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REVIEW

Are coastal habitats important nurseries? A meta-analysis

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Abstract

Nearshore-structured habitats—including underwater grasses, mangroves, coral, and other biogenic reefs, marshes, and complex abiotic substrates—have long been postulated to function as important nurseries for juvenile fishes and invertebrates. Here, we review the evolution of the "nursery habitat hypothesis" and use >11,000 comparisons from 160 peer-reviewed studies to test whether and which structured habitats increase juvenile density, growth, and survival. In general, almost all structured habitats significantly enhanced juvenile density—and in some cases growth and survival—relative to unstructured habitats. Underwater grasses and mangroves also promoted juvenile density and growth beyond what was observed in other structured habitats. These conclusions were robust to variation among studies, although there were significant differences with latitude and among some phyla. Our results confirm the basic nursery function of certain structured habitats, which lends further support to their conservation, restoration, and management at a time when our coastal environments are becoming increasingly impacted. They also reveal a dearth of evidence from many other systems (e.g., kelp forests) and for responses other than density. Although recent studies have advocated for increasingly complex approaches to evaluating nurseries, we recommend a renewed emphasis on more straightforward assessments of juvenile growth, survival, reproduction, and recruitment.

KEYWORDS
coral reef, density, growth, juvenile, mangrove, marsh, seagrass, survival

1 | INTRODUCTION

A defining feature of all shallow waters of coastal and estuarine regions throughout the world is the presence of one or more structured habitats. These habitats range from foundational autotrophs (seagrasses, mangroves, marshes, other submersed vegetation—including tidal freshwater plants— and macroalgae/kelps) to coral reefs and other animal-derived structures (oysters, mussels, sponges) to abiotic substrates

(rock crevices, shell hash, cobble). They are considered "structured" because they have complex three-dimensional shapes that protrude above the benthos compared to unstructured habitats, such as sand and mud, which provide only a relatively flat, two-dimensional surface. Structured habitats are economically and ecologically important to the regions they occupy: they directly or indirectly provide a variety of ecosystem services including carbon sequestration, shoreline protection, nutrient cycling, food products,

disease prevention, and recreation (Barbier et al., 2011; Costanza et al., 1997). Perhaps the most cited function of all is as a nursery in which juveniles of numerous species of vertebrates and invertebrates can grow and mature before migrating elsewhere as adults.

The formal conceptualization of a nursery habitat was first proposed by Beck et al. (2001) who clarified that a habitat should be considered a nursery for juveniles if their density, growth, survival, and/or movement to adult habitats is, on average, greater than in other habitats. A series of quantitative meta-analyses testing this new definition quickly followed for seagrasses (Heck, Hays, & Orth, 2003), salt marshes (Minello, Able, Weinstein, & Hays, 2003), and mangroves (Sheridan & Hays 2003). These showed that juvenile density, growth, and survival were indeed higher in structured habitats than unstructured ones, particularly seagrasses. At the time, there were few tests of recruitment to adult populations, but a contemporaneous review of juvenile dispersal potential suggested that this process is highly variable, with juveniles moving anywhere from 10^{-1} to 10^6 m to reach their adult habitats (Gillanders, Able, Brown, Eggleston, & Sheridan, 2003). More critically, the study by Gillanders et al. (2003) reinforced the idea that, while juvenile and adult habitats can and often do overlap, nurseries should reflect only a subset of potential adult habitats. In other words, a habitat cannot be considered a nursery if a species utilizes it exclusively throughout their entire life history: in this case, the "nursery" would simply be known as its habitat (Beck et al., 2001).

With emerging information on the complex life history strategies of certain species and the multiple interactions that occur during their ontogenetic development to their adult phase, it became clear that the original definition of Beck et al. (2001) required additional nuance. Dahlgren et al. (2006) argued that earlier work ignored habitats that may contribute relatively fewer individuals to the adult population, but are nonetheless critical to maintaining the population, particularly in years of high variability in juvenile recruitment (Kraus & Secor 2005). Dahlgren et al. (2006) thus proposed the "effective juvenile habitat" (EJH), which recognizes the absolute value of certain habitats regardless of their per unit area contributions. A reply by Sheaves, Baker, and Johnston (2006), however, cautioned that the EJH approach was also too simplistic and, like Beck et al. (2001), did not consider the effects of scale, complexity, connectivity, resource availability, and other biotic and abiotic processes occurring within and between habitats, and further did not address reproductive output other than total number of adult recruits. Fodrie, Levin, and Lucas (2009) likewise stressed population growth as a more representative metric of the nursery function of certain habitats.

A penultimate review by Sheaves (2009) formalized the idea that multiple habitats, with all their inherent processes, tightly link to form the "coastal ecosystem mosaic," and this mosaic more than any particular habitat is critical to maintaining the overall nursery function of coastal areas. Multiple habitats, he argued, are necessary to accommodate the varied life histories of organisms, from larva to adult, as well as food web dynamics, differing resources, and abiotic forcing, all of which are central to the growth, survival, and eventual recruitment of juveniles. This idea finally led to the marriage of the principles of the nursery function to landscape ecology to produce the concept of the "seascape nursery" (Boström, Pittman, Simenstad, & Kneib, 2011; Litvin, Weinstein, Sheaves, & Nagelkerken, 2018; Nagelkerken, Sheaves, Baker, & Connolly, 2015). This modern view considers all stages of the life history of an individual, including transient settlement in formerly unrecognized habitats, ascribing each to "hotspots" and establishing migration corridors that connect juvenile and adult populations.

