A meta-analytical review of the effects of environmental and ecological drivers on the abundance of red snapper (*Lutjanus campechanus*) in the U.S. Gulf of Mexico

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REVIEWS

A meta-analytical review of the effects of environmental and ecological drivers on the abundance of red snapper (*Lutjanus campechanus*) in the U.S. Gulf of Mexico

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Abstract We conducted a meta-analysis to summarize current knowledge on the effects of environmental and ecological drivers on the abundance of red snapper (*Lutjanus campechanus*) within the U.S. Gulf of Mexico. We reviewed 1252 published research articles and extracted or calculated effect sizes for 12 drivers from 82 independent studies within 26 articles that met our inclusion criteria. We used a fixed-effect model to calculate the absolute value of the mean effect size of each driver by age class studied and pooled across age classes to estimate effects on the overall abundance of red snapper. Habitat complexity and intra-specific competition had large effects on overall abundance and juvenile abundance, while habitat type and protection from predators showed medium to large effects on age 0 recruits and juvenile red snapper, and the mean effect of all drivers studied for adult red snapper were small or had no effect on abundance. Our results provide systematic support for the role of density-dependent mechanisms (habitat quality and availability, competition, predation) in shaping the regional abundance of red snapper, particularly during the juvenile stages. Sensitivity analyses indicated that issues with non-independence

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(e.g. within-article correlation), between-study heterogeneity, and publication bias influenced the magnitude and certainty of effect size estimates in a subset of drivers. Thus, our meta-analytical review also highlights the need for more empirical research on certain drivers (e.g. temperature, hypoxia) to improve our understanding of the factors that shape the regional abundance of red snapper.

Keywords Meta-analysis · *Lutjanus campechanus* · Red snapper · Ecological drivers · Density-dependence

Introduction

The abundance and distribution of marine fishes are influenced by a suite of environmental and ecological factors. Water temperature determines the broader geographic range of most species, with finer scale patterns in relative abundance modulated by life history traits that have evolved in response to habitat features, biotic interactions, and biophysical and biogeochemical processes that operate at various spatial and temporal scales to generate environmental gradients (Bellwood and Wainwright 2002; Guisan and Thuiller 2005). Life cycles in marine fishes are typically characterized by discrete stages (e.g. recruits, juveniles, adults) that exhibit marked differences in their sensitivity to environmental conditions (Pörtner and Peck 2010; Asch and Erisman 2018) and responses to ecological factors such as habitat availability, predation, and competition. Therefore, the effects of environmental and ecological drivers on specific life stages can be estimated from observed changes in abundance and distribution patterns in response to variations in driver conditions (Werner and Gilliam 1984; Dahlgren and Eggleston 2000; Grober-Dunsmore et al. 2007).

Understanding the environmental and ecological factors that shape the abundance of exploited fish populations and quantifying the magnitude of their effects is critical for the management of recreational and commercial marine fisheries. Fishing can amplify the response of fish populations to environmental stochasticity by increasing variability in population size, which heightens the probability of stock collapse (Hsieh et al. 2006; Anderson et al. 2008; Kirby et al. 2009; Hidalgo et al. 2011). Furthermore, overfishing and environmental change can trigger transformations in species interactions that alter the dynamics of entire ecosystems (Botsford et al. 1997; Travis et al. 2014). Information on the effects of environmental and ecological factors allows fisheries scientists and resource managers to better predict how stocks may respond to various stressors such as fishing, episodic disturbances such as hurricanes or harmful algal blooms, along with regional, seasonal (e.g. hypoxia), annual, and long-term (e.g. climate change) variations in environmental conditions (Craig 2012; Karnauskas et al. 2015). Such information is particularly important for rebuilding plans of overfished stocks in which the response rate to management actions may depend on how well those management actions protect areas (e.g. essential fish habitat), periods (e.g. spawning seasons), and life stages (e.g. juveniles) that are highly sensitive to environmental variability or dependent upon specific ecological (e.g. predator–prey) interactions (Link 2002; Shelton et al. 2006).

The red snapper (*Lutjanus campechanus*) is a large-bodied (up to 1 m in total length and 22.8 kg in body mass), relatively long-lived (up to 57 years) reef fish whose center of abundance and distribution is the U.S. Gulf of Mexico (GOM), where it inhabits coastal to offshore waters from depths of 10 to 190 m (Patterson et al. 2007; Robertson and Van Tassell 2012). An economically important species, red snapper has been highly exploited since the late 1800 s in the GOM, where it supports a large-scale, commercial fishery and contributes to a multi-billion-dollar recreational fishing industry (Hood et al. 2007; Cowan et al. 2011; Rindone et al. 2015). The red snapper population in the GOM was severely depleted from the 1950 s through

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the late 1980 s as fishery landings and shrimping effort (associated with juvenile bycatch) increased, reaching record lows of 5% of historical abundance by 1990 (Goodyear 1995; Porch 2007; Cass-Calay et al. 2015). However, the implementation of numerous regulations to reduce fishing effort, catch, and juvenile bycatch mortality has led to gradual improvements in the status of the population (SEDAR 2013). The most recent assessment, completed in May 2018, determined the stock is rebuilding, is no longer overfished, and overfishing is not occurring (SEDAR 2018).

Due to its abundance in coastal waters and importance to regional fisheries, a wealth of information exists on the life history, ecology, population dynamics, and distribution patterns of red snapper within the GOM (e.g. Render 1995; Patterson et al. 2007; Gallaway et al. 2009). A great deal of research has focused on elucidating relationships between one or more environmental factors (e.g. habitat type and complexity, water temperature, salinity, depth, dissolved oxygen) or ecological factors (e.g. predation, intraspecific competition) and the abundance and distribution of juveniles, adults, or both across a wide range of spatial and temporal scales (e.g. Gallaway et al. 1999; Rooker et al. 2004; Piko and Szedlmayer 2007; Mudrak and Szedlmayer 2012; Switzer et al. 2015; Bolser et al. 2020). Moreover, a few articles have combined information from published literature, fishery-dependent and fishery-independent monitoring programs, and other sources to forecast or map regional patterns in red snapper abundance and distribution in relation to various environmental and ecological parameters to inform assessment, monitoring, and management of the fishery (e.g. Liu et al. 2016; Karnauskas et al. 2017; Dance and Rooker 2019). However, available scientific information has yet to be synthesized into a systematic review of the environmental and ecological factors that determine the abundance of red snapper in the GOM and a quantitative evaluation of their average effects (i.e., a meta-analysis) on different life history stages of the species.

We conducted a meta-analysis of the existing scientific literature to evaluate the average effects of studied environmental and ecological drivers on the abundance of red snapper in the GOM. A meta-analysis is a powerful statistical methodology for combining the magnitude of the outcomes (effect sizes) across independent studies on the same topic in order to draw general conclusions and evaluate the consistency among study findings (Hedges and Olkin 1985). This systematic approach follows the philosophy of ‘Effective Thinking’ (Nakagawa and Cuthill 2007), in which emphasis is placed on the interpretation of the average effect size in terms of biological significance rather than a reliance on statistical significance to generate a more objective and informative summary. We estimated the magnitude of the mean effect size of each environmental and ecological driver across all age classes to summarize their effects on the overall abundance of red snapper. We also calculated mean effect sizes separately by age class (age 0, age 1, juveniles overall, adults) due to known ontogenetic shifts in habitat and differences among life stages in their sensitivity to environmental conditions. Sensitivity analyses on a subset of the data were combined with qualitative examinations of metadata attributes (e.g. study location, effect size metric) to: (1) assess the quality and precision of the effect size estimates and the certainty of our conclusions; (2) identify potential issues related to non-independence, heterogeneity, and bias; and (3) and summarize opportunities for future research. Finally, we discuss our results in light of other empirical studies of environmental and ecological drivers of red snapper abundance as a means to contextualize them within the broader understanding of factors thought to shape the population dynamics of red snapper within the region.

Materials and methods

Literature search and selection criteria

We conducted a systematic and replicable literature search following best practices (Côte et al. 2013; Nakagawa et al. 2017) to identify scientific research that has examined the effects of various environmental and ecological drivers on the abundance of red snapper within the GOM. Our search involved three online databases on 4 June 2018: The Institute for Scientific Information’s Web of Science (WOS), Google Scholar, and Proquest. We used the following four sets of search terms within each database: (1) “red snapper AND abundance”; (2) “red snapper AND distribution*”; (3) “red snapper AND habitat*”; and (4) “red snapper AND dynamic*”. For the Google Scholar database, we reviewed only the first 1000 hits.

We then combined the resulting list of unique references from each database into a single database for further review and consideration of inclusion within the final meta-analysis (Supplementary Material 1).

Each *article*, which for the purpose of this manuscript is defined as an individual peer-reviewed publication or technical report, was initially screened by at least two reviewers. In order to be considered for inclusion, each article had to contain at least one *study* with empirical data on a metric of mean abundance (e.g. density) of red snapper from the Gulf of Mexico. We defined a *study* as a unique analysis within a particular article. The study must have compared the abundance metric in relation to a type of environmental (e.g. temperature, depth, habitat type) or ecological (e.g. protection from predators, intraspecific competition) driver, and the estimated mean abundance must have been measured under two or more conditions of the driver (e.g. shallow vs deep or along a depth gradient). The study was also required to include data on sample size for each condition of the driver, and mean abundances either had to be provided directly in the text, within a data table, or within a figure from which they could be extracted with a graphing program. When not provided directly, the data needed were extracted from graphs within an article using the GetData Graph Digitizer program (http://getdata-graph-digitizer.com/index.php).

To facilitate a replicable and transparent screening and inclusion process, we generated the following protocol comprised of seven sequential criteria to eliminate articles and generate the final list of articles and studies for inclusion in the meta-analysis: (1) duplicate article titles found within the initial list when search results from all three databases were compiled; (2) article titles that were obviously unrelated to the general subject or topic; (3) articles that did not include any specific mentioning of red snapper in the title, abstract, text, figures, or tables (i.e. 'wrong species'); (4) articles that may have contained relevant information on red snapper, but the studies were performed outside the Gulf of Mexico (e.g. south Atlantic coast of the U.S.); (5) articles and studies lacking species-specific data, analyses, results, or text on a measure of abundance of juvenile or adult red snapper in the GOM in relation to an environmental or ecological driver. For example, a few articles contained only information on the mean abundance of all fish species combined in relation to one or more environmental drivers; (6) modeling articles that generated results on the abundance of red snapper in relation to environmental or ecological drivers based on empirical data from other studies were also excluded from the meta-analysis to avoid pseudo-replication (i.e. including the same empirical data sets multiple times in our analysis); (7) articles that did not report an effect size or did not provide sufficient information in the text, data tables, or figures to calculate one. All articles included in the initial list were screened a second time by two or more reviewers to ensure no relevant articles that met our inclusion criteria were excluded from the meta-analysis.

