

Recruitment enhancement varies by taxonomic group and oyster reef habitat characteristics

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Abstract. The rapid loss of coastal and estuarine biogenic habitats has reduced the delivery of valuable ecosystem services, resulting in calls for increased habitat restoration. Yet, a lack of information on how key habitat characteristics (e.g., area, vertical relief, age) influence the ability of restored habitats to deliver these ecosystem services hinders efforts to maximize the return on restoration investments. We conducted a meta-analysis to assess the influence of reef type (natural or restored), taxa, and restored reef size, vertical relief, age, and tidal zone on the presence and magnitude of recruitment enhancement for nekton (i.e., fish and swimming crabs). Both intertidal and subtidal reefs, as well as restored and natural reefs, enhanced nekton recruitment, though there was variation among taxonomic groups with reef types. Recruitment enhancement was more common across taxa on restored (six families) than on natural (one family) reefs. Resident nekton families were more consistently enhanced than transient families. Nekton enhancement varied with a number of restored reef characteristics. Recruitment enhancement increased with greater reef size across taxa, decreased with higher vertical relief for two families, showed maximum recruitment around a single intertidal reef age for one family, and showed minimum recruitment around a single subtidal reef age for three families. Understanding variation across species in response to key design elements will improve restoration success and enhance return on investment. Moving forward, we recommend studies that vary reef habitat characteristics independently and in combination to identify how variation in these characteristics interact to influence nekton recruitment enhancement by oyster reefs.

Key words: design; habitat restoration; meta-analysis; nekton; oyster reef; recruitment enhancement; reef age; reef size; vertical relief.

INTRODUCTION

Coastal ecosystems consist of landscapes of biogenic habitats (e.g., oyster reefs, corals, salt marshes, mangroves, and seagrasses) that provide a range of ecosystem functions. They serve as nursery and foraging grounds for fish and invertebrates (Coen et al. 1999, Beck et al. 2001, Soniat et al. 2004), regulate energy flow and nutrient fluxes (Dame et al. 1984, Piehler and Smyth 2011, Kellogg et al. 2013), stabilize shorelines and slow erosion (Meyer et al. 1997, Piazza et al. 2005), reduce storm surge water levels (Krauss et al. 2009), and enhance biological diversity (Wells 1961, Bahr and Lanier 1981; functions are reviewed in Powers and Boyer 2014). These ecosystem functions result in a host of associated services, such as enhancing economically valuable fisheries

(Peterson et al. 2003, zu Ermgassen et al. 2016), protecting shorelines and infrastructure (Meyer et al. 1997, Krauss et al. 2009, Scyphers et al. 2011), enhancing water quality by removing excess nitrogen (Piehler and Smyth 2011), and providing cultural benefits such as enhancing recreational opportunities (Carlton et al. 2016; services are reviewed in Barbier et al. 2011, Martin et al. 2016). However, degradation and loss of biogenic habitats are intensifying as human populations continue to grow and exert more pressure on coastal systems, leading to reduced areal extent and complexity of these biogenic habitats and threatening the critical ecosystem functions they provide (Alongi 2002, Waycott et al. 2009, zu Ermgassen et al. 2012, 2013). To combat these impacts and restore ecosystem functions, habitat restoration is increasingly employed as a tool (Peterson and Lipcius 2003). Although there are many examples of successful habitat restoration efforts (e.g., oysters in protected areas, Powers et al. 2009; seagrasses in Chesapeake Bay, Lefcheck et al. 2018), overall success rates for many projects, including those in coastal habitats, are

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moderate (Bayraktarov et al. 2016), and ecosystem functions may remain reduced in restored vs. intact habitats (Rey Benayas et al. 2009). Understanding how particular ecosystem functions vary across a range of restored habitat characteristics (e.g., areal extent, age) can inform future habitat restoration efforts by helping decision makers better predict how restoration design elements may influence service delivery.

Re-establishing biodiversity is a common goal of habitat restoration (Peterson and Lipcius 2003, Rey Benayas et al. 2009), yet distribution patterns of fauna among patchy habitats are difficult to predict because they are shaped by processes occurring at various scales of space, time, and ecological organization that often differ from the scales at which patterns are observed (Levin 1992). Understanding how restoration design influences faunal abundances across multiple taxa will enhance the ability of restoration practitioners to increase the return on investments made by future conservation and restoration efforts. Oyster reefs are broadly distributed and augment populations of many faunal species (Zimmerman et al. 1989, Coen et al. 1999, Rodney and Paynter 2006). Although many studies have documented augmented faunal abundances by oyster reefs, the degree of enhancement varies considerably among studies, species, and ocean basins (e.g., Robillard et al. 2010, Kingsley-Smith et al. 2012, Nevins et al. 2014; synthesized in zu Ermgassen et al. 2016). This variation in recruitment enhancement could stem from several differences among studies because of varying habitat characteristics, including reef areal extent, vertical relief, tidal zone (e.g., subtidal vs. intertidal) tidal elevation, salinity, or landscape setting (Lenihan 1999, Lenihan et al. 2001, Lehnert and Allen 2002, Grabowski et al. 2005), but the potential role of these factors has yet to be thoroughly examined.

We synthesized information from eastern oyster (*Crassostrea virginica*) restoration studies across the United States to assess the potential influence of habitat characteristics incorporated into reef restoration designs on the abundance of reef-associated nekton (aquatic animals that can move independently of water currents; specifically fish and swimming crabs in association with oyster reefs). Augmentation of nekton can occur through recruitment enhancement of early life stages (which includes improved settlement, growth, and survival of juveniles; Beck et al. 2001), or enhanced growth and reproductive effort of adults (e.g., by concentrating food resources and enhancing foraging and spawning opportunities; Peterson et al. 2003, Powers et al. 2003) relative to unstructured habitats. Because growth enhancement likely contributes far less to lifetime augmented nekton production by oyster reefs than recruitment enhancement (Peterson et al. 2003, zu Ermgassen et al. 2016), our synthesis focused on recruitment enhancement. We specifically examined whether reef recruitment enhancement varies by taxonomic group and (1) reef type (i.e., natural or restored reefs) or (2) the size, vertical relief, or age of restored reefs. Our ultimate goal was to provide

information for resource managers to guide future habitat restoration efforts.

METHODS

Literature review

First, we determined the variety of reef characteristics reported by studies investigating nekton recruitment enhancement by oyster reefs using citations from the reference list of a recently completed meta-analysis (zu Ermgassen et al. 2016). We identified nekton families that were regularly reported at oyster reef and control habitats, including both resident (i.e., species that feed, breed, and shelter on reefs long after initial recruitment, Coen et al. 1999, Harding and Mann 2000) and transient (i.e., species that recruit to structured habitats but are more widely distributed across multiple habitats after recruitment, Harding and Mann 2001) reef-associated species. We also performed forward searches in Google Scholar on two published syntheses: Peterson et al. (2003) and zu Ermgassen et al. (2016). We retained studies that met the following criteria: (1) authors quantified density or relative abundance of target nekton families at both oyster reefs (or experimental units that contained oyster shell and served as a mimic for reef habitat, e.g., Humphries et al. 2011) and unstructured mud or sand habitats within the same study; (2) restored reefs used oyster shell, including shell piles, cultch, bagged shell, or shell piles from other species (e.g., surf clams) if topped by oyster shell; (3) restored reefs were within the tidal extent of natural reefs (<10 m deep relative to mean low water [MLW] at the base of the reef; Kennedy and Sanford 1999); (4) fishing gear(s) quantitatively censused juveniles; and (5) authors reported densities or abundances of target nekton by species or family.

