

SYNTHESIS

Widespread Heterogeneity in Density-Dependent Mortality of Nearshore Fishes

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ABSTRACT

Debates over whether and how populations are regulated have recently shifted away from detecting and instead towards quantifying the strength of density dependence and its variation among systems. Yet, the degree of variation in density-dependent mortality and the factors driving this variation remain poorly understood. Here, we conducted a meta-analysis of 38 reef fish species across 56 studies, which yielded 147 estimates of intraspecific density-dependent mortality, primarily during early or small life stages. The magnitude of density-dependent mortality (the increase in the per capita mortality rate due to one fish per unit area of habitat) was surprisingly inconsistent both within and among species. Several factors emerged as drivers of variation. Predators amplified the negative effects of density, and density-dependent mortality was greater for species that typically colonize at low densities or achieve larger maximum sizes. However, even within a single species, the strength of density-dependent mortality varied dramatically—often by several orders of magnitude—and sometimes changed sign. This heterogeneity likely reflects multiple processes acting together, including environmental context (e.g., predator density or refuge availability), traits of the focal organism (e.g., size) and methodological differences (e.g., study design) among studies. Our results underscore the need for future efforts to quantify and report ancillary variables and strive to identify how much these factors contribute to population regulation.

1 | Introduction

Scientists have investigated the relationship between population density and population dynamics for centuries (Malthus [1798](#)). This long-standing interest in the effects of intraspecific density on population dynamics is rooted in our search for understanding the factors that regulate populations: that is, enabling them to rebound when they are rare, and preventing them from growing when abundant. Understanding population regulation is paramount to many ecological frameworks, including those developed to manage harvested species, conserve endangered species and predict population dynamics in a variable and uncertain future.

Central to these questions is an understanding of how key vital rates, such as survival, change with population density.

Studies of density-dependent mortality often focus on its detection rather than on estimating the strength of density dependence, and this has sometimes led to erroneous generalisations: for example, about the presence versus absence of density dependence (Osenberg et al. [2002](#)). In contrast, some meta-analyses of studies of plants (Hülsmann et al. [2021, 2024](#); Poulsen et al. [2007](#)), insects (Buddh et al. [2024](#)) and fishes (Osenberg et al. [2002](#); Ruiz-Moreno et al. [2024](#)) use quantitative estimates of the strength of density dependence. These analyses have demonstrated that

mortality generally increases with conspecific density, suggesting that negative density-dependent survival is common for a wide range of taxa. More importantly, these meta-analyses have documented considerable variation in the strength of density dependence, yet these studies seldom have attempted to explain, or succeeded in explaining, this observed heterogeneity. In contrast, the narrative review by White et al. (2010), motivated by past findings of positive (aka inverse) as well as negative (aka direct) density dependence, summarised a wide range of explanations for this diversity of qualitative responses to density, although White et al. (2010), did not attempt to explain quantitative variation in density dependence. Overall, these past syntheses collectively suggest that the next step is a quantitative synthesis that evaluates the role of ecological traits, evolutionary histories or environmental factors that underlie variation in the strength of density dependence—such an analysis would help resolve an outstanding question in much of population and community ecology (e.g., Buddh et al. 2024; Song et al. 2021).

Variation in the effect of density on mortality across studies likely comes from a suite of different sources (White et al. 2010), including variation among different environments (Buddh et al. 2024; Hülsmann et al. 2024) or among species with different life histories or behaviours (Fowler 1981; McCullough 1999), or among researchers who use different methods (Osenberg et al. 2002). For example, some studies examine density dependence in the absence of predators (e.g., in cages), while other studies are done at ambient predator densities (e.g., in uncaged plots). Because predators may aggregate to, or intensify their feeding activities in high-density prey patches (Murdoch and Stewart-Oaten 1989), or because prey compete for refuges (Holbrook and Schmitt 2002), some of the variation in the strength of density dependence could be due to variation in predator density or refuge availability (Frauendorf et al. 2022; Hixon and Carr 1997; Schmitt and Holbrook 2007). Alternatively, heterogeneity in the effects of density on mortality may be driven by variation in the scientific methods we use to study density dependence. For example, the spatial scale of investigation can explain differences in the strength or direction of density dependence (White et al. 2010; White and Warner 2007), and the use of observational approaches (rather than manipulations of density) can give rise to reduced estimates of density dependence if habitat quality and density covary and therefore mask the underlying effects of density—a phenomenon called ‘cryptic density-dependence’ (Shima and Osenberg 2003; Wilson and Osenberg 2002) and comparable to concepts related to ideal free distributions (Fretwell and Lucas 1969). We might also expect the strength of density-dependent mortality to be greater for highly fecund species or those that persist at chronically low density (Comita et al. 2010; Ruiz-Moreno et al. 2024). Although a variety of factors have been implicated in producing variation in density dependence, most of these insights remain study-specific, with few attempts to evaluate their roles across systems.

Understanding how these various ecological, evolutionary and methodological factors drive variation in density-dependent mortality is key to moving the field of population ecology forward from phenomenological description—asking whether density effects exist—to a more quantitative framework able to predict the strength of density dependence under different environmental and system contexts.

Density-dependence in fishes has been particularly well studied, although this research has evolved in two somewhat different directions. The first approach, primarily used by fisheries biologists uses data from time series to estimate spawning stock-recruit relationships (e.g., Meyers 2002; Thorson et al. 2015; Yang and Yamakawa 2022). These studies often rely on large-scale annual sampling of fish stocks in a region as well as natural variation in stock size without any attempts to experimentally manipulate density. The second approach, typically used by field ecologists, often relies on observational studies or experimental manipulations of reef fish conducted at small scales (e.g., <1–100 m²), often over short timescales (e.g., on the order of days to weeks), with fish counts obtained by observers on scuba or snorkel. The second approach, which is the focus of our paper, is taken, in part, because many reef fishes are relatively sedentary, and as such, cohorts of fish can be readily followed and their fates recorded, and individuals can be easily transplanted to local sites to manipulate local density and quantify subsequent mortality (Hixon and Webster 2002). A meta-analysis by Osenberg et al. (2002) extracted available data on reef fishes and showed that effects of density on mortality were demonstrable but also highly variable across studies. However, the factors underlying this heterogeneity in the effects of density were left unexplored.

While the theory of density dependence is central to population dynamics, its application is hampered by uncertainty about its strength in natural systems and the factors that influence its strength. Previous narrative reviews have highlighted context dependency (e.g., White et al. 2010), but we lack a quantitative synthesis to identify general patterns. Our meta-analysis addresses this gap by compiling a dataset on nearshore fishes that quantifies the mean and variance of density-dependent mortality rates. We then test a suite of a priori hypotheses about study-level moderators that might explain the widespread heterogeneity, moving beyond single-study results to identify the general drivers of variation in population dynamics. Our synthesis suggests that environmental context (not inherent biological traits of the target species) most strongly determines the strength and direction of density dependence. Further, other studies have demonstrated that intra-specific density dependence is often much stronger than interspecific effects in reef fishes (Ruiz-Moreno et al. 2024), suggesting that intraspecific density dependence drives population regulation. However, few primary studies report key environmental characteristics making it challenging to infer the relative importance of different factors. Thus, our results suggest that current methodological and reporting approaches are inadequate for identifying the mechanisms driving population regulation in natural systems.

2 | Materials and Methods

2.1 | The System

Most nearshore fishes (hereafter ‘reef fishes’ because most are associated with physical substrates) have a pelagic larval stage that lasts 1–3 months after their eggs are spawned demersally or in the water column. These larvae are then transported over potentially long distances (e.g., among islands) and use various sensory mechanisms to find new reefs (which are typically different from their natal reefs). After these larvae settle and metamorphose, many fishes, especially those of small adult size and those associated

with coral reefs or other physical structures (e.g., kelp), take up residence on their new reef and move relatively little, at least early in their life history. Although most species in our dataset (see below) have this bipartite life history (a planktonic larval stage followed by a more sedentary benthic stage), a few species, such as those in the family Embiotocidae, lack a pelagic larval phase. Studies of density dependence in reef fish often concentrate on the early benthic life stages because of their more limited mobility, and the belief that density-dependent survival is concentrated during this stage. Here for convenience, we use the term ‘settlers’ to refer to the younger fish at the beginning of a study, and ‘recruits’ to refer to fish that survived to the end of the study. Although some fish might have migrated into or away from a focal group of fishes, most investigators argue (indirectly or based on tagging studies) that such movement was absent, or at least negligible. Thus, we interpret the changes in numbers as arising from mortality (as did most of the original investigators) and not migration.

2.2 | Literature Search

We conducted a systematic literature search to identify studies examining density-dependent survival of marine fishes. On August 5, 2024, we searched the Web of Science (WoS) Core Collection database using the following search terms: (TS=((“density-dep*” OR “density-ind*” OR (“density*” AND “dependen*”)) AND “fish*” AND (“reef*” OR “marine*”))) AND PY=(1900–2024). This search yielded 1383 unique records. We screened abstracts using Metagear and WoS tools with inclusion criteria targeting post-settlement, density dependence in nearshore fishes, where mechanisms such as refuge limitation and predator aggregation can be evaluated alongside habitat characteristics. Although we parameterize mortality with the Beverton–Holt form, our objective is stage-specific mortality, not stock–recruit relationships as applied in fisheries management. During screening, we excluded heavily exploited shelf or pelagic species typically managed via stock-assessment frameworks. Our criteria retained 186 records that appeared to quantify intraspecific density-dependent survival in reef fishes. To this, we also added 8 papers from prior reviews by Osenberg et al. (2002), Hixon and Jones (2005), and Bonin et al. (2015), and 4 papers through our personal knowledge that were not tagged in the original search. We then assessed the full texts of these 198 articles for eligibility and excluded 119 due to a lack of data on survival or density effects. We further assessed the 79 remaining papers to determine if they met our final requirements. To be retained for analysis, a paper had to report survival of a group of fishes at two or more densities; the reported data had to be convertible to densities in number per basal habitat area; the data had to provide the density (or number) of fish at the start of the study and the density (number) of those fish that were still present after a specific amount of time; and the censused fish must have been of a single species (in most cases) or genus (in 2 cases). We excluded 24 of the 79 papers for specific reasons: (1) surviving numbers were taken at a common fixed date, but settlers were accumulated through time, such that fish had different durations on the reef ($n=9$); (2) data were appropriate but were reported in another paper already included in our dataset ($n=2$); (3) data were aggregated across multiple genera ($n=1$); (4) the study investigated intercohort effects (e.g., effects of adults on juveniles) ($n=5$); (5) density was reported in a way that could not be converted to number/area ($n=6$); (6) the analyses were too

complex to allow us to recover the original data ($n=1$). Ultimately, we included 55 papers and one unpublished study in our review, yielding a total of 147 effect sizes from 38 species for analysis (see Appendix A in the Supporting Information S1 for the PRISMA diagram; and Appendix B for a list of the papers).

The papers consisted of experimental studies that directly manipulated density (usually of a cohort of young fish) and quantified the number of survivors to a later point in time, as well as observational studies that relied on natural variation in settlement, counted the number of fish on a particular date (after settlement had stopped) and then reported the subsequent number of those fish remaining on the reef after a defined length of time. The duration of these studies ranged from 12 h to over 516 days. Studies focused on local groups of fish at several spatial scales: For example, inhabiting coral colonies (e.g., typically $\leq 1\text{m}^2$), or small patches of habitat (e.g., 10 m^2), or larger reefs (several hundred m^2).

For many of the papers, there was more than one suitable dataset. Some papers reported data for a single species at multiple localities or years; others gave data for > 1 species; and some papers (e.g., Hixon and Carr 1997) reported on an experiment in which density was crossed with another factor. We categorized each of those unique sets of data as a ‘substudy’ (i.e., a density gradient conducted at a particular place, time, and set of conditions for a particular species). As articulated below, we treated subsudies as random effects within papers to help address non-independence of effects within papers. For each subsudy, we either took data from tables, text or appendices, digitized the data from the figures, or contacted the authors directly. The resulting core data set consisted of the initial density of fish (often recent settlers) (N_0 , fish/ cm^2) in each plot (or cage or reef) or an aggregate of replicates at a given density if the data could not be disaggregated, the final density of those fish (N_t , fish/ cm^2), and the amount of time between the two censuses (t , days).

2.3 | Estimating the Recruitment Function

We estimated the strength of density-dependence for each subsudy using a Beverton–Holt recruitment function, which has been shown previously to be a good descriptor of the recruitment function for reef fishes (Shima and Osenberg 2003, Osenberg et al. 2002). We assumed that the instantaneous per capita mortality of group of fish ($1/N$) (dN/dt) was a linear function of fish density, reflecting the strength of density-independent (α) and density-dependent (βN) mortality rates:

$$\left(\frac{1}{N}\right)\frac{dN}{dt} = -\alpha - \beta N \quad (1)$$

where β is a measure of the strength of density dependence (i.e., the effect of one individual (per areal unit) on the per capita mortality rate of conspecifics of a comparable post-settlement life stage).

Equation (1) can be integrated to obtain the continuous-time formulation of the Beverton–Holt recruitment function:

$$N_t = \frac{N_0 e^{-\alpha t}}{1 + \frac{\beta N_0 (1 - e^{-\alpha t})}{\alpha}} \quad (2)$$

Note that negative effects of density on survival are indicated by $\beta > 0$. We expressed all parameters from all studies in common units (e.g., density as fish cm^{-2} , and time in days). Thus, β had units of $\text{cm}^2 \text{fish}^{-1} \text{day}^{-1}$. While β is the focus of our analyses, note that the product βN is the per capita mortality rate (day^{-1}) induced by a conspecific density of N (i.e., over and above the rate induced by density-independent processes). Equation (2) defines the expected density trajectory. To fit empirical data, we mapped this process model into observation models. When raw counts were reported, we applied a binomial likelihood (Approach 2 below); when only densities were reported without survey area, we used a lognormal likelihood (Approach 3 below).

We used three approaches to obtain estimates of β and its variance depending on the available data:

2.3.1 | Approach 1—Reported Estimates

When studies reported estimates of β (i.e., $\hat{\beta}$ where the \wedge indicates an estimate) using eq. 1 or 2 and estimates of uncertainty (e.g., Schmitt and Holbrook 2007; Shima and Osenberg 2003; Wilson and Osenberg 2002), we used those values directly and converted them to $\text{cm}^2 \text{fish}^{-1} \text{day}^{-1}$ when necessary.

2.3.2 | Approach 2—Binomial Likelihood (When Counts Were Available)

For substudies that reported counts (or densities along with the area sampled) we estimated parameters (α, β) using a binomial composite log-likelihood:

$$\ell(\alpha, \beta) = \sum_i [a_i N_{t,i} \log_e p_i(\alpha, \beta) + a_i (N_{0,i} - N_{t,i}) \log_e (1 - p_i(\alpha, \beta))], \quad (3)$$

where p_i is the predicted proportion of fish surviving in observation i within the substudy (i.e., $p_i(\alpha, \beta) = \hat{N}_{t,i} / N_{0,i}$ where $\hat{N}_{t,i}$ is the predicted density of recruits based on Equation 2), a_i is the total area that was sampled to obtain the i th observation of settlers and recruits (i.e., $a_i N_i$ is a total count as required by the binomial distribution). Although p_i was never exactly 0 or 1, it was sometimes arbitrarily close to those boundaries, so as a computational safeguard, we truncated p_i to $[1 \times 10^{-10}, 1 - 1 \times 10^{-10}]$.

2.3.3 | Approach 3—Lognormal Likelihood (When Counts Were Not Available)

In five papers densities were reported, but the area sampled for an observation was not reported, so counts could not be determined. Because Approach 2 could not be applied, we used a lognormal observation model instead:

$$\ell(\alpha, \beta, \sigma) = - \sum_i \left[\frac{(\log_e N_{t,i} - \log_e \hat{N}_{t,i}(\alpha, \beta))^2}{2\sigma^2} + \log_e \sigma \right], \quad (4)$$

where σ is the lognormal error term's standard deviation, quantifying uncertainty and overdispersion in reported densities.

2.3.4 | Uncertainty and Variance Estimates

For Approaches 2 & 3, we quantified uncertainty in $\hat{\beta}$ via profile likelihoods. We used the cutoff $\Delta(-\ell) = 2$ to define 95% confidence intervals for $\hat{\beta}$. Because meta-analysis requires an approximate substudy-specific variance of the effect (i.e., $\text{Var}(\hat{\beta})$), and because the confidence intervals from the profile likelihoods were asymmetric, we converted endpoints of the confidence interval (where U and L are the endpoints) to a variance via

$$\text{Var}(\hat{\beta}) \approx \left(\frac{U - L}{2 \times 1.96} \right)^2 \quad (5)$$

2.4 | Moderators

In addition to estimates of density-dependent survival for each study, we also extracted a series of moderators (i.e., covariates) for each substudy to evaluate hypotheses that could explain the wide variation in the strength of density-dependent mortality that we subsequently observed. Specifically, we recorded the taxonomy of the focal species (family, genus, and species), categorized whether predators were present (e.g., uncaged) or absent (e.g., excluded via the use of cages), the approximate body size of the fish at the start of the study (mm standard length), maximum species length (obtained from FishBase: Froese and Pauly 2010), substudy duration (days), and whether initial density in the substudy was experimentally manipulated or based on observational data.

2.5 | Hypotheses

We framed five a priori hypotheses that we tested using a meta-analytic framework. The paragraphs below elaborate on the biological rationale and statistical specification for each hypothesis.

2.5.1 | H1: Overall Effect of Density Dependence and Its Heterogeneity

We began by estimating the grand mean and heterogeneity of density dependence (β and τ^2), motivated by the expectation that post-settlement fishes experience negative density dependent survival (e.g., due to competition for refuges and size-selective predation). In our analytic approach (here and in all other analyses), we used inverse variance weighting so that substudies with more precise estimates of β received greater weight. We accounted for potential non-independence using a multilevel model that incorporated random effects for paper and substudy (within paper), which enabled us to estimate the overall strength of density-dependent mortality as well as its variation among-papers and within-papers.

2.5.2 | H2: Phylogenetic Signal

We conducted a phylogenetic analysis to determine whether species-level variation in density dependence (β) was influenced by shared evolutionary history. We used the fish

phylogeny from Rabosky et al. (2018) and pruned it to match the species present in our dataset. We then quantified the phylogenetic signal in the data by mapping the mean value of β for each species onto the phylogeny (Siqueira et al. 2020), and asked if there was evidence for a phylogenetic signal using the `phylosig` function in the `phytools` package in the programming language *R* by calculating Blomberg's K (Revell 2012). Blomberg's K compares the observed trait variation to the variation expected under a Brownian Motion model. $K=1$ indicates that traits evolve as expected under Brownian Motion, $K < 1$ suggests lower similarity among closely related species than expected, $K=0$ indicates no phylogenetic signal, and values greater than 1 indicate greater similarity among related species than expected given Brownian Motion (suggesting phylogenetic conservatism). Although we observed only a weak (and nonsignificant) phylogenetic signal, we took a conservative approach and included a phylogenetic variance-covariance matrix in our subsequent models to account for possible phylogenetic non-independence.

2.5.3 | H3: Interspecific Variation

To test whether species differed from one another in the strength of density-dependent mortality, we fit hierarchical meta-analytic models using the `Metafor` package and `rma.mv` function (Viechtbauer 2019). We included random effects for papers, substudies within papers, and a phylogenetic variance-covariance matrix (to account for non-independence), plus a species random intercept that represented differences among species that were not accounted for by the phylogeny. We compared a null model without the species effect to the model with the species random effect using a restricted likelihood ratio test (REML-LRT). Because variance components are on the boundary of the parameter space, we evaluated significance using the $0.5\chi^2_0 + 0.5\chi^2_1$ mixture distribution (Self and Liang 1987). To quantify the magnitude of interspecific heterogeneity, we estimated the species variance component and its 95% confidence interval using a profile-likelihood approach.