While recognizing their value to identify essential fish habitat for red snapper, we did not include data from studies within articles that compared estimated rates of mortality, reproduction, survivorship, or growth in relation to environmental or ecological factors (e.g. Minello 1999; Wells et al. 2008) in order to maintain the scope of this investigation on drivers of abundance patterns. For similar reasons, we excluded articles and information related to the impacts of fishing on red snapper abundance and distribution due to the inherent complexity in clearly disentangling the effect of fishing from environmental and ecological drivers: a task more appropriate for formal stock assessments. However, study data from one article (Wells et al. 2008) that compared fish abundance on trawled sites versus untrawled sites were included, because trawling was considered a form of habitat disturbance in this context. We also excluded studies and articles that produced abundance data in response to environmental or ecological drivers based solely on laboratory experiments (e.g. Bailey et al. 2001).

Calculation of effect sizes

Hedges' *d* is a standardized measure of the difference between means, which allows studies to be compared even if they were measured on different scales (Hedges and Olkin 1985). We chose Hedges' *d* as the standardized effect size measure for the relationship between each environmental or ecological driver and fish abundance, because most data were reported as group means, so this measure served to minimize the number of effect size measures that needed to be converted from other metrics (e.g. *r*, *F*; see below). This measure is particularly useful for estimating overall effects when there are few (< 10) studies, as it is not affected by unequal sampling variances in the paired groups and includes a correction factor for small sample sizes (Rosenberg et al. 2013). Hedges' d is the most commonly used metric of effect size in published meta-analyses in ecology and evolution (Field and Gillett 2010; Koricheva et al. 2013; Rosenberg et al. 2013). Hedges' d is calculated as follows:

$$d = \frac{u_1 - u_2}{SD_{pooled}} \cdot J \tag{1}$$

where u_1 is the mean of fish abundance under one environmental/ecological condition, u_2 is the mean in the comparison condition, SD_{pooled} is the pooled standard deviation, and J is a correction for small sample sizes. SD_{pooled} is calculated as:

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

where n_1 and n_2 are the sample sizes, and s_1 and s_2 are the standard deviations of u_1 and u_2.J, the correction for small sample size, is given as:

$$J = 1 - \frac{3}{4 \cdot (n_1 + n_2 - 2) - 1} \tag{3}$$

To calculate the variance for Hedges' d we used v_d:

$$v_d = \frac{n_1 + n_2}{n_1 \cdot n_2} + \frac{d^2}{2 \cdot (n_1 + n_2)} \tag{4}$$

Original data on effect sizes were also provided in five other formats: r, r^2, X^2, F and H. For those studies, we used the equations provided by Lajeunesse et al. (2013) to calculate d by converting from other formats.

For each study within an article that met our selection criteria, we extracted the data needed to calculate effect size and variance (see Eqs. 1–4). In cases where a single study included comparisons of mean fish abundance among multiple groups or treatments within a specific driver type, we calculated the effect size of each individual pairwise comparison and then calculated the average effect size among them to represent the driver and the study (Cooper 1998; Card 2012; Scammacca et al. 2014).

Several studies have shown a non-linear relationship between environmental gradients and red snapper abundance, such that an optimal condition exists between abundance and factors such as salinity, temperature, and depth (e.g. Gallaway et al. 1999; Reeves et al. 2018; Dance and Rooker 2019). Moreover, the range of environmental or ecological conditions considered (e.g. depth range; specific habitat types; salinity ranges) varied considerably among studies and articles, which produced a mix of positive and negative effect sizes in a somewhat arbitrary manner (e.g. negative effect of depth at 150–300 m versus positive effect of depth at 20–150 m). To account for this variation among studies and estimate the average magnitude of effect sizes, we used the absolute value of Hedges' d when it was converted from another metric. When Hedges' d was calculated directly from data extracted from the text, table, or graph within an article, we selected u_1 as the larger value in comparison with u_2, which resulted in d being a positive value. The use of $|d|$ tends to inflate effect sizes, particularly when study variances are high relative to the true variances (Fritz et al. 2012; Koricheva et al. 2013). However, this approach is valuable when the variables under study have intrinsic meaning and for studies in which the directionality of the phenomena is arbitrary at the level of meta-data (Sullivan and Fein 2012; Morrissey 2016).

Collection and analysis of metadata

Consistent with the approach followed in most articles and studies (e.g. Gallaway et al. 2009; Dance and Rooker 2019), we grouped the estimated effect sizes by age class (Table 1; Supplementary Material 2), because red snapper exhibit ontogenetic shifts in habitat, and different life stages are known to vary in their response to environmental conditions. Studies on juvenile red snapper were separated into three different categories: age 0, age 1, and juveniles non-specific. The latter category refers to studies that focused on juvenile red snapper abundance but did not specify which age classes were studied. Studies from all three categories were pooled to calculate the overall mean effect size for juveniles. Moreover, data were pooled across all categories (age classes) to calculate the mean effect size on the overall abundance of red snapper, including effect size estimates from studies that did not specify any age class of red snapper (i.e. non-specific age, Table 1).

Studies were organized by the type of environmental or ecological driver, which we organized into 12

Table 1 Age-class classification used by studies examining the relationship between environmental drivers and the abundance of red snapper in the U.S. Gulf of Mexico

Age class	Description	Articles
Age 0	Studies that focused on post-settlement juveniles (< 50 mm TL and 66 days of age) post-recruit juveniles less than 1 year of age that available on trawlable bottom habitat as bycatch in the Gulf shrimp fishery	Szedlmayer and Conti (1999), Workman et al. (2002), Rooker et al. (2004), Piko and Szedlmayer (2007), Wells et al. (2008), Mudrak and Szedlmayer (2012), Szedlmayer and Mudrak (2014), Switzer et al. (2015)
Age 1	Studies that focused on juveniles of 1 year of age that are distinguished from age 0 juveniles by their shift in distribution from trawlable bottom to non-trawlable reefs with intermediate relief	Workman et al. (2002), Piko and Szedlmayer (2007), Wells and Cowan 2007, Wells et al. (2008), Mudrak and Szedlmayer (2012), Szedlmayer and Mudrak (2014), Switzer et al. (2015)
Juveniles Non-specific	Studies that combined age 0 and age 1 juveniles in their abundance estimates. These studies were aggregated with age 0 and age 1studies to calculate mean effects on juveniles for the met-analysis	Szedlmayer and Shipp (1994), Workman et al. (2002), Patterson et al. (2005), Piko and Szedlmayer (2007), Mudrak and Szedlmayer (2012), Szedlmayer and Mudrak (2014), Brandt and Jackson (2013), Jaxion-Harm and Szedlmayer (2015), Parsons and Foster (2015)
Adults	Studies that focused on fish 2 years of age or greater, which are available to the directed commercial and recreational snapper fisheries, both on reefs and open areas	Redman and Szedlmayer (2009), Ajemian et al. (2015), Jaxion-Harm and Szedlmayer (2015)
Non-specific Age	Studies whose abundance estimates included all red snapper (i.e. both juvenile and adult red snapper of all age classes). These studies were aggregated with all others to calculate mean effects on overall abundance for the meta-analysis	Stanley and Wilson (2000, 2004), Gledhill and David (2004), Lingo and Szedlmayer (2006), Piko and Szedlmayer (2007), Wells and Cowan (2007), Wells et al. (2008, 2009), Syc and Szedlmayer (2012), Froehlich and Kline (2015), Jaxion-Harm and Szedlmayer (2015), Streich et al. (2017), Barker and Cowan (2018)

categories: artificial light, depth, distance from Mississippi River, dissolved oxygen/hypoxia, habitat complexity (encompassing both natural and artificial reefs), habitat disturbance from trawling, habitat type, intraspecific competition, month/season/temperature (MST), protection from predators (e.g. proximity to other reefs and dedicated predator exclusion devices), reef age, and salinity. We aggregated month/season/temperature into a single driver category due to their covariance; month (e.g. April vs. September) and season (e.g. Spring vs. Fall) were used interchangeably among studies and articles to infer changes in red snapper abundance in response to warmer or colder water temperatures.

We recorded the GPS coordinates of each study and arranged studies into specific geographic regions based on where the study was conducted to characterize the spatial distribution of individual studies in relation to the distribution of red snapper populations in the GOM. Using location information of study areas from selected articles, a 1-degree resolution choropleth map of the GOM was made to display the total number of studies within each spatial extent. Information on the source publication (title, authors, year), research timing (start year, end year, duration), sampling method (e.g. diver surveys, video surveys, trawl surveys), and abundance metric (e.g. CPUE) were recorded as a resource for readers. These data were combined with data related to effect size into a single data frame that was used to run the final meta-analysis (Supplementary Material 2).

Model selection and statistical analyses

The low sample size for most drivers ($n < 10$ studies) precluded the acceptable use of a random-effects or multilevel model (but see Sensitivity Analyses below) to examine the combined, average magnitude of effect of each driver on red snapper abundance in the GOM (Nakagawa and Santos 2012). Therefore, we used a fixed-effect model to calculate the weighted mean $|d|$ and bootstrapped 95% confidence intervals for each of the 12 possible environmental and ecological drivers across all studies for each age class and pooled across age classes. We weighted means by the inverse of the variance for each study to correct for bias associated with studies with large effect sizes based on low sample sizes (Marín-Martínez and Sánchez-Meca 2010; Morrissey 2016). Fixed-effect models assume that studies included in a meta-analysis share a common effect size (meta-analytic mean) irrespective of possible differences among studies (Nakagawa and Santos 2012). For biological meta-analyses, the assumptions of fixed-effect models rarely are met, because they often include studies that differ greatly in design. However, the approach is reasonable in cases where there are few effect sizes and estimates are all obtained for the same species (Nakagawa et al. 2017).

We calculated 95% confidence intervals for each weighted mean $|d|$ using bootstrap resampling of all studies for each age-driver combination (DiCiccio and Efron 1996). For n studies used to calculate the weighted mean, we randomly resampled data from these n studies with replacement and calculated the weighted mean for the resampled subset. Data were resampled 10 000 times to create a vector of 10 000 resampled weighted means, and 95% CIs were calculated as the 0.025 quantile and the 0.975 quantile of the resampled weighted means. The magnitude of $|d|$ was interpreted using Cohen's (1988) convention as small (0.2), medium (0.5), and large (0.8) effect thresholds.

