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Reassessing the nursery role of seagrass habitats from temperate to tropical regions: a meta-analysis

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ABSTRACT: Identifying and protecting coastal nursery habitats is imperative as human impacts to these areas accelerate. Nursery habitats support higher juvenile (1) density, (2) growth, or (3) survival (hereafter nursery role metrics) than other habitats, resulting in a greater contribution to adult populations. Seagrass habitat is commonly referred to as a nursery, but its contribution to each nursery role metric across geographic regions and in comparison to other nursery habitats (e.g. mangroves, coral reefs, salt marshes) remains unclear. We conducted a global meta-analysis of juvenile fish and macro-invertebrate performance in seagrass relative to other habitats to assess the nursery role metric, geographic region, and taxonomic group for which seagrass is most beneficial. We compiled data from 51 papers, spanning temperate, subtropical, and tropical regions and including unstructured and structured comparative habitats. We found that, overall, seagrass provided better nursery habitat than other habitats, particularly for supporting high juvenile density and growth. Seagrass habitat was generally more beneficial in temperate and subtropical regions than in the tropics, and more important for juvenile invertebrates than for fishes. Seagrass appears to be highly valuable for provision of food, but supplies equivalent or less adequate refuge than other nursery habitats. Management efforts may benefit from prioritizing conservation of seagrass habitats as food sources for juveniles in combination with other structured habitats for refuge in temperate regions; in tropical regions, seagrass may be a less important nursery habitat to target for conservation, though the value of nursery habitats may shift with ongoing climate change.

KEY WORDS: Coastal habitat · Fish · Invertebrate · Meta-analysis · Nursery role · Seagrass

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INTRODUCTION

Coastal systems have long been recognized as important nursery habitats for marine species because of the high abundance and diversity of juvenile fauna they support (Drake & Arias 1991, Heck et al. 1995, Desmond et al. 2000). Identifying coastal nursery habitats and understanding the mechanisms by which they serve as nurseries is increasingly important as human populations and associated impacts continue to grow in these areas (Halpern et al. 2008, NOAA 2012). Approximately two-thirds of global seagrass and wetland habitats have been degraded by human activities (Lotze et al. 2006), with 29% of

seagrass lost globally since the late 1800s (Waycott et al. 2009); this has led to poor water quality and increased species invasions (Lotze et al. 2006). Many coastal habitats including seagrass beds, algal mats, salt marshes, mangroves, and coral reefs are considered to be nurseries for juvenile marine species (Haywood et al. 1995, Nagelkerken et al. 2000, Minello et al. 2003, Igulu et al. 2014). Determining their relative importance as nursery habitats, or how they combine to function as a nursery at the landscape level, will aid in the prioritization of management efforts (Huijbers et al. 2013, Kimirei et al. 2013).

The nursery role hypothesis, which was proposed to facilitate a quantitative definition of nursery habi-

that, states that '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' (Beck et al. 2001, p. 635). The production of individuals that recruit to adult populations can stem from increased juvenile (1) density, (2) growth, or (3) survival and (4) successful movement to adult habitat from the nursery habitat (Beck et al. 2001). Several meta-analyses have been conducted to assess the nursery value of different habitats (e.g. Minello et al. 2003, Sheridan & Hays 2003, Igulu et al. 2014), one of which focused on the importance of seagrass habitat (Heck et al. 2003). Despite limited geographical comparisons, 2 meta-analyses found increasing importance of seagrass relative to other habitats with latitude through vote counting (i.e. counting number of papers that found a significant difference, Heck et al. 2003) and in comparison to salt marshes (Minello et al. 2003). Another focused on tropical regions and found that seagrass only served as more important nursery habitat than mangroves and coral reefs when those habitats were less accessible (Igulu et al. 2014). Here, we advance the assessment of the relative importance of seagrass as nursery habitat by incorporating a broader geographic range and making habitat comparisons to a variety of other nursery habitat types.

Seagrass may be a particularly important nursery habitat, as it has been found to support a high number of species at risk (Hughes et al. 2009) and commercially important species (Nagelkerken et al. 2000, Lugendo et al. 2005, Bertelli & Unsworth 2014). Seagrass habitats were recently estimated to enhance fish stocks by approximately € 152 000 ha⁻¹ yr⁻¹ in southern Australia (Blandon & zu Ermgassen 2014) and by €67 000 yr⁻¹ for an eastern Atlantic island (Tuya et al. 2014); though these studies do not directly assess responses of fishes to seagrass loss, others have found that fishes aggregate in remaining seagrass patches (Macreadie et al. 2009). Seagrass also provides a basal food source in the form of edible blades, detritus, and epiphytic algae, supporting a high diversity of specialist consumers (Tewfik et al. 2007). In addition, the blades of seagrass can provide refuge from predation (Heck & Orth 2006). Seagrass species are distributed globally (with the exception of the polar oceans [Orth et al. 2006]), but seagrass area is estimated to be declining at a rate of 110 km² yr⁻¹ (Waycott et al. 2009). Conservation of seagrass habitat is thus a growing priority owing to the habitat's provision of multiple ecosystem services including sediment stabilization (Bos et al. 2007),

nutrient cycling (Ziegler & Benner 1999), long-term carbon storage (Kennedy et al. 2010), and presumed nursery habitat.