Data extraction

We extracted densities or abundances, measures of spread (standard deviation or standard error), and sample sizes of each nekton species from oyster reefs and their paired unstructured control habitat patches. We extracted data for nine nekton families, including reef residents: toadfish (Batrachoididae), blennies (Blenniidae), gobies (Gobiidae), and skiliffish (Gobiesocidae, which were later removed due to limited data availability); and reef transients: grunts (Haemulidae), snappers (Lutjanidae), swimming crabs (Portunidae), drums (Sciaenidae), and porgies (Sparidae; Table 1). We normalized densities to mean individuals/m², abundances to mean individuals per sample (relative abundances), and measures of spread to one standard error of the mean (Appendix S2). We extracted tidal zone (subtidal or intertidal), reef type (restored or natural), restoration method (reefs restored with or without live oysters), and when available, reef size (standardized to square meters), vertical relief (distance from bare sediment to the highest

point on the reef, standardized to meters), tidal elevation (at the base of the reef, in meters relative to MLW), adult oyster density (individuals/m² > 75 mm in shell height, or specified as adult by the authors), and the year of restored reef construction, from which we calculated reef age (Appendix S1: Table S1; Appendix S2).

Analyses

To compare nekton recruitment to oyster reefs vs. unstructured control habitat, we calculated log response ratios (LRRs; Hedges et al. 1999) with 95% confidence intervals (CIs) by family (Appendix S2). An LRR with

TABLE 1. List of species represented in the data set by reef association, family common and scientific name, and species common and scientific names.

Reef association	Family (common)	Common name	Species
Resident	Toadfish (Batrachoididae)	Gulf toadfish	<i>Opsanus beta</i>
		Oyster toadfish	<i>Opsanus tau</i>
		Stiped blenny	<i>Chasmodes bosquianus</i>
		Florida blenny	<i>Chasmodes saburrae</i>
		Crested blenny	<i>Hypleurochilus geminatus</i>
		Feather blenny	<i>Hypsoblennius hentz</i>
		Freckled blenny	<i>Hypsoblennius ionthas</i>
		Highfin blenny	<i>Lupinoblennius nicholsi</i>
		Blenny species	<i>Bleinnidae</i> spp.
	Skilletfish (Gobiesocidae)	Skilletfish	<i>Gobiesox strumosus</i>
	Goby (Gobiidae)	Frillfin goby	<i>Bathygobius soporator</i>
		Darter goby	<i>Ctenogobius boleosoma</i>
		Freshwater goby	<i>Ctenogobius shufeldti</i>
		Emerald goby	<i>Ctenogobius smaragdus</i>
		Highfin goby	<i>Gobionellus oceanus</i>
		Naked goby	<i>Gobiosoma bosc</i>
		Seaboard goby	<i>Gobiosoma ginsburgi</i>
		Code goby	<i>Gobiosoma robustum</i>
		Clown goby	<i>Microgobius gulosus</i>
		Green goby	<i>Microgobius thalassinus</i>
		Goby species	<i>Gobiosoma</i> spp.; <i>Microgobius</i> spp.; Gobiidae
Transient	Grunt (Haemulidae)	Barred grunt	<i>Conodon nobilis</i>
		White grunt	<i>Haemulon plumierii</i>
		Pigfish	<i>Orthopristis chrysoptera</i>
	Snapper (Lutjanidae)	Gray snapper	<i>Lutjanus griseus</i>
		Lane snapper	<i>Lutjanus synagris</i>
	Swimming crab (Portunidae)	Blue crab	<i>Callinectes sapidus</i>
		Lesser blue crab	<i>Callinectes similis</i>
		Iridescent swimming crab	<i>Portunus gibbesii</i>
		Blotched swimming crab	<i>Portunus spinimanus</i>
		Swimming crab species	<i>Callinectes</i> spp.; Portunidae
	Drum (Sciaenidae)	Silver perch	<i>Bairdiella chrysoura</i>
		Sand seatrout	<i>Cynoscion arenarius</i>
		Spotted seatrout	<i>Cynoscion nebulosus</i>
		Silver seatrout	<i>Cynoscion nothus</i>
		Weakfish	<i>Cynoscion regalis</i>
		Banded drum	<i>Larimus fasciatus</i>
		Spot croaker	<i>Leiostomus xanthurus</i>
		Southern kingfish	<i>Menticirrhus americanus</i>
		Northern kingfish	<i>Menticirrhus saxatilis</i>
		Atlantic croaker	<i>Micropogonias undulatus</i>
		Black drum	<i>Pogonias cromis</i>
		Red drum	<i>Sciaenops ocellatus</i>
		American stardrum	<i>Stellifer lanceolatus</i>
		Drum species	<i>Cynoscion</i> spp. Sciaenidae
	Porgy (Sparidae)	Sheepshead	<i>Archosargus probatocephalus</i>
		Spottail seabream	<i>Diplodus holbrookii</i>
		Pinfish	<i>Lagodon rhomboides</i>

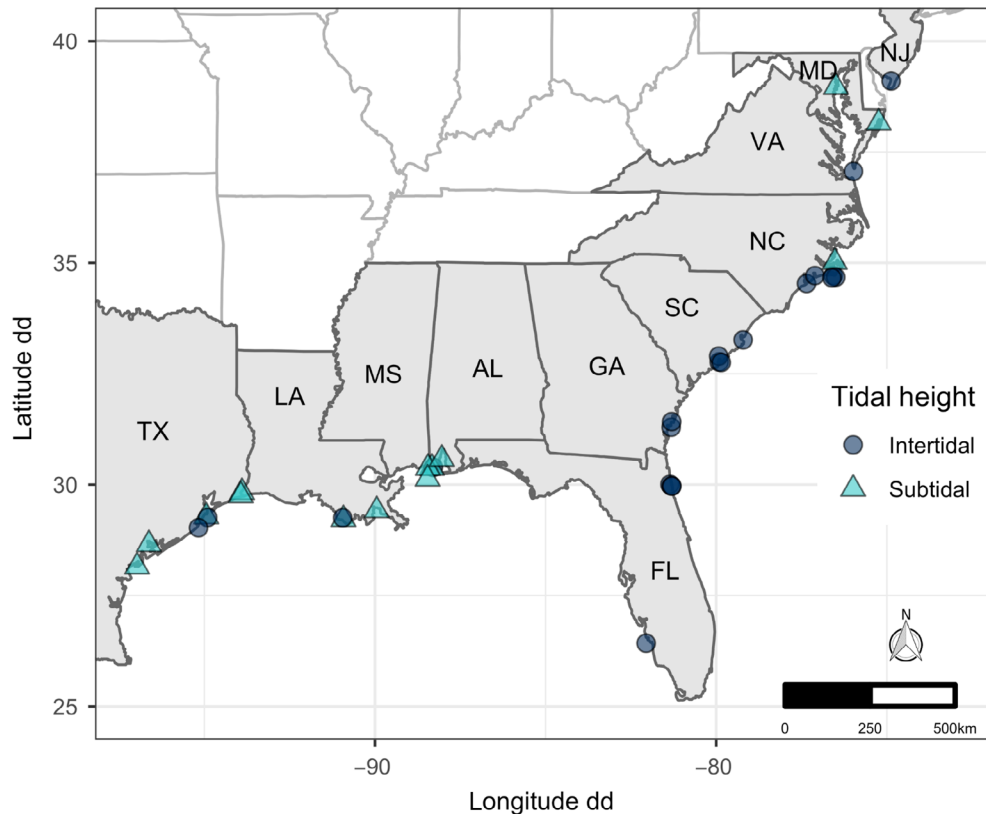


FIG. 1. Map of study sites along the Gulf of Mexico and Atlantic Coasts of the United States, with graticule intervals in decimal degrees (dd). States shaded in gray are represented in the data set. Each point represents an independent study, with shapes representing tidal zone (circles represent intertidal reefs and triangles represent subtidal reefs). Additional study attributes are listed in Appendix S1: Table S1.