2.5.4 | H4: Predators

Predators are thought to mediate density-dependent survival in reef fish because high fish densities intensify competition for refuges from predators (Holbrook and Schmitt 2002; Steele and Forrester 2002; White 2007). Fish that cannot procure shelter space due to crowding within a given reef tend to experience higher per-capita mortality. Therefore, we began our moderator analyses by first examining whether the strength of density-dependent mortality (β) differed between studies in which predators were present versus absent. This included many studies in which predators were not manipulated (i.e., were potentially present at ambient predator densities), studies that excluded predators by examining density-dependence in caged plots, and experiments that manipulated predators and thus had both a predator-present and predator-absent treatment (e.g., Hixon and Carr 1997). To test the hypothesis that predators increased the strength of density-dependent mortality, we used the same model structure as before (random effects of species, paper and substudy, with inverse variance weighting, and the phylogenetic

covariance matrix), but with predators (presence vs. absence) as a categorical fixed effect. We also conducted a secondary analysis on a subset of the papers in which the presence of predators was experimentally manipulated (i.e., each paper provided data on the strength of density-dependent mortality in both the presence and absence of predators). In one case (Carr et al. 2002), predators and interspecific competitions were both manipulated yielding two contrasts of the effect of predators on the strength of density-dependence—one in the presence of interspecific competition and one in its absence. We therefore incorporated substudy and paper as random effects.

2.5.5 | H5: Additional Moderators: Body Size, Density, Study Duration and Methodology

After finding an effect of predators, we focused the remaining analysis of predictor variables on the strength of density dependence in substudies in which predators were present (which was the case for 84% of all substudies). In this meta-regression model, we used the same structure of random effects and phylogenetic covariation as above but simultaneously examined the fixed effects of body size (both at the start of the study and the maximum length for the species), average density, substudy duration and substudy methodology (observational vs. experimental). Below we describe our hypotheses for each of these moderators.

2.5.6 | Initial Body Length

Because predation is thought to be the primary process underlying mortality of reef fishes early in their benthic life history, and because predators on coral reefs are often gape limited (Hixon 1991) and refuges from predators are limiting (Forrester and Steele 2004), fish that were larger at the start of the experiment may incur weaker effects of density-mediated predation. We therefore included initial body size in our main moderator model. Additionally for a subset of the full dataset where species had more than three substudies, we fit a mixed effects model with body size and species as fixed effects and paper and substudy as random effects. This model tested whether there was a consistent effect of body size within species, relying on variation in the size of fish at the start of the experiment.

2.5.7 | Maximum Body Length

We included the maximum body length of each species, as reported in FishBase (Froese and Pauly 2010), to account for broad life history differences that might influence the strength of density-dependent mortality. Body size is a fundamental ecological trait linked to metabolism (Brown et al. 2004), space use (Tamburello et al. 2015) and fecundity (Barneche et al. 2018), and is negatively associated with population density across a wide range of taxa (Ackerman et al. 2004; Ackerman and Bellwood 2003; Cyr et al. 1997; Damuth 1981). Species of large body size tend to occur at lower densities, potentially due to their greater per capita resource demands. Thus, we predicted that species characterised by large maximum size would incur stronger intraspecific density-dependence (i.e., larger β) than species of smaller size.

2.5.8 | Density

We also examined the effect of the mean density of each focal species in each substudy. Our rationale here was similar to that for maximum body length, although density of early life stages is not necessarily correlated with adult density or adult body size. We tested the hypothesis that density (at the start of the substudy) influenced the strength of density-dependent mortality, expecting that species at higher density would have smaller estimates of β . Average density was calculated as the mean density across all levels reported in the paper, which assumed that these densities were representative of the ambient densities for these life stages in the study system.

2.5.9 | Duration

If the strength of density-dependent mortality is stronger early in ontogeny, or if fish in a cohort vary in their frailty (Kendall et al. 2011) then the duration of a substudy may influence the observed strength of density-dependent mortality, with density-dependent mortality being strongest in short-duration studies because newly settled fish are more vulnerable to predation and intraspecific competition (Hixon and Webster 2002) or because of greater variance in frailty in younger cohorts. Study duration was measured as the number of days between the initial and final density censuses (i.e., t in Equation 2), allowing us to assess whether the strength of density dependence declined in studies of longer duration. Ideally, we would quantify how the strength of density-dependent mortality changed over time within a substudy (see Downing et al. 1999; Osenberg et al. 1999), but most studies provided only two point estimates of density (start and end) and not a time series.

2.5.10 | Study Design

Some researchers took an observational approach when investigating potential density dependence, following cohorts of individuals that settled at different ambient densities across different reefs and used this natural spatial variation in density to estimate the relationship between post-settlement survival and density. Other investigators took an experimental approach, capturing fish (typically shortly after settlement), and then deploying groups of fish at different densities to study plots (e.g., patch reefs). The random assignment of treatments (i.e., densities) and individual fish to plots ensured that the effects of density were not confounded with other factors that might affect estimates of density dependence. For example, prior studies of reef fish described ‘cryptic density dependence’ in which effects of density inferred from observational data were weaker than those seen in experiments because larval fish settled at higher densities to higher quality sites masking the effects of density dependence in the observational data sets (Shima et al. 2008; Shima and Osenberg 2003; Wilson and Osenberg 2002). We therefore tested if estimates of density-dependent mortality differed between observational and experimental studies. We also examined if experimental and observational studies differed by pairing an experimental substudy with an observational

substudy conducted on the same species during the closest available site and year.

2.5.11 | Statistical Approach

We conducted all meta-analyses in the programming language *R*, using the package *Metafor* (Viechtbauer 2019). We used the function *rma.mv* (because of the hierarchical structure of the random effects), the option ‘REML’ to estimate the variance components (among papers and among substudies within papers), and the ‘ h ’ option to construct confidence intervals for the mean effect sizes using the t-statistic (rather than z-statistic) because the number of papers was relatively small (e.g., Pappalardo et al. 2020). Because estimates of β spanned positive and negative effects and were skewed, we transformed the estimates of β using the hyperbolic sine function (arcsinh) prior to analysis to produce more normal distributions of effects, as assumed in *Metafor*. Sampling variances, v_i , came from reported variances of $\hat{\beta}_i$ or from Equation (5) and were converted to the transformed scale via the delta method:

$$v_i = \frac{\text{Var}(\hat{\beta}_i)}{1 + \hat{\beta}_i^2}. \quad (6)$$

For ease of interpretation in the text, we back-transformed means and CI’s to the original scale, and for figures, we plotted the untransformed values of $\hat{\beta}$, but on transformed axes. We report variance components based on the transformed data.

For each substudy i , we analysed the transformed effect $e_i = \text{arcsinh}(\hat{\beta}_i)$, where $\hat{\beta}_i$ is the estimated strength of density-dependent mortality on the original scale ($\text{cm}^2 \text{fish}^{-1} \text{day}^{-1}$). We fit a model in which the transformed effect was a linear combination of fixed effects (indicated by η_i), random effects (due to paper, substudy, and phylogeny) plus sampling error (ε) with known variance:

$$e_i = \eta_i + u_{j[i]}^{(\text{paper})} + u_{j[i],k[i]}^{(\text{sub})} + u_{s[i]}^{(\text{phy})} + \varepsilon_i; \varepsilon_i \sim \mathcal{N}(0, v_i) \quad (7a)$$

The fixed effects predictor was:

$$\eta_i = \mu + \gamma_{\text{des}} D_i + \gamma_{\text{den}} \log_e(x_{1,i}) + \gamma_{\text{dur}} x_{2,i} + \gamma_{\text{size}} x_{3,i} + \gamma_{\text{max}} x_{4,i}, \quad (7b)$$

where μ is the grand mean (for an observational study at centered moderators), γ_{des} is the effect of study design ($D_i = 1$ for experimental and 0 for observational), $\log_e(x_{1,i})$ is the centered-and scaled log-transformed average density at the start of the study (where $x_{1,i}$ is in no. cm^{-2}), $x_{2,i}$ is study duration (days), $x_{3,i}$ is initial body size (mm), and $x_{4,i}$ is the maximum adult length of the species (cm).

To account for non-independence, we included (1) a paper-level random intercept, $u_{j[i]}^{\text{paper}} \sim \mathcal{N}(0, \tau_{\text{paper}}^2)$ for paper j containing substudy i , (2) a substudy-within-paper random intercept $u_{j[i],k[i]}^{\text{sub}} \sim \mathcal{N}(0, \tau_{\text{sub}}^2)$ for substudy k nested in paper j , and (3) a phylogenetic random effect $u_{s[i]}^{\text{phy}} \sim \mathcal{N}(0, \sigma_{\text{phy}}^2 V_{\text{phy}})$ for species s ,

where V_{phy} is the variance–covariance matrix extracted from the pruned teleost phylogeny (Rabosky et al. 2018) scaled by shared branch lengths.

Our full model initially contained the five main fixed effects (Equation 7b) plus the ten two-way interactions (unbalanced meta-analytic designs make higher-order interactions hard to interpret). We retained all main effects by design and removed only interaction terms that were not significant at $p > 0.05$. In our analysis, all two-way interactions were non-significant, so the final reported model contained the five main effects and the full random-effects structure described above (Equation 7a).

We conducted several diagnostics to evaluate potential publication bias and the robustness of the pooled mean (Appendix E). Funnel plots, Egger's regression, and null-add sensitivity analyses indicated only weak small-study asymmetry and strong overall model stability. Egger's test yielded an non-zero intercept of 15.91 ($p = 1.747e-07$), with a modest proportion of variance explained ($R^2 = 0.028$), suggesting marginal but statistically detectable asymmetry. However, the pooled effect remained positive and stable even when up to ten hypothetical null studies were added. Although it is plausible that some studies quantifying weak or imprecise density dependence were never published, such omissions would not qualitatively alter our conclusions. The large heterogeneity we observed cannot be explained by selective reporting alone, and any missing and imprecise studies would have been downweighted in our random-effects model. Thus, we consider our results to be a fair representation of studies that have been conducted. Of course, there are likely a wide range of systems (e.g., species that exist at very low densities, or species that are less sedentary) that have never been studied. Our analyses are therefore applicable not to reef fish in general, but to those species and systems that have previously been investigated.

3 | Results

On average, increased density decreased survival ($\bar{\beta} = 10.26 \text{ cm}^2 \text{ fish}^{-1} \text{ d}^{-1}$, 5.56, mean, lower CI, upper CI, Figure 1a). However, the effects were highly heterogeneous ($Q_{146} = 177,054$, $p < 0.0001$), with estimates of β ranging from negative (mortality decreased with increased density) to positive (mortality increased with density): Figure 1b–d. The variance among substudies within papers dwarfed the variation among papers (back transformed estimates: $\hat{\sigma}_{\text{paper}}^2 = 34.40$; $\hat{\sigma}_{\text{substudy}}^2 = 1252$).

There was some evidence for a phylogenetic signal in the strength of density-dependent mortality (Figure 2, $K = 0.530$, $p = 0.16$), although this estimate did not differ from 0 (which would indicate phylogenetic independence). For example, species in the family Pomacentridae were characterised by relatively weak density-dependence compared to fishes in the families Labridae and Sparidae. This suggests that while not statistically significant, closely related species tended to share similar strengths of density dependent mortality. Including species as a random effect with a phylogenetic variance–covariance structure substantially improved model

fit ($\Delta AIC = 7.96$; REML LRT = 9.95, boundary-corrected $p = 0.0016$; Figure 3). The estimated among-species variance was 5.26 (95% profile-likelihood CI: 0.82–4.13). These results indicate strong evidence for interspecific heterogeneity in the strength of density-dependent mortality beyond what is explained by phylogenetic relationships. In contrast, in the simpler model with only species, study, and substudy as random effects, species identity accounted for roughly 20% of the variance, with the majority ($\approx 80\%$) attributable to variation among substudies within species. For example, the bluehead wrasse, (*Thalassoma bifasciatum*) had substudies with both negative and positive estimates of β . Another wrasse (*Halichoeres garnoti*) has estimates of β that varied by several orders of magnitude. This highlights that most of the heterogeneity in density dependence arose from differences among substudies within species, rather than consistent differences between species. Although the test of phylogenetic non-independence was not significant, we retained the phylogenetic information in subsequent analyses as a conservative approach.

Across the entire data set, density-dependent mortality was stronger in the presence (vs. absence) of predators ($p = 0.048$; Figure 4): in the absence of predators there was no detectable effect of density on survival ($\hat{\beta}_{\text{nopred}} = 5.02$, lower CI: -0.35, Upper CI: 72.50), whereas in the presence of predators the effect of density was strong and demonstrable ($\hat{\beta}_{\text{pred}} = 35.44$, lower CI: 5.10, Upper CI: 244.20). On average, predator presence increased the strength of density-dependent mortality by 606%. A direct test of predator effects comes from the 11 experimental studies that included paired predator-absence and predator-presence treatments. In every case, density dependence was stronger when predators were present. The paired meta-analytic model estimated a predator effect of 2.79 ± 0.85 on the arcsinh-transformed β scale ($t = 3.27$, $df = 14$, $p = 0.0056$). Back-transformed predictions indicated that mean β was $12.83 \text{ cm}^2 \text{ fish}^{-1} \text{ day}^{-1}$ (95% CI = -0.82 to 695.99) in the absence of predators and $208.75 \text{ cm}^2 \text{ fish}^{-1} \text{ day}^{-1}$ (95% CI = 4.26 to 10103.99) in their presence—an average increase of $\sim 1527\%$. A corroborating maximum-likelihood likelihood-ratio test comparing models with and without the predator term within pairs was also significant (LRT = 7.88, $df = 1$, $p = 0.0050$). While predator presence/absence clearly plays a role in driving heterogeneity in $\hat{\beta}$, the strength of density-dependent mortality still varied by several orders of magnitude among studies with predators present (Figure 4). Because most substudies (84%) were conducted in the presence of predators, we focused subsequent analyses on the studies with predators and explored possible drivers of that variation.

All ten 2-way interactions in the full moderator model were not significant (all $p > 0.2$), so we retained only the five main effects (along with random effects) in the final model, which explained a significant portion of variation in the strength of density dependence ($F_{5,91} = 7.17$, $p < 0.0001$). However, residual heterogeneity remained substantial ($QF_{91} = 20,166.5$, $p < 0.0001$), suggesting that the fixed effects did not capture all sources of heterogeneity. The variance estimates indicated that this unexplained heterogeneity was primarily from variation among substudies within papers and species: there was negligible heterogeneity among papers ($\sigma^2 = 0.00$) and among

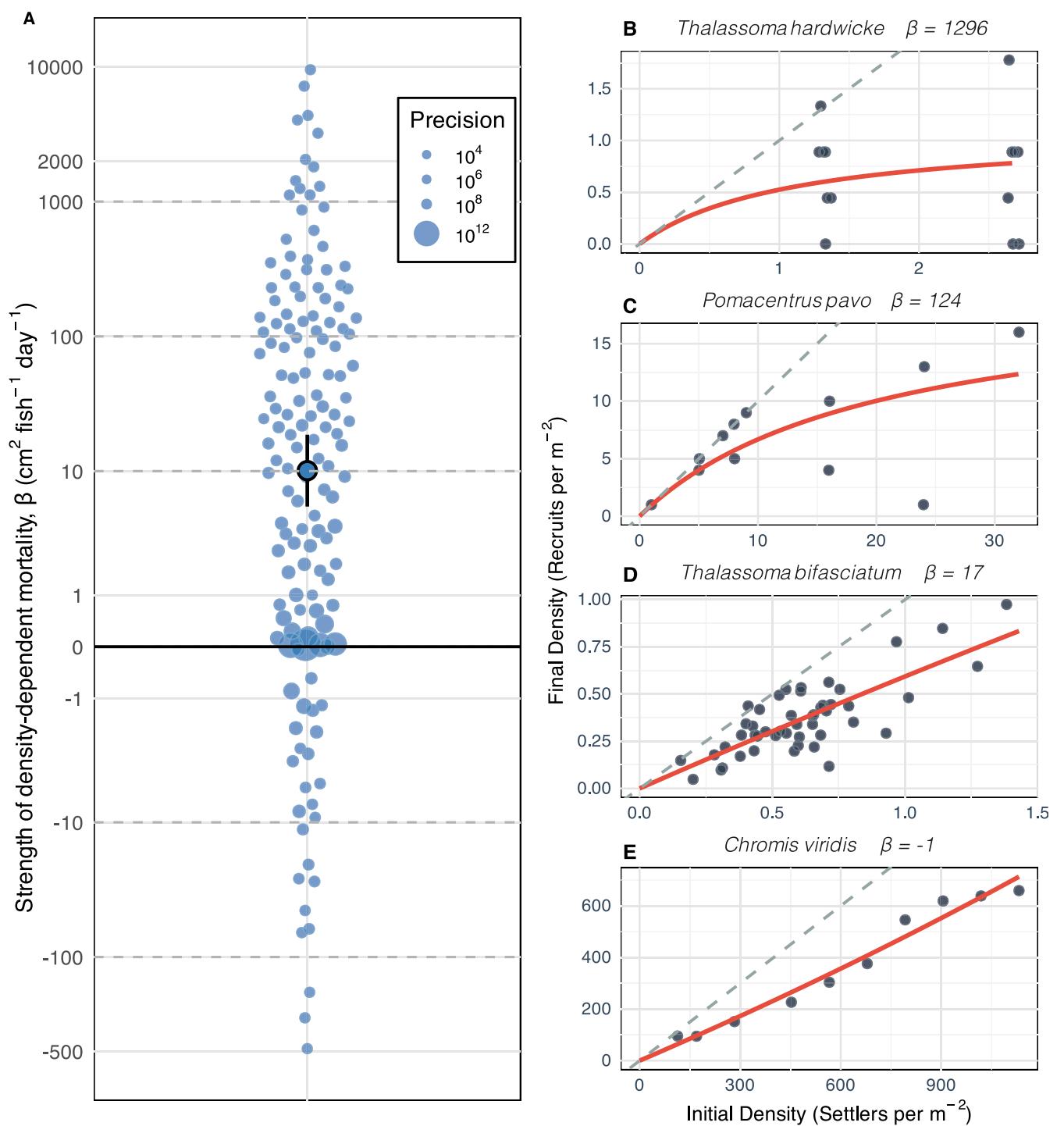


FIGURE 1 | The strength of density-dependent mortality ($\hat{\beta}$) and its precision vary widely across studies of coastal fishes. (A) The y -axis gives $\hat{\beta}$ values (density-dependent mortality expressed as $\text{cm}^2 \text{fish}^{-1} \text{day}^{-1}$) on a inverse hyperbolic sine transformation (arcsinh) scale to capture a broad range of negative to positive effects. The size of the point is proportional to the square root of the inverse variance of $\hat{\beta}$. (B–E) Four representative sub-studies illustrating original data for species with a range of effects of density as indicated by $\hat{\beta}$.

species ($\sigma^2=0.113$), but substantial variation among sub-studies ($\sigma^2=8.15$).