The evolution of this nursery habitat hypothesis, as originally defined by Beck et al. (2001), has occurred rapidly and stimulated considerable reflection and refinement on what constitutes a nursery. At the same time, researchers have been empirically testing this hypothesis both in the field and laboratory. Two synthetic analyses have updated the earlier suite of quantitative reviews (Heck et al., 2003; Minello et al., 2003; Sheridan & Hays 2003) to include more recent studies. First, Igulu et al. (2014) summarized 14 studies testing the use of mangroves, seagrasses, and coral reefs by juvenile fishes, showing that while structured habitats supported higher densities of fauna than coral reefs, abiotic properties such as tidal amplitude and salinity played a much larger role than habitat per se in defining juvenile properties. McDevitt-Irwin, Iacarella, and Baum (2016) analyzed 51 papers focusing only on seagrasses and showed that—like Heck et al. (2003) before—seagrass habitat supported higher densities and increased growth of juveniles relative to bare sediment or other structured habitats. Moreover, these effects were stronger in temperate than in subtropical regions, and more important for invertebrates than for fishes.

Despite the considerable conceptual advances made to the nursery habitat hypothesis over the past two decades—and substantial effort by many state, federal and international organizations to protect and restore many of these important structured habitats in part on the basis of their nursery function—most empirical tests have reported on the three juvenile attributes originally proposed by Beck et al. (2001): density, growth, and survival. With repeated calls for scaling-up to seascape-level investigations, we find it valuable to first assess the current body of evidence that has accumulated since Beck et al. (2001) to see whether their original and simpler definition has been satisfactorily addressed. To that end, we conducted a search of the peer-reviewed literature and identified 160 studies on the role of structured habitats in promoting juvenile performance. We then applied formal meta-analysis to provide the most comprehensive test of the

nursery habitat hypothesis to date. Our goals were to assess the strength of evidence for coastal habitats as nurseries based on all available data, and to determine the degree to which empirical tests have or have not kept up with the evolution of the nursery concept in the past several decades.

2 | METHODS

We adhered to the PRISMA standard for meta-analysis reporting (Moher et al., 2009). A flowchart of the evaluation process and PRISMA checklist are available in the Supporting Information. We performed a Google Scholar search on October 3, 2016, using the following search string:

> *(nurser* OR "habitat complex*" OR EJH OR "effective juvenile habitat" OR "structural* complex*") AND (marine OR estuar* OR coast* OR nearshore OR seascape OR seagrass* OR SAV OR mangrove* OR marsh* OR saltmarsh* OR wetland* OR reef* OR macroalga* OR kelp* OR macrophyte* OR lagoon* OR brackish) AND (juvenile* OR recruit* OR post-larva* OR post-settle* OR sub-adult* OR young OR YOY OR anadromous OR age-0 OR natal OR pup OR fry OR fingerling OR smelt) AND (growth OR surviv* OR recruit* OR densit* OR abundance* OR product* OR movement OR connect* OR emigrat* OR migrat*)*

The initial search returned 2,607 abstracts from peer-reviewed journals. We conducted an additional forward search on Beck et al. (2001), which yielded 527 additional unique abstracts. We also added 50 unique abstracts from two recent reviews (McDevitt-Irwin et al., 2016; Nagelkerken, 2009;) for a total of 3,184 abstracts.

To be included in our analysis, a study must have: (a) tested the role of structure relative to an unstructured control or other structured habitat (i.e., the study had to be comparative); (b) identified at least one habitat as a potential "nursery"; (c) not included artificial habitats (e.g., bulkheads, shipwrecks); (d) explicitly stated that at least one of the organisms considered were juveniles; and (e) reported a quantitative measure of performance such as density, growth, etc. If both juvenile and adults were censused, we chose only responses pertaining to juveniles. If studies reported aggregate measures (e.g., total community abundance) but did not discriminate among juveniles and adults, we excluded them from our analysis.

Assessment was conducted by two separate evaluators: if both agreed, the study was retained for further consideration; if both disagreed, the study was rejected; and if there was no consensus, the study was reviewed in committee until a decision was reached. Of the 3,184 initial abstracts, 2,900

were rejected for not meeting our initial criteria based on content in the abstract. We then obtained copies of the 284 remaining references and conducted a second round of evaluation based on the content of the entire paper, of which 123 were deemed unsuitable (Table S1). Our final list for data extraction included 160 references from the peer-reviewed literature.

Means/sums/proportions, sample sizes, and standard deviations (when reported) were extracted from text, figures, or tables presented in the main text or Supporting Information. For graphical presentations, we used the Measure Tool in Adobe PDF Reader (Adobe Systems, Inc.) to estimate the data points. We also collected metadata on the location, experimental design, abiotic environment (e.g., salinity regime), habitat type and their characteristics, response type and units, and characteristics of the response organisms (e.g., taxonomy, trophic group), when reported.

To analyze the response data, we used the log response ratio, hereafter *LRR* (Hedges, Gurevitch, & Curtis, 1999). The *LRR* is computed as follows:

$$LRR = \ln\left(\frac{\overline{X_T}}{\overline{X_C}}\right), \tag{1}$$

where $\overline{X_T}$ is the mean value of a response in one habitat and $\overline{X_C}$ is the mean of the same response in the comparison habitat. These comparisons were only conducted within the same species, in the same treatment, in the same study. Unlike other estimates of effect size, the *LRR* does not require information about the variance of the observations. As we encountered many situations in which variance was not reported or was not estimable (e.g., survival, total density), the *LRR* is the only meta-analytical metric that can harness the full power of our dataset. However, to test the robustness of our conclusions to our choice of metric, we computed several additional effect sizes that do incorporate sampling variance into their calculations: Hedges' *d* (Hedges & Olkin 1985) and bias-adjusted LRR^Δ and LRR^Σ (Lajeunesse, 2015; see Supporting Information).