CIs >0 implies that nekton recruitment was enhanced by oyster reefs, an LRR with CIs <0 implies the opposite, and an LRR with CIs that include 0 implies no difference in recruitment between oyster reef and control habitats. For each research question, we assessed data publication bias with funnel plots (Appendix S3) and data availability with mosaic and violin plots (Appendix S4).

To assess whether recruitment enhancement varied as a function of reef type (natural or restored) and nekton family, we conducted linear mixed model analyses separately for intertidal and subtidal reefs that included two categorical factors (reef type and nekton family) and their interaction as fixed effects, with study as a random effect. We conducted mixed model analyses separately by tidal zone, because subtidal and intertidal habitats harbor different nekton communities (Lehnert and Allen 2002), and subtidal and intertidal oyster reefs are distributed unevenly in our database: intertidal reefs are more prevalent on the Atlantic coast and subtidal reefs are more common in the Gulf of Mexico (Fig. 1; Appendix S1: Table S1). Furthermore, the reef characteristics in our database differed across tidal zones (Appendix S4: Figs. S1–S12). We removed any family that was represented by fewer than three independent

studies and/or fewer than 10 independent LRRs (“NA” on Fig. 2). Results of randomization and resampling in support of these criteria are presented in Appendix S5.

To evaluate the effects of restored reef characteristics (i.e., reef size, vertical relief, and age) on recruitment enhancement, we focused on restored reefs only, and performed linear mixed effect regression models with orthogonal polynomials (first and second order) for the continuous reef characteristics as fixed effects, and study as a random effect. We conducted separate analyses for each reef characteristic, nekton family, and tidal zone. We did not model families represented by fewer than three independent studies and/or 10 independent LRRs covering different values of the reef characteristics (e.g., reef sizes, vertical reliefs, or ages; “insufficient data” in Figs. 3–8), and results are not reported or plotted for models that did not converge. Because not all families were represented at all values of each reef characteristic (e.g., all vertical reliefs or sizes), we performed separate analyses for each family and included all available data (but for combined-family approaches, see Appendix S2 for methods and Appendix S5 for results). We also examined the influence of tidal elevation on recruitment enhancement for each family using linear mixed effect

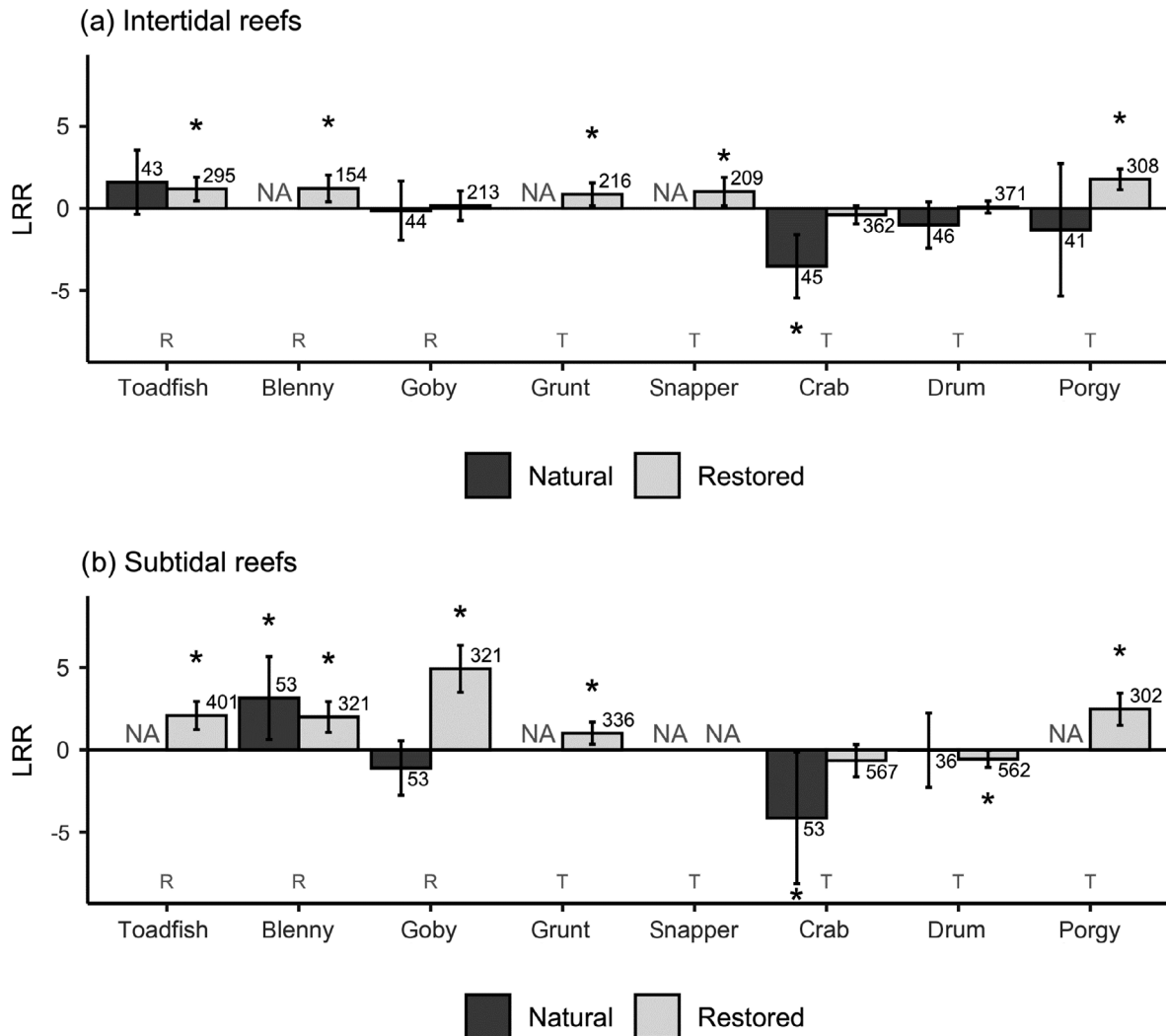


FIG. 2. (a), (b) Mean and 95% confidence intervals of the log response ratios (LRR) of nekton densities at oyster compared to unstructured sedimentary control habitats for each family (toadfish = Batrachoididae, blenny = Blenniidae, goby = Gobiidae, grunt = Haemulidae, snapper = Lutjanidae, crab = Portunidae, drum = Sciaenidae, porgy = Sparidae), at natural vs. restored reefs, for (a) intertidal reefs, and (b) subtidal reefs. Numbers indicate the total number of LRRs that contributed to the mean LRR for each family. Asterisks indicate 95% confidence intervals that do not overlap 0. NA indicates that data were insufficient to include in analyses, as there were fewer than 10 LRRs included in the mean.

regression models with orthogonal polynomials (first and second order) for tidal elevation as a fixed effect and study as a random effect (Appendix S5). Where models indicated that predictor variables are on substantially different scales (i.e., reef size) we rescaled using natural log transformation.

All models were weighted by sample size (Appendix S2). All analyses were conducted in R 3.6.1 (R Development Core Team, 2019) on the RStudio IDE 1.2.1335 (RStudio Team, 2019).

RESULTS

We extracted density or relative abundance comparisons from 28 studies (Appendix S1: Table S1) that

generated 1,820 LRRs across eight target nekton families (excluding skillefish), represented by 51 species (Table 1). Studies were distributed along the Atlantic and Gulf of Mexico coastlines from New Jersey to Texas, USA, across 25 embayments (Fig. 1). Funnel plots indicated no evidence of publication bias (Appendix S3: Fig. S1).