We conducted a global meta-analysis of peer-reviewed literature to evaluate the importance of seagrass as a nursery habitat for juvenile fishes and macro-invertebrates. Specifically, we tested the hypotheses that juveniles have higher density, growth, and survival (hereafter nursery role metrics) in seagrass relative to other habitats. We analyzed seagrass comparisons to unstructured and structured habitats for each nursery role metric and assessed whether the geographic region, comparative habitat, and taxonomic group (e.g. fish or invertebrate) influenced the relative importance of seagrass as a nursery. Our study builds on the meta-analysis conducted by Heck et al. (2003) by adding over a decade of relevant studies that have since been published and applying meta-analysis methods (Viechtbauer 2010) that have greatly improved since the previous study, thus strengthening the inferences that can be made from such synthetic analyses. We aim to (1) strengthen the understanding of how the nursery role of seagrass varies geographically, (2) compare the importance of seagrass to other recognized nursery habitats (e.g. mangroves, coral reefs, and salt marshes), and (3) determine if the results from Heck et al.'s (2003) meta-analysis are substantiated after 14 more years of research and development of meta-analysis techniques. Advancing understanding of the importance of seagrass habitats is essential to focus and motivate conservation efforts, especially in light of continued global coastal development and seagrass habitat loss (Waycott et al. 2009).

MATERIALS AND METHODS

Literature search and selection criteria

To identify the primary literature that examines the nursery role of seagrass habitats, we conducted a systematic literature search of all databases in the Institute for Scientific Information's Web of Science (WOS) using the following 3 sets of search terms: (1) seagrass OR phyllospadix OR zostera OR halophila OR posidonia OR amphibolis OR cymodocea OR halodule OR syringodium OR thalassodendron OR enhalus OR halophila OR thalassia OR ruppia OR lepilaena, (2) nurser* OR juvenile*, and (3) densit* OR abundance* OR survival OR growth OR movement* AND adult. Seagrass species in our search terms followed those of Short et al. (2011). We also

included review papers and meta-analyses that were identified in our WOS search or that we knew about previously.

We selected papers for inclusion in our meta-analysis using the following criteria from Beck et al.'s (2001) definition of a nursery: (1) the paper provided data on juvenile density, abundance, growth, or survival in seagrass for at least 1 species; (2) the paper compared this metric for the species between seagrass and at least 1 other habitat type; (3) at least 1 species in the study had a transient life history (i.e. juvenile and adult stages live in separate habitats); (4) the work included the variance and sample size; and (5) the study was not conducted in artificial seagrass. If papers included different experiments or sampling that was done at different seagrass densities, we only collected data from those components of the study with $\geq 50\%$ seagrass density. For criterion (3), we considered a species to have a transient life history if it was suggested in any part of the paper, if the study showed differences in adult and juvenile densities (indicating one habitat is primarily used as nursery for juveniles and the other is used by adults), if we determined the species was transient based on another study in the meta-analysis, or if it was included in either Beck et al.'s (2001) list of nursery species or Nagelkerken et al.'s (2000) list of tropical nursery species.

For each paper that met our selection criteria, we extracted the data needed to calculate effect size and variance. If a paper presented sample size as a range, we took the most conservative value. For papers that did not present their data in numerical form, we used the program GraphClick (www.arizona-software.ch/graphclick) to extract values from the figures. When studies quantified multiple species and/or habitats, we treated each species-specific comparison as a separate data point. If the study had repeated measures of a variable, we considered these to be separate data points when a full year had passed between them or took the most recent measurement if the study was repeated within the same year (as in Alofs & Jackson 2014, Magrach et al. 2014). If more than 1 response variable was presented, we took the most commonly presented measurement (e.g. length for growth instead of weight) following Alofs & Jackson (2014) and Parker et al. (2006). We standardized all mean density measures to per square meter and combined growth measurements of diameter, standard length, volume, otolith increment, and instantaneous growth rate. We did not use any papers that included a form of growth rate that was not comparable (e.g. RNA:DNA growth rate ratio). Survival was always measured in percent units.

We applied length criteria to exclude adult densities reported by studies that combined measurements of juvenile and adult density. When observed species had average sizes presented in the data, we used FishBase (Froese & Pauly 2014) to determine which of these were juveniles using their reported length at maturity (L_m). If L_m was not available, we used one-third of the maximum species length (following Dorenbosch et al. 2005). For papers that evaluated multiple habitats utilized by nursery species, we only included habitats and species densities when the species mean size in the habitat was below or equal to L_m or one-third of the maximum species length.

We recorded any study variables that may have affected the habitat comparison and were commonly provided across studies, including the geographic region, habitat comparison, taxonomic group (fishes or invertebrates), taxonomic family of the fauna studied, and taxonomic genus of the seagrass. Geographic regions were categorized as temperate (38° to $66^\circ 33'$ N and S), subtropical ($23^\circ 27'$ to 38° N and S), and tropical (0° to $23^\circ 27'$ N and S) (Fig. 1a,b, see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m577p133_supp.xlsx for map of study regions). We classified the habitats that were compared to seagrass as habitat types and habitat categories. Habitat types included bare (sand, limestone pavement, water column, mud, and unvegetated), algae, marsh, mangrove, coral reef, and rock/rubble/shell (oyster beds, coral and/or shell rubble, cobble, and boulders) (Fig. 1c,d). Studies that compared seagrass to channel habitats were excluded, as channels may contain any of the different habitat types. Habitat category combined these types as unstructured (bare habitat) or structured (all other habitat types). Faunal family was labeled as unknown for 3 studies in which species were not identified.