We conducted two analyses of the raw data: in the first, we focused only on structured versus unstructured habitats (e.g., submersed aquatic vegetation [SAV] vs. bare sand). In the second, we compared structured against other structured habitats (e.g., SAV vs. mangroves). In both cases, we computed the mean $\overline{LRR}$ for each response category (density, growth, and survival) as the average of individual *LRR*s $\pm$ 1 standard error of the mean. We also computed the inverse variance-weighted and sample size weighted *LRR*s (when reported) to assess how the precision of each study influenced our overall conclusions (Hedges et al., 1999). Finally, we performed several tests of bias and sensitivity (see Supporting Information).

We used a modeling approach to identify the important predictors of the structured versus unstructured *LRR*s. For each

response category (density, growth, survival), we fit a general linear mixed effects model using the *nlme* package (Pinheiro, Bates, DebRoy, & Sarkar, 2017) in R version 3.5.0 (R Core Team 2017) including the following fixed effects:

$$LRR_{ij} \sim \alpha_{ij} + \text{Habitat} + \text{Salinity Regime} + \text{Latitude}$$
$$+ \text{Trophic Level} + \text{Lab or Field} + \varepsilon_{ij}, \quad (2)$$

where LRR_{ij} is the ith observation in the jth study. We also allowed the intercept α to vary randomly by study j to account for any variation arising from being within a particular study:

$$\alpha_j \sim \alpha_0 + b_0 u_j + \eta_j. \quad (3)$$

For the model of density LRRs, we included the additional fixed effect of phylum, which could not be fit for the other responses due to model convergence errors arising from lack of representation in certain phyla. We obtained and plotted the model-estimated partial means for each level of each covariate using the *effects* package (Fox, 2003).

3 | RESULTS

Our final dataset included 160 studies spanning the years 1986–2016 and 11,236 total comparisons for the final analysis. Studies were distributed among six continents but concentrated in North America and Europe (Figures 1A and S1). Studies overwhelmingly reported on juvenile density (e.g., abundance, biomass, etc. per unit area), although a smaller number reported on growth and survival (Figure 1B). No studies reporting on recruitment met our criteria for inclusion, despite being one of the original response variables identified by Beck et al. (2001). Almost all studies reported on data from an unstructured control, and most studies also included SAV (including marine and freshwater grasses) as a structured comparison (Figure 1C). Mangroves, coral reefs, marshes, macroalgae (including both drift and turf), and other biogenic reefs (including oysters, mussels, and sponges) were also represented, while abiotic habitats (such as rubble and shell) and kelp forests (distinguished from macroalgae by the original authors) reported the fewest tests (Figure 1C). Studies considered largely carnivores and omnivores, with a fewer number of studies considering exclusively herbivores or mixed assemblages (Figure 1C). Taxonomically, ray-finned fishes were overwhelmingly represented (85% of all measurements), with fewer values reported for crustaceans (14%), gastropods (1%), and sharks and rays (<1%).

Compared to unstructured habitats, juvenile density was enhanced by the presence of SAV, mangroves, coral reefs, other biogenic reefs, and rubble or shell hash, with macroal-

gae having no effect and kelp being slightly worse than the unstructured habitat (Figure 2). SAV also enhanced growth and survival, whereas most other structured habitats revealed no significant effect (Figure 2). Exceptions included rubble, shell, and rock, which significantly enhanced growth, and macroalgae, and biogenic reefs, which additionally enhanced survival (Figure 2). We note that the values for many habitats, including biogenic reefs, kelps, and abiotic substrates, reflect averages over only 3–10 independent studies, and thus should be interpreted with caution relative to better represented habitats such as SAV. Regardless of sample size, however, within-study variance tended to be consistent and low across studies (Figure S2).

When we repeated our analysis using Hedges' d as our effect size, we observed equivalent or stronger effects: all habitats, for example, significantly enhanced juvenile density, and most enhanced growth and survival (Figure S3). We note, however, that these averages were derived from the 54% of studies that reported sample variances, which may explain deviations from the larger analysis (Figure 2). Similarly, weighting the LRR by the inverse of the variance or sample size (Figures S4 and S5), and adjusting the LRR for additional sampling bias using the methods in Lajeunesse (2015; Figures S6 and S7), revealed nearly identical trends to the main analysis. Thus, for the studies reporting variances, there appeared to be no systematic bias introduced by low precision or low replication relative to the entire dataset.

Although SAV consistently and generally enhanced density, growth, and survival relative to an unstructured control, it was generally inferior to mangroves (Figure 3). However, SAV did enhance juvenile densities beyond those observed in coral reef, marsh, and macroalgal habitats (Figure 3). In turn, coral reefs also significantly increased juvenile density relative to macroalgae. There was little difference among the habitats in effects on growth or survival, except for coral reefs, which had somewhat greater juvenile growth compared to SAV, mangroves, or macroalgae (Figure 3). Due to low sample sizes, comparisons to other structured habitats were omitted (e.g., rubble, rock). Nearly identical trends were observed for Hedges' d and variants of the LRR (Figures S8–S10), with the exception of macroalgae being slightly better than coral reefs for juvenile density.