Restored vs. natural reefs (reef type)

Recruitment enhancement on intertidal reefs varied interactively by family and reef type (Fig. 2a; family * reef type, $F_{4, \text{hairsp}; 790} = 8.25$, $P < 0.001$). In the intertidal, recruitment was frequently enhanced on restored reefs (i.e., $\text{LRR} > 0$ for two resident families:

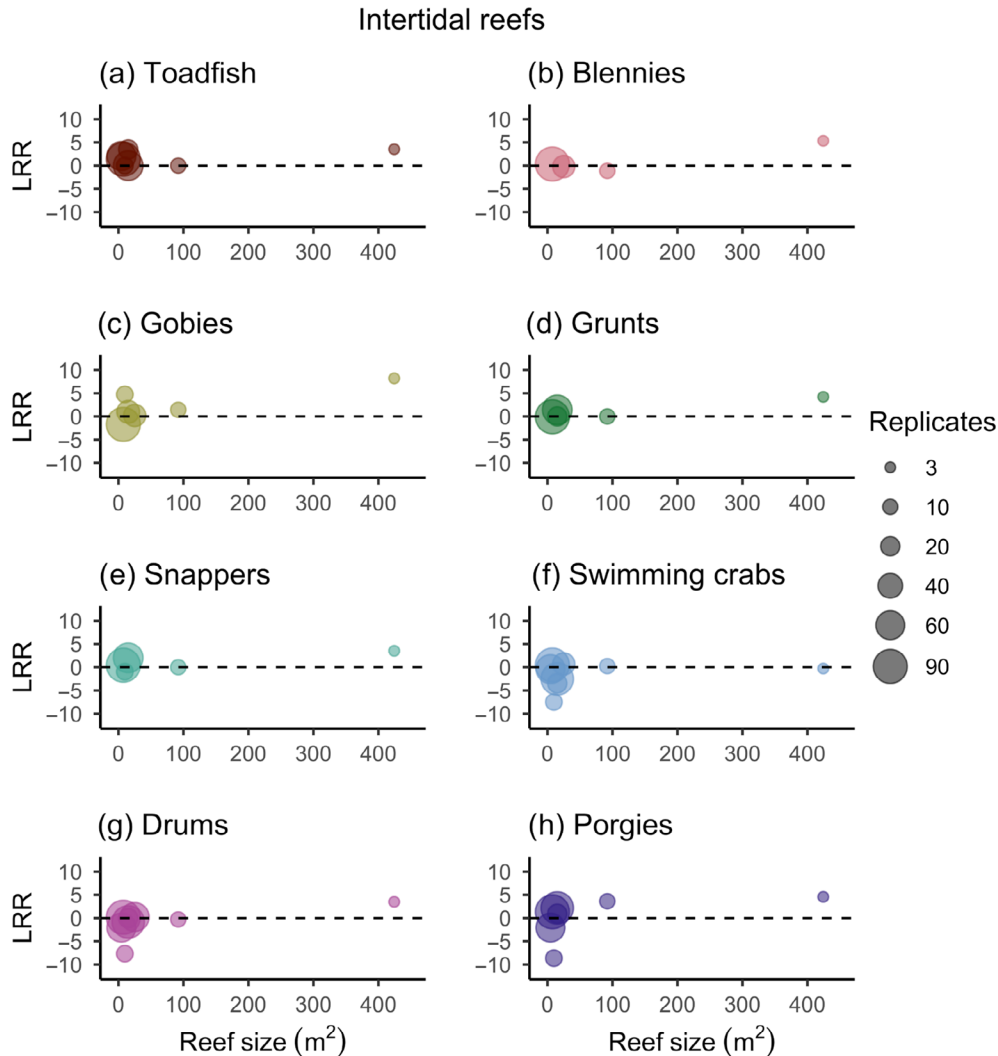


FIG. 3. (a)–(h) Variation in mean log response ratios (LRR) of nekton densities by reef size (square meters) on intertidal reefs. Point size is weighted by the number of independent replicates for each reef. The model for toadfish (a) has a singular fit and should be interpreted with caution.

toadfish and blennies and three transient families: grunts, snappers, and porgies; Fig. 2a), but not on natural oyster reefs (i.e., $LRR = 0$; Fig. 2a). Recruitment enhancement on subtidal reefs varied by family and was marginally related to reef type, but not their interaction (Fig. 2b; family, $F_{3,513} = 8.19$, $P < 0.001$; reef type, $F_{1,11} = 3.53$, $P = 0.09$; family * reef type, $F_{3,513} = 1.81$, $P = 0.15$). Five families (three resident: toadfishes, blennies, and gobies; two transient: grunts and porgies) were enhanced at subtidal restored reefs (Fig. 2b), and one resident family (blennies) was enhanced on subtidal natural reefs (Fig. 2b). Swimming crabs were more abundant on unstructured sedimentary habitat than natural reefs in both intertidal and subtidal zones (i.e., $LRR < 0$; Fig. 2a, b), though they did not differ

between restored reefs and unstructured habitat in either zone (Fig. 2a, b). In the subtidal zone, drums were more abundant on unstructured sedimentary habitat than restored reefs, but did not differ between natural reefs and controls (Fig. 2b).

Restored reef characteristics (reef size, vertical relief, and age)

Recruitment enhancement differed with reef size for only one family (blennies; Figs. 3, 4). On intertidal reefs, there was no relationship between blenny recruitment and reef size (natural log transformed). On subtidal reefs, there was a marginal U-shaped relationship between blenny recruitment enhancement and subtidal

