that are most critical to the maintenance of target populations. Moreover, EJH can be more easily defined under data and funding constraints typically facing managers (e.g. lack of habitat mapping data or funds to acquire them). Thus, incorporating EJH into habitat assessments and management strategies will improve our ability to manage and conserve nearshore systems critical for supporting fisheries and providing other ecosystem services.

Acknowledgements. This manuscript arose from discussions associated with the Backreef II Workshop held on Lee Stocking Island, Bahamas, in January 2005 and sponsored by NOAA Fisheries and the Perry Institute for Marine Science. Funding for manuscript preparation was provided by Mote Scientific Foundation (A.J.A.), National Fish and Wildlife Foundation and NSF OCE-0119976 (C.P.D.), an ARC QEII Fellowship (B.M.G.), and a Vidi grant from the Netherlands Organisation for Scientific Research (I.N.). M. Beck and K. Heck and 4 anonymous reviewers provided helpful comments that improved the paper.

LITERATURE CITED

Adams AJ, Ebersole JP (2002) Use of back-reef and lagoon habitats by coral reef fishes. Mar Ecol Prog Ser 228: 213–226

Adams AJ, Ebersole JP (2004) Processes influencing recruitment inferred from distributions of coral reef fishes. Bull Mar Sci 75:153–174

Adams AJ, Dahlgren CP, Kellison GT, Kendall MS, Layman CA, Ley JA, Nagelkerken I, Serafy JE (in press) The juvenile contribution function of tropical backreef systems. Mar Ecol Prog Ser

Appeldoorn RS, Recksiek CW, Hill RL, Pagan FE, Dennis GD (1997) Marine protected areas and reef fish movements: the role of habitat in controlling ontogenetic migration. Proc 8th Int Coral Reef Symp 2:1917–1922

Beck MW, Heck KL Jr, Able KW, Childers DL and 9 others (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. BioScience 51:633–641

Beck MW, Heck KL Jr, Able KW, Childers DL and 9 others (2003) The role of nearshore ecosystems as fish and shellfish nurseries. Issues Ecol 11:1–12

Blaber SJM, Brewer DT, Salini JP (1989) Species composition and biomasses of fishes in different habitats of a tropical northern Australian estuary: their occurrence in the adjoining sea and estuarine dependence. Estuar Coast Shelf Sci 29:509–531

Chittaro PM, Fryer BJ, Sale PF (2004) Discrimination of French grunts (*Haemulon flavolineatum*, Desmarest, 1823) from mangrove and coral reef habitats using otolith microchemistry. J Exp Mar Biol Ecol 308:169–183

Cocheret de la Morinière E, Pollux BJA, Nagelkerken I, van der Velde G (2002) Post-settlement life cycle migration patterns and habitat preference of coral reef fish that use seagrass and mangrove habitats as nurseries. Estuar Coast Shelf Sci 55:309–321

Gillanders BM (2002) Connectivity between juvenile and adult fish populations: do adults remain near their recruitment estuaries? Mar Ecol Prog Ser 240:215–223

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. Mar Ecol Prog Ser 141:13–20

Gillanders BM, Able KW, Brown JA, Eggleston DB, Sheridan PF (2003) Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. Mar Ecol Prog Ser 247:281–295

Gunter G (1967) Some relationships of estuaries to the fisheries of the Gulf of Mexico. In: Lauff GH (ed) Estuaries. American Association for the Advancement of Science, Washington, DC, p 621–638

Heck KL, Hays G, Orth RJ (2003) Critical evaluation of the nursery role hypothesis for seagrass meadows. Mar Ecol Prog Ser 253:123–136

Kraus RT, Secor DH (2005) Application of the nursery-role hypothesis to an estuarine fish. Mar Ecol Prog Ser 291: 301–305

Lenanton RCJ (1982) Alternative non-estuarine nursery habitats for some commercially and recreationally important fish species of south-western Australia. Aust J Mar Freshw Res 33:881–900

Nagelkerken I, Dorenbosch M, Verberk WCEP, Cocheret de la Morinière E, van der Velde G (2000a) Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. Mar Ecol Prog Ser 194:55–64

Nagelkerken I, Dorenbosch M, Verberk WCEP, Cocheret de la Morinière E, van der Velde G (2000b) Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns in biotope association, community structure and spatial distribution. Mar Ecol Prog Ser 202:175–192

Nagelkerken I, van der Velde G, Gorissen MW, Meijer GJ, van't Hof T, den Hartog C (2000c) Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. Estuar Coast Shelf Sci 51:31–44

Orth RJ, Heck KL, 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

Sheridan P, Hays C (2003) Are mangroves nursery habitat for transient fishes and decapods? Wetlands 23:449–458

Shulman MJ (1985) Recruitment of coral reef fishes: effects of distribution of predators and shelter. Ecology 66: 1056–1066

Yamashita Y, Otake T, Yamada H (2000) Relative contributions from exposed inshore and estuarine nursery grounds to the recruitment of stone flounder, *Platichthys bicoloratus*, estimated using otolith Sr:Ca ratios. Fish Oceanogr 9:316–327

Editorial responsibility: Otto Kinne (Editor-in-Chief), Oldendorf/Luhe, Germany

Submitted: May 9, 2005; Accepted: October 6, 2005
Proofs received from author(s): March 16, 2006