Calculation of effect sizes

We calculated the effect size Hedges' d (Hedges & Olkin 1985) for each nursery role metric (metafor package in R; Viechtbauer 2010):

$$d = \left(\frac{\mu_1 - \mu_2}{SD_{\text{pooled}}} \right) \times J \quad (1)$$

where μ_1 is the mean of juvenile density, growth, or survival in the seagrass habitat, μ_2 is the mean in the comparison habitat, SD_{pooled} is the pooled standard deviation and J is a correction for small sample sizes.

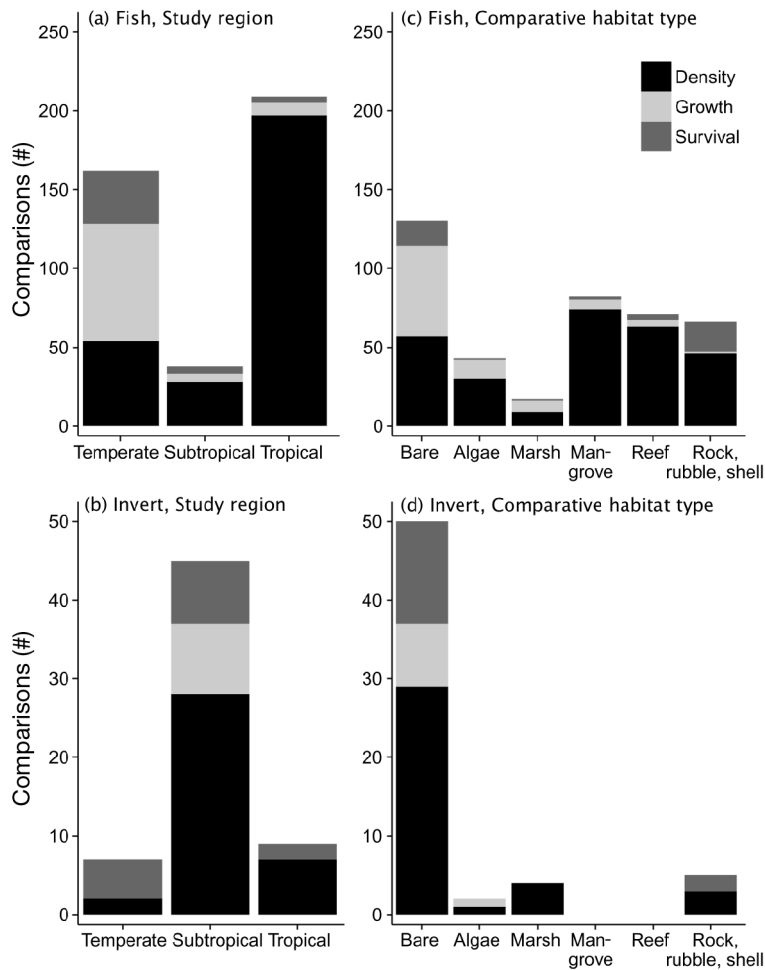


Fig. 1. Comparisons of seagrass with other habitats (i.e. no. of data points) by geographic region and comparative habitat type that were included in the meta-analysis. Studies assessed the nursery role of habitats by measuring juvenile density, growth, or survival for (a,c) fishes and (b,d) invertebrates across (a,b) temperate, subtropical, and tropical regions. Seagrass was compared to (c,d) 6 other habitat types across studies. Bare habitat type includes sand, limestone pavement, water column, mud, and unvegetated

SD_{pooled} is calculated as:

$$SD_{\text{pooled}} = \sqrt{\frac{(n_1 - 1)(s_1)^2 + (n_2 - 1)(s_2)^2}{(n_1 + n_2 - 2)}} \quad (2)$$

where n_1 and n_2 are the sample sizes, and s_1 and s_2 are the standard deviations of μ_1 and μ_2 .

J , the correction for small sample size, is given as:

$$J = 1 - \left(\frac{3}{4(n_1 + n_2 - 2) - 1} \right) \quad (3)$$

and v_d is the variance for Hedges' d :

$$v_d = \left(\frac{(n_1 + n_2)}{n_1 n_2} \right) + \left(\frac{d^2}{2(n_1 + n_2)} \right) \quad (4)$$

Here, Hedges' d weights the difference between the mean responses from the 2 habitat types by the pooled standard deviation. We chose to use Hedges' d , as this effect size metric permits the use of reported zero values (e.g. zero juvenile density or growth) and was used in past meta-analyses on nursery habitats, allowing for direct comparison of results (Heck et al. 2003, Minello et al. 2003, Igulu et al. 2014).