Parameter estimates from the final additive model indicated that study design (experimental vs. observational: $\beta=1.27 \pm 1.06$ SE, $t_{91}=1.20$, $p=0.23$), average body size ($\beta=0.09 \pm 0.45$ SE, $t_{91}=0.20$, $p=0.84$), and maximum

length ($\beta=0.29 \pm 0.50$ SE, $t_{91}=0.58$, $p=0.57$) had no significant effects on density dependence (see Appendix C,D; Figure SC-2,5,SD-1). The results for the 6 species with paired observation and experimental subsudies suggested, however, that the contrast between experimental and observational estimates of β was species-specific (Appendix D). In contrast, density-dependent mortality was significantly stronger when

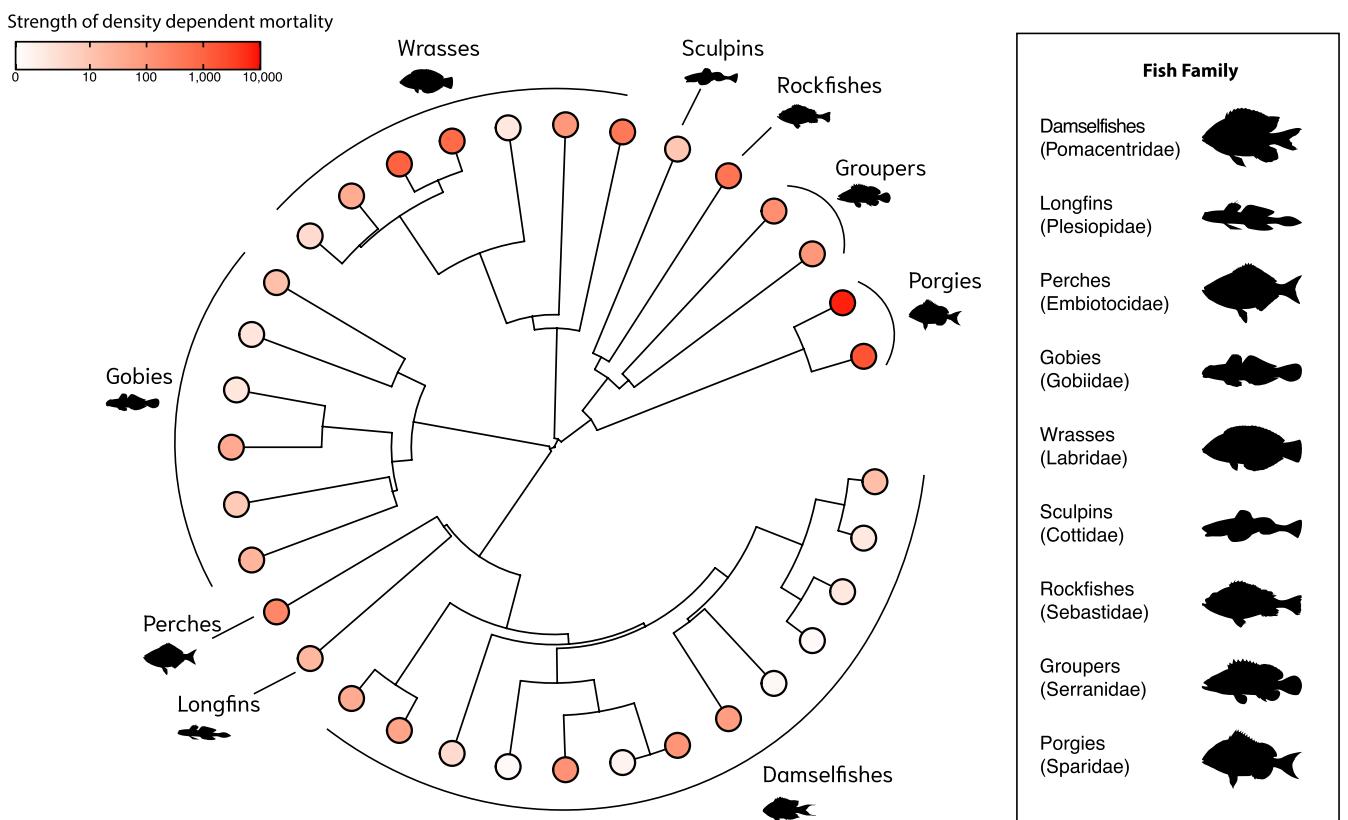


FIGURE 2 | Phylogenetic mapping reveals mild clustering of density-dependent mortality across fish species. The phylogeny of Rabosky et al. (2018) was pruned to show only the species present in our dataset, with circles at each tip representing the mean estimate of density-dependent mortality ($\hat{\beta}$). Most intense colours indicate stronger density dependence. Silhouettes of fish are representative shapes of fish from families mapped on the phylogeny.

initial fish densities were lower ($t_{91} = -3.60$, $p = 0.0005$) and study duration was longer ($t_{91} = -3.17$, $p = 0.0021$): Figure 5.

4 | Discussion

Our findings reveal considerable heterogeneity in the strength and direction of density-dependent mortality in reef fishes. While higher densities within a substudy generally reduced survival, our meta-analysis uncovered striking intraspecific variation, with some species exhibiting both positive and negative effects of density on mortality. In several cases, the magnitude of density dependence varied by orders of magnitude—even within a single species—suggesting that density-dependent processes are highly context-dependent. This variability is not random but instead arises from an interplay of ecological interactions, evolutionary history, and methodological influences. Specifically, we found that predators amplified density-dependent mortality (e.g., Hixon and Carr 1997; Schmitt and Holbrook 2007), and that species that exhibited weak density-dependence occurred at higher average densities. However, a large portion of the variation remained unexplained, underscoring the need to identify additional environmental and behavioural drivers of density dependence. Without a clearer understanding of these factors, our ability to predict population regulation in reef fishes remains incomplete.

4.1 | Causes and Consequences of Widespread Intraspecific Variation

Prior work identified several drivers that can generate considerable heterogeneity in addition to those highlighted by our analyses. For example, habitat complexity (Beukers and Jones 1997), predator assemblages (Hixon and Carr 1997), and resource availability (Forrester and Steele 2004) can all alter the mortality–density relationship, yet these factors are rarely reported unless they are the focus on the primary study. Since they are rarely reported, we could not incorporate them into our meta-analysis. Below we review the factors that have been implicated as modifying the strength (and possibly direction) of density-dependent survival and then discuss future directions.

4.2 | Predators as Agents Driving Variation in Density-Dependent Mortality

Predators can readily induce high mortality (upwards of 90%) on newly settled fishes (Almany and Webster 2006). Thus, predation plays a key role in driving reef fish abundance, biodiversity (Almany and Webster 2006; Hixon 1991; Stier et al. 2017), and density-dependent mortality (Figure 4, Carr et al. 2002; Hixon and Carr 1997; Schmitt and Holbrook 2007). Predators are hypothesized to induce density-dependent mortality by

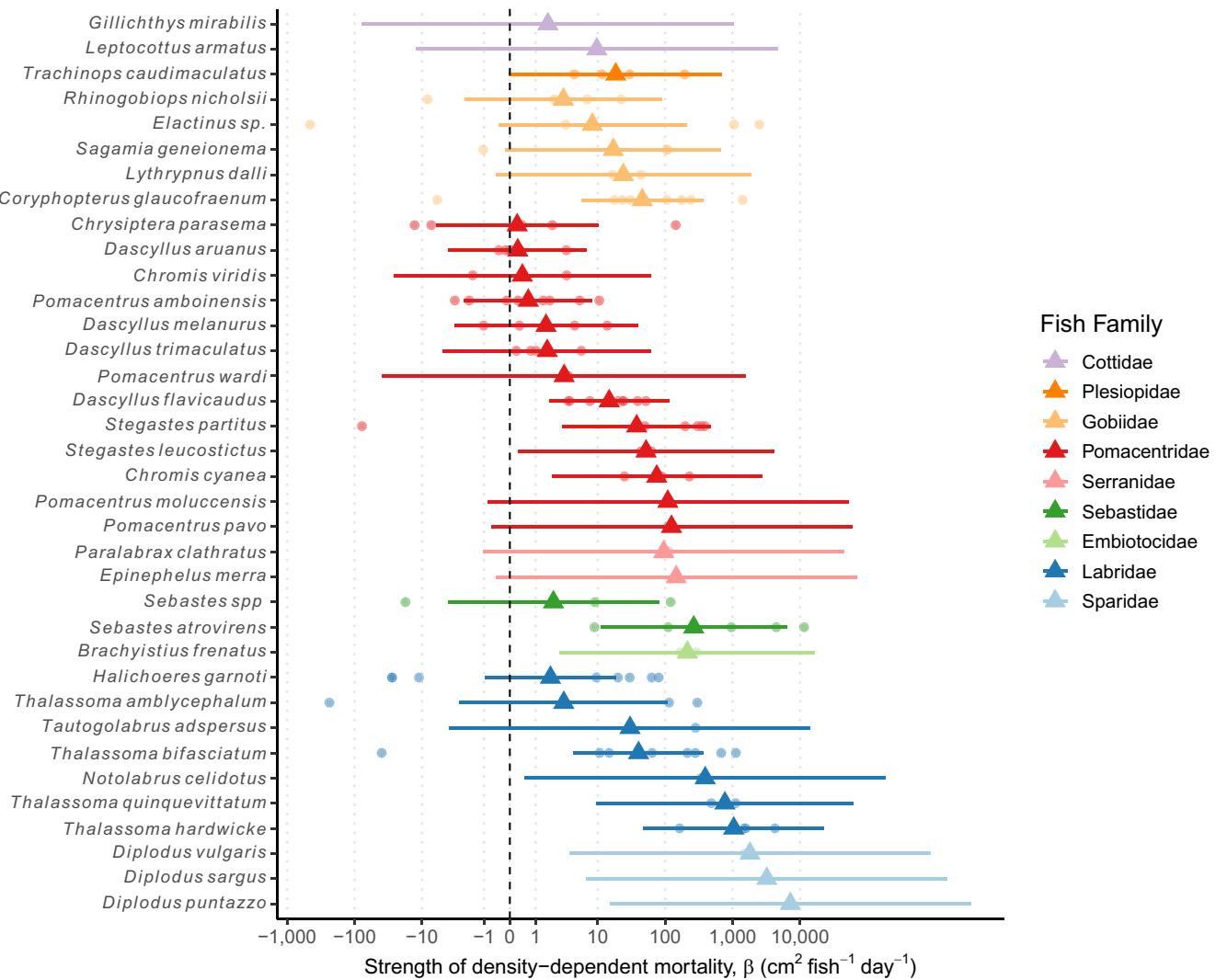


FIGURE 3 | Studies revealed significant variation in the strength of density-dependent mortality, both within and among fish species. Each species' mean $\hat{\beta}$ (triangle) and 95% confidence interval (horizontal line) was estimated from the rma.mv model, with colours corresponding to fish family. Individual points give estimates of density-dependent mortality ($\hat{\beta}$, $\text{cm}^2 \text{fish}^{-1} \text{day}^{-1}$) for each substudy within a species. Species that lack points had only 1 estimate. The dashed vertical line at $\hat{\beta} = 0$ indicates no density-dependent mortality and separates positive and negative density-dependent mortality effects. $\hat{\beta}$ values are displayed on an inverse hyperbolic sine (arcsinh) scale to effectively display a wide range of values.

consuming fishes unable to find shelter space (Holbrook and Schmitt 2002), so the strength of density-dependence should not only depend on predator density but it also should be greater in low complexity systems that lack predator-free refuges. For example, Forrester and Steele (2004) manipulated refuge availability from low to high (without manipulating predators) and found that the strength of density-dependence was 5.3× greater in the low versus high shelter treatments. Shima and Osenberg (2003) applied Equation (2) to observational data on settlement-recruitment patterns in *Thalassoma hardwicke* and used a suite of environmental parameters to describe spatio-temporal variation in $\hat{\beta}$. They found estimates of β ranging from 0.015 to 0.61 $\text{cm}^2 \text{fish}^{-1} \text{day}^{-1}$, with weaker density-dependence in sites with more shelter (branching corals), but in contrast to other studies, these better sites also had more predators. Subsequent experimental work confirmed the role of shelter availability (Shima et al. 2008). Thus, variation in predator density (or identity or composition) and shelter

availability might explain considerable variation in estimates of β , yet these variables are not consistently reported in studies of density-dependence.

Furthermore, considerable variation remains unexplained even when accounting for predator density. For example, *Dascyllus flavicaudus* exhibited 13-fold variation in $\hat{\beta}$ in response to variation in predator density (Schmitt and Holbrook 2007), but in our meta-analysis β 's estimated for *D. flavicaudus* varied 380-fold, suggesting that predators, while important, explain only a small portion of the heterogeneity observed in studies of *D. flavicaudus*. While some of this unresolved variation might be the result of variation in shelter availability, it is surprising that despite being one of the best-studied species in the world, *D. flavicaudus* exhibits a tremendous amount of (currently) unexplained variability in the strength of density-dependent mortality, pointing to the need for additional research and more extensive reporting of potential moderators.

4.3 | Spatial Scale and Habitat Configuration

The spatial scale at which density-dependence is assessed could affect estimates of density-dependence (White et al. 2010). For example, predators might aggregate to areas with high prey

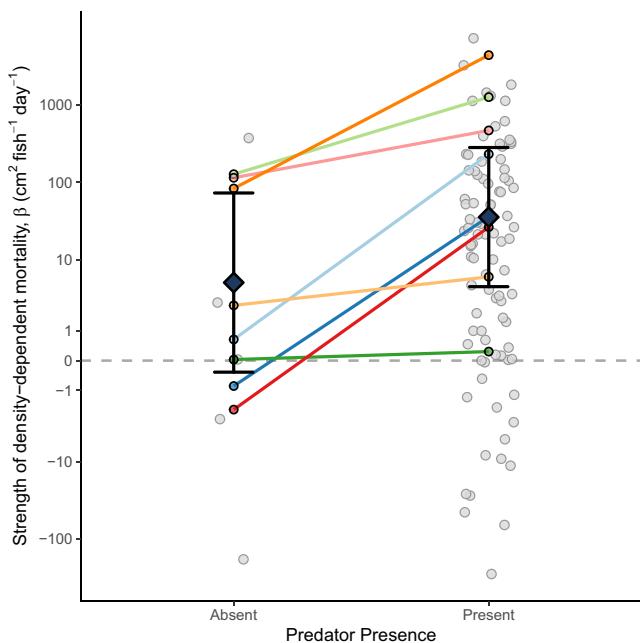


FIGURE 4 | Predator presence enhances the strength of density-dependent mortality ($\hat{\beta}$, $\text{cm}^2 \text{fish}^{-1} \text{day}^{-1}$). Points represent substudies, diamonds and 95% confidence intervals are for the two groups, and lines connect corresponding substudies from the same experiment (open symbols) that included predator-absent and predator-present treatments. Substudies without a paired design are shown with grey circles. More positive values of $\hat{\beta}$ indicate stronger density-dependent mortality, while negative values suggest inverse density dependence.

densities intensifying negative density-dependence. On the other hand, if predators don't move among prey patches, positive density-dependent prey survival might result if a predator has a Type II functional response (Overholtzer-McLeod 2006; Sandin and Pacala 2005). *Thalassoma bifasciatum* exhibited a scale-dependent pattern of density dependence (White and Warner 2007). At the scale of small groups, fish exhibited positive density dependence (possibly due to schooling and safety in numbers), while at the reef scale, survival was negatively density dependent (possibly due to predator aggregation or a Type III functional response). In contrast, large-scale manipulations of the schooling snapper *Lutjanus apodus* revealed that higher population density increased both recruitment and survival, consistent with benefits of group-living at high density (Wormald et al. 2013). Habitat configuration can also generate variation in density-dependence: on continuous reefs, prey aggregation can lower per-capita predation, whereas on more isolated patches with little shelter, mortality tends to rise sharply with density (Overholtzer-McLeod 2004, 2006; Sandin and Pacala 2005).

4.4 | Stronger Density Dependence in Species Living at Low Population Densities

Our results also suggest that the strength of density dependence is weaker in systems that tend to occur at higher average densities. This pattern suggests that species that persist at high densities (which are usually small in body size) can do so because they have mitigated the negative effects of conspecific crowding. This finding aligns with theoretical work showing that negative conspecific density dependence is expected to be stronger in species that are less abundant (Chisholm and Muller-Landau 2011). Studies of plant communities support this expectation (Comita et al. 2010; Kliromanos 2002; Mangan et al. 2010). These observations are further bolstered by other studies of reef fish showing that intraspecific density dependence is stronger than interspecific effects (Ruiz-Moreno et al. 2024), suggesting that

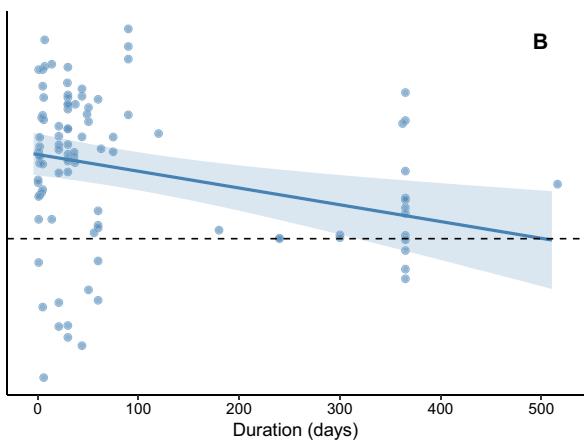
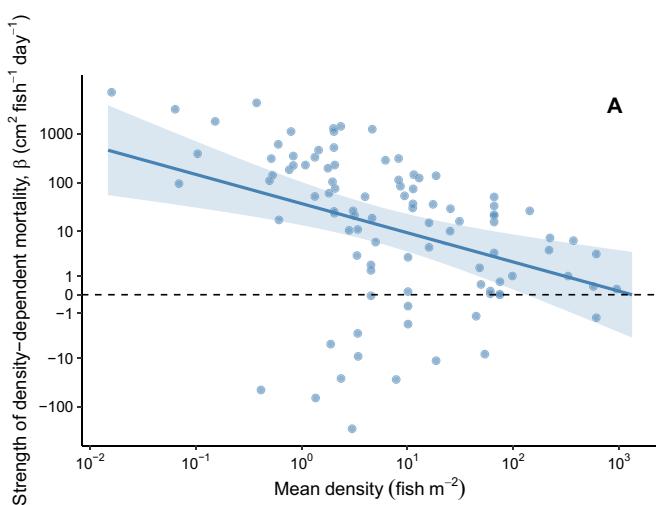


FIGURE 5 | Variation in density-dependent mortality ($\hat{\beta}$) with two key study moderators. (A) $\hat{\beta}$ ($\text{cm}^2 \text{fish}^{-1} \text{day}^{-1}$) versus mean density (fish m^{-2}) on a \log_{10} scale. (B) $\hat{\beta}$ versus study duration (days). In each panel, semi-transparent steel-blue circles are the raw substudy estimates and the solid navy line with pale-blue ribbon is the meta-regression prediction \pm 95% CI from an rma.mv model holding all other moderators at their mean (centered = 0). A horizontal dashed line at $\hat{\beta} = 0$ indicates the absence of density-dependence. The y-axis uses an inverse hyperbolic sine (arcsinh) transformation to symmetrically accommodate large negative and positive values.

ambient densities may be more determined by conspecific interactions rather than interactions with heterospecifics.

4.5 | The Need for Improved Reporting and Methods

Based on these insights, we recommend several improvements to primary studies of density dependence that will facilitate future comparative analyses designed to understand the factors that influence density-dependence and population regulation: (i) report predator identity and density, and, when possible, their typical foraging scale, as well as the availability of refugia; (ii) report both areal density and group/aggregation sizes of the focal species; (iii) quantify and report habitat configuration (e.g., patch size, interpatch spacing, reef continuity) and state the observation grain; and (iv) where feasible, estimate density effects at more than one spatial scale (e.g., aggregation vs. reef) and across both patchy and continuous habitats. Adopting these practices would allow future syntheses to explicitly evaluate the role of moderators directly rather than infer them post hoc.