Subtidal reefs

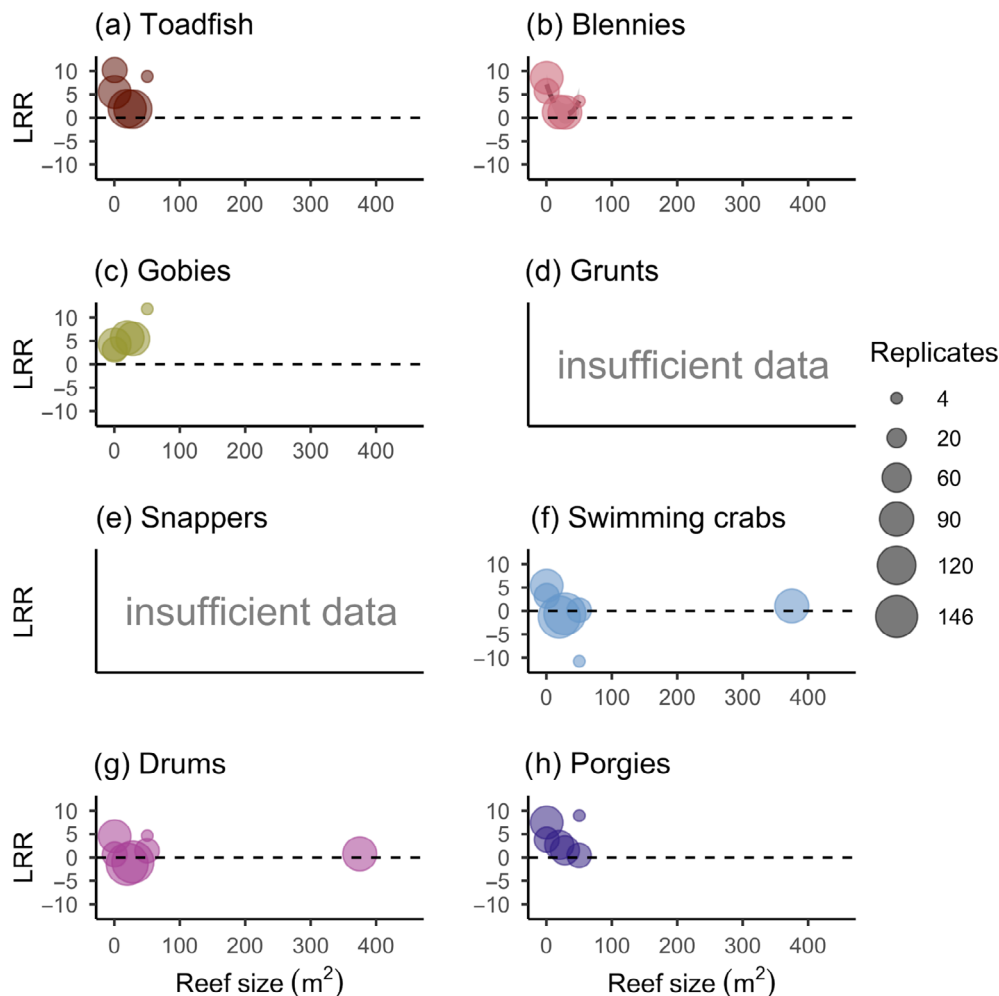


FIG. 4. (a)–(h) Variation in mean log response ratios (LRR) of nekton densities by reef size (square meters) on subtidal reefs. Studies that included multiple experiments with reefs of different sizes are assigned separate points for each reef. Point size is weighted by the number of independent replicates for each reef. For readability, mean LRRs (0.921 for toadfish, 0.679 for drums, and 1.63 for porgies) for the study with the largest subtidal reef ($>8,000 \text{ m}^2$; Appendix S1: Table S1) are not pictured. The model for gobies (c) has a singular fit and should be interpreted with caution.

reef size ($t_{54.7} = 1.78$, $P = 0.08$), with recruitment enhancement decreasing from 0.5 to 28.3 m^2 and increasing from 28.3 to 50.3 m^2 (Fig. 4b).

Recruitment enhancement of several families (grunts, drums, and blennies) varied with reef vertical relief (Figs. 5, 6). Drum enhancement varied with vertical relief on intertidal reefs in a U-shaped pattern (Fig. 5g, $t_{6.9} = 2.66$, $P = 0.03$), though a single experiment, at a vertical relief of 0.48 m with 20 independent replicates, appears to drive this relationship (Fig. 5g). Enhancement of blennies on subtidal reefs tended to decrease with increasing vertical relief (Fig. 6b; $t_{6.6} = -1.96$, $P = 0.09$). On subtidal reefs, drum enhancement decreased as vertical relief increased (Fig. 6g; $t_{7.44} = -2.52$, $P = 0.04$).

Recruitment enhancement of some families was also correlated with reef age (Figs. 7, 8). On subtidal reefs, toadfish enhancement varied with reef age in a U-shaped pattern, decreasing from reefs that were between 0 and approximately 4 yr of age, and then increasing from reefs aged approximately 4–6 yr ($t_{77.6} = 2.43$, $P = 0.02$; Fig. 8a). Drum enhancement responded similarly to reef age on subtidal reefs ($t_{126.8} = 7.25$, $P < 0.0001$; Fig. 8g), decreasing from 0- to 4-yr-old reefs, then increasing on 6-yr-old reefs (Fig. 8g). Porgy enhancement on subtidal reefs also varied similarly with reef age ($t_{56.2} = 2.56$, $P = 0.01$; Fig. 8h), decreasing on reefs between 0 and 3 yr old, and then increasing on 6-yr-old reefs (Fig. 8h). Porgy enhancement on intertidal reefs tended to vary with reef age in a hump-shaped pattern (Fig. 7h,

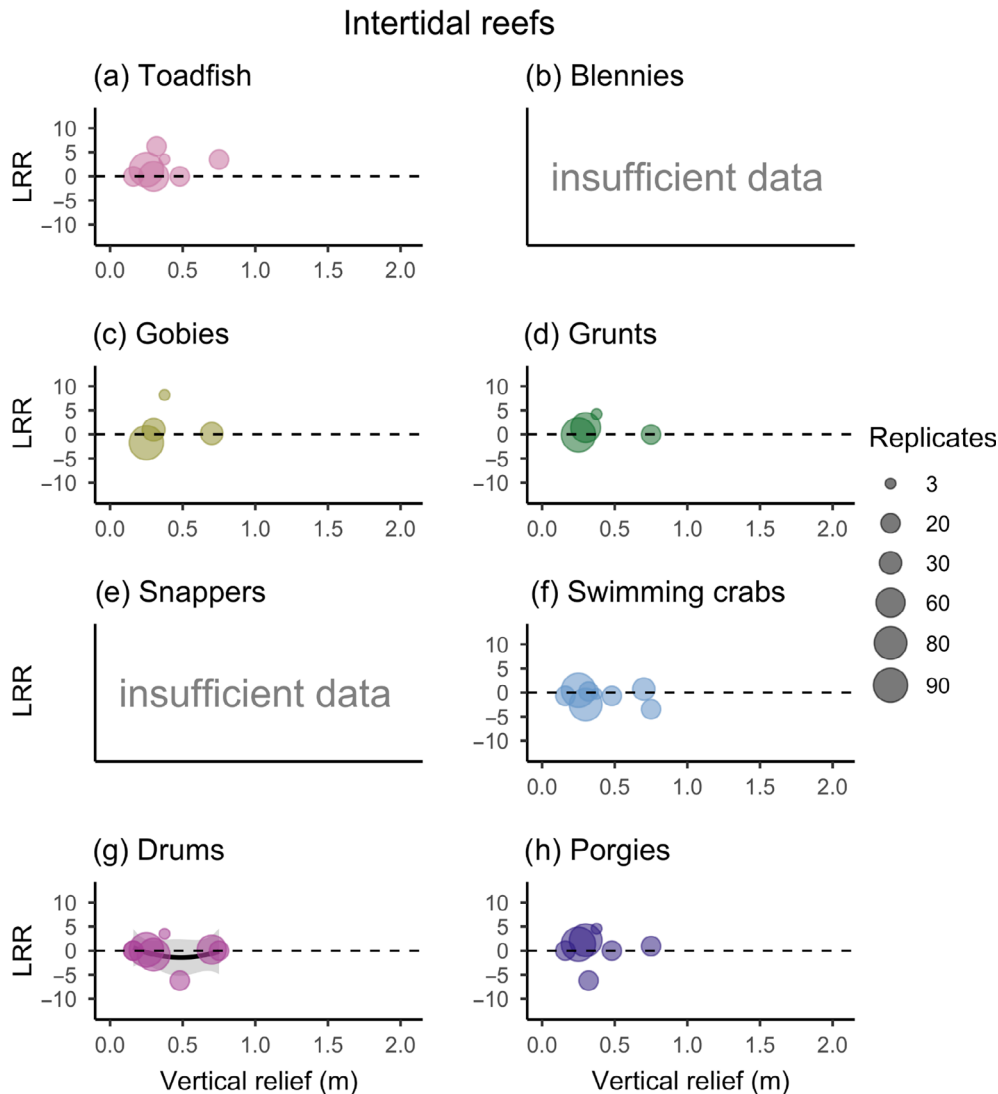


FIG. 5. (a)–(h) Variation in mean log response ratios (LRR) of nekton densities by vertical relief (meters) on intertidal reefs. Studies that included multiple experiments with reefs of different reliefs are assigned separate points for each reef. Point size is weighted by the number of independent replicates for each reef. Plots with a solid trend line and 95% confidence intervals (gray areas) indicate a significant effect of vertical relief from single-family mixed model analysis. The model for grunts (d) has a singular fit and should be interpreted with caution.

$t_{17,7} = -2.04$, $P = 0.06$), with recruitment enhancement increasing from 0 to 7 yr, and decreasing from 7 to 13 yr.