Statistical analyses

We conducted separate maximum likelihood mixed-effects meta-regressions with inverse-variance weighting (metafor in R; Viechtbauer 2010) for each of the 3 nursery role metrics. We included study ID as a random effect in all models to account for non-independence of effect sizes taken from the same study. Intraclass correlation coefficients (ICC package in R; Wolak et al. 2012) revealed low correlation of effect sizes within studies (0.21, $n = 51$) and faunal taxonomic families (0.12, $n = 32$). We chose to include study ID, and not family, as a random effect owing to the higher correlation compared to family and because the majority of studies only observed 1 family (36 of 51).

We included geographic region, habitat category, nursery taxonomic group, and seagrass family as main effects for all nursery role metrics; habitat type was assessed separately owing to overparameterization of full models. Full models were constructed differently for each nursery role metric to maximize the interactions that could be tested without

overparameterization: the density model included all main effects and their interactions; the growth model included an interaction between habitat category and taxonomic group, but no interactions with geographic region; the survival model could include any 2 interactions simultaneously, but not all 3 (i.e. habitat category \times geographic region \times taxonomic group). Seagrass genus could not be included, as the high number of levels overparameterized the models; thus, seagrass family was used instead, with factor levels indicating if more than 1 family was identified in the study (e.g. Cymodoceaceae or Cymodoceaceae and Hydrocharitaceae). We used Akaike's information criterion for small sample sizes to find the best-fit model (Bolker et al. 2009) by testing all pos-

sible combinations of main effects and interactions within the full models (glmulti package in R; Calcano & de Mazancourt 2010). We tested the effect of habitat type in separate models for nursery role metrics that retained habitat category as a significant predictor; habitat types that had less than 4 measures were excluded from this analysis (Fig. 1c,d).

We conducted post hoc analyses on each retained model term by contrasting term levels with Tukey's HSD and Bonferroni corrections (multcomp package in R; Hothorn et al. 2008). We also determined whether effect sizes for each level were significantly above or below zero by calculating 95% CIs. A significantly positive Hedges' d indicates a higher nursery role metric in seagrass compared to another habitat type, whereas a significantly negative Hedges' d indicates a higher metric in the other habitat type. We determined the overall effect size and CIs for each nursery role metric by running models without any moderator terms.

To evaluate our meta-analysis for publication bias, we verified that funnel plots for each nursery role metric were symmetric and calculated a fail-safe number (Rosenberg 2005) that indicated 5525 non-significant studies for density, 1176 for growth, and 225 for survival would have to be added to change the statistical significance of the overall effect of each nursery role metric. All analyses were done in R (R Core Team 2015).

RESULTS

Overall, our meta-analysis revealed that juvenile density and growth were significantly higher in seagrass compared to other habitats and that survival also tended to be higher (Fig. 2). The importance of seagrass as nursery habitat was mediated by whether the habitat was in a temperate, subtropical, or tropical region. Juvenile density was more consistently higher in seagrass across geographic regions than either growth or survival (Fig. 3).

The extent to which seagrass supported higher densities of juveniles than other habitats was influenced by the geographic region and whether the comparative habitat was unstructured or structured (heterogeneity explained by the model, $QM = 66.57$, $p < 0.001$, $df = 5$; Fig. 3a). Juvenile densities were higher in seagrass across all regions and habitat category comparisons, except in the tropics. In the tropics (Trop), densities were significantly higher in seagrass relative to unstructured (Unstr) habitats, whereas no difference was found between seagrass

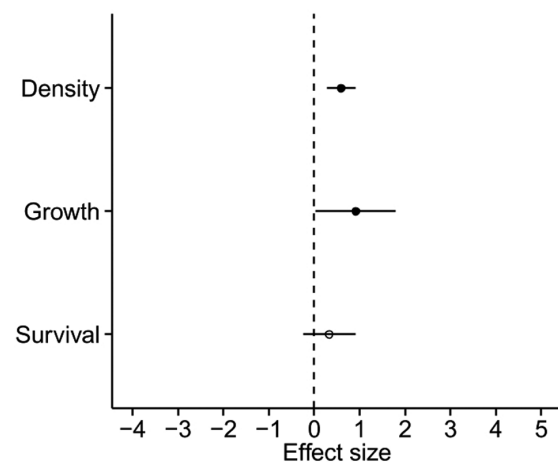


Fig. 2. Positive effect sizes (Hedges' d) indicate seagrass supports higher levels of juvenile density, growth, and survival compared to other habitat types. CIs (95%) that do not overlap 0 indicate significant effect sizes (solid circles); no significant difference indicated with unfilled circles

and structured (Str) habitats (Trop, Unstr vs. Str, $z = 7.55$, $p < 0.001$; Fig. 3a). Juvenile densities were also significantly higher in seagrass habitats than in bare, algal, and marsh habitats but were similar to mangrove, coral reef, and rock/rubble/shell habitats ($QM = 128.63$, $p < 0.001$, $df = 5$; Fig. 4a).