The modeling results revealed few significant predictors for the LRR of structure versus no structure for any of the response categories (Table 1). The major exception was habitat, for which we have already described the major differences (Figure 2). One of the few other significant predictors was a positive relationship between latitude and juvenile density, with a stronger effect of structured habitats at higher latitudes (Figure 4). Similarly, there were slightly higher benefits of structured habitats for arthropod invertebrates than for vertebrates, primarily Actinopterygian fishes (Figure 5). Otherwise, there was remarkable consistency in the expected
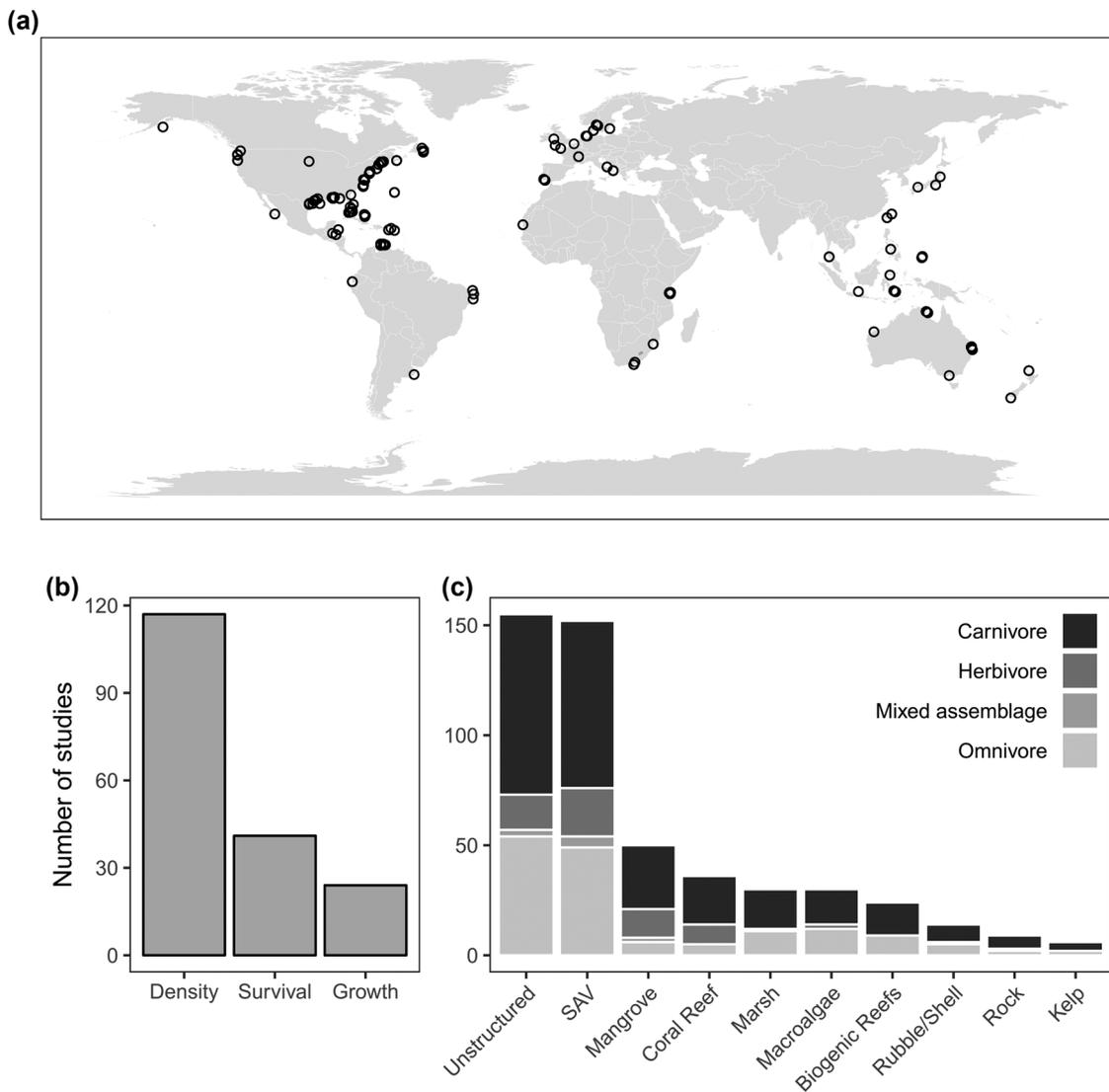
(a)

(b)

(c)

FIGURE 1 (a) Geographic distribution of 160 studies used in the final meta-analysis. (b) The number of studies reporting on each of the three juvenile attributes (density, growth, and survival). (c) The number of studies reporting on different habitats, and the trophic composition within each habitat

effect sizes by trophic level, salinity regime, and whether studies were conducted in the laboratory or field (Table 1 and Figure 5).

4 | DISCUSSION

In our meta-analysis of 160 published articles, we found substantial evidence for the role of structured habitats in enhancing the density, growth, and survival of juvenile fishes and invertebrates. There were, however, differences among habitats in both magnitude of the effect size and degree of support. SAV (including marine and freshwater grasses), for example, had 3× more tests than the next most studied habitat (Figure 1) . Consequently, studies incorporating SAV yielded unequivocal support for the role of this habitat in

increasing all three responses variables relative to unstructured habitats (Figures 2 and S3–S7). When compared to other structured habitats, SAV was superior to all habitats other than mangroves (Figures 3 and S8–S10). Thus, based on available evidence, SAV and mangroves appear to confer the greatest nursery benefits, a result that is consistent with several prior syntheses (Heck et al., 2003; Igulu et al., 2014; McDevitt-Irwin et al., 2016).