DISCUSSION

Our analyses confirmed that both natural and restored oyster reefs enhance nekton recruitment, and we further demonstrate that the magnitude of this enhancement is as strong or stronger on restored reefs as natural reefs for five nekton families (Fig. 2). The magnitude of enhancement also varied by family and tidal zone, and key characteristics of restored reef design (i.e., reef size, reef vertical relief, and reef age) also influenced

recruitment enhancement of fishes and swimming crabs. Nekton recruitment enhancement tended to increase with intertidal reef size, though increases in vertical relief decreased enhancement, particularly at subtidal reefs. Enhancement of many nekton species occurred immediately, though enhancement of porgies peaked around 6 yr on intertidal reefs, and enhancement of toadfish, drums, and porgies was lowest at intermediate ages (about 3–4 yr) on subtidal reefs. Further data are needed to examine whether recruitment enhancement is sustained over longer time periods.

Review of past restoration projects suggest that enhancement of nekton recruitment is generally greater on restored than on natural reefs. The enhancement by

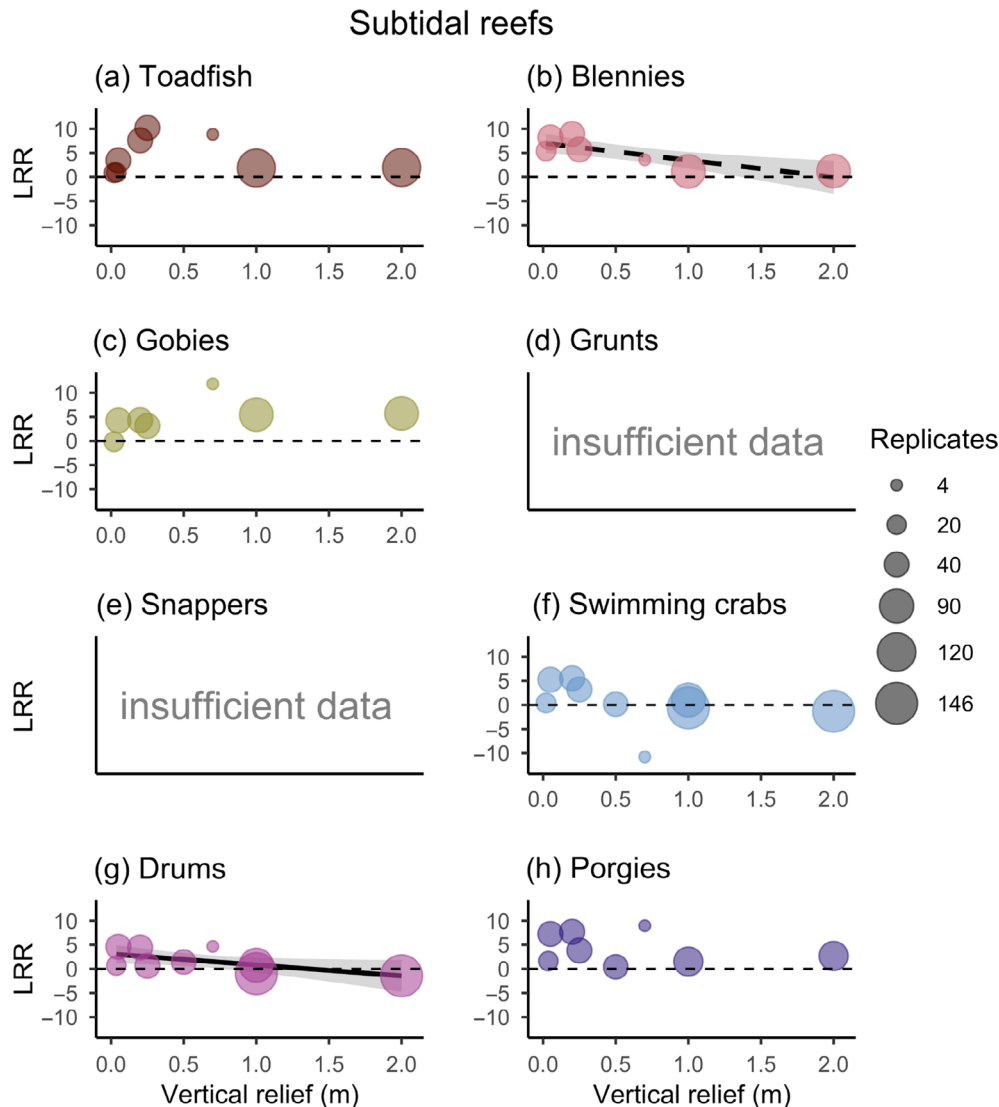


FIG. 6. (a)–(h) Variation in mean log response ratios (LRR) of nekton densities by vertical relief (meters) on subtidal reefs. Studies that included multiple experiments with reefs of different reliefs are assigned separate points for each reef. Point size is weighted by the number of independent replicates for each reef. Plots with a solid trend line and 95% confidence intervals (gray areas) indicate a significant effect of reef age from single-family mixed model analysis. Dashed lines indicate vertical relief effects for which $0.05 \leq P \leq 0.1$.

restored reefs supports earlier findings that nekton communities respond rapidly to oyster reef restoration efforts (Lenihan et al. 2001, Grabowski et al. 2005, La Peyre et al. 2014) and highlights the utility of reef restoration as a technique to recover nekton abundances. We do not know why restored reefs more consistently augmented nekton than natural reefs, but past or current exposure of natural reefs to destructive harvesting practices that reduced their habitat quality may have contributed to this difference. Given the dramatic losses of oyster populations to overharvesting and other contributing factors (reviewed in Kirby 2004), remaining natural reefs may be degraded and exhibit reduced

function (zu Ermgassen et al. 2012, 2013), whereas restored reefs are often protected from harvest (e.g., Dunnigan 2015). Only 10 of 29 studies in our analysis reported susceptibility to harvest, with even fewer providing specific harvest methods and amounts, precluding an analysis of the effects of harvest on nekton recruitment enhancement in this study.

Habitat patch size can mediate the population dynamics of mobile species (Hanski 1999): Larger habitat patches have lower metapopulation extinction rates (MacArthur and Wilson 1967, Hanski 1999) and alleviate negative edge effects in fragmented landscapes (Ries et al. 2004). Thus, we expected enhancement of fish and