Sensitivity analyses

To assess potential biases associated with the effect size metric chosen, we re-calculated the mean absolute value of the effect size across all age classes and drivers using the same fixed-effect model but with $|r|$ as the effect size measure. We then compared the results with those generated by calculating $|d|$ to evaluate the impact of our study design on the estimated magnitude of the mean effect size (Noble et al. 2017). Pearson's r statistics were either extracted directly from the original study or were converted from other reported test statistics. Because the distribution of r values becomes skewed when r approaches ± 1, r values were transformed into Z-scores using Fisher's z-transformation (Rosenberg et al. 2013). We accounted for the positive bias associated with Fisher's z-transformations by applying the correction recommended by Overton (1998). Modelled effect sizes and 95% confidence intervals (CIs) around our estimates were back transformed from Fisher's Z to r by taking the hyperbolic tangent of the estimate (Rosenberg et al. 2013). The magnitude of $|r|$ was interpreted using Cohen's (1988) convention as small (0.1), medium (0.3), and large (0.5) effect thresholds, which differ from the thresholds of $|d|$ (see above).

Non-independence within data from primary studies can affect the calculation of effect size statistics and the certainty of conclusions of the meta-analysis (Nakagawa and Santos 2012; Noble et al. 2017). Multiple effect sizes collected from a single article may exhibit within-article correlation (a form of non-independence) that influence effect size estimates and can produce erroneous conclusions (Nakagawa and Santos 2012; Noble et al. 2017). Within several articles, there were multiple effect size estimates reported for a particular age class or driver (Table S1). The sample size of studies on habitat type ($n = 18$) and MST ($n = 20$) were sufficient to test for non-independence of effect sizes among studies taken from the same article using a multilevel model that relaxes assumptions of independence made by the fixed-effect model (Nakagawa et al. 2017). We ran a multivariate meta-analysis ("metafor" package in R; Viechtbauer 2010) on $|d|$ with *article* treated as a random effect to test for its influence on the estimated effect size for each driver. This procedure was repeated separately with *age class* (to avoid overfitting) as the random effect to test for the effect of pooling data across age classes when calculating the overall effect size of each driver. As a third method to assess (non)independence, we explored the metadata on the spatial and temporal distribution of studies for evidence of between-study correlations (Noble et al. 2017).

Heterogeneity refers to variation in effect size estimates among studies that are not explained by sampling error, which can impact the reliability of the meta-analytical mean and requires investigation to properly interpret the results of a meta-analysis (Nakagawa et al. 2017; Noble et al. 2017). We partially addressed potential heterogeneity in the data by running separate meta-analyses by age class. In addition, we calculated Cochran's Q to test for heterogeneity and quantify how much of variation in effect sizes were due to the level of between-study variance (and not sampling error) for the effects of MST and habitat type. We then examined variations in the ranges of data used among studies (e.g. temperature and number of habitat types) in comparison with the results of heterogeneity tests to qualitatively evaluate the influence of between-study heterogeneity on mean effect size estimates.

Publication bias in meta-analysis can have numerous causes but is often associated with the overrepresentation of positive results due the preferential publication of statistically significant results in the literature (Sutton 2009). We generated funnel plots comparing the average magnitude of the effect size |*d*| for MST and habitat type with its variance (reversed). Plots were constructed to visualize the degree of asymmetry, which can be caused by publication bias (Nakagawa and Santos 2012).

Results

Literature search

Our initial literature search identified 1252 articles for potential inclusion within the meta-analysis (Fig. 1; Supplementary Material 1). Of these, 770 articles were removed after a review of titles and abstracts, because they were duplicates (criteria 1; n = 51) or focused on topics unrelated to red snapper (criteria 2; n = 719). An additional 209 articles were removed after reviewing the full texts, because they studied a different species, including fishes described as "red snapper" or "snapper" that were not *L. campechanus* (criteria 3). Ten articles were excluded despite containing relevant information on the abundance of red snapper, because the study regions were outside the GOM (criteria 4). Another 212 articles that covered topics relevant to the distribution and abundance of red snapper in the GOM were not included, because they lacked specific data, graphs, analyses, or results (criteria 5). The final review resulted in the exclusion of 15 modelling articles (criteria 6) and 10 articles with highly relevant information on environmental drivers of red snapper abundance from which we were unable to extract the necessary data to calculate effect size (criteria 7). This process led to a final list of 82 studies from 26 articles that met all our criteria for inclusion within the meta-analysis.

Distribution of research effort

Fifty-five of 82 (67.1%) studies concentrated their sampling efforts east of the Mississippi River, in waters offshore of Mobile Bay, Alabama and Pascagoula, Mississippi (Fig. 2). The area with the next highest study effort was off the coast of Central and South Texas (6 studies, 7.3%), followed by equal effort along the eastern coast of Texas in waters off Galveston and Freeport (4 studies, 4.9%), and off Louisiana (4 studies, 4.9%). One study was conducted in the Madison Swanson area off the west Florida shelf (1.2%), and twelve (14.6%) studies spanned more than one of the previously identified areas. Research effort (i.e. number of articles) was distributed evenly over time from 1988 through 2015 and ranged in duration from 1 year (n = 18) to over 9 years (n = 1), with a mean study duration of 1.65 years.

Seven of the 26 articles (26.9%) contained studies of multiple age classes of red snapper. The majority of the study effort (23 of 82 studies, 28.0%) was focused on both adult and juvenile red snapper combined (i.e. non-specific age; Fig. 3a). Nineteen studies (23.2%) focused only on age 0 red snapper, and fourteen studies (17.1%) focused exclusively on age 1 red snapper. Juvenile (non-specific for age) and adult red snapper were the subject of 13 studies (15.9%) each.

Among the 26 articles selected for this meta-analysis, the majority of study effort was focused on the effect of MST (20 studies, 24.4%) and habitat type (18 studies, 22.0%) (Fig. 3b). The effect of protection from predators was studied ten times (12.2%), the effect of dissolved oxygen levels (i.e. hypoxia) was studied eight times (9.8%), and the effect of depth was studied seven times (8.5%). The effects of reef age, habitat complexity, salinity, intraspecific competition, habitat disturbance (from trawling), and distance from the Mississippi River, were examined by two to four studies (2.4–4.9%), and the effect of artificial light was the subject of only one study (1.2%). Fourteen articles (53.8%) selected for the meta-analysis contained studies on the effects of multiple environmental drivers.

Survey methods were grouped into one of eight different categories (Fig. 4a), with diver surveys (i.e. underwater visual censuses; n = 33 studies) and bottom trawl surveys (n = 24 studies) being the most common methods employed to estimate fish abundance. The mean number of sampling units per study was variable. The mean number of sampling units for the trawl surveys was 2514, vertical longlines used an average of 106 sampling units, and all other methods had a mean of 33 to 66 sampling units (Fig. 4b).

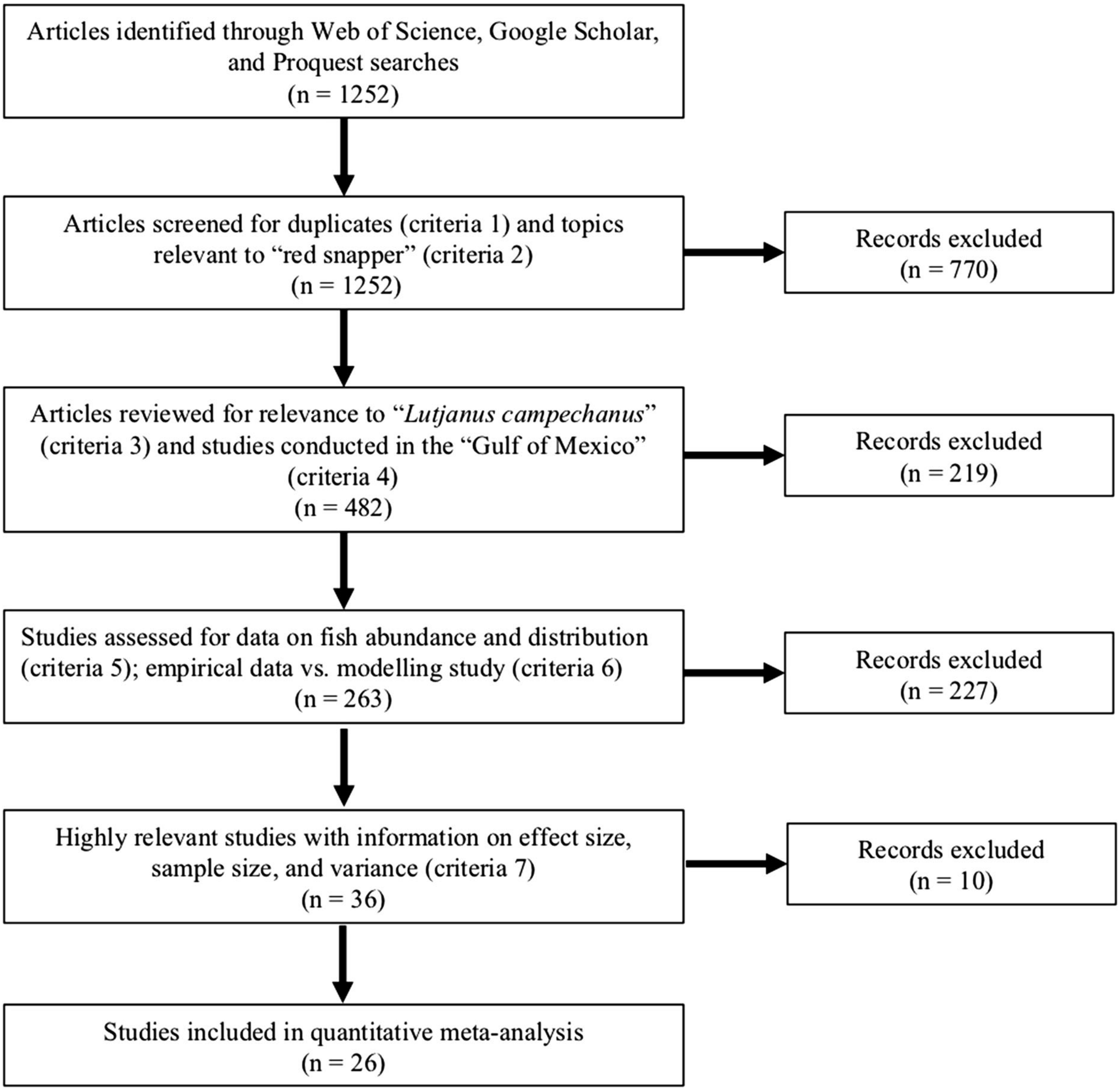

Fig. 1 Preferred Reporting Items for Systems Reviews and Meta-Analyses (PRISMA) diagram detailing literature review process and selection criteria

Effects of drivers by age class

Habitat complexity and intraspecific competition had large effects on the abundance and distribution of red snapper pooled across all age classes (i.e. overall abundance), while habitat type had medium effects (Table 2, Fig. 5a). Protection from predators, artificial light, reef age, depth, salinity, MST, and distance from the Mississippi River all had small effects on overall abundance. Both habitat disturbance and DO/hypoxia had no effect on the overall abundance of red snapper.