Given likely interactions among some factors, future work could, for example, use factorial experiments that cross juvenile density with predator access and with refuge availability, while also quantifying predator identity, activity and foraging scale. Designs that measure β simultaneously at different grains can reveal the spatial scale at which density-dependence operates or changes in sign or magnitude (e.g., schooling benefits change to crowding costs), and whether the results from small-plot results scale up to the reef scale (e.g., Steele and Forrester 2005). Finally, establishing coordinated multi-site studies using common protocols, as has been successfully applied in other contexts (e.g., in the Nutrient Network: Borer et al. 2014), would allow us to better disentangle site-specific drivers from methodological effects.

4.6 | Implications for Ecological Theory

Our meta-analysis reveals substantial heterogeneity in density dependent mortality within and among species. This variation demonstrates that density dependent mortality is not a static property of reef fishes but a contingent outcome that depends critically on ecological context. Such heterogeneity challenges the traditional ‘density paradigm,’ which assumes uniform, repeatable relationships between population growth and density (Krebs 2002). Similar context dependence appears across taxa: in plants, host quality and induced chemical defences fundamentally alter the outcomes of intraspecific competition (Rotem and Agrawal 2003). In amphibian larvae, the presence of predator cues can reduce intraspecific competition in bullfrog larvae through predator-mediated changes in foraging activity (Peacor and Werner 2001). Thus, the effects of conspecific density routinely shift in magnitude and sign depending on environmental conditions, resource quality or life-history (Agrawal et al. 2004; Hunter and Elkinton 1999; Rotem and Agrawal 2003). Such parallels demonstrate that widespread intraspecific heterogeneity in density dependence is a fundamental feature of population dynamics rather than an anomaly of marine fishes.

Beyond ecological factors, methodological choices also can substantially influence the detection and apparent strength of density dependence, contributing to heterogeneity in ways that can obscure underlying ecological patterns. Observational studies may fail to detect ‘cryptic density dependence’ when population density covaries with unmeasured attributes of habitat quality, as documented in some reef fishes (Shima and Osenberg 2003) and paralleled in terrestrial systems where long-term observational datasets initially failed to detect density dependence that experimental manipulations later revealed (Fowler et al. 2006). Similarly, statistical models that ignore the nested structure of the data (e.g., substudies within papers) or variation in ecological context (e.g., habitat quality, predator abundance) risk conflating true ecological heterogeneity with statistical noise, leading to erroneous conclusions about the prevalence and strength of density dependence (Krüger et al. 2002).

5 | Conclusion

Our synthesis demonstrates that conspecific density is a pervasive and powerful driver of mortality in reef fishes, even though its strength and direction vary widely. Alongside other key demographic processes like density-dependent growth (Booth 1995; Forrester and Steele 2004) and reproduction (Samhouri 2009), these mechanisms can play important roles in population recovery following disturbances (e.g., due to coral bleaching or cyclones) and for regulating population size. Despite decades of research, substantial variation in density dependence—particularly within species—remains unexplained. This suggests that overlooked ecological or methodological factors are at play. Advancing our understanding of these mechanisms is essential for predicting population dynamics across space and time and moving our discipline beyond the binary question of whether populations are regulated and instead focusing on understanding the strength of density dependence and resolving when, where and through which mechanisms density feedbacks arise.

Author Contributions

C.W.O. conceived the project and A.C.S. kept it alive. A.C.S. and C.W.O. supervised and performed data extraction. A.C.S. performed the analyses and drafted the figures with input from C.W.O., A.C.S. wrote the first draft, and A.C.S. and C.W.O. contributed substantially to revisions.

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Data Availability Statement

Data accessibility statement: All code and processed data supporting the results are archived in Zenodo (<https://doi.org/10.5281/zenodo.17371596>).

Peer Review

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References

- Ackerman, J. L., and D. R. Bellwood. 2003. "The Contribution of Small Individuals to Density-Body Size Relationships." *Oecologia* 136: 137–140.
- Ackerman, J. L., D. R. Bellwood, and J. H. Brown. 2004. "The Contribution of Small Individuals to Density-Body Size Relationships: Examination of Energetic Equivalence in Reef Fishes." *Oecologia* 139: 568–571.
- Agrawal, A. A., N. Underwood, and J. R. Stinchcombe. 2004. "Intraspecific Variation in the Strength of Density Dependence in Aphid Populations." *Ecological Entomology* 29: 521–526.
- Almany, G. R., and M. S. Webster. 2006. "The Predation Gauntlet: Early Post-Settlement Mortality in Reef Fishes." *Coral Reefs* 25: 19–22.
- Barneche, D. R., D. R. Robertson, C. R. White, and D. J. Marshall. 2018. "Fish Reproductive-Energy Output Increases Disproportionately With Body Size." *Science* 360: 642–645.
- Beukers, J. S., and G. P. Jones. 1997. "Habitat Complexity Modifies the Impact of Piscivores on a Coral Reef Fish Population." *Oecologia* 114: 50–59.
- Bonin, M. C., L. Boström-Einarsson, P. L. Munday, and G. P. Jones. 2015. "The Prevalence and Importance of Competition Among Coral Reef Fishes." *Annual Review of Ecology, Evolution, and Systematics* 46: 169–190.
- Booth, D. J. 1995. "Juvenile Groups in a Coral-Reef Damselfish: Density-Dependent Effects on Individual Fitness and Population Demography." *Ecology* 76: 91–106.
- Borer, E. T., W. S. Harpole, P. B. Adler, et al. 2014. "Finding Generality in Ecology: A Model for Globally Distributed Experiments." *Methods in Ecology and Evolution* 5: 65–73.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. "Toward a Metabolic Theory of Ecology." *Ecology* 85: 1771–1789.
- Buddh, S., S. Krishna, and D. Agashe. 2024. "Density Dependent Survival Drives Variation in Density Dependent Population Growth of an Insect Pest." *Oikos* 2024: e10813.
- Carr, M. H., T. W. Anderson, and M. A. Hixon. 2002. "Biodiversity, Population Regulation, and the Stability of Coral-Reef Fish Communities." *Proceedings of the National Academy of Sciences* 99: 11241–11245.
- Chisholm, R. A., and H. C. Muller-Landau. 2011. "A Theoretical Model Linking Interspecific Variation in Density Dependence to Species Abundances." *Theoretical Ecology* 4: 241–253.
- Comita, L. S., H. C. Muller-Landau, S. Aguilar, and S. P. Hubbell. 2010. "Asymmetric Density Dependence Shapes Species Abundances in a Tropical Tree Community." *Science* 329: 330–332.
- Cyr, H., J. A. Downing, and R. H. Peters. 1997. "Density-Body Size Relationships in Local Aquatic Communities." *Oikos* 79: 333–346.
- Damuth, J. 1981. "Population Density and Body Size in Mammals." *Nature* 290: 699–700.
- Downing, J. A., C. W. Osenberg, and O. Sarnelle. 1999. "Meta-Analysis of Marine Nutrient-Enrichment Experiments: Variation in the Magnitude of Nutrient Limitation." *Ecology* 80: 1157–1167.
- Forrester, G. E., and M. A. Steele. 2004. "Predators, Prey Refuges, and the Spatial Scaling of Density-Dependent Prey Mortality." *Ecology* 85: 1332–1342.
- Fowler, C. W. 1981. "Density Dependence as Related to Life History Strategy." *Ecology* 62: 602–610.
- Fowler, N. L., R. D. Overath, and C. M. Pease. 2006. "Detection of Density Dependence Requires Density Manipulations and Calculation of λ ." *Ecology* 87: 655–664.
- Frauendorf, M., A. M. Allen, E. Jongejans, et al. 2022. "Love Thy Neighbour?—Spatial Variation in Density Dependence of Nest Survival in Relation to Predator Community." *Diversity and Distributions* 28: 624–635.
- Fretwell, S. D., and H. L. Lucas. 1969. "On Territorial Behavior and Other Factors Influencing Habitat Distribution in Birds." *Acta Biotheoretica* 19: 16–36.
- Froese, R., and D. Pauly. 2010. *FishBase*. Fisheries Centre, University of British Columbia.
- Hixon, M. A. 1991. "Predation as a Process Structuring Coral Reef Fish Communities." In *In 'the Ecology of Fishes on Coral Reefs'*, 475–508. Academic Press.
- Hixon, M. A., and M. H. Carr. 1997. "Synergistic Predation, Density Dependence, and Population Regulation in Marine Fish." *Science* 277: 946–949.
- Hixon, M. A., and G. P. Jones. 2005. "Competition, Predation, and Density-Dependent Mortality in Demersal Marine Fishes." *Ecology* 86: 2847–2859.
- Hixon, M. A., and M. S. Webster. 2002. "Density Dependence in Reef Fish Populations." In *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*, edited by P. F. Sale, 303–325. Academic Press.
- Holbrook, S. J., and R. J. Schmitt. 2002. "Competition for Shelter Space Causes Density-Dependent Predation Mortality in Damselfishes." *Ecology* 83: 2855–2868.
- Hülsmann, L., R. A. Chisholm, L. Comita, et al. 2024. "Latitudinal Patterns in Stabilizing Density Dependence of Forest Communities." *Nature* 627: 564–571.
- Hülsmann, L., R. A. Chisholm, and F. Hartig. 2021. "Is Variation in Conspecific Negative Density Dependence Driving Tree Diversity Patterns at Large Scales?" *Trends in Ecology & Evolution* 36: 151–163.
- Hunter, A. F., and J. S. Elkinton. 1999. "Interaction Between Phenology and Density Effects on Mortality From Natural Enemies." *Journal of Animal Ecology* 68: 1093–1100.
- Kendall, B. E., G. A. Fox, M. Fujiwara, and T. M. Noguire. 2011. "Demographic Heterogeneity, Cohort Selection, and Population Growth." *Ecology* 92: 1985–1993.
- Klironomos, J. N. 2002. "Feedback With Soil Biota Contributes to Plant Rarity and Invasiveness in Communities." *Nature* 417: 67–70.
- Krebs, C. J. 2002. "Two Complementary Paradigms for Analysing Population Dynamics." *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 357: 1211–1219.
- Krüger, O., R. Liversidge, and J. Lindström. 2002. "Statistical Modelling of the Population Dynamics of a Raptor Community in a Semi-Desert Environment." *Journal of Animal Ecology* 71: 603–613.
- Malthus, T. R. 1798. *An Essay on the Principle of Population, as it Affects the Future Improvement of Society, With Remarks on the Speculations of Mr. Godwin, M. Condorcet, and Other Writers*, 1st ed. J. Johnson.
- Mangan, S. A., S. A. Schnitzer, E. A. Herre, et al. 2010. "Negative Plant-Soil Feedback Predicts Tree-Species Relative Abundance in a Tropical Forest." *Nature* 466: 752–755.
- McCullough, D. R. 1999. "Density Dependence and Life-History Strategies of Ungulates." *Journal of Mammalogy* 80: 1130–1146.
- Meyers, R. A. 2002. "Recruitment: Understanding Density-Dependence in Fish Populations." In *Handbook of Fish Biology and Fisheries*, edited by P. J. B. Hart, vol. 2. Blackwell Science.
- Murdoch, W. W., and A. Stewart-Oaten. 1989. "Aggregation by Parasitoids and Predators: Effects on Equilibrium and Stability." *American Naturalist* 134: 288–310.

- Osenberg, C. W., O. Sarnelle, S. D. Cooper, and R. D. Holt. 1999. "Resolving Ecological Questions Through Meta-Analysis: Goals, Metrics, and Models." *Ecology* 80: 1105–1117.
- Osenberg, C. W., C. M. St Mary, R. J. Schmitt, S. J. Holbrook, P. Chesson, and B. Byrne. 2002. "Rethinking Ecological Inference: Density Dependence in Reef Fishes." *Ecology Letters* 5: 715–721.
- Overholtzer-McLeod, K. L. 2004. "Variance in Reef Spatial Structure Masks Density Dependence in Coral-Reef Fish Populations on Natural Versus Artificial Reefs." *Marine Ecology Progress Series* 276: 269–280.
- Overholtzer-McLeod, K. L. 2006. "Consequences of Patch Reef Spacing for Density-Dependent Mortality of Coral Reef Fishes." *Ecology* 87: 1017–1026.
- Pappalardo, P., K. Ogle, E. A. Hamman, J. R. Bence, B. A. Hungate, and C. W. Osenberg. 2020. "Comparing Traditional and Bayesian Approaches to Ecological Meta-Analysis." *Methods in Ecology and Evolution* 11: 1286–1295.
- Peacor, S. D., and E. E. Werner. 2001. "The Contribution of Trait-Mediated Indirect Effects to the Net Effects of a Predator." *Proceedings of the National Academy of Sciences* 98: 3904–3908.
- Poulsen, J. R., C. W. Osenberg, C. J. Clark, D. J. Levey, and B. M. Bolker. 2007. "Plants as Reef Fish: Fitting the Functional Form of Seedling Recruitment." *American Naturalist* 170: 167–183.
- Rabosky, D. L., J. Chang, P. O. Title, et al. 2018. "An Inverse Latitudinal Gradient in Speciation Rate for Marine Fishes." *Nature* 559: 392–395.
- Revell, L. J. 2012. "Phytools: An R Package for Phylogenetic Comparative Biology (And Other Things)." *Methods in Ecology and Evolution* 3: 217–223.
- Rotem, K. A., and A. A. Agrawal. 2003. "Density Dependent Population Growth of the Two-Spotted Spider Mite, *Tetranychus urticae*, on the Host Plant *Leonurus cardiaca*." *Oikos* 103: 559–565.
- Ruiz-Moreno, A., M. J. Emslie, and S. R. Connolly. 2024. "High Response Diversity and Conspecific Density-Dependence, Not Species Interactions, Drive Dynamics of Coral Reef Fish Communities." *Ecology Letters* 27: e14424.
- Samhouri, J. F. 2009. "Food Supply Influences Offspring Provisioning but Not Density-Dependent Fecundity in a Marine Fish." *Ecology* 90: 3478–3488.
- Sandin, S. A., and S. W. Pacala. 2005. "Fish Aggregation Results in Inversely Density-Dependent Predation on Continuous Coral Reefs." *Ecology* 86: 1520–1530.
- Schmitt, R. J., and S. J. Holbrook. 2007. "The Scale and Cause of Spatial Heterogeneity in Strength of Temporal Density Dependence." *Ecology* 88: 1241–1249.
- Self, S. G., and K.-Y. Liang. 1987. "Asymptotic Properties of Maximum Likelihood Estimators and Likelihood Ratio Tests Under Nonstandard Conditions." *Journal of the American Statistical Association* 82: 605–610.
- Shima, J. S., and C. W. Osenberg. 2003. "Cryptic Density Dependence: Effects of Covariation Between Density and Site Quality in Reef Fish." *Ecology* 84: 46–52.
- Shima, J. S., C. W. Osenberg, and C. M. St. Mary. 2008. "Quantifying Site Quality in a Heterogeneous Landscape: Recruitment of a Reef Fish." *Ecology* 89: 86–94.
- Siqueira, A. C., R. A. Morais, D. R. Bellwood, and P. F. Cowman. 2020. "Trophic Innovations Fuel Reef Fish Diversification." *Nature Communications* 11: 2669.
- Song, X., J. Y. Lim, J. Yang, and M. S. Luskin. 2021. "When Do Janzen-Connell Effects Matter? A Phylogenetic Meta-Analysis of Conspecific Negative Distance and Density Dependence Experiments." *Ecology Letters* 24: 608–620.
- Steele, M. A., and G. E. Forrester. 2002. "Early Postsettlement Predation on Three Reef Fishes: Effects on Spatial Patterns of Recruitment." *Ecology* 83: 1076–1091.
- Steele, M. A., and G. E. Forrester. 2005. "Small-Scale Field Experiments Accurately Scale Up to Predict Density Dependence in Reef Fish Populations at Large Scales." *Proceedings of the National Academy of Sciences of the United States of America* 102, no. 38: 13513–13516.
- Stier, A. C., C. D. Stallings, J. F. Samhouri, M. A. Albins, and G. R. Almany. 2017. "Biodiversity Effects of the Predation Gauntlet." *Coral Reefs* 36: 601–606.
- Tamburello, N., I. M. Côté, and N. K. Dulvy. 2015. "Energy and the Scaling of Animal Space Use." *American Naturalist* 186: 196–211.
- Thorson, J. T., J. M. Cope, K. M. Kleisner, J. F. Samhouri, A. O. Shelton, and E. J. Ward. 2015. "Giants' Shoulders 15 Years Later: Lessons, Challenges and Guidelines in Fisheries Meta-Analysis." *Fish and Fisheries* 16: 342–361.
- Viechtbauer, W. 2019. The R Package Metafor: Past, Present, and Future.
- White, J. W. 2007. "Spatially Correlated Recruitment of a Marine Predator and Its Prey Shapes the Large-Scale Pattern of Density-Dependent Prey Mortality." *Ecology Letters* 10: 1054–1065.
- White, J. W., J. F. Samhouri, A. C. Stier, C. L. Wormald, S. L. Hamilton, and S. A. Sandin. 2010. "Synthesizing Mechanisms of Density Dependence in Reef Fishes: Behavior, Habitat Configuration, and Observational Scale." *Ecology* 91: 1949–1961.
- White, J. W., and R. R. Warner. 2007. "Safety in Numbers and the Spatial Scaling of Density-Dependent Mortality in a Coral Reef Fish." *Ecology* 88: 3044–3054.
- Wilson, J., and C. W. Osenberg. 2002. "Experimental and Observational Patterns of Density-Dependent Settlement and Survival in the Marine Fish *Gobiosoma*." *Oecologia* 130: 205–215.
- Wormald, C. L., M. A. Steele, and G. E. Forrester. 2013. "High Population Density Enhances Recruitment and Survival of a Harvested Coral Reef Fish." *Ecological Applications* 23: 365–373.
- Yang, Y., and T. Yamakawa. 2022. "Re-Examination of Stock-Recruitment Relationships: A Meta-Analysis." *ICES Journal of Marine Science* 79: 1380–1393.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** Supporting Information.

SUPPLEMENTAL INFORMATION
ECOLOGY LETTERS
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Widespread heterogeneity in density-dependent mortality of nearshore fishes

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Appendix A: PRISMA diagram

Appendix B: Summary of substudies included in the meta-analysis

Appendix C: Supporting Figures, C1-C5.

Figure C-1. Geographic distribution of substudies.

Figure C-2. Effect of initial body size on the strength of density-dependent mortality (β , $\text{cm}^2 \text{ fish}^{-1} \text{ day}^{-1}$).

Figure C-3. Variation in effect of body size on density-dependent mortality (β , $\text{cm}^2 \text{fish}^{-1} \text{day}^{-1}$) for 10 different species.

Figure C-4. Relationship between experiment duration and density-dependent mortality for reef fish with ≥ 4 substudies.

Figure C-5. Relationship between maximum adult body size (cm) density-dependent mortality.