The next most important structured habitat after SAV and mangroves was coral reefs (Figures 2 and 3). Historically, coral reefs have been ignored as potential nurseries: neither the Beck et al. (2001) paper nor any of the early synthesis efforts considered coral reefs, presumably because, for most fishes, the reef also functions as the final adult habitat. Yet, a handful of studies around the same time showed that shallow coral reefs supported equivalent or higher juvenile
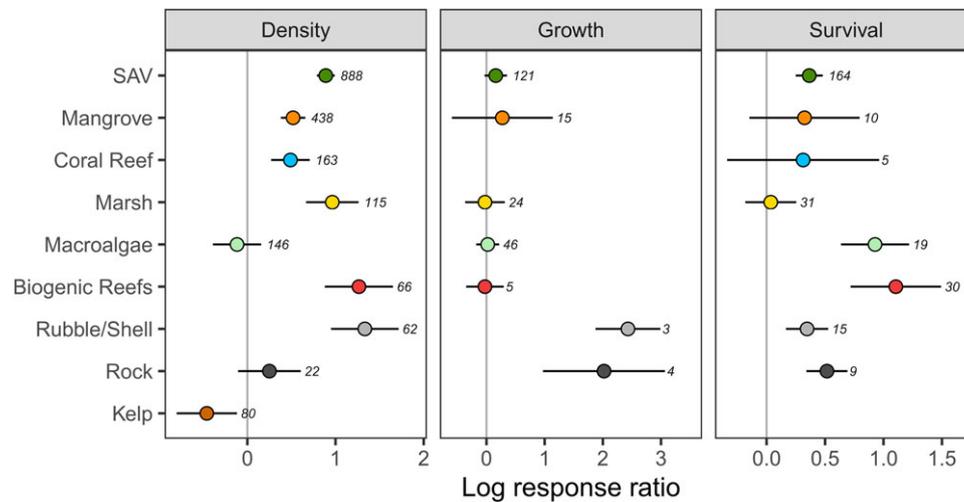
FIGURE 2 Log response ratios (*LRR*s) comparing each structured habitat (y-axis) to the unstructured control (e.g., bare sediment). Values are grand means ±95% confidence intervals. Values >0 indicate a positive effect of structure on density, growth, or survival, and values <0 indicate a negative effect of structure on those properties. The number of comparisons is given next to each point

TABLE 1 Analysis of variance (ANOVA) results from general linear mixed effects models predicting the log response ratio of structured versus unstructured habitats

Response	Predictor	Num. *df*	Denom. *df*	*F*-value	*p*-Value
Density	Intercept	1	1,863	58.951	<.001***
Density	Structured habitat	8	1,863	16.717	<.001***
Density	Salinity	2	1,863	0.686	.504
Density	Latitude	1	1,863	8.059	.005**
Density	Trophic level	2	1,863	0.791	.454
Density	Phylum	2	1,863	3.392	.034*
Density	Lab/field	1	1,863	0.111	.739
Growth	Intercept	1	189	4.420	.037*
Growth	Structured habitat	6	189	4.622	<.001***
Growth	Salinity	1	189	1.986	.160
Growth	Latitude	1	189	0.677	.412
Growth	Trophic level	2	17	1.160	.337
Growth	Lab/field	1	189	0.022	.883
Survival	Intercept	1	241	24.166	<.001***
Survival	Structured habitat	7	241	1.323	.240
Survival	Salinity	2	28	0.049	.952
Survival	Latitude	1	28	0.140	.711
Survival	Trophic level	2	28	0.134	.875
Survival	Lab/field	1	28	0.020	.888

Significant predictors are indicated with asterisks ($^*.05 > p \geq .01$;$^{**}.01 > p \geq .001$;$^{***}p < .001$).

densities than other habitats such as SAV and mangroves (Nagelkerken et al., 2000, 2002). Several later studies also supported this assertion (Dorenbosch et al., 2004; Eggleston et al., 2004; Kimirei et al., 2011), even showing that density and growth was greater on coral reefs than in other structured habitats (Grol et al., 2008; Tupper, 2007). Such studies might otherwise be excluded under the definition of Beck