The role of seagrass in supporting increased juvenile growth relative to other habitats varied depending on the geographic region and whether juveniles were fishes or invertebrates ($QM = 222.87$, $p < 0.001$, $df = 3$; Fig. 3b). Seagrass was more important for higher growth of juveniles in subtropical regions than in temperate ($z = -3.77$, $p < 0.001$) and tropical regions ($z = -3.34$, $p < 0.001$). Growth in seagrass compared to other habitats was also significantly lower for fishes than for invertebrates ($z = 10.10$, $p < 0.001$; Fig. 3b).

Survival of juveniles was the only metric in which we found cases of other habitats playing a more important nursery role than seagrass, and this was influenced by geographic region, habitat category, and taxonomic group ($QM = 141.45$, $p < 0.001$, $df = 7$; Fig. 3c). In temperate (Temp) regions, survival was higher in seagrass compared to unstructured habitats but significantly lower compared to other structured habitats (Temp, Unstr vs. Str, $z = 11.33$, $p < 0.001$; Fig. 3c). In the tropics, there were no significant differences in survival between seagrass and unstructured or structured habitats. Both fishes (Fish) and invertebrates (Invert) had higher survival in seagrass compared to unstructured habitats but tended to have lower survival in seagrass compared to structured habitats (Fish, Unstr vs. Str, $z = 9.26$, $p < 0.001$; Invert,

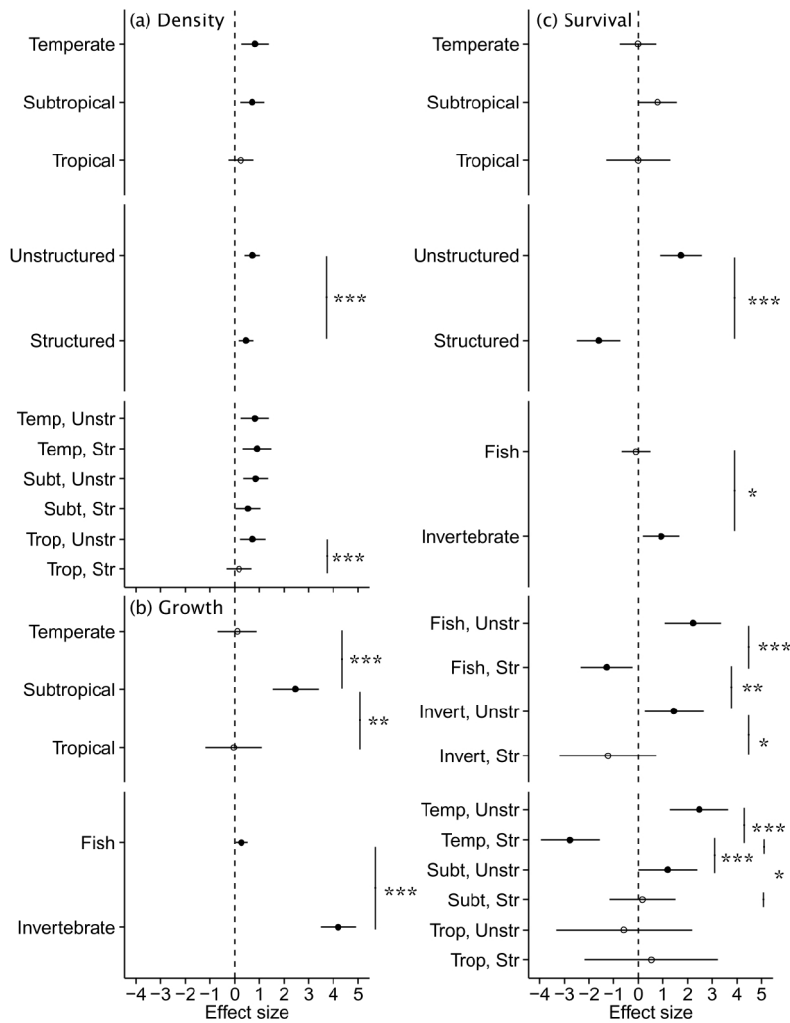


Fig. 3. Importance of seagrass over other habitats for juvenile (a) density, (b) growth, and (c) survival is indicated by significant positive effect sizes (Hedges' d) with 95% CIs that do not overlap 0 (solid circles); no significant difference indicated with unfilled circles. Model terms that best explained variation in seagrass–other habitat comparisons are depicted for each nursery role metric. Lines and asterisks indicate contrasts within model terms that were significantly different: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Temp: temperate; Unstr: unstructured; Str: structured; Subt: subtropical; Trop: tropical; Invert: invertebrate

Unstr vs. Str, $z = 2.82$, $p = 0.03$; Fig. 3c). Specifically, survival was higher in seagrass compared to bare habitat, similar to coral reef habitat, and significantly lower in seagrass than in rock/rubble/shell ($r/r/s$) habitat (bare and reef vs. $r/r/s$, $p < 0.001$; QM = 130.74, $p < 0.001$, $df = 3$; Fig. 4b). Residual heterogeneity was significant for density (QE [test statistic for test of heterogeneity] = 1939.23, $p < 0.001$, $df = 310$), growth (QE = 233.92, $p < 0.001$, $df = 92$), and survival metrics (QE = 228.87, $p < 0.001$, $df = 50$).