Appendix D: Experimental and observational substudies

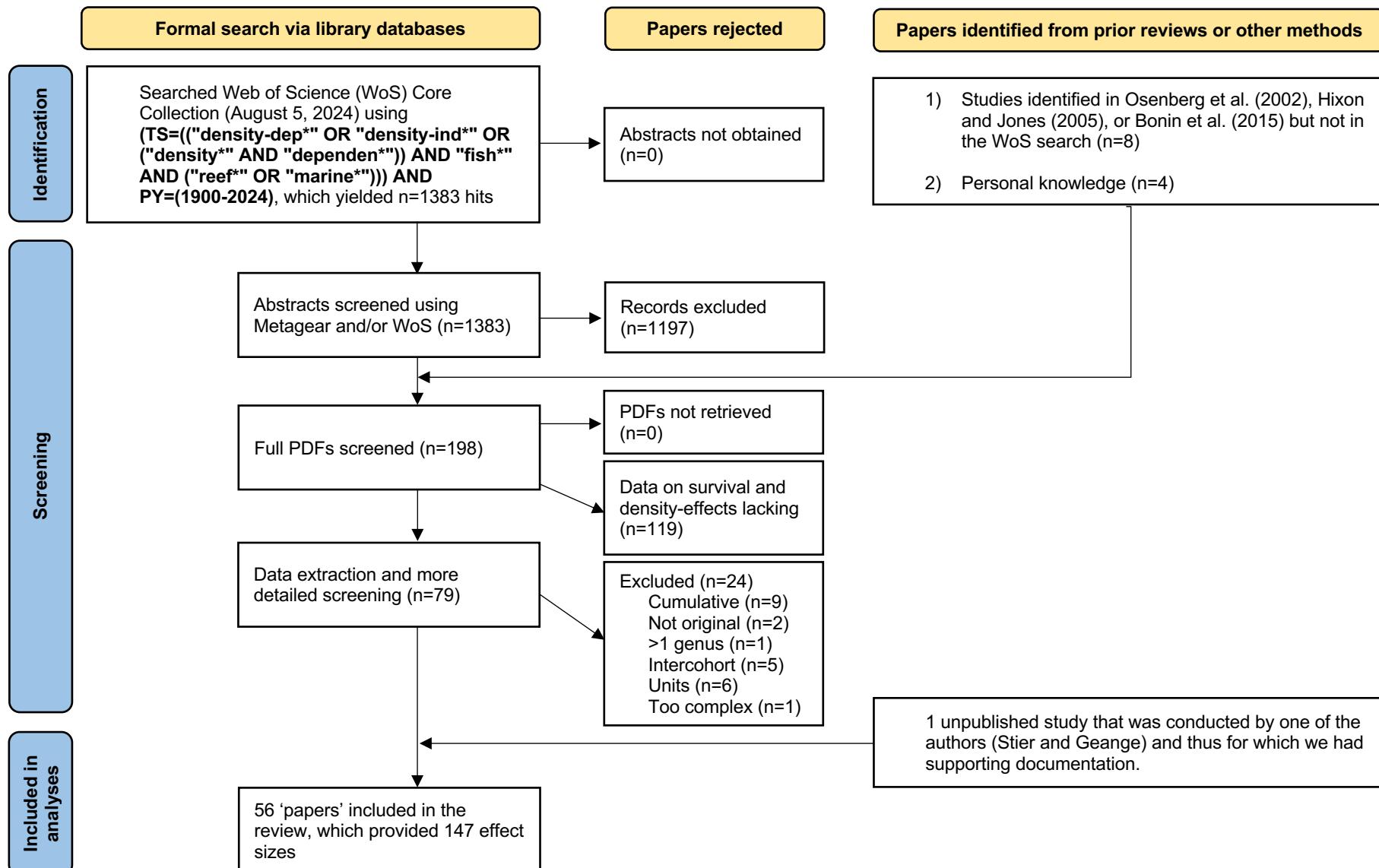
Figure D-1. Comparison of density-dependent mortality (β , $\text{cm}^2 \text{ fish}^{-1} \text{ day}^{-1}$) between experimental and observational substudies.

Appendix E: Analyses to identify influential substudies or publication bias

Figure E-1. Sensitivity and publication-bias diagnostics.

Appendix A. PRISMA diagram

After screening of 1383 papers, 79 papers were retained, but subsequent review and attempts at data extraction reduced this pool to 55, to which we added one unpublished study, bringing the total to 56. Reasons for exclusion included: "Cumulative" (initial 'cohort' of fish were followed for different durations), "Not original" (data were reported and used in another publication); ">1 genus" (data were aggregated across 5 different families of fishes); "Intercohort" (data on density-dependent survival were from effects between different age-classes, such as adults on young); "Units" (densities could not be converted to fish/cm²); "Too complex" (data were not reported and analyses were too complex to facilitate recovery).



77 **Appendix B. Summary of substudies included in the meta-analysis**

78 Each row represents a unique “substudy” reporting the strength of intraspecific density-
79 dependent mortality (β) in reef fishes. Substudies are defined as an experimental or observational
80 dataset that allowed an estimate of β , the increase in per capita mortality rate per additional fish
81 per unit area (units: $\text{cm}^2 \text{ fish}^{-1} \text{ day}^{-1}$). Each substudy was conducted under a distinct ecological
82 condition (e.g., site, time, predator regime). β estimates were derived from fits to the Beverton–
83 Holt recruitment function (Equation 2 in the main text). This dataset synthesizes 147 effect sizes
84 drawn from 56 studies (55 published papers and 1 unpublished study) spanning 38 species across
85 diverse families, geographic locations, and methodological designs. The estimates include both
86 predator-present and predator-absent treatments, as well as experimental and observational
87 designs.

88 **Column descriptions:**

- 89 • **Paper [Substudy]:** Unique identifiers corresponding to each paper (i.e., study) and the
90 substudy within the paper that generated an estimate of density-dependent mortality, β .
- 91 • **Description:** A summary of where the data were presented in the paper.
- 92 • **Beta (β):** The estimated effect of conspecific density on per capita mortality, in $\text{cm}^2 \text{ fish}^{-1}$
93 day^{-1} ; positive values indicate that mortality increases with density.
- 94 • **Variance:** Estimated variance of β , typically derived from profile likelihoods or reported
95 confidence intervals.
- 96 • **Citation:** Author(s) and year of the original substudy.
- 97 • **Family:** Taxonomic family of the focal species.
- 98 • **Species:** *Scientific name* (italicized) of the focal species.
- 99 • **Predators:** Indicates whether predators were present (pres) or absent (abs) during the
100 substudy. Similar numbers in brackets indicate the predator presence/absence treatments
101 that were explicitly paired or contrasted within the same paper.
- 102 • **Duration:** Duration of the substudy or time between initial and final censuses (in days).
- 103 • **Study Design:** Substudies were either experimental (Expt) if densities were manipulated
104 or observation (Obs) if they relied on natural variation in density. Similar numbers in
105 brackets indicate an experimental and observational substudy on the same species that we
106 paired based on their proximity in space and time.
- 107 • **SizeStart:** Mean standard length (mm) of fish at the start of the study or treatment.
- 108 • **MaxLen:** Maximum length (cm) of the focal species from FishBase.
- 109 • **MeanDensity:** Mean conspecific density (individuals per m^2) at the start of the study.

110

Paper [substudy]	Description	Beta (β)	Variance	Citation	Family	Species	predation [pair]	Duration	Study Design	SizeStart	MaxLen	MeanDensity
1 [1]	From text	0.03	3.00E-05	Chua & Teng 1979	Serranidae	<i>Epinephelus malabaricus</i>	abs	240	Exp	125.04	234	93.33
2 [5]	Fig3, large fish, 2 wks	12.42	1.34E+02	Kneib 1981	Fundulidae	<i>Fundulus heteroclitus</i>	abs	14	Exp	56.00	15	2.33
2 [6]	Fig3, medium fish, 2 wks	-5.49	5.15E+01	Kneib 1981	Fundulidae	<i>Fundulus heteroclitus</i>	abs	14	Exp	47.60	15	2.33
2 [7]	Fig3, small fish, 2 wks	136.73	9.80E+02	Kneib 1981	Fundulidae	<i>Fundulus heteroclitus</i>	abs	14	Exp	36.00	15	2.33
3 [8]	Fig1a,b	3.11	1.85E+00	Doherty 1982	Pomacentridae	<i>Pomacentrus wardi</i>	pres	365	Exp	17.00	8	3.33
4 [9]	Fig6	392.93	1.24E+03	Jones 1984	Labridae	<i>Notolabrus celidotus</i>	pres	365	Obs	50.00	23.9	0.10
5 [10]	Fig 3, with adults-small	-0.05	1.70E-01	Jones 1987	Pomacentridae	<i>Pomacentrus amboinensis</i>	pres	365	Exp	18.07	9	4.51
5 [11]	Fig 3, without adults-small	1.42	3.18E-01	Jones 1987	Pomacentridae	<i>Pomacentrus amboinensis</i>	pres	365	Exp	18.30	9	4.51
5 [12]	fig 6,without adults-large	10.90	6.60E+00	Jones 1987	Pomacentridae	<i>Pomacentrus amboinensis</i>	pres	365	Exp	38.43	9	3.38
5 [13]	Fig 6, with adults-large	-3.03	1.63E+00	Jones 1987	Pomacentridae	<i>Pomacentrus amboinensis</i>	pres	365	Exp	38.33	9	3.38
6 [14]	Fig4 +LR, Expt4)- late recruits	1.92	3.00E-01	Jones 1987	Pomacentridae	<i>Pomacentrus amboinensis</i>	pres	365	Exp	14.40	9	4.52
6 [15]	Fig2 Expt 3+R), with adults	0.02	1.80E-04	Jones 1987	Pomacentridae	<i>Dascyllus aruanus</i>	pres	240	Exp	15.40	10	74.67
6 [16]	Fig2 Expt 3, -R) – without adults	0.00	9.73E-03	Jones 1987	Pomacentridae	<i>Dascyllus aruanus</i>	pres	240	Exp	15.40	10	74.67
7 [17]	Fig. 2 -poc	2.85	4.22E-01	Jones 1988	Pomacentridae	<i>Dascyllus aruanus</i>	pres	365	Exp	15.40	10	10.13
7 [18]	Fig. 2 - por	-0.57	3.07E+00	Jones 1988	Pomacentridae	<i>Dascyllus aruanus</i>	pres	365	Exp	15.40	10	10.13
7 [19]	Fig. 1 - poc	0.15	5.01E-02	Jones 1988	Pomacentridae	<i>Pomacentrus amboinensis</i>	pres	365	Exp	18.00	9	10.13
7 [20]	Fig. 1 - por	-1.89	1.17E-01	Jones 1988	Pomacentridae	<i>Pomacentrus amboinensis</i>	pres	365	Exp	18.00	9	10.13
9 [27]	Fig3- with adults	0.05	3.30E-04	Forrester 1990	Pomacentridae	<i>Dascyllus aruanus</i>	pres	300	Exp	9.12	10	60.85
9 [28]	Fig3- without adults	0.17	9.10E-04	Forrester 1990	Pomacentridae	<i>Dascyllus aruanus</i>	pres	300	Exp	9.12	10	60.85
11 [30]	Fig 8	60.61	9.56E+00	von Herbing & Hunte 1991	Labridae	<i>Thalassoma bifasciatum</i>	pres	120	Obs	40.00	25	1.81
13 [49]	Fig4B.	190.91	4.84E+01	Anderson 1994	Embiotocidae	<i>Brachyistius frenatus</i>	pres	365	Obs [5]	50.00	22	0.59

15 [52]	Expt - art reefs	51.53	1.17E+02	Forrester 1995	Gobiidae	<i>Coryphopterus glaucofraenum</i>	pres	75	Exp [1]	26.68	8	3.98
15 [53]	Obs - nat reefs	26.27	5.58E+01	Forrester 1995	Gobiidae	<i>Coryphopterus glaucofraenum</i>	pres	75	Obs [1]	28.68	8	3.06
16 [54]	Figs. 5 and 6	288.29	8.75E+19	Tupper & Boutilier 1995	Labridae	<i>Tautogolabrus adspersus</i>	pres	60	Exp	21.00	44	6.20
17 [55]	Fig. 1a	109.70	1.60E+02	Beukers & Jones 1997b	Pomacentridae	<i>Pomacentrus moluccensis</i>	pres	365	Obs	17.45	9	0.50
18 [57]	Fig. 2 all preds	230.00	2.35E+03	Hixon & Carr 1997	Pomacentridae	<i>Chromis cyanea</i>	pres [1]	30	Exp	10.00	15	2.06
18 [58]	Fig. 2 no preds	0.67	6.30E+01	Hixon & Carr 1997	Pomacentridae	<i>Chromis cyanea</i>	abs [1]	30	Exp	10.00	15	2.01
18 [59]	Fig. 2 resident preds	23.46	2.00E+02	Hixon & Carr 1997	Pomacentridae	<i>Chromis cyanea</i>	pres	30	Exp	10.00	15	2.04
18 [60]	Fig. 2 transient preds	75.80	2.39E+02	Hixon & Carr 1997	Pomacentridae	<i>Chromis cyanea</i>	pres	30	Exp	10.00	15	2.07
19 [61]	Fig4-1992	88.99	2.63E+02	Sano 1997	Gobiidae	<i>Sagamia geneionema</i>	pres	165	Obs	53.00	7.1	0.85
19 [62]	Fig4-1993	-1.17	5.39E+00	Sano 1997	Gobiidae	<i>Sagamia geneionema</i>	pres	165	Obs	54.00	7.1	1.16
19 [63]	Fig4-1994	129.16	5.45E+02	Sano 1997	Gobiidae	<i>Sagamia geneionema</i>	pres	165	Obs	54.00	7.1	0.10
20 [64]	Fig. 2, 3, 6 - cn	18.96	5.91E+01	Steele 1997	Gobiidae	<i>Rhinogobiops nicholsii</i>	pres	86	Exp	27.50	15	6.55
20 [65]	Fig. 2, 3, 6 - ld	16.06	7.68E+00	Steele 1997	Gobiidae	<i>Lythrypnus dalli</i>	pres	37	Exp	17.50	6.4	31.05
22 [68]	Fig. 5 - em	145.96	1.20E+02	Letourneau <i>et al.</i> 1998	Serranidae	<i>Epinephelus merra</i>	pres	49	Obs	39.70	36.5	11.48
23 [69]	Fig2 - dp	7171.72	1.27E+06	Planes <i>et al.</i> 1998	Sparidae	<i>Diplodus puntazzo</i>	pres	90	Obs	6.40	60	0.012
23 [70]	Fig2 - ds	3212.12	1.10E+05	Planes <i>et al.</i> 1998	Sparidae	<i>Diplodus sargus</i>	pres	90	Obs	6.40	45	0.07
23 [71]	Fig2 - dv	1808.08	2.23E+04	Planes <i>et al.</i> 1998	Sparidae	<i>Diplodus vulgaris</i>	pres	90	Obs	6.40	45	0.15
24 [72]	Pg 113 - gm - author	1.70	2.36E+00	Brooks 1999	Cottidae	<i>Gillichthys mirabilis</i>	pres	30	Exp	45.60	21	14.67
24 [73]	Pg. 113 - la - author	9.70	7.38E+00	Brooks 1999	Cottidae	<i>Leptocottus armatus</i>	pres	30	Exp	48.80	46	14.67
25 [74]	Fig2	-45.15	2.44E+03	Caselle 1999	Labridae	<i>Thalassoma bifasciatum</i>	pres	30	Exp	10.00	25	0.41
25 [75]	Fig3	1119.43	1.52E+05	Caselle 1999	Labridae	<i>Thalassoma bifasciatum</i>	pres	1	Exp	10.00	25	0.79
25 [76]	Fig4	17.16	3.08E+02	Caselle 1999	Labridae	<i>Thalassoma bifasciatum</i>	pres	30	Exp [4]	12.00	25	0.61
25 [77]	Fig7	312.12	9.34E+01	Caselle 1999	Labridae	<i>Thalassoma bifasciatum</i>	pres	30	Obs [4]	12.00	25	0.52

26 [80]	Fig 4	1.00	6.05E-02	Schmitt & Holbrook 1999	Pomacentridae	<i>Dascyllus trimaculatus</i>	pres	14	Exp [3]	11.00	14	98.28
28 [87]	Fig2.	0.40	2.03E-03	Schmitt & Holbrook 1999	Pomacentridae	<i>Dascyllus trimaculatus</i>	pres	180	Exp	10.00	14	573.76
30 [90]	Fig 2, with preds	35.86	5.39E+01	Forrester & Steele 2000	Gobiidae	<i>Lythrypnus dalli</i>	pres [2]	21	Exp	32.00	6.4	17.48
30 [91]	Fig 2 without preds	-0.83	7.68E-03	Forrester & Steele 2000	Gobiidae	<i>Lythrypnus dalli</i>	abs [2]	21	Exp	32.00	6.4	20.74
30 [92]	Fig 3a with preds	-7.34	5.53E+02	Forrester & Steele 2000	Gobiidae	<i>Rhinogobiops nicholsii</i>	pres [3]	30	Exp	38.50	15	5.71
30 [93]	Fig 3a without preds	-3.46	3.17E+00	Forrester & Steele 2000	Gobiidae	<i>Rhinogobiops nicholsii</i>	abs [3]	30	Exp	38.50	15	5.65
30 [94]	fig3b-with preds	1.93	4.22E+00	Forrester & Steele 2000	Gobiidae	<i>Rhinogobiops nicholsii</i>	pres [4]	59	Exp	44.20	15	5.42
30 [95]	fig3b-without preds	0.78	2.23E+00	Forrester & Steele 2000	Gobiidae	<i>Rhinogobiops nicholsii</i>	abs [4]	59	Exp	44.20	15	5.56
30 [96]	fig3c-with preds	7.09	1.57E+01	Forrester & Steele 2000	Gobiidae	<i>Rhinogobiops nicholsii</i>	pres	140	Exp	57.50	15	4.63
30 [97]	fig5-with preds	1249.50	2.59E+05	Forrester & Steele 2000	Gobiidae	<i>Coryphopterus glaucofraenum</i>	pres [5]	30	Exp	40.00	8	4.65
30 [98]	fig5-without preds	126.67	6.12E+02	Forrester & Steele 2000	Gobiidae	<i>Coryphopterus glaucofraenum</i>	abs [5]	30	Exp	40.00	8	4.67
31 [99]	Fig3, expt	1428.49	1.11E+05	Shima 2001	Labridae	<i>Thalassoma hardwicke</i>	pres	14	Exp [6]	10.00	25	2.34
32 [101]	Fig3	239.39	5.38E+02	Anderson 2001	Embiotocidae	<i>Brachyistius frenatus</i>	pres	14	Exp [5]	55.50	22	2.59
33 [102]	Fig4. caged	0.03	2.40E-04	Nanami & Nishihira 2001	Pomacentridae	<i>Dascyllus aruanus</i>	abs [6]	56	Exp	15.00	10	952.39
33 [103]	Fig4. uncaged	0.27	4.85E-03	Nanami & Nishihira 2001	Pomacentridae	<i>Dascyllus aruanus</i>	pres [6]	56	Exp	15.00	10	952.39
37 [109]	Figure 1A - no pred no compet	-2.75	1.11E+02	Carr <i>et al.</i> 2002	Pomacentridae	<i>Stegastes partitus</i>	abs	44	Exp	17.00	10	1.36
37 [110]	Figure 1B: no pred, + comp	113.94	1.16E+03	Carr <i>et al.</i> 2002	Pomacentridae	<i>Stegastes partitus</i>	abs [7]	44	Exp	17.00	10	1.36
37 [111]	Figure 1C: +pred, - comp	-65.85	1.36E+03	Carr <i>et al.</i> 2002	Pomacentridae	<i>Stegastes partitus</i>	pres	44	Exp	17.00	10	1.36
37 [112]	Figure 1D: +pred, +comp	464.49	2.58E+04	Carr <i>et al.</i> 2002	Pomacentridae	<i>Stegastes partitus</i>	pres [7]	44	Exp	17.00	10	1.44
37 [113]	Figure 2A: +pred, - dams - continuous reef	52.02	1.78E+03	Carr <i>et al.</i> 2002	Pomacentridae	<i>Stegastes partitus</i>	pres	44	Exp	17.00	10	1.33
37 [114]	Figure 2B: +pred, +damsel	331.10	4.96E+03	Carr <i>et al.</i> 2002	Pomacentridae	<i>Stegastes partitus</i>	pres	44	Exp	17.00	10	1.33
38 [115]	Figure 1 authors)- Caged	-2.03	2.47E-01	Holbrook & Schmitt 2002	Pomacentridae	<i>Dascyllus flavicaudus</i>	abs [8]	1	Exp	10.00	12	143.24