Habitat type and protection from predators had large effects on age 0 red snapper abundance (Table 2, Fig. 5b). Habitat complexity had a medium effect on abundance, whereas MST, salinity, depth, and distance from the Mississippi River each had a small effect. Habitat disturbance and dissolved oxygen had no effect on the abundance of age-0 red snapper. We

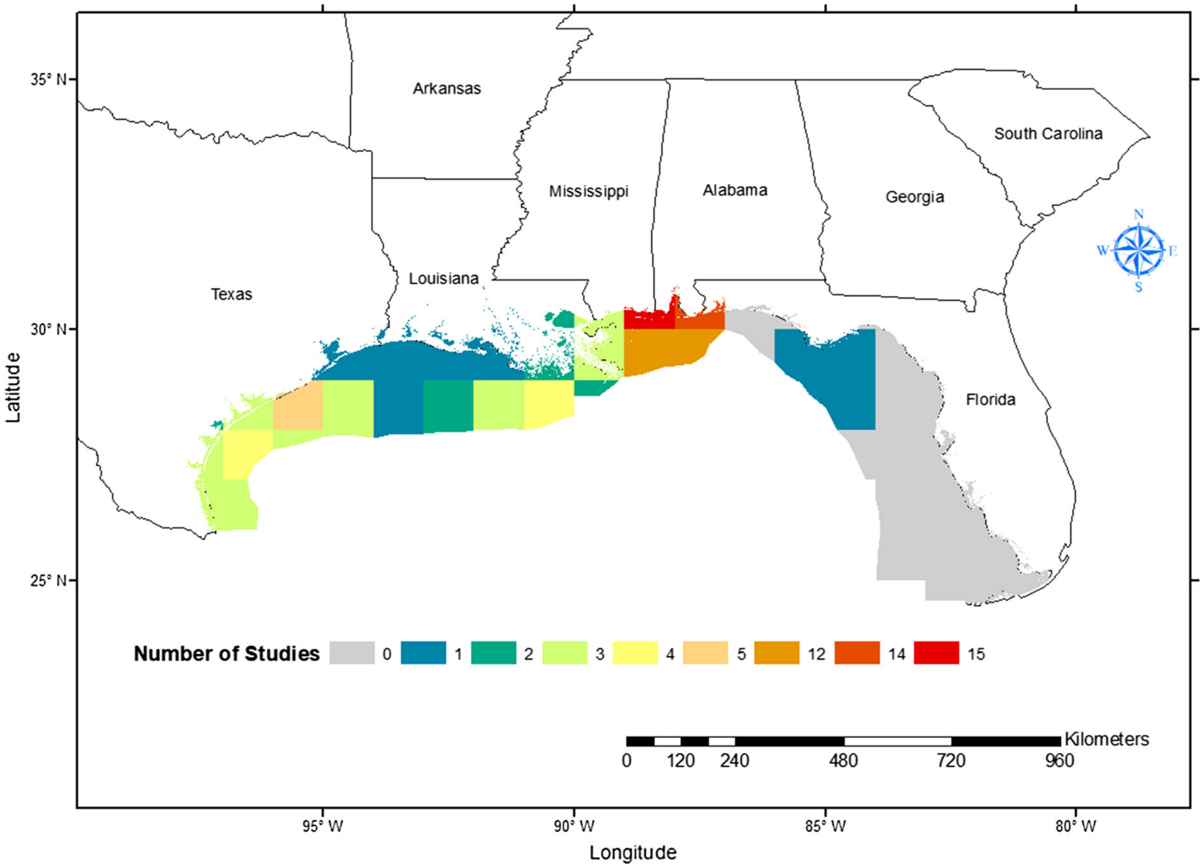

Fig. 2 Map of the U.S. Gulf of Mexico showing the spatial distribution of studies that have investigated the effect of environmental conditions on the abundance and distribution of red snapper (*Lutjanus campechanus*) in the region. Only studies that met the meta-analysis criteria are included

found no studies of the effects of artificial light, reef age, or intraspecific competition on the abundance of age 0 red snapper.

Very few studies focused on age 1 red snapper (Table 2, Fig. 5c). Protection from predators, habitat type, depth, and distance from the Mississippi River each had a small effect. Salinity, MST, and DO/hypoxia had no effect, and there were no studies of reef age, intraspecific competition, habitat disturbance from trawling, habit complexity, or artificial light that focused only on age 1 red snapper.

Habitat complexity, intraspecific competition, and habitat type had large effects on the overall abundance of juvenile red snapper (i.e. effect size data pooled across studies on age 0, age 1, juveniles non-specific; Table 2, Fig. 5d). MST and habitat type had small effects, while protection from predators had a moderate effect. A suite of drivers (depth, salinity, MST, distance from the Mississippi River) had a small effect on juvenile red snapper abundance, and both DO/hypoxia and habitat disturbance showed no effect. We found no studies on the effects of artificial light or reef age on juvenile red snapper abundance.

No drivers had either a large or medium effect on the abundance of adult red snapper (Table 2, Fig. 5e). Habitat type had a low to medium ($|d| = 0.48$) effect on adult abundance, while habitat complexity, reef age, depth, and protection from predators all showed small effects. MST had no effect on adult abundance, and there were no studies of the effects of intraspecific competition, artificial light, salinity, distance from the Mississippi River, habitat disturbance, or DO/hypoxia that focused solely on adult red snapper.

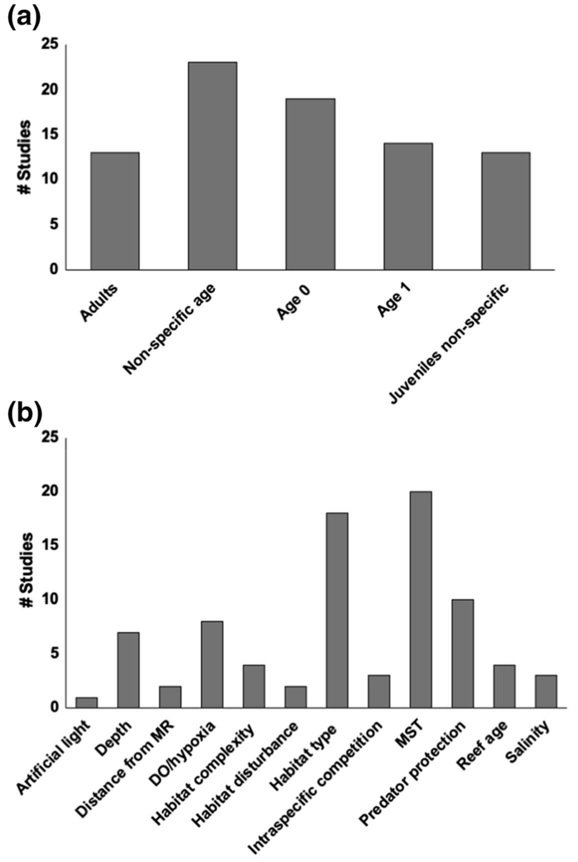

Fig. 3 Bar graphs showing distribution of research effort (# studies) by age class of red snapper (**a**) and by environmental or ecological driver (**b**)

Sensitivity analyses

The relative magnitude (i.e. small, medium, large) of the mean effect sizes for |*d*| versus |*r*| were the same across nearly all drivers and age classes for the fixed-effect model (Supplementary Material 3: Fig. S1, Tables S1and S2), with |*r*| values being slightly lower for juveniles in relation to intraspecific competition and protection from predators and slightly higher for adults in relation to habitat type. While the even distribution of research efforts among studies by year indicated that temporal correlation was not present, the clustering of studies in the regions surrounding Alabama and Mississippi was evidence of potential between-study spatial correlations.

The results of the multilevel model showed that *article* influenced effect size estimates for both habitat type and MST. In both cases, the effect size estimate and the associated variance increased markedly (compared to the fixed-effect model) when *article* was treated as a random effect. This result indicated that within-article correlation influenced the effect size estimates from the fixed-effect model (as compared to the mixed-model, which allows for multiple studies within articles). However, the effect size estimates and associated variances did not change when *age class* was treated as a random effect, demonstrating that pooling data across age classes produced a reliable estimate of the overall effects of each driver on red snapper abundance.

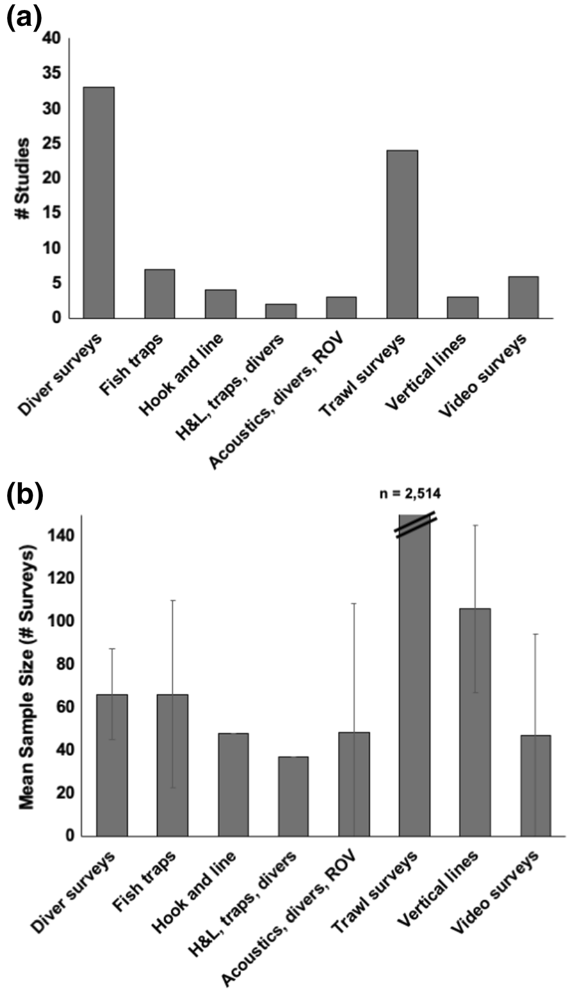

Fig. 4 Bar graphs showing distribution of sampling methods used to measure the effects of environmental drivers on red snapper (*Lutjanus campechanus*) abundance and distribution. **a** sampling method by sampling effort (# studies): **b** sampling effort by mean sample size (mean # surveys per study). Error bars represent 95% confidence intervals

Table 2 Summary of the magnitude of mean effect sizes (|*d*|) by environmental driver and age class for red snapper (*Lutjanus campechanus*) in the U.S. Gulf of Mexico (n = #studies)