Our meta-analysis of 51 papers provided a global assessment of the nursery role of seagrass relative to other habitats. Nursery role habitat comparisons

were more prevalent for juvenile fishes than invertebrates for density ($n = 279$ vs. 37, respectively), growth ($n = 87$ vs. 9), and survival ($n = 43$ vs. 15) metrics. The most frequent regional habitat comparisons for each taxonomic group measured density of fish in tropical regions ($n = 197$) and density of invertebrates in subtropical regions ($n = 28$) (Fig. 1a,b). Seagrass was most often compared to bare habitat for fishes ($n = 130$, 32% of all habitat type comparisons) and invertebrates ($n = 50$, 82%) for all nursery role metrics combined (Fig. 1c,d). Seagrass was more frequently compared to unstructured habitats in temperate regions (Unstr vs. Str, $n = 117$ vs. 52) but more often compared to other structured habitats in tropical regions ($n = 19$ vs. 199); subtropical comparisons were relatively evenly distributed ($n = 44$ vs. 39). Fishes represented 27 taxonomic families spanning a range of habitat-use traits (e.g. benthic vs. mid-water dwelling), and invertebrates represented 4 families including shrimps, crabs, and sea snails (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m557p133_suppl.xlsx for details of studies and data included in the meta-analysis).

DISCUSSION

Our meta-analysis confirms the value of seagrass as nursery habitat but also shows that its importance relative to other habitats varies across geographic regions. Our results corroborate past meta-analyses, which found that the importance of seagrass for supporting high juvenile densities increases with latitude (Heck et al. 2003, Minello et al. 2003), and also highlight the influence of latitude on the nursery role metrics of growth and survival. Seagrass was found to be particularly beneficial for juvenile density and growth, whereas survival was similar or higher in other structured habitats.

Geographic region was a dominant mediator of the nursery function of seagrass. The importance of seagrass in different regions also varied based on the nursery role metric and whether seagrass was compared to unstructured or structured habitats. Heck et al.'s (2003) meta-analysis also found seagrass impor-

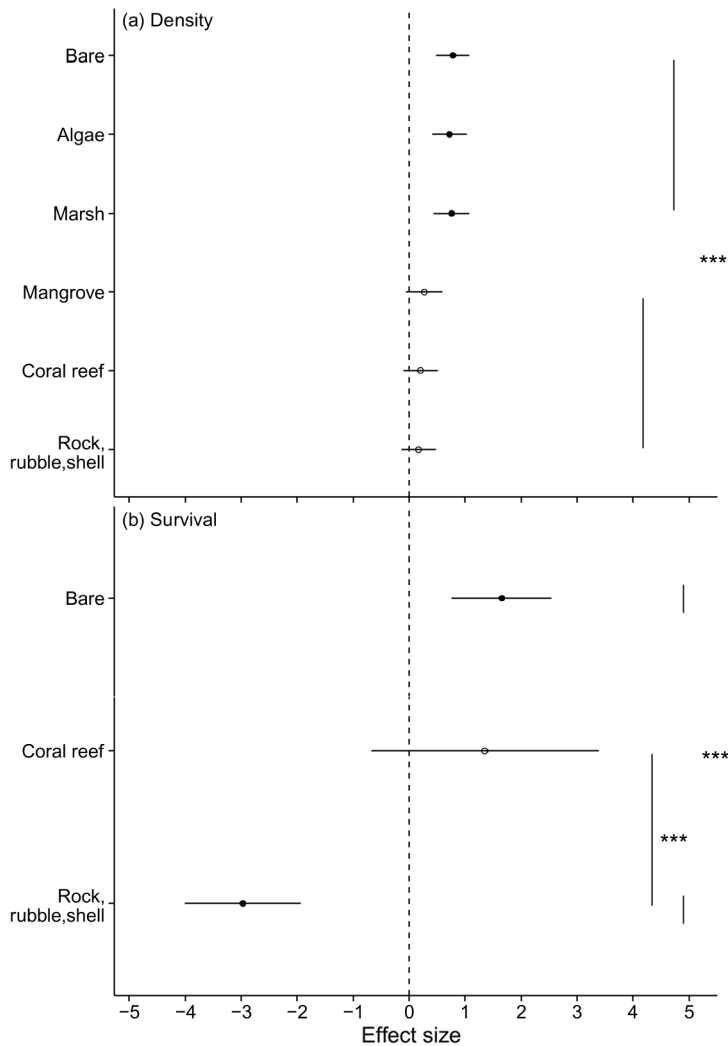


Fig. 4. Seagrass comparisons to different habitat types for supporting juvenile (a) density and (b) survival. CIs (95%) that do not overlap 0 indicate significant effect sizes (solid circles); no significant difference indicated with unfilled circles. Bare habitat type includes sand, limestone pavement, water column, mud, and unvegetated. Lines and asterisks indicate contrasts within model terms that were significantly different: *** $p < 0.001$

tance was driven by geography, with seagrass acting as a more important habitat for supporting high juvenile densities in North America than in Australia. In comparison, our results showed higher density and survival in seagrass compared to structured and unstructured habitats, respectively, in temperate regions but not in tropical regions. Structured habitats in the tropics include mangroves and coral reefs, both of which are widely recognized nursery habitats (Nagelkerken et al. 2000, Igulu et al. 2014). Seagrass in the tropics has been found to contain higher juvenile densities than mangroves and coral reefs only in locations where these other habitats were less acces-

sible owing to large tidal amplitudes (Igulu et al. 2014). Previous meta-analyses were unable to determine the importance of seagrass to growth and survival of juveniles across geographic gradients owing to lack of habitat comparisons for these metrics (Heck et al. 2003, Minello et al. 2003). Though we found that seagrass was only important for growth in subtropical regions, this may be a reflection of missing habitat comparisons for invertebrate growth in temperate and tropical regions.