et al. (2001) due to reef also serving as the adult habitat, except that many fishes appear to partition their use of different subhabitats on the reef throughout their development. For example, several common reef fishes utilize the shallow back reef before migrating to the deeper fore reef as adults (Adams & Ebersole 2002; Nagelkerken et al., 2000).
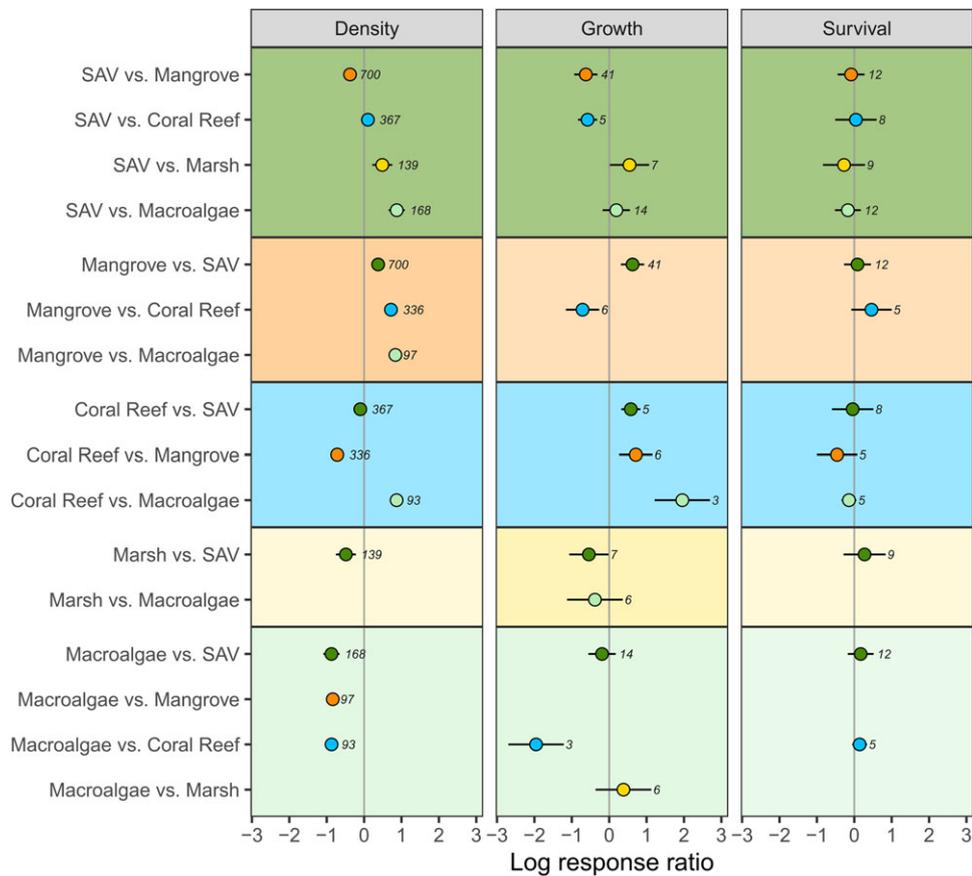
FIGURE 3 Log response ratios comparing each structured habitat to another structured habitat. Values are means ±95% confidence intervals. Values >0 indicate higher performance in the first habitat, while values <0 indicate higher performance in the second habitat. The number of comparisons is given next to each point
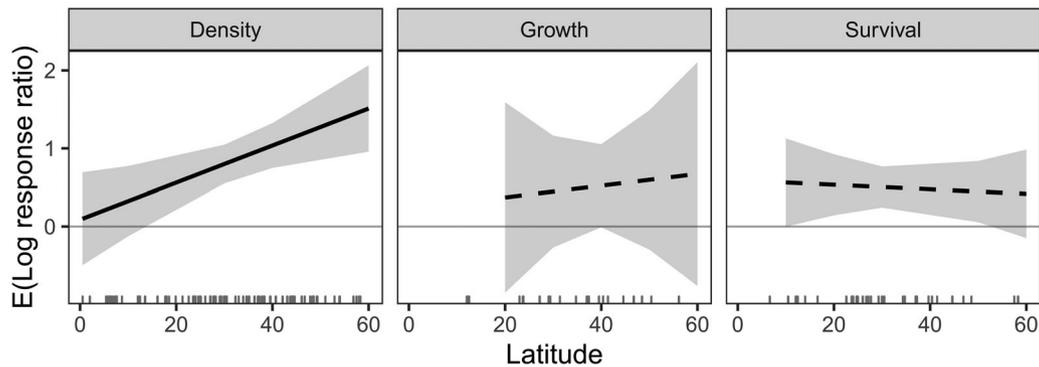

FIGURE 4 The model-estimated (expected) log response ratio as a function of latitude for each of the juvenile response categories. Estimates are (partial) predicted fits ±95% confidence intervals and account for the other covariates in the model. The significant fits are given in solid lines, while dashed lines reflect nonsignificant relationships ($p > .05$). Rug plots along the x-axis reflect the distribution of raw observations

This notion of "subhabitats" complicates the identification of coral reefs as a nursery per se, as a fine understanding of each species' ontogenetic habitat requirements is required. Indeed, many coral reef fishes have complex life cycles, such as those in the families Haemulidae, Lutjanidae, and Serranidae, which utilize different habitats throughout their juvenile development (e.g., seagrass → mangroves → coral reef)

or even different subhabitats within those habitats (e.g., coral or rubble embedded within seagrass beds; reviewed in Adams et al., 2006). Similar life histories are also present in other systems such as the ontogenic shift of bay scallops from the seagrass canopy to the benthos at a certain size (Thayer & Stuart 1974). Although our data support the notion that coral reefs can enhance juvenile densities, they were most often invoked
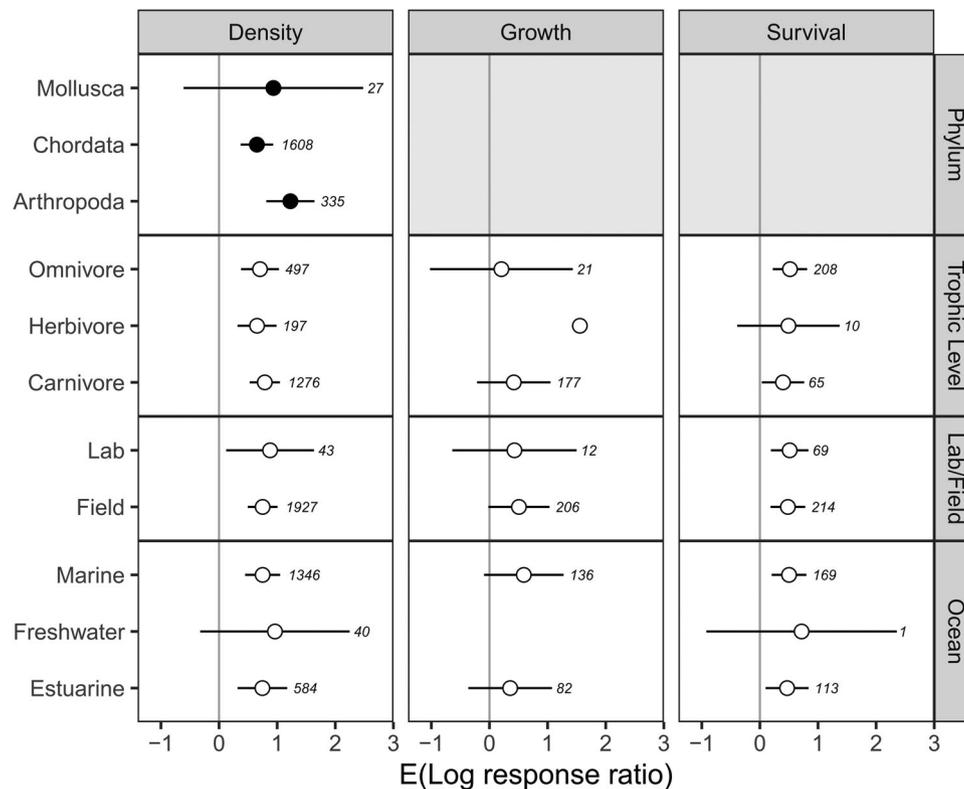
FIGURE 5 The model-estimated (expected) log response ratio as a function of various predictors for each of the juvenile response categories. Estimates are (partial) predicted means ±95% confidence intervals and account for the other covariates in the model. The significant ($p < .05$) covariates are filled in black. Sample sizes are given next to each point