Driver	Overall			Age 0			Age 1			Juveniles			Adults		
	n	$\lvert d \rvert$	*95% CIs*	*n*	$\lvert d \rvert$	*95% CIs*	*n*	$\lvert d \rvert$	*95% CIs*	*n*	$\lvert d \rvert$	*95% CIs*	*n*	$\lvert d \rvert$	*95% CIs*
Habitat complexity	4	0.90	0.48,1.88	1	0.62	–	0	–	–	2	1.00	0.62,1.99	1	0.31	–
Intraspecific competition	3	0.89	0.65,1.02	0	–	–	0	–	–	3	0.89	0.65,1.02	0	–	–
Habitat type	18	0.59	0.39,0.94	3	2.39	0.67,6.88	2	0.21	0.07,0.80	7	0.87	0.24,2.26	3	0.48	0.16,4.90
Predator protection	10	0.46	0.17,0.88	3	1.10	0.17,1.81	2	0.33	0.05,0.61	6	0.58	0.16,1.19	2	0.21	0.20,0.23
Artificial light	1	0.44	–	0	–	–	0	–	–	0	–	–	0	–	–
Reef age	4	0.42	0.24,0.82	0	–	–	0	–	–	0	–	–	2	0.25	0.22,0.28
Depth	7	0.27	0.20,1.01	1	0.33	–	1	0.20	–	4	0.27	0.20,1.58	2	0.24	0.17,0.30
Salinity	3	0.27	0.14,0.40	1	0.40	–	1	0.14	–	2	0.27	0.14,0.40	0	–	–
MST	20	0.26	0.07,0.69	5	0.42	0.39,1.50	4	0.07	0.05,2.51	12	0.25	0.07,0.89	3	0.14	0.13,0.15
Distance from MR	2	0.23	0.19,0.27	1	0.27	–	1	0.19	–	2	0.23	0.19,0.27	0	–	–
Habitat disturbance	2	0.18	0.09,0.20	1	0.09	–	0	–	–	1	0.09	–	0	–	–
DO/hypoxia	8	0.12	0.07,0.25	3	0.11	0.06,2.72	3	0.12	0.12,0.13	7	0.12	0.07,0.24	0	–	–

The results of the heterogeneity tests for both habitat type ($Q = 228$; $p < 0.001$) and MST ($Q = 729$; $p < 0.001$) indicated that between-study variance not due to sampling error was significant (Supplementary Material 3: Figure S2). The survey methods, research durations, sample sizes, response measurements (e.g. CPUE, density), and ranges of conditions investigated all varied greatly among studies for both drivers, providing further evidence that between-study variance (heterogeneity) was high. Funnel plots (i.e. half-funnel plots due to presentation of absolute values only) for both drivers were quasi-symmetrical (Supplementary Material 3: Figure S3) but with gaps near the bottom left corner of the data, which may be indicative of underreporting of non-significant studies (publication bias).

Discussion

For the highly-exploited red snapper, it is critical to understand the environmental factors that shape their abundance and distribution due to the long history of overfishing, the continued rebuilding status of the stock, and widespread debate over the management of the fishery (Cowan et al. 2011; Shipp and Bortone 2009; SEDAR 2018). Given the significant investment in understanding red snapper population dynamics, it is also important to identify understudied regions and the key environmental and ecological drivers of red snapper abundance within the GOM so that future research effort may be directed toward the areas of greatest need.

Red snapper exhibit ontogenetic shifts in behavior and habitat preferences (Boland et al. 1983; Render 1995; Patterson et al. 2001; Rooker et al. 2004; Wells and Cowan 2007; Jaxion-Harm and Szedlmayer 2015; Switzer et al. 2015; Dance and Rooker 2019), and as such, it was expected that the average effects of environmental and ecological factors on red snapper abundance would differ among age classes. Although our sensitivity analysis revealed that there were not strong differences between age classes for the effects of MST and habitat type, we analyzed age classes separately based on the aforementioned justification in the literature. We found that habitat complexity, habitat type, and intraspecific competition each had large mean effects on the abundance of juvenile red snapper. Fewer studies focused specifically on age 0 red snapper but revealed large mean effects for habitat

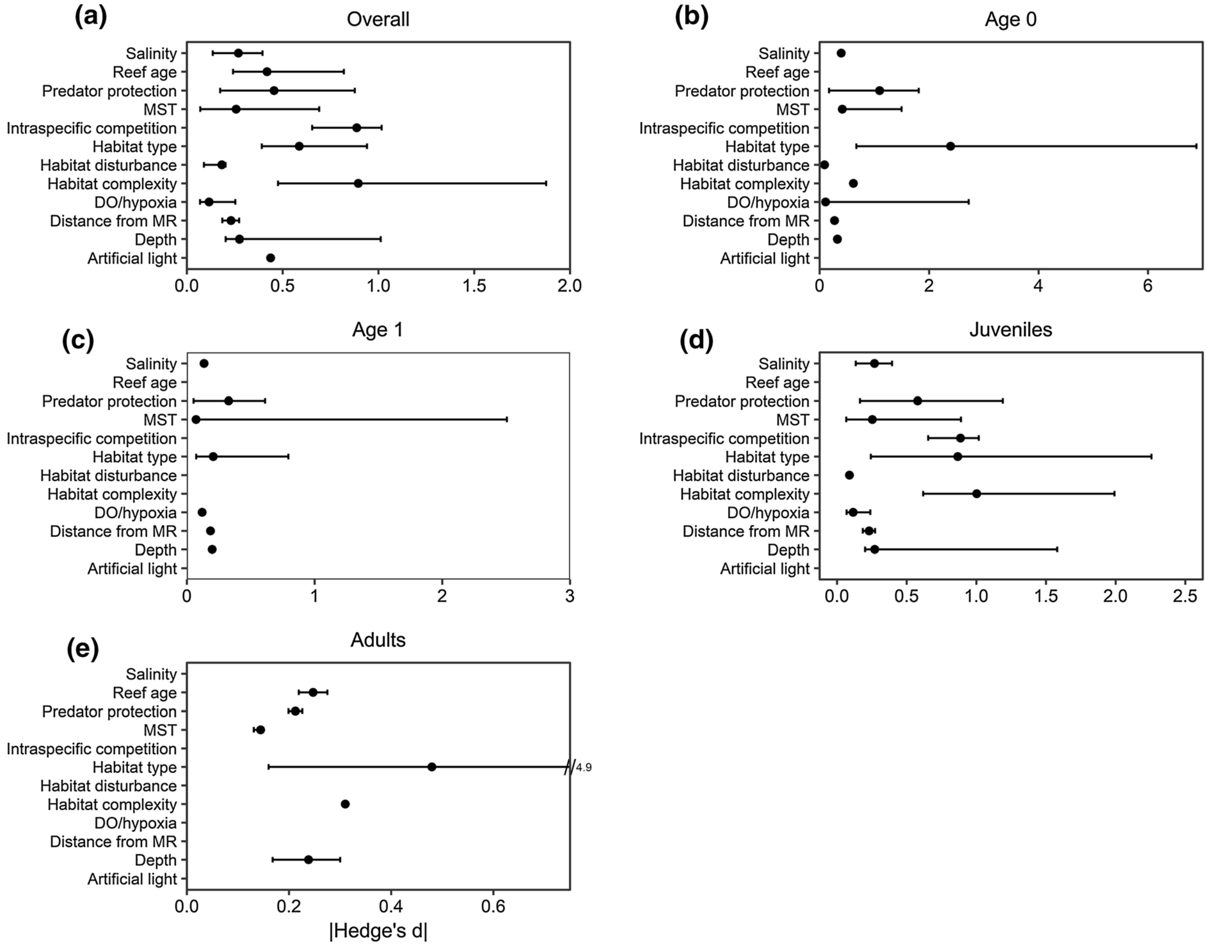

Fig. 5 Forest plots showing the absolute value of the mean effect size of environmental parameters on the abundance and distribution of red snapper, including all ages combined (Overall; **a**), age 0 recruits (**b**), age 1 juveniles (**c**), juveniles pooled (**d**), and adults (**e**)

type and predator protection on the abundance of newly recruited juveniles. Collectively, these results were consistent with previous reviews emphasizing the role of density-dependent mechanisms related to suitable habitat, competition, and predation in determining survivorship during the early life history of the species and shaping population dynamics of red snapper (Gallaway et al. 1999; Patterson et al. 2007; Gallaway et al. 2009; Karnauskas et al. 2017).

Among studies focused specifically on adult red snapper, all factors either showed small effects (habitat complexity, reef age, depth, protection from predators) or no effect at all (MST), although the effect size of habitat type could be considered moderate (|*d*| = 0.48). The lack of large effects of most environmental drivers on the abundance of adult red snapper is consistent with its life history strategy and tolerance of a broad range of environmental conditions associated with the diverse habitats used by adults. The species exhibits several life history traits that are associated with high resilience to environmental variability, including an early age of sexual maturity (2 years), a long lifespan (57 years), a protracted spawning season (April to September), and a high spawning frequency (every 3–10 days) (Wilson and Nieland 2001; Woods et al. 2003; Kulaw 2012; Porch et al. 2015; Glenn et al. 2017).

When studies were pooled across age classes to identify factors that affected the overall abundance of red snapper within the GOM, habitat complexity had a large mean effect based on four studies comprising multiple age classes. The mean overall effect of intraspecific competition on red snapper abundance was large based on three studies of juveniles, as investigations on competition for resources among adults have yet to be undertaken. Results of the fixed-effect model produced a medium effect of habitat type on overall abundance, but the multilevel model predicted a large mean effect of habitat type and indicated that within-article correlation (non-independence) and between-study variance (heterogeneity) influenced the lower estimate of the fixed-effect model. Results on the mean effect of MST on the overall abundance of red snapper were somewhat inconclusive due to a high level of heterogeneity in the data; studies varied considerably with respect to sample size, survey method, variables measured, months or seasons compared, and effect size metric used. As a result, the meta-analytical model selected greatly influenced the magnitude of the effect size estimate, with the multilevel model predicting a large, mean effect of MST on overall red snapper abundance (compared to a small effect from the fixed-effect model) when multiple effect sizes from the same article were adequately considered. Similarly, the magnitude of the effect sizes varied considerably among studies focused on the effect of depth on red snapper abundance, which reflected differences in depth ranges measured, survey method (e.g. diver surveys, trawls, hook and line, hydroacoustics), habitats surveyed (e.g. oil platforms vs. trawlable bottoms) both within and among age classes. Consequently, the mean effect of depth was small among age class and on overall abundance. Dissolved oxygen exhibited a large effect on juvenile red snapper in two studies with small sample sizes conducted at the scale of one or more reefs within Mobile Bay (Szedlmayer and Shipp 1994; Szedlmayer and Mudrak 2014), but the effect of dissolved oxygen on juvenile red snapper abundance was estimated to be low due to the high variance associated with these studies. The mean effect of dissolved oxygen on overall red snapper abundance was also small based on several larger-scale trawl studies. The remaining five drivers (artificial light, reef age, salinity, distance from the Mississippi River, and habitat disturbance) investigated in this meta-analysis either showed no effect on red snapper abundance, comprised very few studies, or both. These drivers are not discussed further, as additional research is needed to draw meaningful conclusions about their relative influence on red snapper population dynamics in the GOM.