Intertidal reefs

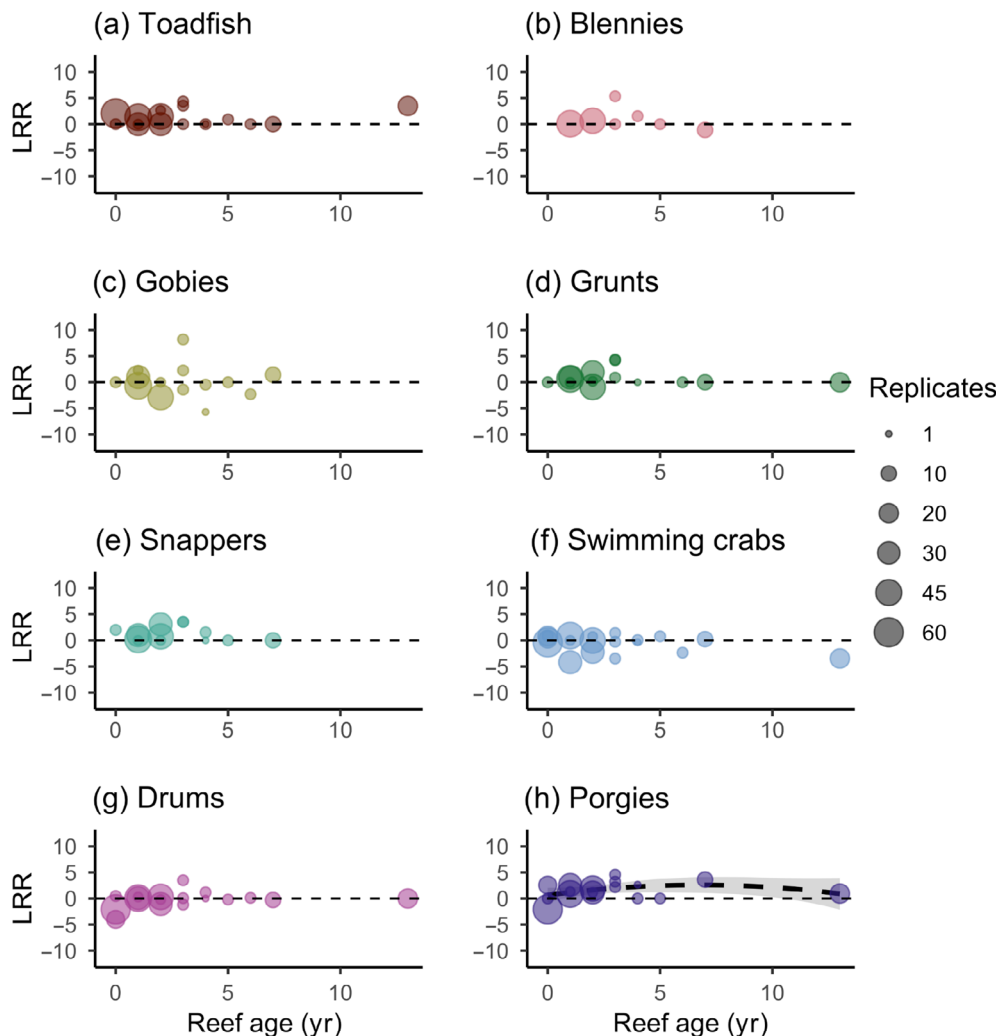


FIG. 7. (a)–(h) Variation in mean log response ratios (LRR) of nekton densities by reef age (years) on intertidal reefs. Studies that included multiple experiments with reefs of different ages are assigned separate points for each reef. Point size is weighted by the number of independent replicates for each reef. Plots with a dashed trend line and 95% confidence intervals (gray areas) indicate a reef age from single-family mixed model analysis for which $0.05 \leq P \leq 0.1$. The model for toadfish (a) has a singular fit and should be interpreted with caution.

mobile crustacean recruitment to increase with restored reef (patch) size. Our analyses of individual families were not significant, but there were positive trends at intertidal reefs, and our combined-family analysis provided additional support that recruitment enhancement increases with intertidal reef size (Appendix S5: Fig. S2a). For subtidal reefs, the influence of reef size was taxon-dependent (Appendix S5: Fig. S2b), consistent with findings from the habitat fragmentation literature (Eggleston et al. 1999, Johnson and Heck 2006). Relationships between fish recruitment enhancement and reef size may be more consistent within a region than across regions. For instance, the density of commercial fishes within marine reserves increased with reserve

size when marine reserves within a single region were compared to unprotected spaces (Edgar and Barrett 1997, Claudet et al. 2008), yet Lester et al. (2009) found no relationship between density enhancement and MPA size when synthesizing MPAs globally. Additionally, an overrepresentation of small reef sizes in our analysis, as in the global analysis of MPAs (Lester et al. 2009), may have hindered our ability to detect an impact of habitat size. Reefs in our analysis ranged in size over four orders of magnitude (0.45 to $>8,000$ m²), though greater than 70% of restored reefs that reported sizes were ≤ 50 m² (Appendix S4: Fig. S3). Given the magnitude of degradation that has occurred in many estuaries in the United States and elsewhere, extensive restoration efforts are

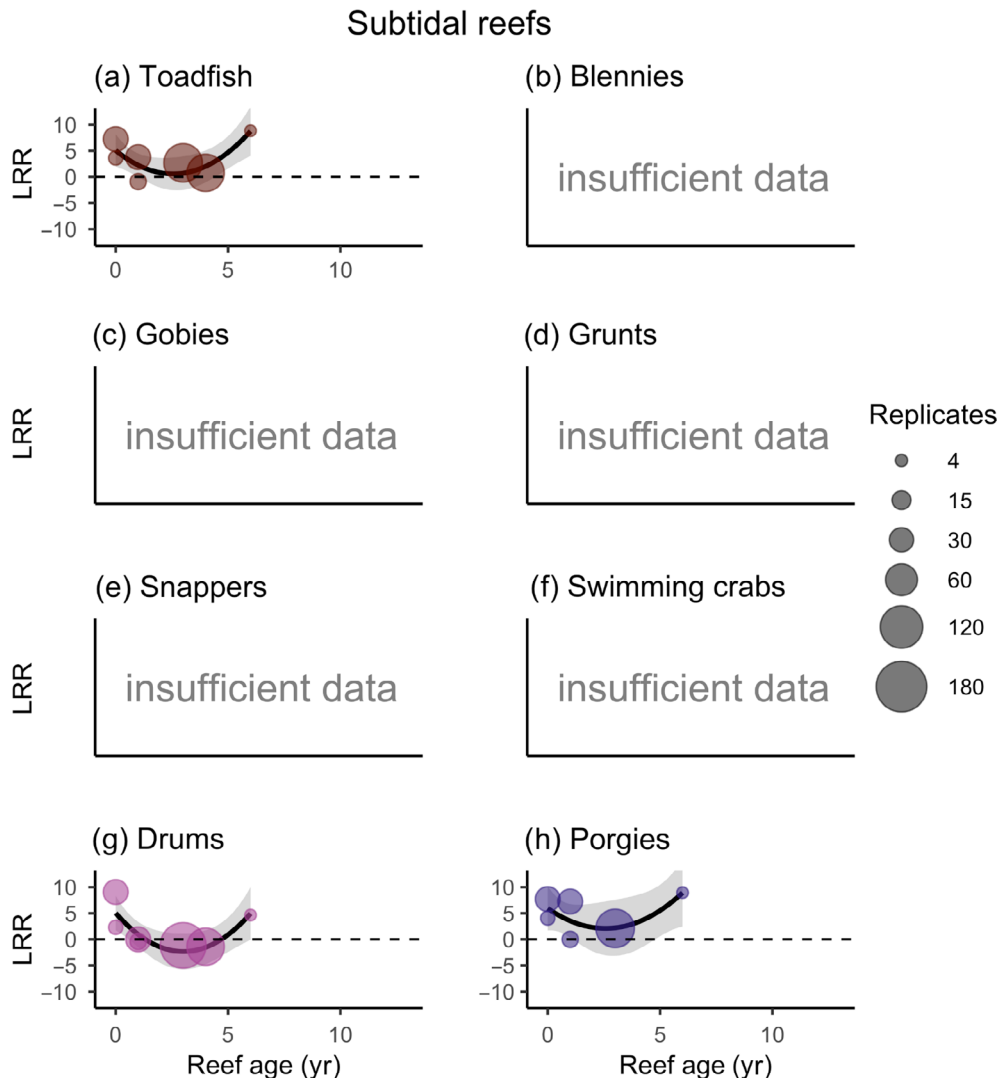


FIG. 8. (a)–(h) Variation in mean log response ratios (LRR) of nekton densities by reef age (years) on subtidal reefs. Studies that included multiple experiments with reefs of different ages are assigned separate points for each reef. Point size is weighted by the number of independent replicates for each reef. Plots with a trend line and 95% confidence intervals (gray areas) indicate a significant effect of reef age from single-family mixed model analysis.

necessary. Studies that include larger (i.e., ~100–1,000 m²) restored reefs are needed to define the relationship between reef size and recruitment enhancement better and to determine whether there are optimal or minimum sizes necessary to benefit target species.