Differences in food availability and refuge from predation provided to juveniles likely regulates the extent to which various habitats act as nurseries (Nagelkerken 2009). Our results suggest seagrass habitats may provide better food sources for juveniles than other habitats (as indicated by our growth analysis) but provide less adequate shelter than other structured habitats (as indicated by our survival analysis); both factors likely influence juvenile density. Density and growth were generally higher in seagrass than in both unstructured and structured habitats in our meta-analysis; however, densities in seagrass were similar to mangroves, coral reefs, and rock/rubble/shell habitats. Another meta-analysis comparison between seagrass and salt marsh similarly found that seagrass habitats supported higher juvenile densities (Minello et al. 2003). Seagrass is also thought to provide a better food source than mangroves; behavioural observations in the tropics have shown that some fishes move between seagrass and mangroves for food and refuge, respectively (Verweij et al. 2006a, Hammerschlag et al. 2010). Growth is a more direct measure of food provision, whereas the relative similarity in densities

between seagrass and mangroves, coral reefs, and rock/rubble/shell could also be an indication of refuge provided by these other habitats (Verweij et al. 2006a, Hammerschlag et al. 2010, Igulu et al. 2014). Both Heck et al. (2003) and our meta-analysis show that survival is higher in non-vegetated structure habitats (i.e. rock/rubble/shell) than in seagrass, driving the result of higher survival in structured habitats compared to seagrass in temperate regions. Conversely, coral reefs may be the most similar to seagrass as nursery habitat (Nagelkerken et al. 2000, Igulu et al. 2014), reducing the importance of seagrass in tropical regions.

Seagrass was more beneficial for juvenile invertebrate growth and survival than for fishes. Another meta-analysis also found that juvenile decapod crustacean densities were more positively influenced by seagrass relative to non-vegetated marsh than fish densities (Minello et al. 2003). Macro-invertebrates within seagrass habitats are often suspension or deposit feeders, whereas most fishes consume benthic invertebrates and thus are only indirectly supported by basal seagrass food sources (Luczkovich et al. 2002). Growth of invertebrate detritivores may be especially linked to seagrass habitat, as detrital pathways are thought to be an important energy source that structures food webs in seagrass (Tewfik et al. 2007, Rooney & McCann 2012). Benthic invertebrates may also benefit more from seagrass as a refuge from predation compared to more conspicuous midwater-dwelling fishes (see review by Heck & Orth 2006). All invertebrates included in our meta-analysis were benthic, whereas the fishes included benthic and midwater-dwelling species.

Although seagrass structural complexity and morphology can clearly influence faunal density and predation risk (Nelson & Bonsdorff 1990, Curtis & Vincent 2005, Verweij et al. 2006b), our meta-analysis did not find that seagrass family (a metric for morphological differences) influenced the nursery role of seagrass. Different species of seagrass vary in morphology; for example, *Enhalus acoroides* and *Zostera marina* have long, ribbonlike leaves, whereas *Halophila engelmanni* has short leaves (Kuo & den Hartog 2006). Tethered crabs were 3 times more likely to be eaten in seagrass characterized by thin stems with clusters of small leaves (*Amphibolis* spp.) than in seagrass with straplike leaves (*Posidonia sinuosa*) (Vanderklift et al. 2007). Responses of fishes to alterations in seagrass height, density, and total seagrass clearance have been found to vary by species (Horinouchi 2007). Seagrass shoot biomass can also affect species densities, whereas percent cover and total linear edge explain little variation (Hovel et al. 2002). The lack of effect of these morphological differences in our meta-analysis may reflect the greater influence of habitat type than seagrass morphology or the fact that we were unable to test for differences among seagrass genera.

Remaining unexplained heterogeneity for each nursery role metric suggests that factors other than those we could test also influence the efficacy of seagrass as a nursery habitat. Salinity, temperature, and tidal range can, for example, each affect recruitment and juvenile densities (Minello et al. 2003, Schaffler et al. 2013, Igulu et al. 2014). Seagrass area and con-

nectivity, as well as harvesting of adults, also mediates the nursery value of seagrass. For instance, blue crab *Callinectes sapidus* populations are best supported by large, continuous seagrass beds when there is no crab harvesting, but smaller, fragmented seagrass patches are better when there are higher harvesting rates (Mizerek et al. 2011).