Habitat complexity and habitat type

Only four studies investigated patterns of red snapper abundance along a gradient of habitat complexity, but they collectively produced a large mean effect size on juveniles and red snapper overall. The magnitude of effect sizes varied among individual studies, which could be due to differences in the age class studied, the study design, survey method, and the magnitude of habitat complexity gradients among those studies. Redman and Szedlmayer (2009) found a small effect of increasing complexity of artificial reef designs on adult abundance by conducting diver surveys, whereas Lingo and Szedlmayer (2006) found a large relationship between artificial reef complexity and the density of adult and juvenile red snapper using a similar approach. Patterson et al. (2005) found a large effect of sponge density on the CPUE of juvenile red snapper from trawl surveys, but Rooker et al. (2004) showed that the density of shell material on trawled reefs had a medium effect on the density of age 0 snapper.

Habitat type was the second most studied of all the environmental factors considered and showed medium to large mean effects on the abundance of all age classes studied except age 1 red snapper. The fixed-effect model predicted a medium effect of habitat type on overall red snapper abundance, but the results of the sensitivity analysis (multilevel model) showed that the true mean effect size was large when multiple effect sizes from the same article were adequately considered. Moreover, the high degree of between-study variance (heterogeneity) also influenced the effect size estimates produced by both models.

Among the studies we examined, large effects of habitat type were found across studies on age 0 (Rooker et al. 2004; Piko and Szedlmayer 2007), age 1 (Workman et al. 2002), adults (Jaxion-Harm and Szedlmayer 2015), and juveniles and adults combined (Wells and Cowan 2007; Froehlich and Kline 2015; Streich et al. 2017). For example, based on trawl surveys, Rooker et al. (2004) found the density of age 0 red snapper to be much higher on shell banks compared to inshore and offshore mud banks. Conversely, Wells and Cowan (2007) showed that juvenile and adult red snapper preferred natural reefs over shell or mud habitat, and Froehlich and Kline (2015) found that adult and juvenile snapper densities were much higher on natural reefs than artificial reefs. Streich et al. (2017) demonstrated that adult and juvenile abundance of red snapper increased dramatically several years after the deployment of artificial reefs onto bare substrates. Jaxion-Harm and Szedlmayer (2015) showed the highest densities of adult red snapper on small artificial reefs compared to other artificial reef types (e.g. tanks, pyramids, large reefs).

The meta-analytical results on the effects of habitat complexity and habitat type support expert opinion on age-specific habitat preferences of red snapper and the role of habitat limitation in regulating the population capacity of red snapper in the GOM (see Gallaway et al. 2009), many of which were excluded from the analysis due to a lack of extractable data. New recruits (age 0) and juvenile (< 2 years) red snapper tend to be closely affiliated with low-profile, shell bank or patch reef structures until moving to larger reefs (both natural and artificial) with greater structural complexity as they increase in size over the first two years of life (Boland et al. 1983; Gutherz and Pellegrin 1988; Workman and Foster 1994; Render 1995; Szedlmayer and Howe 1997; Szedlmayer and Conti 1999; Patterson et al. 2001; Workman et al. 2002; Nieland and Wilson 2003; Mitchell et al. 2004; Rooker et al. 2004; Szedlmayer and Lee 2004; Lingo and Szedlmayer 2006; Wells and Cowan 2007; Gallaway et al. 2009; Cowan 2011). Young adults (ages 2–3) are most abundant at oil platforms, but few adult red snapper survive or remain at these sites beyond age 5 or 6 years of age (Stanley 1994; Gitschlag et al. 2003; Gallaway et al. 2009; Powers et al. 2018). Adults in general are most abundant on shelf and shelf-edge habitat with an affinity for vertical structures such as pinnacles, rock ledges, artificial reefs, shipwrecks, oil and gas platforms and pipelines (Patterson et al. 2001; Gallaway et al. 2009; Powers et al. 2018). Based on many tagging and telemetry studies, adults show high site fidelity, long residence times, and limited movement in relation to these habitats (Beaumariage and Bullock 1976; Fable 1980; Szedlmayer and Shipp 1994; Patterson et al. 2001; Diamond et al. 2007; Strelcheck et al. 2007; Topping and Szedlmayer 2011; Williams-Grove and Szedlmayer 2016).

The affiliation of adult red snapper with high-relief structures decreases with size and age such that older fishes (8 to 10 + years) demonstrate larger home ranges, lower site fidelity to reefs, an ability to inhabit a wider range of structural habitat types, and an increased association with soft-bottom habitats areas with sea bottom depressions and lumps (Boland et al. 1983; Render 1995; Nieland and Wilson 2003; Szedlmayer 2007; Gallaway et al. 2009; Cowan 2011; Topping and Szedlmayer 2011; Powers et al. 2018). While the distribution and abundance of older fish is still likely to be influenced by their proximity to reef structures (Dance and Rooker 2019), this shift in behavior may reflect their ability to forage over open habitat with negligible threat from predation and a need to do so to meet energetic demands as food resources on reefs become depleted (Gallaway et al. 2009).

The high study effort on the influence of habitat type and habitat complexity on the abundance of red snapper is not surprising, given that the GOM contains the largest artificial reef complex in the world (Dauterive 2000), particularly if the thousands of offshore petroleum platforms, pipelines, and related structures are included. There is growing support for the idea that artificial reefs and platforms can enhance red snapper populations in the GOM by increasing the area of suitable habitat, prey resources, and shelter (Shipp and Bortone 2009; Syc and Szedlmayer 2012; Brandt and Jackson 2013; Streich et al. 2017; Karnauskas et al. 2017); however, several studies contend that fish are merely attracted to artificial reefs (Cowan et al. 1999; Patterson and Cowan 2003). While artificial reefs comprise only a small fraction of available high-relief habitats, the current fishery relies heavily on catches of young adults (2–3 years) from artificial reefs, suggesting that increases in the number of artificial reefs are linked to production increases (Shipp 1999; Szedlmayer 2007; Gallaway et al. 2009). As a result, artificial reef programs have become prevalent in the region (Szedlmayer and Shipp 1994; Kaiser and Pulsipher 2005; Fikes 2013).

Karnauskas et al. (2017) found that artificial reefs harbored high densities of age 1 and 2 red snapper, but the fraction of the population that is associated with artificial structures is relatively low. Therefore, while artificial structures are crucial for red snapper in some areas, their impact on the overall population is relatively low (Karnauskas et al. 2017). Karnauskas et al. (2017) and Gallaway et al. (2009) reached different conclusions on the relative importance of petroleum platforms on red snapper populations. Gallaway et al. (2009) estimated that platforms held 70–80% of age 2 red snapper, while Karnauskas et al. (2017) estimated that only 3.3% of age 1 and 2 red snapper reside on platforms. This discrepancy was partially due to the use of different estimates of natural mortality; when the current estimate (1.6 and 0.7 year^{-1} for age 1 and 2, respectively; SEDAR 2013) was applied with Gallaway's method, only 7–25% of age 1 and 2 red snapper were estimated to be associated with platform structure (Karnauskas et al. 2017).

While clearly important to the population dynamics and productivity of red snapper, artificial reefs may not reproduce all of the functions of natural reefs. Individuals associated with natural reefs have been shown to occupy these areas for extended periods, feeding on and above the reef, while individuals associated with artificial reefs have been shown to feed on the surrounding seabed and in the water column, and feed on species occupying lower trophic levels (Davis et al. 2015; Schwartzkopf et al. 2017; but see Simonsen et al. 2015 and Tarnecki and Patterson 2015). These foraging and habitat use differences may lead to the reported disparity in energy reserves and reproductive potential between red snapper associated with natural and artificial reefs (Glenn et al. 2017; Schwartzkopf and Cowan 2017). From a resource management perspective, the specific habitat preferences of each age class and the effects of habitat type on feeding habits and nutrition seem to be important considerations when developing the goals of artificial reef programs and evaluating their effectiveness for protecting or enhancing red snapper populations.

Intraspecific competition and protection from predators

Based on the results of three studies, intraspecific competition between age classes of juveniles had a large mean effect on the abundance of red snapper. Using diver surveys of juvenile (age 0 vs. age 1) red snapper, studies by Workman et al. (2002), Mudrak and Szedlmayer (2012), and Szedlmayer and Mudrak (2014) all found a moderate to large negative impact of the density of age 1 snapper on the density of age 0 recruits. While not included in the meta-analysis, Bailey et al. (2001) also showed that larger red snapper excluded smaller individuals from reef structures.

A total of 10 studies from four articles investigated the effects of protection from predators. The largest effects were found by Mudrak and Szedlmayer (2012), in which visual diver surveys were combined with photos and video (e.g. baited and unbaited videos, ROV surveys). Surveys found higher abundances of age 0 and age 1 red snapper on artificial reefs that were far away from large, natural reefs (i.e. 500 m vs. 50 m distance) and on artificial reefs in which predators were excluded (Mudrak and Szedlmayer 2012). Conversely, Jaxion-Harm and Szedlmayer (2015) found a small (non-significant) effect of the proximity of artificial reefs to large, natural reefs on the abundance of adult red snapper. Piko and Szedlmayer (2007) also found a small, positive effect of predator exclusion (caged treatments) on the abundance of age 0 and age 1 red snapper on artificial reefs and an increased association with complex habitats with exposure to predators in laboratory experiments. Using a combination of hook and line sampling, fish traps, and diver surveys, Syc and Szedlmayer (2012) found no relationship between the abundance of red snapper (adults and juveniles combined) on artificial reefs and distance to other reefs.

The results of the meta-analysis on the effects of predation and competitive exclusion of older, larger juveniles (age 1 fish) on newly settled juveniles (age 0 fish) are consistent with the role of density-dependent mechanisms in regulating reef fish populations (Hixon and Carr 1997; Hixon and Webster 2002). More specifically, they reflect the vulnerability of juvenile red snapper to predation by adult red snapper and other reef fishes, the influence of predation pressure on habitat selection by recruits and juvenile snapper to increase survivorship, and decreased predation pressure with increasing size and age (Stanley 1994; Bailey et al. 2001; Piko and Szedlmayer et al. 2007; Wells and Cowan 2007; Gallaway et al. 2009; Mudrak and Szedlmayer 2012).