38 [116]	Figure 1 authors)-Uncaged	26.31	1.17E+01	Holbrook & Schmitt 2002	Pomacentridae	<i>Dascyllus flavicaudus</i>	pres [8]	1	Exp	10.00	12	143.24
38 [117]	Figure 2authors)-cage	2.71	2.13E-01	Holbrook & Schmitt 2002	Pomacentridae	<i>Dascyllus flavicaudus</i>	abs	4	Exp	10.00	12	218.27
38 [118]	Figure 2 authors)-nocage	4.06	3.13E-01	Holbrook & Schmitt 2002	Pomacentridae	<i>Dascyllus flavicaudus</i>	pres	4	Exp	10.00	12	218.27
38 [119]	Figure 5a authors) - day+night combined	7.27	1.55E+00	Holbrook & Schmitt 2002	Pomacentridae	<i>Dascyllus flavicaudus</i>	pres	0.5	Exp	10.00	12	222.82
38 [121]	Figure 5b authors) - day+night combined	6.41	3.92E-01	Holbrook & Schmitt 2002	Pomacentridae	<i>Dascyllus trimaculatus</i>	pres	0.5	Exp	10.00	14	371.37
41 [132]	Figs4 (expt), 5a (obs)	866.22	1.55E+04	Wilson & Osenberg 2002	Gobiidae	<i>Elactinus sp.</i>	pres	12	Exp [2]	8.00	4	65.75
41 [133]	Figs4 (expt), 5a (obs)	3.67	5.42E+01	Wilson & Osenberg 2002	Gobiidae	<i>Elactinus sp.</i>	pres	32	Obs [2]	8.00	4	66.75
43 [136]	Fig2a	142.00	2.81E+03	Shima & Osenberg 2003	Labridae	<i>Thalassoma hardwicke</i>	pres	90	Obs [6]	10.00	25	0.53
45 [139]	Fig1-low-refuge	197.61	1.40E+03	Forrester & Steele 2004	Gobiidae	<i>Coryphopterus glaucofraenum</i>	pres	50	Exp	25.00	8	1.77
45 [140]	Fig1-med-refuge	104.17	6.43E+02	Forrester & Steele 2004	Gobiidae	<i>Coryphopterus glaucofraenum</i>	pres	50	Exp	25.00	8	1.96
45 [141]	Fig1-high-refuge	-5.12	7.34E+01	Forrester & Steele 2004	Gobiidae	<i>Coryphopterus glaucofraenum</i>	pres	50	Exp	25.00	8	1.88
45 [142]	Fig2-low-refuge	229.73	4.07E+03	Forrester & Steele 2004	Gobiidae	<i>Coryphopterus glaucofraenum</i>	pres	37	Exp	25.00	8	1.09
45 [143]	Fig2-med-refuge	25.68	1.36E+02	Forrester & Steele 2004	Gobiidae	<i>Coryphopterus glaucofraenum</i>	pres	36	Exp	25.00	8	2.02
45 [144]	Fig2-high-refuge	21.21	4.15E+01	Forrester & Steele 2004	Gobiidae	<i>Coryphopterus glaucofraenum</i>	pres	36	Exp	25.00	8	3.16
46 [163]	Figure 2AL-large reef	-9.20	4.56E+02	Overholtzer-McLeod 2004	Labridae	<i>Halichoeres garnoti</i>	pres	21	Exp	20.50	19.3	3.42
46 [164]	Figure 2AS-small reef	-27.52	3.78E+01	Overholtzer-McLeod 2004	Labridae	<i>Halichoeres garnoti</i>	pres	21	Exp	20.50	19.3	7.83
46 [165]	Figure 2BL-large reef separated by 50 m	84.43	3.99E+02	Overholtzer-McLeod 2004	Labridae	<i>Halichoeres garnoti</i>	pres	21	Exp	20.50	19.3	8.59
46 [166]	Figure 2BS-small reef separated by 50 m	29.14	5.15E+01	Overholtzer-McLeod 2004	Labridae	<i>Halichoeres garnoti</i>	pres	21	Exp	20.50	19.3	25.53
46 [167]	Figure 2CL-large reef separated by 5 m	53.60	4.43E+02	Overholtzer-McLeod 2004	Labridae	<i>Halichoeres garnoti</i>	pres	21	Exp	20.50	19.3	9.39
46 [168]	Figure 2CS-small reef separated by 5 m	10.04	4.54E+01	Overholtzer-McLeod 2004	Labridae	<i>Halichoeres garnoti</i>	pres	21	Exp	20.50	19.3	25.34
48 [170]	Fig3 +pred	2.48	3.51E-01	Hixon & Jones 2005	Pomacentridae	<i>Pomacentrus amboinensis</i>	abs [9]	516	Exp	14.00	9	5.00
48 [171]	Fig3 -pred	5.97	1.35E+00	Hixon & Jones 2005	Pomacentridae	<i>Pomacentrus amboinensis</i>	pres [9]	516	Exp	14.00	9	5.00

49 [172]	Figure 3a-Patch Reef-Halichoeres garnoti	18.63	7.03E+01	Overholtzer-McLeod 2005	Labridae	<i>Halichoeres garnoti</i>	pres	30	Exp	22.50	19.3	4.63
49 [173]	Figure 3b-PatchReef-THBI	10.46	8.27E+01	Overholtzer-McLeod 2005	Labridae	<i>Thalassoma bifasciatum</i>	pres	30	Exp	22.50	25	2.81
49 [174]	Figure 3a-ContinousReef-HAGA	-26.23	1.64E+02	Overholtzer-McLeod 2005	Labridae	<i>Halichoeres garnoti</i>	pres	30	Exp	22.50	19.3	2.35
49 [175]	Figure 3b-ContinousReef-THBI	184.13	5.71E+03	Overholtzer-McLeod 2005	Labridae	<i>Thalassoma bifasciatum</i>	pres	30	Exp	22.50	25	0.76
51 [185]	Fig2a - 1999 - blue	35.05	4.38E+02	Johnson 2006a	Sebastidae	<i>Sebastes atrovirens</i>	abs	365	Exp	30.00	42	0.28
51 [186]	Fig 2b 1999 - KGB	4022.86	7.76E+07	Johnson 2006a	Sebastidae	<i>Sebastes atrovirens</i>	pres	365	Exp	30.00	42	0.07
51 [187]	Fig 2a 2000 - blue	232.32	9.59E+03	Johnson 2006a	Sebastidae	<i>Sebastes atrovirens</i>	abs	365	Exp	30.00	42	0.09
51 [188]	Fig 2b 2000 - KGB	97.78	1.71E+04	Johnson 2006a	Sebastidae	<i>Sebastes atrovirens</i>	pres	365	Exp	30.00	42	0.36
51 [189]	Fig 2a 2001 - blue	49.09	9.04E+01	Johnson 2006a	Sebastidae	<i>Sebastes atrovirens</i>	abs	365	Exp	30.00	42	0.36
51 [190]	Fig 2b2001 - KGB	909.08	1.34E+06	Johnson 2006a	Sebastidae	<i>Sebastes atrovirens</i>	pres	365	Exp	30.00	42	0.21
51 [191]	Fig 2a 2002 - blue	-61.82	1.24E+02	Johnson 2006a	Sebastidae	<i>Sebastes atrovirens</i>	abs	365	Exp	30.00	42	0.88
51 [192]	Fig 2b 2002 - KGB	9494.95	1.45E+09	Johnson 2006a	Sebastidae	<i>Sebastes atrovirens</i>	pres	365	Exp	30.00	42	0.81
52 [193]	Fig 1. Pred -	0.77	5.51E-01	Johnson 2006a	Sebastidae	<i>Sebastes atrovirens</i>	abs [10]	27	Exp	30.00	42	12.12
52 [194]	Fig1. Pred +	9.11	2.04E+00	Johnson 2006a	Sebastidae	<i>Sebastes atrovirens</i>	pres [10]	27	Exp	30.00	42	12.29
53 [197]	Fig2B-50m	36.66	4.81E+01	Overholtzer-McLeod 2006	Pomacentridae	<i>Stegastes leucostictus</i>	pres	30	Exp	19.50	10	11.27
53 [198]	Fig2B-5m	74.44	4.39E+02	Overholtzer-McLeod 2006	Pomacentridae	<i>Stegastes leucostictus</i>	pres	30	Exp	19.50	10	11.34
55 [200]	Fig 2. Site 1--SH07	33.22	7.24E+00	Schmitt & Holbrook 2007	Pomacentridae	<i>Dascyllus flavicaudus</i>	pres	2	Exp	10.00	12	66.05
55 [201]	Fig 2. Site 2-SH07	50.89	8.04E+01	Schmitt & Holbrook 2007	Pomacentridae	<i>Dascyllus flavicaudus</i>	pres	2	Exp	10.00	12	66.05
55 [202]	Fig 2. Site 3 -SH07	3.53	8.93E-02	Schmitt & Holbrook 2007	Pomacentridae	<i>Dascyllus flavicaudus</i>	pres	2	Exp	10.00	12	66.05
55 [203]	Fig 2. Site 4-SH07	21.91	1.43E+00	Schmitt & Holbrook 2007	Pomacentridae	<i>Dascyllus flavicaudus</i>	pres	2	Exp	10.00	12	66.05
55 [204]	Fig. 2 Site 5-SH07	15.55	8.04E-01	Schmitt & Holbrook 2007	Pomacentridae	<i>Dascyllus flavicaudus</i>	pres	2	Exp	10.00	12	66.05

55 [205]	Fig. 2 Site 6-SH07	21.21	3.22E+00	Schmitt & Holbrook 2007	Pomacentridae	<i>Dascyllus flavicaudus</i>	pres	2	Exp	10.00	12	66.05
57 [209]	Fig 3	95.46	1.92E+01	White & Caselle 2008	Serranidae	<i>Paralabrax clathratus</i>	pres	362	Obs	10.00	72	0.070
58 [212]	Fig 2. Simultaneous compet	1295.96	1.60E+05	Geange & Stier 2009	Labridae	<i>Thalassoma hardwicke</i>	pres	7	Exp	10.00	25	2.00
60 [214]	Fig 1. low-complexity-simultaneous	525.25	7.74E+04	Geange & Stier 2010	Labridae	<i>Thalassoma quinquevittatum</i>	pres	5	Exp	25.00	17	2.02
60 [215]	Fig. 1 high-complexity-simultaneous	1118.18	6.99E+04	Geange & Stier 2010	Labridae	<i>Thalassoma quinquevittatum</i>	pres	5	Exp	25.00	17	2.02
62 [225]	Fig4.	0.65	2.47E-02	Bosström-Einarsson et al. 2013	Pomacentridae	<i>Chrysiptera parasema</i>	pres	60	Exp	16.50	7	74.97
63 [226]	Fig. 3 – 12 fish treatment	3.85	3.16E-02	Ford & Swearear 2013	Plesiopidae	<i>Trachinops caudimaculatus</i>	pres	14	Exp	35.00	15	46.75
61 [220]	Fig 1A. - no Hawkfish	370.49	7.45E+04	Stier et al. 2013	Labridae	<i>Thalassoma amblycephalum</i>	abs	6	Exp	13.00	16	8.25
61 [221]	fig 3A - control	-182.63	7.30E+04	Stier et al. 2013	Labridae	<i>Thalassoma amblycephalum</i>	abs	6	Exp	13.00	16	3.00
61 [222]	Fig 1A - 1 Hawkfish	313.11	5.29E+03	Stier et al. 2013	Labridae	<i>Thalassoma amblycephalum</i>	pres	6	Exp	13.00	16	8.25
61 [223]	Fig 1A- 2 Hawkfish	113.64	7.04E+02	Stier et al. 2013	Labridae	<i>Thalassoma amblycephalum</i>	pres	6	Exp	13.00	16	8.25
61 [224]	Fig 3a - with Pavo	-282.42	3.65E+03	Stier et al. 2013	Labridae	<i>Thalassoma amblycephalum</i>	pres	6	Exp	13.00	16	3.00
67 [244]	Fig1a-L (3 shelter tts)	165.67	2.88E+04	Ford et al. 2016	Plesiopidae	<i>Trachinops caudimaculatus</i>	pres	90	Obs	30.00	15	0.50
67 [245]	Fig1a-M (3 shelter tts)	12.01	5.45E+01	Ford et al. 2016	Plesiopidae	<i>Trachinops caudimaculatus</i>	pres	90	Obs	30.00	15	2.62
67 [246]	Fig1a-H (3 shelter tts)	24.53	2.28E+15	Ford et al. 2016	Plesiopidae	<i>Trachinops caudimaculatus</i>	pres	90	Obs	30.00	15	3.57
68 [248]	fig2_large_scale	611.11	2.37E+03	White & Warner 2007	Labridae	<i>Thalassoma bifasciatum</i>	pres	29	Obs	15.00	25	0.60
69 [249]	Unpublished from Stier and Geange	124.37	6.44E+02	unpublished	Pomacentridae	<i>Pomacentrus pavo</i>	pres	4	Exp	15.00	8.5	12.91
70 [250]	Fig 5.	1.00	1.13E+11	Schmitt & Holbrook 1996	Pomacentridae	<i>Dascyllus trimaculatus</i>	pres	1	Obs [3]	10.00	14	330.14
71 [251]	Fig 1-caged	82.83	1.82E+05	Shima 2002	Labridae	<i>Thalassoma hardwicke</i>	abs [11]	7	Exp	10.00	25	0.38
71 [252]	Fig 1- uncaged	4349.09	5.96E+05	Shima 2002	Labridae	<i>Thalassoma hardwicke</i>	pres [11]	7	Exp	10.00	25	0.37
72 [255]	Fig. 7 3 sites	30.20	1.59E+00	Nitschke et al. 2002	Labridae	<i>Tautogolabrus adspersus</i>	pres	63	Obs	45.00	44	11.21

73 [256]	Fig. 1 10 mm	-1.31	4.70E-01	Lecchini <i>et al.</i> 2006	Pomacentridae	<i>Chromis viridis</i>	pres	1	Obs	10.00	10	611.21
73 [257]	Fig. 1 20 mm	3.36	1.14E+00	Lecchini <i>et al.</i> 2006	Pomacentridae	<i>Chromis viridis</i>	pres	1	Obs	20.00	10	611.21
74 [258]	Fig4a – chap – acr	-11.30	8.85E+00	Bonin <i>et al.</i> 2009	Pomacentridae	<i>Chrysiptera parasema</i>	pres	5	Exp	9.30	7	18.67
74 [259]	Fig 4b – chap - poc	138.59	1.27E+04	Bonin <i>et al.</i> 2009	Pomacentridae	<i>Chrysiptera parasema</i>	pres	5	Exp	9.30	7	18.67
74 [260]	Fig 4 – dm - poc	14.99	8.14E+01	Bonin <i>et al.</i> 2009	Pomacentridae	<i>Dascyllus melanurus</i>	pres	5	Exp	10.00	8	16.00
74 [261]	Fig 5 – dm – acr	4.64	2.41E+01	Bonin <i>et al.</i> 2009	Pomacentridae	<i>Dascyllus melanurus</i>	pres	5	Exp	10.00	8	16.00
76 [265]	Fig2-chpa-healthy	1.64	1.35E-01	Boström-Einarsson <i>et al.</i> 2014	Pomacentridae	<i>Chrysiptera parasema</i>	pres	60	Exp	16.50	7	48.12
76 [266]	Fig2-chpa-degraded	-8.29	2.51E-01	Boström-Einarsson <i>et al.</i> 2014	Pomacentridae	<i>Chrysiptera parasema</i>	pres	60	Exp	16.50	7	53.93
76 [267]	Fig2-dame-healthy	0.51	1.19E-02	Boström-Einarsson <i>et al.</i> 2014	Pomacentridae	<i>Dascyllus melanurus</i>	pres	60	Exp	16.50	8	49.58
76 [268]	fig2-dame-degadet	-1.20	1.70E-02	Boström-Einarsson <i>et al.</i> 2014	Pomacentridae	<i>Dascyllus melanurus</i>	pres	60	Exp	16.50	8	44.67
80 [276]	Fig3a-highcondition	225.25	2.76E+03	Johnson 2008	Pomacentridae	<i>Stegastes partitus</i>	pres	30	Exp	19.50	10	0.83
80 [277]	Fig3a-lowcondition	351.72	6.73E+03	Johnson 2008	Pomacentridae	<i>Stegastes partitus</i>	pres	30	Exp	17.00	10	0.83
81 [278]	Fig 2b-settlers	2053.03	5.30E+05	Wilson 2005	Gobiidae	<i>Elactinus sp.</i>	pres	1	Exp	12.00	4	15.45
81 [282]	Fig2a-older fish	-477.78	4.43E+04	Wilson 2005	Gobiidae	<i>Elactinus sp.</i>	pres	1	Exp	20.00	4	15.17
82 [279]	fig1a-1pred	-20.61	2.45E+01	Johnson 2006b	Sebastidae	<i>Sebastes spp</i>	pres	2	Exp	22.50	42	6.54
82 [280]	fig1b-3pred	9.05	6.67E+01	Johnson 2006b	Sebastidae	<i>Sebastes spp</i>	pres	2	Exp	22.50	42	6.26
82 [281]	fig1c-5pred	107.39	2.14E+02	Johnson 2006b	Sebastidae	<i>Sebastes spp</i>	pres	2	Exp	22.50	42	6.25