as the "control" case to ensure that juvenile and adult densities were not conflated. On the other hand, coral reefs are among the most complex three-dimensional coastal habitats and thus should not be treated in the same way as sand and mud. Continued exploration of when and how coral reefs function as nurseries, with a particular focus on subhabitats, is a crucial frontier, and may prove analogous to differences observed in edge versus interior habitats (Boström, Jackson, & Simenstad, 2006).

Other coastal habitats, such as marshes, biogenic reefs, and rubble and shell hash, also appear important in our dataset, although they had many fewer tests than SAV or mangroves (Figures 2 and 3). The trends, however, are promising: biogenic reefs and shell/rubble had the strongest effect sizes relative to unstructured controls (Figures 2 and S3–S7), but reduced sample sizes precluded testing them relative to other habitats. Oyster reefs in particular were highlighted by Beck et al. (2001) for needing further research, and although it appears there has been some progress, many more tests are required to generate evidence on par with that of SAV beds. Macroalgae, which includes both upright seaweeds and turf-forming algae, appeared no better than bare substrate, perhaps owing to both high spatial and temporal variance in habitat complexity afforded by their different forms (especially drift macroalgae) and the relatively

low sample size. In some cases, macroalgae also reflected an undesirable or degraded state after eutrophication or climate shifts (Aburto-Oropeza, Sala, Paredes, Mendoza, & Ballesteros, 2007; Wennhage, 2002; Wennhage & Pihl 1994), or as an alternative habitat after the preferred habitat had been severely reduced, such as SAV in Chesapeake Bay (Johnston & Lipcius 2012).

Kelps, a subset of macroalgae, appeared to be the only habitat that was worse for juveniles than even bare substrate (Figure 2), although this inference is based on only four studies in the Gulf of Maine (Lazzari, 2008, 2013; Lazzari & Stone 2006; Lazzari, Sherman, & Kanwit, 2003). This result may reflect region-specific patterns in foundational species composition—these four studies consider only laminarian kelps—but also a community-level perspective that obscured responses by individual species. For example, the Atlantic cod *Gadus morhua* tended to have higher densities in kelps (Lazzari, 2013), but its signal was negated, on average, by a diversity of other species. Thus, kelps provide a critical reminder that species of particular commercial interest, such as cod, may require a less community-oriented perspective when evaluating their association with potential nurseries. Although previous work has also demonstrated the benefits of kelp for juvenile fishes (Anderson, 1994; Carr, 1989), these studies were not comparative (often focusing on differing

complexities within kelp habitat), and thus were not suitable for inclusion in our analysis. Future efforts in kelp forests should therefore adopt a comparative approach.

Beyond habitat differences, we found very little variation in the effect size of structured versus unstructured habitat as a function of trophic level, laboratory versus field studies, and salinity regime (Table 1). The two notable exceptions were effects of latitude and phyla on density, both of which have been observed previously. The increasing effect of structured habitats on juvenile density with increasing latitude was most recently reported in the meta-analysis by McDevitt-Irwin et al. (2016) in which they proposed the availability of alternative nurseries in tropical regions could explain the weaker effects of seagrass habitat. Removing SAV comparisons from the dataset yielded a nonsignificant effect of latitude ($p = .063$), indicating that this trend in our analysis was also driven primarily by SAV. An alternative but not mutually exclusive explanation might be the paradigm of decreasing predation with increasing latitude (Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009), which leads to higher juvenile survival and increased densities in temperate regions, as has been shown recently in a global comparative seagrass experiment (Reynolds et al., 2017).

Like McDevitt-Irwin et al. (2016) and Minello et al. (2003), we also found a stronger effect of habitat on some invertebrates (arthropods) than vertebrates (Actinopterygian fishes). They attributed these patterns to the greater availability of food resources for invertebrates in seagrass habitats. Invertebrates may also benefit from the vertical structure: higher habitats leave benthic invertebrates less exposed to predators. In our case, the simplest explanation may be mobility: invertebrates are less mobile, especially as they transition to their adult phase (Gillanders et al., 2003), and thus depend more on structure to both hide from predators and provide food. In contrast, juvenile fishes can forage more broadly within a habitat and move to other, more suitable habitats to avoid predation. Invertebrates were also 6× less represented than vertebrates in our dataset, which may have also contributed to the observed difference between the two.