The vertical relief of a reef can influence oyster survival (Taylor and Bushek 2008, Colden et al. 2017). We expected that greater relief would also increase augmentation of fish and mobile crustacean abundances, as taller reefs are less likely to be influenced by bottom-water hypoxia (Lenihan et al. 2001), more likely to avoid sedimentation and sustain oyster populations (Taylor and Bushek 2008, Colden et al. 2017), and potentially provide greater reef complexity and refuge quality. Recruitment enhancement of individual families did not vary

consistently with vertical relief on intertidal reefs, which may be more strongly influenced by seldom-reported tidal emersion (determined by a combination of vertical relief, tidal elevation, and tidal range in the embayment; Fodrie et al. 2014, Walles et al. 2016) than vertical relief alone. On subtidal reefs, we found evidence that increasing reef vertical relief decreased recruitment enhancement of two families. Perhaps greater vertical relief on these reefs provided more accessible area to support a wider variety of predators, leading to these negative relationships. Prior studies have described thresholds in initial height of subtidal restored oyster reefs (~0.2–0.45 m) for the persistence of oyster growth (Lenihan 1999, Powers et al. 2009, Schulte et al. 2009, Lipcius et al. 2015, Colden et al. 2017, Grizzle and Ward 2017). Our results

suggest a threshold under which nekton recruitment is enhanced (<1 m) by greater reef height; from 0 to 1 m reef height, small gains in reef height can lead to substantial increases in nekton recruitment enhancement until they reach a maximum and then decline above around 1 m reef height. Thus, designing reefs to optimize oyster recruitment will likely influence enhancement of fish families. Although the mechanisms driving this relationship are not clear, if reefs are preferentially restored in areas that are not typically subjected to hypoxia, then reefs with higher vertical relief may not be necessary. Given that constructing high-relief reefs is more expensive and requires greater amounts of shell material, restoration decision makers could increase the aerial extent of restored reefs in areas where low-relief reefs will be effective.

Variability in recruitment enhancement across families may also be attributable to their degree of reef fidelity (e.g., reef residents vs. transients). Oyster habitat is considered an essential habitat for resident species long after initial recruitment (Coen et al. 1999, Harding and Mann 2000), whereas transient species spend less time on reefs and are more widely distributed across multiple structured habitats (Harding and Mann 2001). In our database, some intriguing potential differences between residents and transients emerged. Each resident species we examined demonstrated recruitment enhancement, whereas only two families of transient species were enhanced (grunts and porgies), and two demonstrated lower recruitment at some oyster reefs (drums and crabs; Fig. 2). Drums are transient among estuarine habitats and utilize oyster reefs over nonvegetated habitat in some studies (Lenihan et al. 2001, Kingsley-Smith et al. 2012), though they utilize marsh edges and subtidal areas over oyster reefs in other studies (Stunz et al. 2010). Low or no recruitment of drums to oyster reefs may therefore reflect functional redundancy of structured habitats (Grabowski et al. 2005, Geraldini et al. 2009) and/or alternative habitat selection, particularly in intertidal zones where alternative structured habitats are often readily available. Understanding the influence of coastal habitat landscapes, rather than just individual habitats, on faunal abundance is a key research priority for informing habitat restoration efforts (Gilby et al. 2018). In the case of the Blue crab (*Callinectes sapidus*), previous studies found blue crab to be enhanced by oyster reef in the Gulf of Mexico, but not in the Atlantic coast (zu Ermgassen et al. 2016). It is possible that by using data from both regions in this analysis, this regional enhancement was masked in our results.

Several other factors not included in our analysis likely influence nekton recruitment enhancement by oyster reefs. For instance, nekton densities on oyster reefs, including many of our target families, fluctuate seasonally (Lehnert and Allen 2002, Shervette and Gelwick 2008). Many studies in our synthesis reported densities pooled across repeated time points, precluding an analysis of seasonality. Further, our synthesis included studies conducted across

different latitudes where seasonality effects may differ. Although we were not able to evaluate the effects of seasonality explicitly, assuming nekton do not change their relative use of oyster vs. unstructured habitats by season, this omission should not confound our results.

We are often forced to make assumptions about whether ecosystem services from restored habitats are consistent over time because of the lack of temporal data on service delivery (Barbier et al. 2011, Grabowski et al. 2012). Although many studies reviewed in this meta-analysis have documented that fish and invertebrate communities respond quickly to restoration efforts, ecological theory predicts that recruitment enhancement will vary through time. For example, as restored reefs age, we expect their associated communities will undergo succession (Connell and Slatyer 1977, Manley et al. 2010, Quan et al. 2012). Recruitment was reported at intertidal restored reefs 0–13 yr old in our study. Though reef age was not a strong predictor of recruitment enhancement in our analyses, porgies provided some evidence for a maximum recruitment enhancement at intermediate reef ages, whereas recruitment enhancement data for intertidal reefs aged 8–12 yr are not available for any family and represent a data gap (Fig. 7). For restored reefs in the subtidal zone, a minimum recruitment enhancement value at reefs aged 3–4 yr were represented by data from a single study that reported annual recruitment on reefs >1 yr old (Lenihan et al. 2001). Additional studies are needed to provide further evidence for this relationship and address the data gap beyond 6 yr old for subtidal reefs. Several studies pooled densities across years (4 of 21 studies that reported reef construction date; Appendix S1: Table S1), indicating that services were consistent over the time these studies were sampled (e.g., La Peyre et al. 2014). However, the limited data for nekton recruitment enhancement over a decadal timescale (but see Ziegler et al. 2018) challenges our ability to project whether ecosystem service delivery remains constant or varies temporally at the scale of several years to decades. Thus, long-term studies investigating the degree to which nekton enhancement varies with reef age would be particularly useful.

Reef habitat complexity (the physical structure of an environment) is predicted to increase with reef age as oysters settle atop one another and grow vertically in the water column (Bahr and Lanier 1981, Grabowski et al. 2005, Rodriguez et al. 2014, Ziegler et al. 2018). Such habitat complexity has been linked to habitat quality for associated communities, with interstitial refuges that decrease interaction strengths (i.e., predation, Humphries et al. 2011) and increase rugosity, which alters water flow and enhances larval settlement opportunities (Breitburg et al. 1995). Oyster density and biomass are often used as quantitative measures of reef complexity (Baggett et al. 2015); thus, we expected augmentation of fish and mobile crustaceans to increase with oyster density and biomass on oyster reefs, even in the absence of explicit information about reef age. However, we could not

assess nekton responses to oyster density, as only 5 out of the 22 studies of restored reefs in our database reported oyster density, and fewer yet reported biomass.

Syntheses across restoration efforts can identify potential influences of reef characteristics on recruitment enhancement, determine restoration designs that are most beneficial to target species, and help assess trade-offs among targeted services. Future experiments that manipulate multiple restoration design factors orthogonally will further our understanding and predictive capacity of how they potentially interact to influence ecosystem service delivery by restored habitats, including nekton recruitment enhancement at oyster reefs. Such manipulations are difficult at scales relevant for restoration, so data syntheses are also a critical tool for advancing restoration science. Future synthesis efforts will be facilitated by consistent reporting across restoration efforts; therefore, we highlight the Baggett et al. (2015) recommendations for reporting universal oyster reef metrics (project footprint and reef area, reef vertical relief, oyster density, and oyster size-frequency distribution) and environmental variables (water temperature, salinity, and for subtidal reefs, dissolved oxygen) from all oyster restoration projects, in addition to densities of target species when reefs are intended to benefit nekton. We also support the Walles et al. (2016) recommendation to add tidal emersion for intertidal reefs to this set of recommendations, and we further suggest that tidal elevation, reef age at the time of sampling, and exposure to oyster harvest be reported for effective comparisons across restored reefs. Given the magnitude of restoration needed to recover lost ecosystem services from biogenic habitats, experimental and synthetic efforts aimed at guiding restoration decision making are critical.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2340/full>

OPEN RESEARCH

Citations for the studies included in this synthesis are available in Appendix S1. Data (Davenport et al. 2021) are available from the Biological and Chemical Oceanography Data Management Office (BCO-DMO). <https://doi.org/10.26008/1912/bco-dmo.845755.1>