112 LITERATURE CITED
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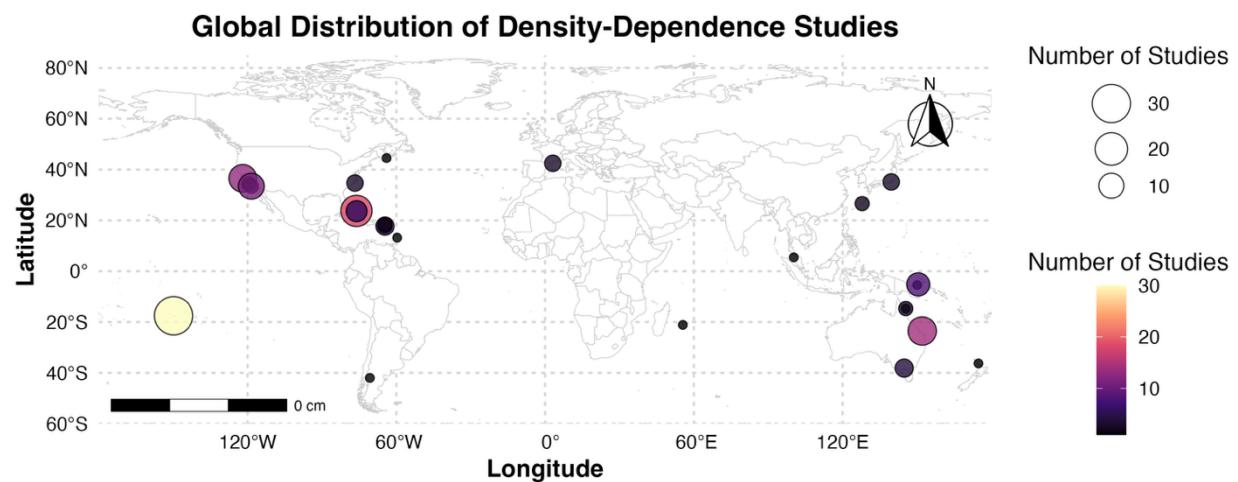
- 114 Anderson, T.W. (1994). Role of macroalgal structure in the distribution and abundance of a
115 temperate reef fish. *Mar. Ecol. Prog. Ser. Oldendorf*, 113, 279–290.
116 Anderson, T.W. (2001). Predator responses, prey refuges, and density-dependent mortality of a
117 marine fish. *Ecology*, 82, 245.
118 Beukers, J.S. & Jones, G.P. (1997). Habitat complexity modifies the impact of piscivores on a
119 coral reef fish population. *Oecologia*, 114, 50–59.
120 Bonin, M.C., Srinivasan, M., Almany, G.R. & Jones, G.P. (2009). Interactive effects of
121 interspecific competition and microhabitat on early post-settlement survival in a coral
122 reef fish. *Coral Reefs*, 28, 265–274.
123 Boström-Einarsson, L., Bonin, M.C., Munday, P.L. & Jones, G.P. (2013). Strong intraspecific
124 competition and habitat selectivity influence abundance of a coral-dwelling damselfish. *J.
125 Exp. Mar. Biol. Ecol.*, 448, 85–92.
126 Boström-Einarsson, L., Bonin, M.C., Munday, P.L. & Jones, G.P. (2014). Habitat degradation
127 modifies the strength of interspecific competition in coral dwelling damselfishes.
128 *Ecology*, 95, 3056–3067.
129 Brooks, A.J. (1999). Factors influencing the structure of an estuarine fish community: the role of
130 interspecific competition. UC Santa Barbara.
131 Carr, M.H., Anderson, T.W. & Hixon, M.A. (2002). Biodiversity, population regulation, and the
132 stability of coral-reef fish communities. *Proc. Natl. Acad. Sci.*, 99, 11241–11245.
133 Caselle, J.E. (1999). Early post-settlement mortality in a coral reef fish and its effect on local
134 population size. *Ecol. Monogr.*, 69, 177.
135 Chua, T. & Teng, S. (1979). Relative growth and production of the estuary grouper *Epinephelus
136 salmonoides* under different stocking densities in floating net-cages. *Mar. Biol.*, 54, 363–
137 372.
138 Doherty, P.J. (1982). Some effects of density on the juveniles of two species of tropical,
139 territorial damselfish. *J. Exp. Mar. Biol. Ecol.*, 65, 249–261.
140 Ford, J.R., Shima, J.S. & Swearer, S.E. (2016). Interactive effects of shelter and conspecific
141 density shape mortality, growth, and condition in juvenile reef fish. *Ecology*, 97, 1373–
142 1380.
143 Ford, J.R. & Swearer, S.E. (2013). Two's company, three's a crowd: Food and shelter limitation
144 outweigh the benefits of group living in a shoaling fish. *Ecology*, 94, 1069–1077.
145 Forrester, G.E. (1990). Factors influencing the juvenile demography of a coral reef fish. *Ecology*,
146 71, 1666–1681.
147 Forrester, G.E. (1995). Strong density-dependent survival and recruitment regulate the
148 abundance of a coral reef fish. *Oecologia*, 103, 275–282.
149 Forrester, G.E. & Steele, M.A. (2000). Variation in the presence and cause of density-dependent
150 mortality in three species of reef fishes. *Ecology*, 81, 2416–2427.
151 Forrester, G.E. & Steele, M.A. (2004). Predators, prey refuges, and the spatial scaling of density-
152 dependent prey mortality. *Ecology*, 85, 1332–1342.
153 Geange, S.W. & Stier, A.C. (2009). Order of arrival affects competition in two reef fishes.
154 *Ecology*, 90, 2868–2878.
155 Geange, S.W. & Stier, A.C. (2010). Priority effects and habitat complexity affect the strength of
156 competition. *Oecologia*, 163, 111–118.

- 157 von Herbing, I.H. & Hunte, W. (1991). Spawning and recruitment of the bluehead wrasse
158 *Thalassoma bifasciatum* in Barbados, West Indies. *Mar. Ecol. Prog. Ser.*, 49–58.
- 159 Hixon, M.A. & Carr, M.H. (1997). Synergistic predation, density dependence, and population
160 regulation in marine fish. *Science*, 277, 946–949.
- 161 Hixon, M.A. & Jones, G.P. (2005). Competition, predation, and density-dependent mortality in
162 demersal marine fishes. *Ecology*, 86, 2847–2859.
- 163 Holbrook, S.J. & Schmitt, R.J. (2002). Competition for shelter space causes density-dependent
164 predation mortality in damselfishes. *Ecology*, 83, 2855–2868.
- 165 Johnson, D.W. (2006a). Density dependence in marine fish populations revealed at small and
166 large spatial scales. *Ecology*, 87, 319–325.
- 167 Johnson, D.W. (2006b). Predation, habitat complexity, and variation in density-dependent
168 mortality of temperate reef fishes. *Ecology*, 87, 1179–1188.
- 169 Johnson, D.W. (2008). Combined effects of condition and density on post-settlement survival
170 and growth of a marine fish. *Oecologia*, 155, 43–52.
- 171 Jones, G.P. (1984). Population ecology of the temperate reef fish *Pseudolabrus celidotus* Bloch
172 & Schneider (Pisces: Labridae). I. Factors influencing recruitment. *J. Exp. Mar. Biol.
Ecol.*, 75, 257–276.
- 173 Jones, G.P. (1987). Competitive interactions among adults and juveniles in a coral reef fish.
174 *Ecology*, 68, 1534–1547.
- 175 Jones, G.P. (1988). Experimental evaluation of the effects of habitat structure and competitive
176 interactions on the juveniles of two coral reef fishes. *J. Exp. Mar. Biol. Ecol.*, 123, 115–
177 126.
- 178 Kneib, R.T. (1981). Size-specific effects of density on the growth, fecundity and mortality of the
179 fish *Fundulus heteroclitus* in an intertidal salt marsh. *Mar. Ecol. Prog. Ser.*, 203–212.
- 180 Lecchini, D., Nakamura, Y., Grignon, J. & Tsuchiya, M. (2006). Evidence of density-
181 independent mortality in a settling coral reef damselfish, *Chromis viridis*. *Ichthyol. Res.*,
182 53, 298–300.
- 183 Letourneau, Y., Chabanet, P., Vigliola, L. & Harmelin-Vivien, M. (1998). Mass settlement and
184 post-settlement mortality of *Epinephelus merra* (Pisces: Serranidae) on Réunion coral
185 reefs. *J. Mar. Biol. Assoc. U. K.*, 78, 307.
- 186 Nanami, A. & Nishihira, M. (2001). Survival rates of juvenile coral reef fishes differ between
187 patchy and continuous habitats. *Bull. Mar. Sci.*, 69, 1209–1221.
- 188 Nitschke, P., Mather, M. & Juanes, F. (2002). Evidence for density-dependent mortality in
189 recruitment of a temperate reef fish, cunner *Tautogolabrus adspersus*, among similar
190 reefs in the vicinity of an anthropogenic disturbance. *Mar. Ecol. Prog. Ser.*, 226, 165–
191 178.
- 192 Overholtzer-McLeod, K.L. (2004). Variance in reef spatial structure masks density dependence
193 in coral-reef fish populations on natural versus artificial reefs. *Mar. Ecol. Prog. Ser.*, 276,
194 269–280.
- 195 Overholtzer-McLeod, K.L. (2005). Post-settlement emigration affects mortality estimates for two
196 Bahamian wrasses. *Coral Reefs*, 24, 283–291.
- 197 Overholtzer-McLeod, K.L. (2006). Consequences of patch reef spacing for density-dependent
198 mortality of coral reef fishes. *Ecology*, 87, 1017–1026.
- 199 Planes, S., Jouvenel, J.-Y. & Lenfant, P. (1998). Density dependence in post-recruitment
200 processes of juvenile sparids in the littoral of the Mediterranean Sea. *Oikos*, 83, 293.

- 202 Sano, M. (1997). Temporal variation in density dependence: recruitment and postrecruitment
203 demography of a temperate zone sand goby. *J. Exp. Mar. Biol. Ecol.*, 214, 67–84.
- 204 Schmitt, R. & Holbrook, S. (1996). Local-scale patterns of larval settlement in a planktivorous
205 damselfish—do they predict recruitment? *Mar. Freshw. Res.*, 47, 449.
- 206 Schmitt, R.J. & Holbrook, S.J. (1999). Settlement and recruitment of three damselfish species:
207 larval delivery and competition for shelter space. *Oecologia*, 118, 76–86.
- 208 Schmitt, R.J. & Holbrook, S.J. (2007). The scale and cause of spatial heterogeneity in strength of
209 temporal density dependence. *Ecology*, 88, 1241–1249.
- 210 Shima, J.S. (2001). Recruitment of a coral reef fish: roles of settlement, habitat, and
211 postsettlement losses. *Ecology*, 82, 2190–2199.
- 212 Shima, J.S. (2002). Mechanisms of density- and number-dependent population regulation of a
213 coral-reef fish. *Mar. Freshw. Res.*, 53, 175.
- 214 Shima, J.S. & Osenberg, C.W. (2003). Cryptic density dependence: effects of covariation
215 between density and site quality in reef fish. *Ecology*, 84, 46–52.
- 216 Steele, M.A. (1997). Population regulation by post-settlement mortality in two temperate reef
217 fishes. *Oecologia*, 112, 64–74.
- 218 Stier, A.C., Geange, S.W. & Bolker, B.M. (2013). Predator density and competition modify the
219 benefits of group formation in a shoaling reef fish. *Oikos*, 122, 171–178.
- 220 Tupper, M. & Boutilier, R.G. (1995). Effects of conspecific density on settlement, growth and
221 post-settlement survival of a temperate reef fish. *J. Exp. Mar. Biol. Ecol.*, 191, 209–222.
- 222 White, J.W. & Caselle, J.E. (2008). Scale-dependent changes in the importance of larval supply
223 and habitat to abundance of a reef fish. *Ecology*, 89, 1323–1333.
- 224 White, J.W. & Warner, R.R. (2007). Safety in Numbers and the Spatial Scaling of Density-
225 Dependent Mortality in a Coral Reef Fish. *Ecology*, 88, 3044–3054.
- 226 Wilson, J. & Osenberg, C.W. (2002). Experimental and observational patterns of density-
227 dependent settlement and survival in the marine fish *Gobiosoma*. *Oecologia*, 130, 205–
228 215.
- 229 Wilson, J.A. (2005). Age class interactions in a marine goby, *Elacatinus prochilos* (Böhlke and
230 Robins, 1968). *J. Exp. Mar. Biol. Ecol.*, 327, 144–156.
- 231
- 232

233 **Appendix C. Supporting Figures, C1-C5.**

234 **Figure C-1. Geographic distribution of substudies.** The size of the circles represents the
235 number of substudies conducted at each location, with larger circles (and lighter colors)
236 indicating a higher number of studies.

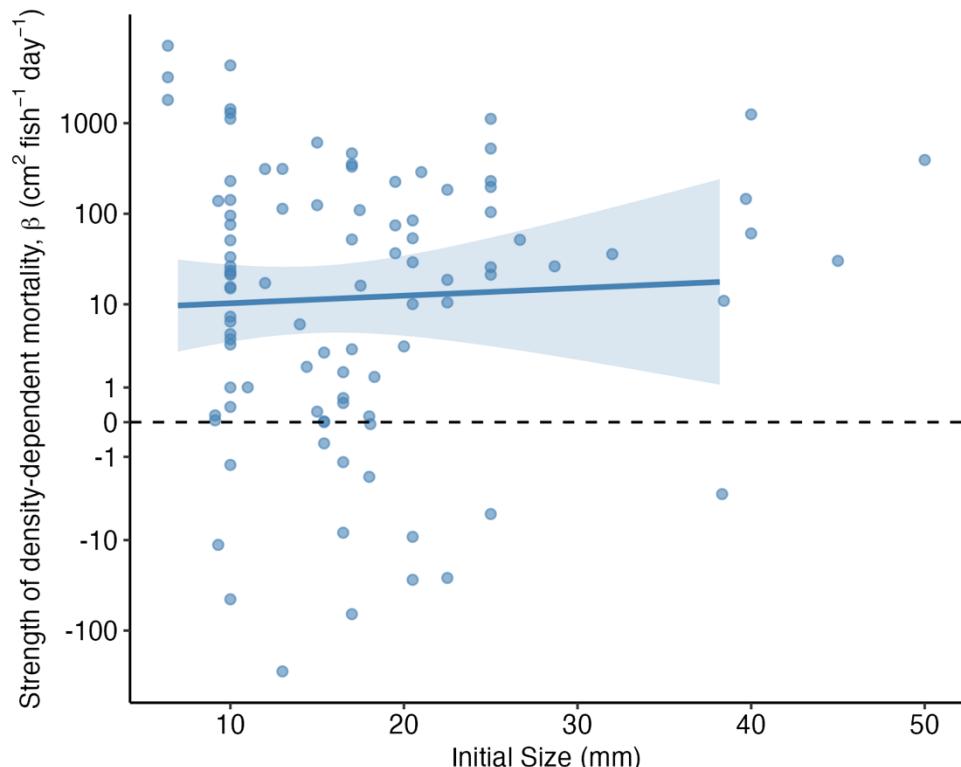


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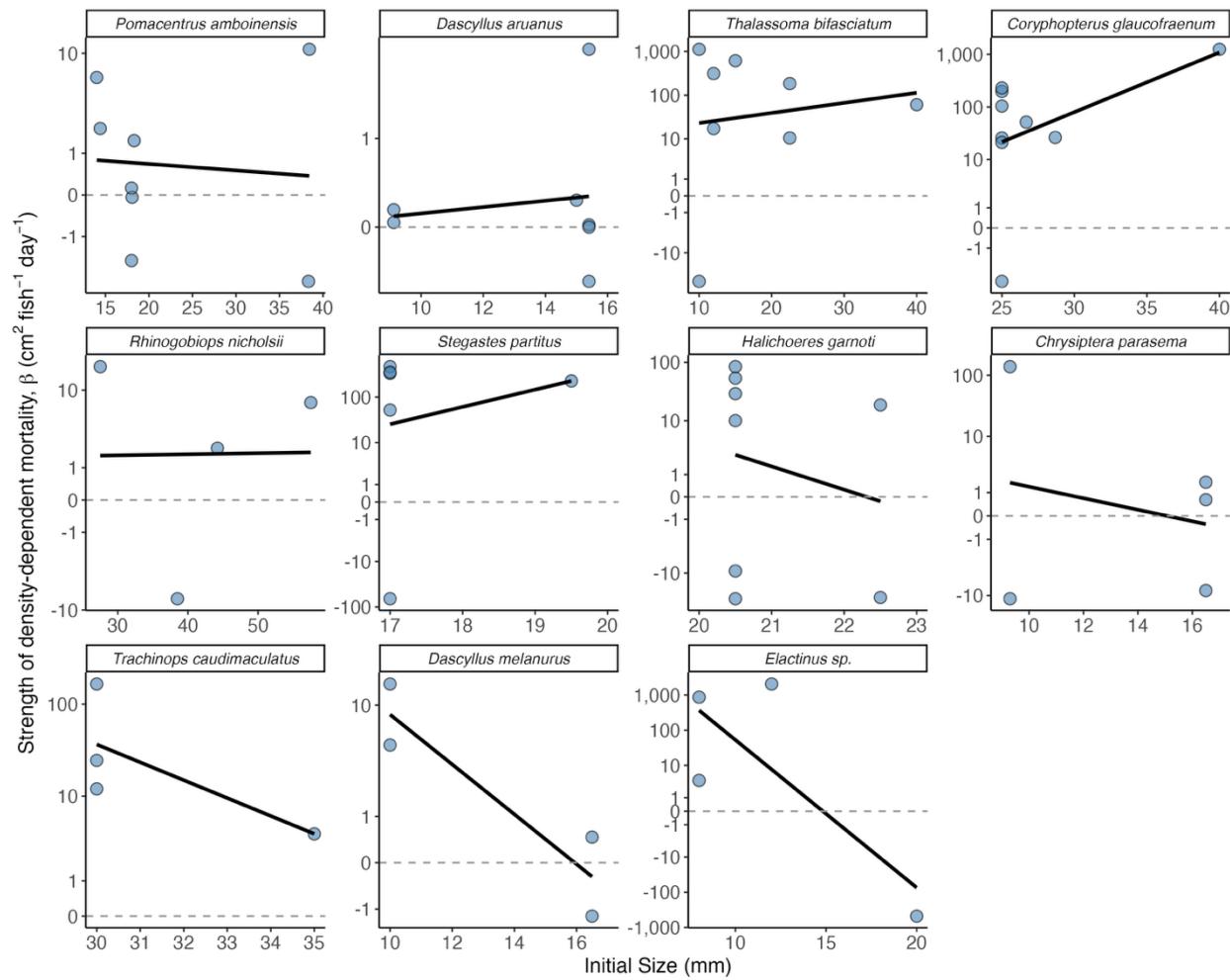
239 **Figure C-2. Effect of initial body size on the strength of density-dependent mortality (β , cm^2
240 $\text{fish}^{-1} \text{day}^{-1}$).** Effects of body size across the entire dataset. Each point represents a substudy. The
241 black line represents a fitted regression model using rma.mv, whose slope is not significantly
242 different from 0. The y-axis uses an inverse hyperbolic sine scale (arcsinh) to display both
243 negative and positive values of β effectively.

244



245

246 **Figure C-3. Variation in effect of initial size on density-dependent mortality (β , $\text{cm}^2 \text{ fish}^{-1}$
 247 day^{-1}) for 10 different species.** Panels show scatterplots of the relationship between initial body
 248 size at the start of the experiment (mm) and the strength of density-dependent mortality (β). Each
 249 point represents a substudy. Black lines represent fitted regression models for each species. Note
 250 that the scale in each plot varies, and the y-axis is on the arcsinh scale to accommodate wide
 251 variation in β . The effect of body size was not significant for any species.