Studies on patterns of red snapper abundance and distribution not included in the meta-analysis have reached similar conclusions regarding the importance of competition and predation on habitat selection of juvenile red snapper and the influence of density-dependence on red snapper population dynamics. Using trawl data from the Southeastern Area Monitoring and Assessment Program (SEAMAP), both Gallaway et al. (1999) and Dance and Rooker (2019) found a negative relationship between the abundance of age 0 red snapper and the proximity or density of petroleum platforms and other artificial structures that could increase exposure of juveniles to predators. Natural mortality rates of juvenile red snapper have been shown to be higher for stronger year classes compared to weaker year classes, which is indicative of density-dependence mechanisms associated with competition among juveniles for the limited amount of suitable habitat (Szedlmayer and Conti 1999; SEDAR 2005; Szedlmayer 2007; Gazey et al. 2008). Froehlich and Kline (2015) observed that adult red snapper exhibited a density-dependent effect, in which the mean length of snapper was higher on low density reefs than on high density areas. Using standard monitoring units for the recruitment of reef fishes, Arney et al. (2017) showed that newly recruited snapper were more attracted to low-relief structures than high-relief structures that harbored predators.

Month/season/temperature (MST) and depth

MST was the most studied environmental factor, but the fixed-effect model predicted a small mean effect on the abundance of red snapper overall, age 0 recruits, and juveniles and no effect on the abundance of age 1 and adult red snapper. The effect of MST on abundance was large for a few studies of age 0 post-settlement fish (Szedlmayer and Conti 1999; Workman et al. 2002; Mudrak and Szedlmayer 2012;) but small in others (Piko and Szedlmayer 2007; Switzer et al. 2015). Among these studies, the effect of MST was associated with elevated abundances of fish during the late summer and fall months, which represent peak periods for spawning and larval recruitment (see below). Similarly, MST showed small to large effects among studies of multiple age classes of juveniles (Workman et al. 2002; Patterson et al. 2005; Brandt and Jackson 2013) and studies that included both juveniles and adults (Stanley and Wilson 2000, 2004; Piko and Szedlmayer 2007; Wells et al. 2007; Jaxion-Harm and Szedlmayer 2015) with abundance peaking from late summer to fall. Effects from studies focused only on age 1 juveniles were also highly variable (Workman et al. 2002; Piko and Szedlmayer 2007; Mudrak and Szedlmayer 2012; Switzer et al. 2015), while studies on adults (Redman and Szedlmayer 2009; Jaxion-Harm and Szedlmayer 2015) consistently showed no effect of MST on abundance.

While representing the most common environmental factor available in most studies and articles, results for MST were often associated with studies focused on other environmental drivers (e.g., habitat type, predation, dissolved oxygen). The large variation of mean effect sizes reported among age classes likely reflects this association with other factors. For example, a study by Mudrak and Szedlmayer (2012) showed the highest effect of MST on red snapper abundance; the density of age-0 fish quadrupled between August and September 2009 on reefs distantly located from natural reefs that was attributed both to an influx of newly settled fish (i.e. a recruitment pulse) onto reefs as well as the absence of predators on distant reefs that facilitated recruitment success. Similarly, Stanley and Wilson (2004) also showed a large seasonal effect on red snapper abundance on offshore petroleum platforms, but this was due to a large increase in juvenile and adult abundance during a single survey period in Fall 1995, and the overall effect of seasonality was deemed to be non-significant.

The importance of MST to explain age 0 red snapper abundance and distribution is not surprising, since red snapper spawn at specific times of year (May to September; peaking from June to August; Collins et al. 1996; Woods et al. 2003; Kulaw 2012; Porch et al. 2015; Glenn et al. 2017; summarized in Kobara et al. 2017), the appearance of post-settlement individuals follows this pattern after a time lag (peak densities in July–August; Rooker et al. 2004; Szedlmayer 2007; Gallaway et al. 2009), and favorable survey conditions that permit field studies are most common during these seasons. As a result, peaks in the abundance of age 0 fish occur during studies conducted during the fall, whereas studies carried out during the summer months are often dominated by age 1 fish (e.g. Gallaway et al. 1999; Dance and Rooker 2019).

Results from the sensitivity analyses showed that the meta-analytical model selected determined the magnitude of the estimated mean effect size of MST on red snapper abundance. When *article* was selected as a random effect within the multilevel model, studies within individual articles were correlated (i.e. non-independent), which influenced the estimated effect size and variance within the data. This result partially explains why the estimated effect size predicted by the fixed-effect model was different than that of the multilevel model (low vs. high, respectively), as the former assumes independence between studies. In addition, the high level of heterogeneity observed among studies (e.g. range of environmental conditions measured, effect size estimates, sample size, variables measured, survey method) and differences between the two models in their treatment of between-study variance also influenced effect size estimates.

We posit that the results of the multilevel model represent a more accurate estimate of the effects of MST on red snapper, because the model relaxes the assumption of independence and adequately considers multiple studies within articles (Nakagawa et al. 2017). Moreover, its results are consistent with conclusions drawn by seminal studies excluded from this meta-analysis on the relative importance of monthly and seasonal variations in temperature on red snapper abundance in the GOM. As more empirical studies become available, it may be possible to understand the influence of temperature independently of time. For example, in a study of the distribution of fishes on Gulf of Mexico petroleum platforms in the summer months, Bolser et al. (2020) showed that temperature influenced the depth distribution of red snapper but not their geographic distribution. The ability to discriminate the influence of temperature from season and other co-varying environmental parameters will be important to predict the impacts of increased climate variability and climate trends on the abundance and distribution of red snapper.

We extracted data on the effects of depth on red snapper abundance and distribution patterns from seven studies within four articles. The fixed-effect model predicted a small mean effect of depth across all age classes and for the overall abundance of red snapper. However, the direction and magnitude of effect size estimates varied greatly among studies due to large differences in the depth ranges and metrics (e.g. substrate or bottom depth vs. water column strata) investigated. For example, Parsons and Foster (2015) conducted trawl surveys for juvenile (age 0 and 1) red snapper to compare their relative abundance between inshore and offshore waters along the continental shelf and found a large negative relationship between depths greater than 40 m and the density of juveniles. In contrast, Stanley and Wilson (2000) estimated the combined abundance of juvenile and adult red snapper between two petroleum platforms from the surface to 60 m and showed a positive relationship between depth and fish abundance. In addition, the disproportionately large sample size (and low variance) of studies by Switzer et al. (2015), which included over ten thousand trawl surveys, likely influenced the low mean effect sizes of depth on red snapper abundance predicted by the fixed-effect model. While differences in study design make it difficult to draw any definitive conclusions about the effect of depth on red snapper distributions in the GOM from the studies included in our meta-analysis, the patterns generated by these studies support the general understanding that juvenile red snapper (age 0 post-settlement and age 1) are concentrated on the continental shelf over bottom depths between 20 and 50 m, whereas adults occupy a wider depth range that includes deeper reefs and open habitats (reviewed by Gallaway et al. 2009).

Using SEAMAP trawl data, previous studies provided useful summaries on the depth ranges of peak abundance for juvenile and adult red snapper in unconsolidated (non-trawlable) habitat in the northern GOM. Age 0 red snapper are most abundant on the continental shelf in waters shallower than 50 m (Dance and Rooker 2019). The highest densities of age 1 fish occurs at 18–55 m, with a peak habitat suitability at depths of 28–37 m (Gallaway et al. 1999), whereas sub-adults (1–2 years) are found at slightly deeper depths of 20–55 m in the eastern GOM and 25–70 m in the western GOM (Dance and Rooker 2019). Gallaway et al. (2009) concluded that adult red snapper are most abundant from 55 to 92 m, declining both inshore and offshore of these depths; however, Dance and Rooker (2019) found that adult abundance was positively related to depths greater than 30 m with a peak in abundance at 100–150 m. A study by Powers et al. (2018) off Alabama showed that juvenile red snapper were found primarily in shallower water on the inner shelf at depths of 20–40 m, while older adults (5–42 years) occupied all depth strata and showed no prevalence in deeper waters.

Dissolved oxygen (hypoxia)

Based on the eight studies from four articles that were included in the meta-analysis, dissolved oxygen levels, and more specifically hypoxia, showed no measurable effect on the overall abundance of red snapper in the GOM or any specific age classes. However, the overall effect size was driven by the large sample size (i.e. $> 10\,000$ trawls) and low variance of four studies from an article by Switzer et al. (2015), which masked moderate to large effects of hypoxia on juvenile red snapper found in studies that involved smaller sample sizes (Szedlmayer and Shipp 1994; Szedlmayer and Mudrak 2014). Moreover, while the results of studies by Switzer et al.

(2015) concluded that hypoxia had "had moderate but discernible effects on the distribution of" juvenile red snapper, the extraction of useable data and subsequent calculation of effect sizes produced low effect sizes for both age 0 and age 1 fish.

From a small number of trawl surveys conducted off the northeastern GOM in summer and fall of 1991, Szedlmayer and Shipp (1994) found a very large effect (d = 32) of a hypoxia event on the density of juvenile red snapper, in which CPUE decreased from ca. 800 fish per hour in July to almost zero in August when DO levels decreased from normoxic to anoxic conditions. Importantly, temperature and salinity showed little difference between the two periods (Szedlmayer and Shipp 1994). Similarly, results from diver surveys in a study by Szedlmayer and Mudrak (2014) showed that dissolved oxygen levels had a very large effect on the density of age 0 red snapper (d = 2.7) at one artificial reef site southwest of Mobile Bay, where fish density decreased from nearly 70 fish per m^3 to nearly zero between early and late August due to dissolved oxygen levels that dropped to 0.4 mg/L.

Switzer et al. (2015) studied the effects of dissolved oxygen and hypoxia on the abundance of juvenile red snapper (age 0 and age 1) in the northwest GOM due to the potential threat that the seasonal formation of hypoxic bottom water along the Louisiana-Texas coast poses to larval settlement, survival, and other processes associated with juvenile recruitment on a regional scale. Using retrospective SEAMAP data from over ten thousand trawl surveys conducted during the summer and fall months from 1988 to 2009, they found that juvenile recruitment in the northwest GOM was weakest during years of severe hypoxia. In particular, they showed that the abundance of age 0 and age 1 individuals was significantly reduced during years when the areal extent of summer hypoxia exceeded 20 000 km^2, and age 1 fish shifted towards deeper, cooler, more saline waters during these years. While it was concluded that the occurrence of severe hypoxia had a moderate effect on the distribution of juvenile red snapper, it was unclear whether reductions in juvenile recruitment during years of severe hypoxia are reflected in the adult population or the fishery, and the authors suggested that examinations of the distribution of red snapper and hypoxia at much finer spatial scales are necessary to elucidate the effects of hypoxia (Switzer et al. 2015).