Our meta-analysis advances that of Heck et al. (2003) in that we include over 30 new studies, providing more tropical habitat comparisons, and use advanced meta-analytic methods that account for the non-independence of data (Hedges & Olkin 1985, Viechtbauer 2010) and do not rely on vote counting (Koricheva et al. 2013). Many of Heck et al.'s (2003) original conclusions are substantiated by our new analysis, thus strengthening support for the idea that seagrass is a valuable nursery habitat (see Table 1 for comparisons between Heck et al.'s [2003] results and ours). Our study also shows the importance of seagrass relative to different nursery habitats and underscores the complexity of determining important habitat, as the value of nurseries depends on the geographic region, faunal taxon, and nursery role metric. However, despite an additional 14 yr of research, there remains a dearth of studies comparing juvenile survival and growth in seagrass to other habitats, few studies on other macrophytes such as kelp and salt marshes (but see Minello et al. 2003), a bias to evaluate invertebrates in subtropical bare habitats, and limited research on juvenile movement. We recommend future studies focus on these areas to improve our understanding of the nursery role of different habitats.

Our results provide further support for the general importance of protecting and maintaining seagrass as nursery habitat but also identify potential differences in management strategies based on the focal geographic region and nursery metric. In case studies of pink shrimp and blue crabs, Heck et al. (2003) found little evidence that seagrass loss was related to changes in production of these fisheries species. However, seagrass habitats have also been found to enhance commercially important fisheries (Blandon & zu Ermgassen 2014, Tuya et al. 2014) such as Atlantic cod *Gadus morhua* (Lilley & Unsworth 2014), and loss of seagrass habitats can cause declines in the abundance and biomass of fishes (Hughes et al. 2002). Active management and restoration of seagrass is required to maintain these habitats, as they face a multitude of stressors including eutrophication (van Katwijk 2010), competition with algae (Hauxwell et al. 2003), and herbivory from invasive crabs (Garbary et al. 2014). However, seagrass in tropical re-

Table 1. Comparison of meta-analysis results assessing the nursery role of seagrass (SG) relative to other habitats from Heck et al. (2003) and this study. Only results from comparisons of means and variance (using Hedges' *d*) or percentage of papers showing significant differences (using vote counting) were included from Heck et al. (2003); discussion of possible trends without these direct comparisons was considered not tested. **Bold** text under 'Current study' highlights differences between the 2 studies. > and < indicate significant differences, ≥ and ≤ indicate a trend but no significant difference, and = indicates no difference

| Comparison | Nursery role | Heck et al. (2003) | Current study |
|--|--------------|---|--|
| Overall importance of density, growth, survival | Density | 46 % of papers showed SG > other habitats | SG > other habitats |
| | Growth | SG > other habitats | SG > other habitats |
| | Survival | SG ≥ other habitats | SG ≥ other habitats (Fig. 2) |
| Importance of seagrass across geographic regions | Density | 75 % of papers show SG > in northern hemisphere | SG > for unstructured habitats in all regions |
| | Growth | Not tested | SG > in subtropical regions |
| | Survival | Not tested | SG > in temperate and subtropical regions for unstructured habitats, but SG < for structured habitats in temperate regions (Fig. 3) |
| Seagrass vs. habitat categories | Density | Not tested | SG > for unstructured and structured habitats but not for tropical structured habitats |
| | Growth | SG > for unstructured and structured (unvegetated) habitats, SG = vegetated habitats | Not significant |
| | Survival | SG > for unstructured habitats, SG < for structured (unvegetated) habitats, SG = vegetated habitats | Significant interactions with geographic region and taxonomic group (see other survival rows, Fig. 3) |
| Seagrass vs. other nursery habitat types | Density | Not tested | SG > salt marsh, SG ≥ coral reefs and mangroves |
| | Growth | Not tested | Not significant |
| | Survival | Not tested | SG ≥ coral reefs (Fig. 4) |
| Seagrass importance to fishes and invertebrates | Density | Not tested | Not significant |
| | Growth | Not tested | SG > for fishes and invertebrates |
| | Survival | Not tested | SG > for fishes and invertebrates in unstructured habitats, but SG ≤ for fishes and invertebrates in structured habitats (Fig. 3) |

regions did not improve any of the nursery role metrics compared to other structured habitats. As the survival of coral reefs is severely threatened with rising temperatures (Graham et al. 2015), management efforts may choose to prioritize conservation of coral reef habitats in light of their value as nursery habitat or may find that seagrass could become an important surrogate habitat for some species. Seagrass may also decline with climate change, though, with deleterious effects caused by sea level rise and increased storms as well as rising temperatures for temperate species (Connolly 2012).

Seagrass alone does not appear to adequately fulfill each aspect of a nursery habitat (Beck et al. 2001). Different structured habitats may be valuable for each nursery role metric, and management of different

focal species may require strategies that prioritize one nursery role metric over another. For instance, a population that has high larval recruitment may benefit from conservation of seagrass for support of high juvenile densities, whereas a population that has low recruitment may benefit from protection of other structured habitats that improve survival rates. An emerging concept that recognizes the importance of multiple habitat types as nurseries suggests managing these habitats as a seascape that considers all connected nursery habitats and identifies hotspots of juvenile abundance and productivity (Boström et al. 2011, Pittman et al. 2011, Nagelkerken et al. 2015). As seagrass habitats decline worldwide (Waycott et al. 2009), it is vital that we prioritize conservation of these and other coastal nursery habitats.

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