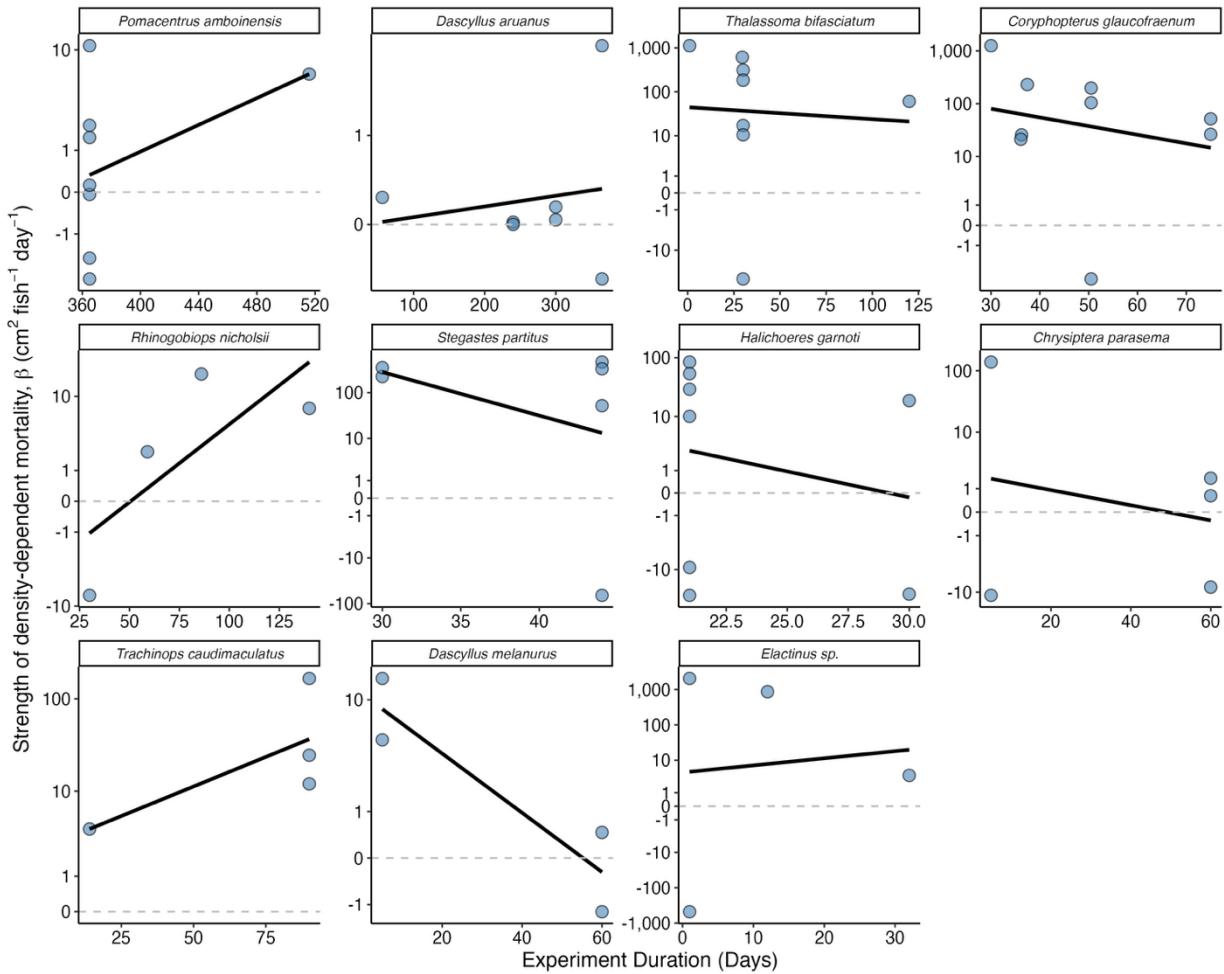


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253

254 **Figure C-4. Relationship between experiment duration and density-dependent mortality**
 255 **within fish species with four or more substudies.** Each facet, labeled with the species name in
 256 italics, displays individual estimates of density-dependent mortality, β ($\text{cm}^2 \text{ fish}^{-1} \text{ day}^{-1}$) plotted
 257 against the duration of the substudy (days). Solid black line in each panel shows the linear
 258 regression fits for each species. The vertical axis is scaled using the inverse-hyperbolic-sine
 259 (arcsinh) function so that both small and large values—including negative mortality estimates—
 260 can be visualized. The effect of duration was not significant for any species.

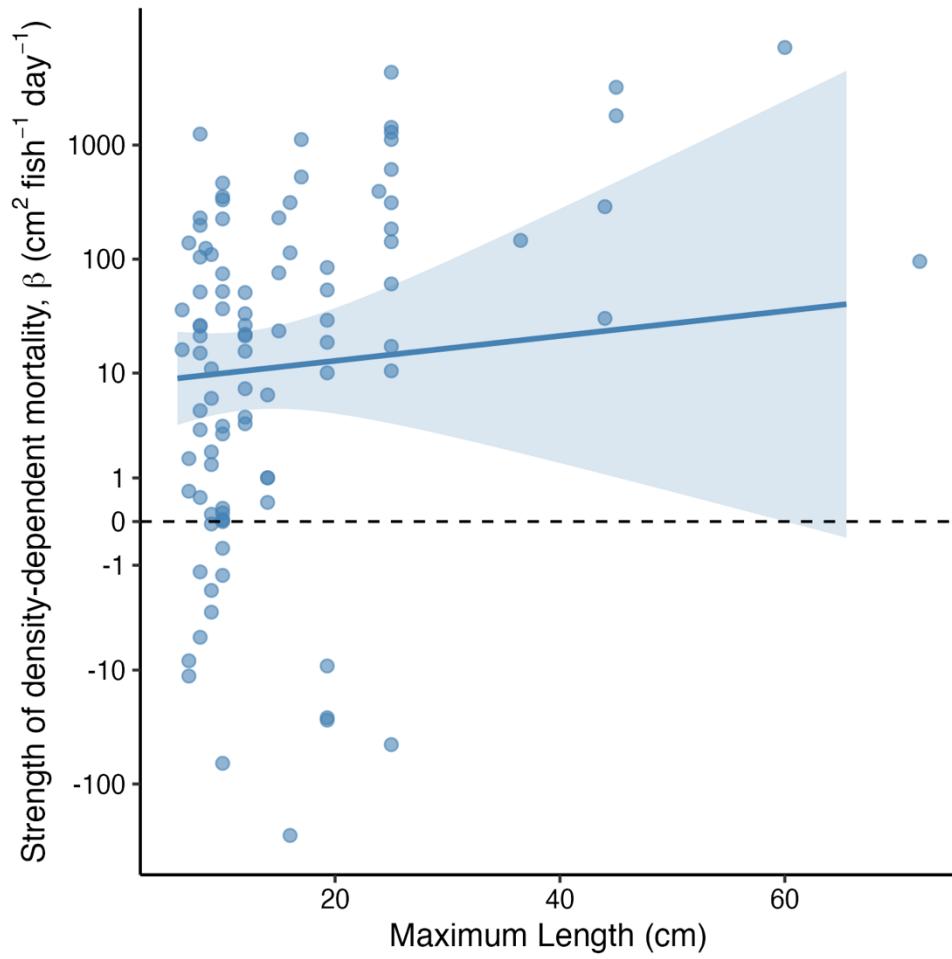
261



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263

264 **Figure C-5. Relationship between maximum adult body size (cm) density-dependent**
265 **mortality.** The semi-transparent steel-blue circles are the raw substudy estimates and the solid
266 navy line with pale-blue ribbon is the meta-regression prediction \pm 95% CI from an rma.mv
267 model holding all other moderators at their mean (centered = 0). A horizontal dashed line at $\hat{\beta} = 0$
268 indicates no effect of density on mortality. The y-axis uses an inverse hyperbolic sine (arcsinh)
269 scale to accommodate large negative and positive values.



270

271

272 **Appendix D: Paired Observational and Experimental Substudies.**

273 To test whether experimental and observational studies conducted within the same system
274 differed in the strength of density-dependent mortality (β), we performed a paired meta-analysis
275 restricted to cases in which estimates of β were available from an experimental and observational
276 substudy for the same species, at comparable locations and times, and in the presence of
277 predators. This resulted in data for six species, each represented by a paired experimental and
278 observational substudy ($n = 12$ total observations). Effect sizes were analyzed on the arcsinh-
279 transformed scale, with a minimum variance floor of 1×10^{-8} imposed to prevent singularities.

280 We fit two multilevel meta-analytic models using the metafor package:

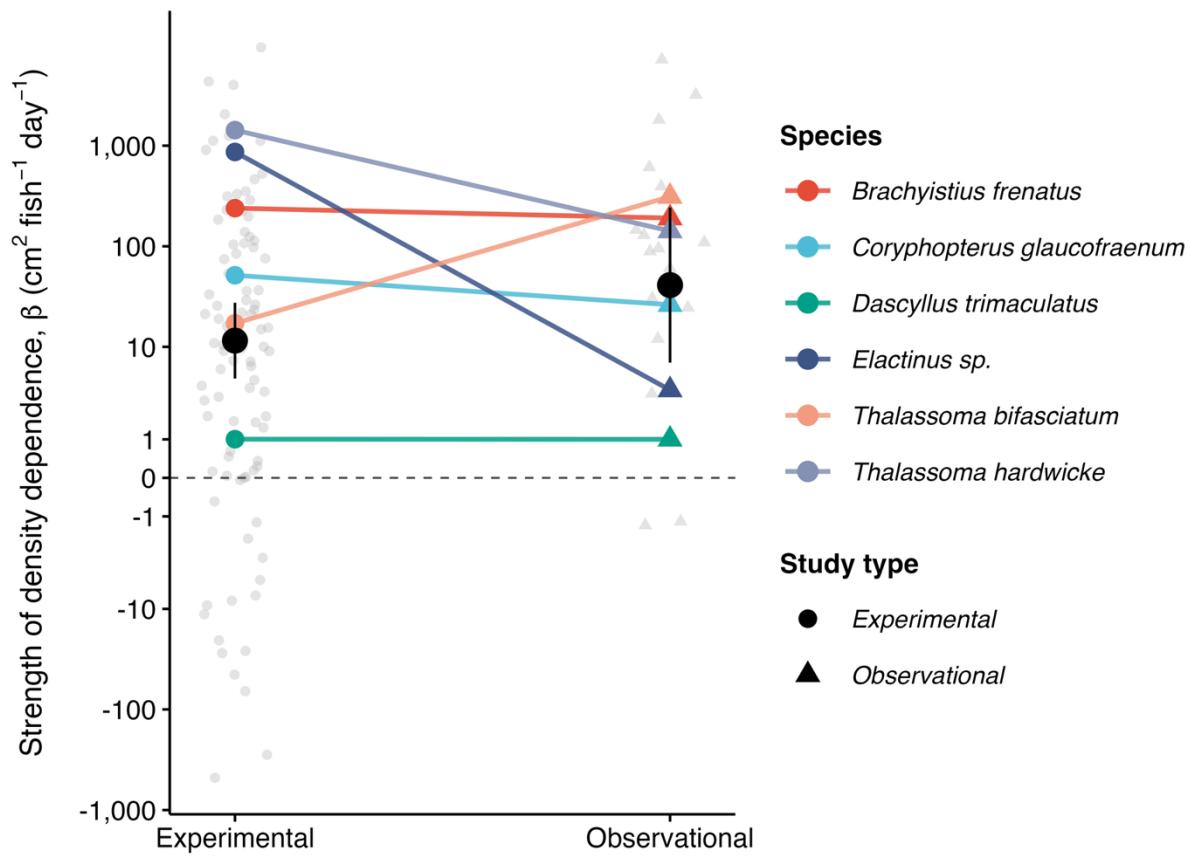
- 281 1. Main-effects model, assuming a common experimental–observational difference across
282 species.
283 2. Random-slopes model, allowing the experimental–observational difference to vary
284 among species (i.e., species-specific slopes).

285 Both models were estimated via restricted maximum likelihood (REML) and compared using a
286 likelihood-ratio test (LRT). Model coefficients were back-transformed (sinh) to obtain estimates
287 on the raw β scale.

288 Five of the six species had larger estimates of density-dependence in the experimental substudy
289 compared to the observational substudy, and the main-effects model indicated a significant
290 overall difference between experimental and observational substudies (estimated $\Delta\beta = -0.34 \pm$
291 0.10 SE, $t_{10} = -3.54$, $p = 0.0053$). However, the random-slopes model provided a significantly
292 better fit than this main-effects model (LRT = 27.6, $p < 0.0001$), indicating strong heterogeneity
293 in the experimental–observational effect across species (i.e., a statistically significant interaction
294 term). Under this model, the overall experimental–observational contrast was not significant
295 (estimate = 0.24 ± 1.36 SE, $t_{10} = 0.18$, $p = 0.8638$), indicating that the direction and magnitude of
296 substudy-type effects varied considerably among species.

297 In summary, while experimental substudies often suggested stronger density dependence than
298 observational ones, this pattern was not consistent across species. The random-slopes model
299 demonstrates that the experimental–observational difference varied substantially by species
300 (LRT $p < 0.0001$), indicating that species-specific ecological and methodological factors drive
301 heterogeneity in the strength of density-dependent mortality.

302 **Figure D-1.** Comparison of density-dependent mortality (β , $\text{cm}^2 \text{ fish}^{-1} \text{ day}^{-1}$) between
 303 experimental (Exp) and observational (Obs) studies. Gray points show individual substudies.
 304 Black points (and vertical lines) give the model-estimated marginal means ($\pm 95\%$ CI) for
 305 Experimental and Observational substudies from the full meta-analysis (REML, rma.mv),
 306 evaluated at the mean of centered moderators and with random effects for paper, substudy, and
 307 phylogenetic correlation. Colored points and connecting line segments show species-specific
 308 means for observational and experimental studies paired for six species. The y-axis is arcsinh-
 309 scaled to match the analysis; the dashed line at $\beta = 0$ indicates no effect of density on mortality.



310

311

312 **Appendix E: Sensitivity and Publication Bias Analyses**

313 In this appendix, we detail the diagnostic procedures we conducted to evaluate the stability of the
314 pooled mean effect and the extent of publication bias across the 147 estimates of density-
315 dependent mortality (β). We analyzed all effect sizes on the arcsinh-transformed scale to match
316 our core analysis with our sensitivity analysis: all diagnostics were performed on this
317 transformed scale.

318 E.1. Model Robustness and Heterogeneity

319 We used a multilevel random-effects meta-analysis to estimate the overall strength of density-
320 dependent mortality (β). Effect sizes were transformed using the inverse hyperbolic sine
321 function. All model fitting was conducted on this arcsinh(β) scale to stabilize variance and
322 accommodate both positive and negative values and near-zero effects. Accordingly, all reported
323 effect sizes (β) represent $sinh$ -back-transformed estimates of the corresponding arcsinh-
324 transformed model coefficients, whereas μ refers to results on the analysis scale.

325 The pooled mean on the analysis scale was $\mu = 3.02$ (95% CI = 2.42–3.63). Back-transformation
326 yielded a mean effect of $\beta = 10.26 \text{ cm}^2 \text{ fish}^{-1} \text{ day}^{-1}$ (95% CI = 5.56–18.86 $\text{cm}^2 \text{ fish}^{-1} \text{ day}^{-1}$).

327 Between-paper heterogeneity was extreme ($Q_e = 1.77 \times 10^5$, $p < 0.0001$; $I^2 \approx 99.9\%$), confirming
328 that observed variability exceeded that expected from sampling error. Variance components were
329 $\sigma^2_{\text{paper}} = 0.3240$ and $\sigma^2_{\text{substudy}} = 11.7896$ on the arcsinh scale, indicating substantial
330 ecological and/or methodological heterogeneity among substudies.

331 To evaluate the influence of individual substudies, we performed a leave-one-out (LOO)
332 sensitivity analysis. For each of the 147 substudies, a new model was fit after removing that
333 study, using the same random-effects structure and REML estimation procedure as the full
334 model. Each iteration yielded a new pooled mean $\mu_{(-i)}$ on the arcsinh scale, which was then back-
335 transformed via $\beta_{(-i)} = sinh(\mu_{(-i)})$. The resulting LOO distribution (Figure E-1A) was narrow: $\mu_{(-i)}$
336 ranged from 2.95 to 3.14 ($\Delta\mu = 0.19$), corresponding to $\beta_{(-i)}$ values of 9.56 to 11.56 $\text{cm}^2 \text{ fish}^{-1}$
337 day^{-1} . The largest change was relatively small ($\Delta\beta \approx 1.3$), indicating that no single study
338 materially altered the pooled mean, confirming model stability across the dataset.

339 E.2. Publication and Small-Study Bias

340 Potential publication and small-study bias were evaluated using funnel-plot symmetry and
341 Egger's regression. The funnel plot (Figure E-1B) displays a greater preponderance of
342 observations to the right of the mean suggesting that smaller, less-precise substudies tended to
343 report somewhat larger positive effects, consistent with weak small-study bias.

344 We formally tested this pattern using Egger's regression, in which standardized effects were
345 regressed against precision ($1/\text{SE}$). The fitted model yielded an intercept of 15.91 which differed
346 from zero ($p = 1.747e-07$), with a modest proportion of variance explained ($R^2 = 0.028$). This
347 result indicates marginal asymmetry consistent with small-study effects, but the magnitude of
348 bias is weak and does not alter the qualitative conclusion of a positive overall effect.

349 E.3. Null-Add Sensitivity

350 To test whether the pooled mean could be substantially altered by unreported or missing “null”
351 results, we performed a null-add sensitivity analysis (Figure E-1D). In this procedure, we
352 sequentially added hypothetical substudies with no density dependence ($\beta = 0 \text{ cm}^2 \text{ fish}^{-1} \text{ day}^{-1}$,
353 corresponding to 0 on the arcsinh scale) and assigned them precision corresponding to observed
354 quantiles of the standard errors of arcsinh β (Q50 = 0.236, Q75 = 0.575, Q90 = 1.39, Q95 =
355 2.92). After each addition, we refit the same multilevel random-effects model and recorded the
356 updated pooled mean (μ), and its difference from the baseline ($\mu = 3.023$): i.e., $\Delta\mu$.

357 As progressively more nulls were added, the pooled mean declined modestly. For the Q95 cases,
358 adding 5 null substudies, resulted in $\Delta\mu = -0.070$, corresponding to a decrease from $\beta = 10.26$
359 $\text{cm}^2 \text{ fish}^{-1} \text{ day}^{-1}$ to $\beta = 9.56 \text{ cm}^2 \text{ fish}^{-1} \text{ day}^{-1}$.

360 After adding 10 null substudies, $\Delta\mu = -0.135$, corresponding to a reduction in β to 8.96 cm^2
361 $\text{fish}^{-1} \text{ day}^{-1}$.

362 Using more precise estimates for the null studies (e.g., based on Q50), reduced the mean effect
363 somewhat more (e.g., for 10 null studies, $\Delta\mu$ was reduced by another ~ 0.1 .

364 Despite the addition of null substudies, the estimated effect size remained strongly positive,
365 indicating that the overall conclusion of a positive density-dependent mortality relationship is
366 robust to the possible presence of several unreported null studies.

367

368 **Figure E-1. Sensitivity and publication-bias diagnostics for density-dependent mortality.**

369 Panels summarize robustness and bias diagnostics on the arcsinh analysis scale. A) Leave-one-
 370 out evaluation showing the pooled mean re-estimated after excluding each of 147 substudies.
 371 The dashed line marks the full-sample mean ($\mu = 3.02$; $\beta = 10.26 \text{ cm}^2 \text{ fish}^{-1} \text{ day}^{-1}$ after back-
 372 transformation). B) Funnel plot of $\text{arcsinh}(\beta)$ against its standard error, showing the pooled
 373 random-effects mean ($\mu = 3.02$) as a dashed vertical line. The gray shaded area denotes the 95%
 374 confidence funnel ($\pm 1.96 \times \text{SE}$), and light dashed boundary lines indicate the 99% limits (± 2.58
 375 $\times \text{SE}$). Three substudies with extreme variance ($\text{SE}[\text{asinh } \beta] > 7.0$) were excluded from display
 376 but retained in all analyses. C) Egger's regression of standardized effects [$\text{arcsinh}(\beta)/\text{SE}$] on
 377 precision [1/ SE of $\text{arcsinh}(\beta)$] led to an estimated intercept of 15.91 ($p = 1.747\text{e-}07$), consistent
 378 with mild small-study bias. Egger's plot excludes the same 3 points as in the funnel plot. D)
 379 Null-add sensitivity test showing the effect of sequentially adding hypothetical null substudies (β
 380 = 0 $\text{cm}^2 \text{ fish}^{-1} \text{ day}^{-1}$) with $\text{SE}(\text{arcsinh } \beta)$ values corresponding to observed quantiles (Q50 =
 381 0.236, Q75 = 0.575, Q90 = 1.39, Q95 = 2.92).