Consideration of studies from articles not included in the meta-analysis due to data limitations provided additional insights on the effects of hypoxia on the abundance and distribution of red snapper in the GOM. Gallaway et al. (1999) found lower abundances of juvenile red snapper in areas with dissolved oxygen levels less than 4 mg/L, estimated that ideal juvenile habitat contained dissolved oxygen levels greater than 5 mg/L, and contended that the expansion of the hypoxic area offshore of the mouth of the Mississippi River and westward had reduced the potential carrying capacity for juvenile red snapper as much as 25% in some areas. Chesney and Baltz (2001) showed that the seasonal timing of hypoxic bottom water coincides with the peak settlement period of larval red snapper, which could reduce larval settlement success through a reduction in habitat quality. The detrimental effects of low dissolved oxygen levels to red snapper have also been shown in laboratory studies, in which levels lower than 3 mg/L caused significant mortality of larval red snapper (Bardon-Albaret and Sailliant 2016). On petroleum platforms, red snapper are less likely to be encountered on platforms with lower average dissolved oxygen (Bolser et al. 2020) and tend to constrain their vertical distribution to avoid hypoxia in deeper waters (Stanley and Wilson 2004; Reeves et al. 2018; Munnelly et al. 2019; Bolser et al. 2020), which may have sublethal effects at both individual (e.g. growth, reproduction, competition) and ecosystem scales (e.g. trophic interactions; predator–prey interactions). Craig (2012) found that shrimp and fishes aggregate just beyond (1 to 3 km) the margins of the hypoxic zone and concluded that the sublethal and indirect effects of hypoxia manifest themselves within a narrow region along the hypoxic edge that induce small-scale shifts in species distributions.

In summary, the results of the meta-analysis and those from other studies on the effects of dissolved oxygen and hypoxia on red snapper populations in the GOM indicate that the magnitude of impacts are dependent upon the spatio-temporal scale of individual studies. The largest effects have been observed as reductions in the presence and abundance of juvenile red snapper at the scale of individual reefs or petroleum platforms, whereas studies conducted at regional scales suggest that red snapper shift their vertical and horizontal distributions towards more favorable conditions but do not decrease in overall abundance. Transient hypoxic and permanent anoxic zones are a regular occurrence in the summer months for the waters of the northern GOM, and their effects are expected to intensify in the future due to climate change (Justić et al. 1996; Rabalais et al. 2002). Therefore, long-term studies on the lethal and sublethal effects of hypoxia (e.g. across a gradient of dissolved oxygen levels) on all age classes of red snapper are needed to understand subsequent impacts on population stability and fisheries production.

Spatial distribution of research effort

The majority of studies on the effects of environmental drivers on red snapper abundance and distribution have occurred in the waters off Mobile Bay, Alabama, and used diver or trawl surveys to collect data on relationships between habitat features (e.g. artificial reef type, structural complexity) and the relative abundance (as measured by fish density or CPUE) of one or more age classes of red snapper. The artificial and natural habitats off Freeport and Galveston, Texas were the second most studied areas and involved studies using similar methods. Therefore, the distribution of research effort seems to correspond to areas estimated to hold the largest abundance and preferred habitat of red snapper juveniles and adults (Mitchell et al. 2004; Gallaway et al. 2009; Karnauskas et al. 2017; Dance and Rooker 2019). Likewise, the area off Mobile Bay contains the highest density and diversity of artificial reefs in the GOM and numerous oil and gas structures. Given the importance of habitat type and complexity on the abundance of red snapper, this region is ideal for surveys and field experiments focused on these topics. However, the relative importance of specific environmental drivers on the population structure and dynamics of red snapper differ between the western and eastern GOM (Liu et al. 2016; Dance and Rooker 2019), which points to the need for continued monitoring and assessments in both regions.

Limitations

A meta-analysis is a useful and powerful analytical technique designed to summarize the knowledge of a research field by critically evaluating and statistically combining the results of multiple studies to identify the overall measure of a treatment's effect with greater statistical power (Spector and Thompson 1991; Greco et al. 2013). However, it can be a controversial tool, as opportunities to introduce bias arise throughout the stepwise process (Morrissey 2016; Noble et al. 2017). Like any scientific study, the strength of the conclusions depend upon the type, quality, and amount of available data.

Overall, the approach used and conclusions drawn by this meta-analysis were reasonable for investigating and summarizing the average effect of ecological and environmental drivers studied on the abundance of red snapper in the GOM. The magnitude of the mean effect sizes produced by the fixed-effect model were not influenced by the effect size metric. Further, the pooling of data across age classes to summarize overall effects was valid, as results from the multilevel model on habitat data and MST demonstrated no effect of age class on the estimated effect size. Most importantly, the results of the meta-analysis were consistent with expert opinion on the most influential factors driving population dynamics of red snapper, including the findings and conclusions within seminal studies that were not directly incorporated within the meta-analysis due to the inclusion criteria.

Nevertheless, explorations of a subset of data using a suite of sensitivity analyses revealed issues with the type, quality, and amount of data available for the meta-analysis, which reduced the precision of our results and the reliability of the conclusions for certain drivers (e.g. MST, habitat type). First, estimates of mean effect sizes included multiple studies collected from the same article, which were shown to influence the effect size estimate produced by the fixed-effect model for both habitat type and MST. When this issue of non-independence was accounted for by using a multilevel model, the estimated mean effect size increased from a small to a large effect. While not tested directly, most studies were conducted in two regions within the Gulf (i.e. potential spatial correlation), which may have also influenced effect size estimates to disproportionately reflect relationships from those two regions. Thus, our study confirms the limitations of using a fixed-effect model for summarizing topics in ecology, particularly in dealing with issues of non-independence (Koricheva et al. 2013; Morrissey 2016).

The large variation in study design among studies produced high variance around the mean effect sizes for several drivers, which was confirmed by the heterogeneity tests. In some cases, studies on certain drivers were likely conducted at improper spatial or temporal scale, which could obscure the true effect size based on studies that were conducted at the appropriate scale. For example, trawling studies typically covered large areas, involved disproportionately large sample sizes, and were conducted over multiple seasons or years. These studies typically produced a small effect or showed no effect of hypoxia on red snapper abundance (e.g. Switzer et al. 2015). When these large-scale studies were combined with small-scale studies that showed large effects of hypoxia, and all were weighted based on variance (calculated based on sample size; see Eq. 4), a small mean effect size was produced. However, if we assume that the impacts of hypoxia are acute, episodic, and occur at fine spatial scales, then the mean effect size produced by the meta-analysis was somewhat biased. A similar argument could be made for studies on the effects of depth and MST on red snapper abundance, which were highly variable in terms of the range of depths investigated (e.g. 5–50 m vs. 30–200 m). We attempted to control for this bias by comparing the absolute value of effect sizes between metrics, evaluating patterns in effect size in relation to a suite of metadata attributes, and separating effect size calculations among age classes. However, results of the Cochran's Q test on the MST data set found between-study variance (heterogeneity) to be very high even after such steps were taken.

Conclusions

This meta-analytical review is intended to serve as a resource for ecologists, fishery scientists, resource managers, and stakeholders in their efforts to better understand the key environmental drivers of red snapper population dynamics and distribution. Our study catalogued the frequency and scale (spatial and temporal) at which various environmental drivers have been studied, reviewed which geographic regions have received the most research attention, and highlighted specific drivers and regions that warrant more research attention. We hope our findings may assist efforts to: (1) generate informed, science-based predictions about the spatio-temporal distribution of red snapper populations in the GOM; (2) identify environmental information needed to improve predictions of how red snapper populations may respond to oil spills, climate change, and other stressors; (3) foster ideas to better integrate environmental and ecological drivers within stock assessments; and (4) identify and delineate essential fish habitat for this ecologically and economically important fish species in the GOM.

The results of this study provide systematic, quantitative support for the role of density-dependent mechanisms (i.e. habitat quality and availability, predation, competition) in shaping the population structure and dynamics of red snapper, particularly during the larval, recruitment, and juvenile stages. Suitable habitat for red snapper includes both artificial and natural reefs of varying levels of vertical relief and rugosity, making it quite "weedy" in comparison to most reef fishes. However, structural complex habitats constitute only a very small portion of shelf area in the northern GOM but appear to determine the population structure and dynamics of red snapper (Gallaway et al. 2009) through its relationship with shelter from predators, food availability, and competition among conspecifics for these resources. Although large, old adults may be influenced less by these factors, persistent and intense fishing pressure by both the recreational and commercial sectors means that such fish are rare and contribute very little to the regional population.

In contrast to ecological drivers, the effects of most environmental drivers were typically small in average magnitude, were highly variable in magnitude among studies, and less important for adult snapper. While it is clear that additional research is needed to elucidate the spatiotemporal scale and relative effect of certain environmental variables (e.g. dissolved oxygen, temperature), this finding is not surprising if we consider the evolutionary history and biogeography of the red snapper. This species has maintained a center of distribution within the northern GOM, a subtropical biome characterized by large seasonal and regional fluctuations in most physical and biotic features, including nutrients and sediments, air and water temperatures, salinity, dissolved oxygen, turbidity, surface circulation patterns, as well as large-scale, episodic weather events (hurricanes) associated with rapid changes to environmental conditions (Darnell 2015). Fishes like red snapper that evolve and persist within these types of seasonally variable and productive environments often adopt a periodic life history strategy (Winemiller 1992; Winemiller and Rose 1992; King and McFarlane 2003) that consists of a long lifespan, high fecundity, protracted breeding seasons, and frequent (daily) spawning. This ‘bet-hedging’ strategy maximizes survival and recruitment rate during favorable conditions while also maintaining population age structure during long periods of unfavorable conditions.

The results of the meta-analysis were limited by the number of studies and articles that contained results, figures, or tables that permitted extraction of measurable response variables. The literature review process revealed well over 200 articles that covered topics relevant to the distribution and abundance of red snapper in the GOM, but only 82 studies from 26 articles met all the necessary inclusion criteria. We compared the results of our meta-analysis with the findings of these and other studies in order to summarize the current state of knowledge in a balanced manner. However, the process would have been more robust and streamlined if more data from previous studies were able to be included. For example, red snapper GOM articles that were excluded due to the lack of extractable metrics (criteria 7) would have increased our sample size of analyzed articles by 38% if qualitative or quantitative metrics had been available. Therefore, perhaps the most important take-home message of this review is that despite the wealth of information that has been compiled on the ecology of the red snapper (see Rindone et al. 2015), large gaps in knowledge remain. Indeed, there is a need for more empirical investigations that are designed in a more systematic manner to accurately measure relationships between various eco-environmental factors and the abundance of red snapper conducted. For new studies to be quantitatively compared and examined, it is crucial that they include controls and sample the full range of variability of the parameter of interest where possible, as comparisons between effect sizes are often confounded without true controls and when ranges differ (O’Keefe 2017). With the addition of new data, it would be possible to perform a more comprehensive meta-analysis with more precise conclusions that are free of issues of non-independence, heterogeneity, and other sources of bias.

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Compliance with ethical standards

Conflict of interest No potential conflict of interest were reported by the authors.

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