There are undoubtedly many other factors that mediate the nursery function but could not be tested in our dataset. We relied on the authors of the original publications to supply information on such variables, but unfortunately these were not consistently reported enough to support rigorous analysis (see Supporting Information). A recent meta-analysis also suggested that abiotic conditions can greatly influence the nursery function of coastal habitats (Igulu et al., 2014), and other reviews of nurseries along the Northeast Pacific (Hughes et al., 2014) and Northeast Atlantic coasts (Brown et al., 2018) found that numerous human-induced stressors can pose a risk to the nursery function (Toft et al., 2018). To date, however, explicit examples of nursery impairment due to anthropogenic or other environmental factors are rare and should be considered as an important next step for nursery research.

Our study has several implications for conservation and management. First, of the 315 organisms identified to species in our dataset, 230 are considered commercially fished or farmed somewhere in the world according to Food and Agriculture Organization of the United Nations (http://www.fao.org/fishery/collection/asfis/en): 215 fishes, 14 crustaceans (mostly Penaeid shrimps), and 1 gastropod (the queen conch *Strombus gigas*). Although many species were undoubtedly targeted by the original authors specifically because they are of interest to fisheries, this statistic underlies the key role coastal systems play in supporting coastal economies. For example, a recent global analysis revealed that the nursery value of seagrass meadows may account for one fifth of the world's largest 25 fisheries (Unsworth, Nordlund, & Cullen-Unsworth, 2018). Moreover, five species in our dataset are considered "threatened" by the IUCN (http://www.iucnredlist.org/), four are "endangered," and one is listed as "critically endangered" (the European eel, *Anguilla anguilla*, in Polte & Asmus 2006). Although such organisms are, by definition, rare, their inclusion in 13 studies does suggest that nursery habitats can sometimes serve as refuge for juveniles of vulnerable marine species.

Second, our comparative analysis may provide justification for the prioritization of resources toward certain habitats. SAV, for example, provided the greatest benefit to unstructured controls (Figure 2), but was generally inferior to mangroves in cases where only the two were compared (Figure 3). Similarly, SAV conferred greater nursery benefits relative to other temperate habitats, such as marshes and macroalgae, which also happen to be regions where SAV loss is most prominent (Waycott et al., 2009). Thus, maintenance of SAV might be prioritized in temperate areas or in cases where fragmentation or conversion to unvegetated substrate is underway, but less so in tropical regions where SAV and mangroves still coexist.

Finally, despite its prominence in Beck et al. (2001), no study in our 30-year dataset reported on measures of recruitment in a systematic, comparative manner that allowed for inclusion in our analysis. This result likely stems from the historical difficulties in linking adult populations with their juvenile origins, although new techniques—such as stable isotopes (Herzka, 2005), otolith microchemistry (Gillanders, 2005; Gillanders & Kingsford 2000), and environmental or eDNA—may provide some solutions. Yet, the concept of the "nursery habitat" has accelerated to consider the interaction between multiple habitats, the abiotic environment, and human impacts in driving recruitment over increasingly larger temporal and spatial scales (Litvin et al., 2018; Nagelkerken et al., 2015; Sheaves, 2009).

Inarguably, the "seascape nursery" provides the most realistic perspective on the functioning of coastal nurseries.

However, this reality can be sobering and potentially discouraging to managers, especially those in developing countries where the funds to study and unravel multifaceted relationships are limited or nonexistent. Even in the United States, where resources are comparatively very high, a focus on the complexity of the relationship between fish and habitat has arguably not benefited management. The difficulty in managing for increasing realism may be best illustrated in the application of the "Essential Fish Habitat" (EFH) policy. In theory, the EFH concept aimed to clearly prioritize a few key places and habitats. In practice, nearly everywhere was identified as "essential" to some species at some time in their life history, which is to say that there were few to no priority areas identified (Fluharty, 2013; Meissner, German, Aiken, & Wolter, 2000). In contrast, relatively simple characterizations of juvenile success captured in our analysis show a clear and consistent hierarchy in the importance of different habitats for juveniles across a range of locations and taxa.

Although we far from discourage investigations of the multifaceted and complex function of coastal systems, the utility of the original definition by Beck et al. (2001) lies in its simplicity and generality, and the clarity that it provides for prioritization of efforts by resources managers and conservation practitioners. The lack of tests in many habitats for response variables such as growth and survival, no suitable tests of recruitment from any nursery habitat, and overwhelming focus on vertebrate fishes indicate that there is still considerable progress to be made at a fundamental level before advancing to more realistic, and therefore more complicated and challenging, investigations. Thus, we propose that, where the resources exist to adopt a seascape-level perspective, researchers should strive to link these simple measures of density, growth, and survival across space and time to new estimates of adult recruitment, and further test how these relationships change under different scenarios of global change. In places where resources are scarce or in underrepresented habitats, the simpler approach advocated by Beck et al. (2001) can establish a stronger foundation and, beyond that, relevant information for managers. Given that almost all coastal habitats are under threat from human activities, tests of the nursery function—at any level—are critical in protecting this essential service. Our quantitative analysis is the next iteration in empirically validating the most basic tenets of the nursery habitat hypothesis, but there is still much more to be done to reveal and confirm the nursery benefit provided by coastal ecosystems.

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SUPPORTING INFORMATION

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