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Are Habitat Fragmentation Effects Stronger in Marine Systems? A Review and Meta-analysis

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Abstract

Purpose of the Review The importance of habitat fragmentation in driving biodiversity loss has been recently debated. While the negative effects of habitat loss are well-documented, the effects of habitat fragmentation independent of habitat loss (e.g., habitat configuration) are more equivocal. Marine ecosystems have been underrepresented in past reviews, yet may differ fundamentally from terrestrial systems in their responses to habitat fragmentation because of the nature of energy/material flow, open population structure of most marine species, and narrow habitat extents. We conducted a systematic literature review and meta-analysis on the effects of habitat fragmentation in marine ecosystems.

Recent Findings In our review of 180 studies from 28 articles, we found that habitat fragmentation effects were more often negative than positive, although the overall mean effect did not differ from zero. Interestingly, the mean effect was positive when the response was a measure of abundance, biodiversity, or population/ecosystem stability. Habitat fragmentation had overwhelmingly negative effects when it involved hydrological fragmentation. We found some support for the fragmentation threshold hypothesis via a weak negative relationship between habitat percent cover in the landscape and the habitat fragmentation effect.

Summary Results of this review on the effects of habitat fragmentation in marine ecosystems are largely consistent with another recent review finding that habitat fragmentation (independent of habitat loss) does not have consistent, negative impacts on biodiversity, and in many cases may increase biodiversity. Future work should focus on factors driving this variability and employ multi-scale frameworks to test for congruence between patch- and landscape-scale studies.

Keywords Habitat fragmentation per se · Matrix quality · Fragmentation threshold hypothesis · Marine · Biodiversity · Ecosystem function

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Introduction

Habitat fragmentation is often cited as a primary driver of contemporary biodiversity loss and the associated degradation of natural ecosystems. Habitat fragmentation is a process whereby a large expanse of habitat is broken into smaller and more numerous fragments separated by a matrix unlike the original [1]. During this process, multiple habitat attributes change, including reductions in total habitat area, decreasing patch size, increasing amount of edge, increasing patch number, and increasing patch isolation. In the aggregate, habitat fragmentation is typically associated with declines in organismal abundance and diversity [2–5], but the primary mechanism underlying this loss is often unclear. Specifically, it may be useful to conceptualize habitat fragmentation as two distinct processes: habitat loss and independent changes in spatial configuration (termed habitat fragmentation per se, [6]). The negative effects of habitat loss on biodiversity are well-documented [7–9], and the positive relationship between habitat area and species richness is among the most universally supported in ecology [10]. In contrast, the effects of habitat fragmentation per se (hereafter "habitat fragmentation"), are much more equivocal [6, 11]. For example, a recent review by Fahrig [11••] found that effects of habitat fragmentation on ecological responses were highly variable across studies and more likely to be positive than negative. This has led to much debate surrounding the relative importance of habitat fragmentation as a driver of biodiversity loss [12, 13].

Understanding when habitat fragmentation should be important in impacting the biodiversity and function of ecosystems is key in making effective management recommendations (e.g., reserve design or land-use planning). Several factors have been suggested to be important in mediating the effect of habitat fragmentation including traits of focal species and aspects of landscape configuration [14]. Specifically, species with lower dispersal abilities, narrow environmental requirements, or those more sensitive to small population sizes may be more sensitive to habitat fragmentation [15, 16]. Additionally, matrix quality may be another important driver of variance in effects of habitat fragmentation across studies [14]. Although, conceptual models of habitat fragmentation often involve habitat patches nested within a non-habitat matrix, real-world landscapes exist along gradients of matrix quality (e.g., agriculture or secondary forests) where matrix habitat may serve as secondary habitat or have varying effects on organismal dispersal [17, 18]. Lastly, interactions among habitat loss and habitat fragmentation may determine the expected ecological outcome. Studies using simulation models have predicted that negative effects of habitat fragmentation should manifest primarily when habitat area is low (below 20%–30% cover, [19–21]). Termed the fragmentation threshold hypothesis, this hypothesis predicts that non-linear declines in patch size and isolation concomitant with reduced total habitat area below this threshold should have significant negative impacts on species persistence. As testing this hypothesis requires replication of landscapes along both area and fragmentation gradients, there have been relatively few empirical tests which have provided variable results [22–26]. Identifying a habitat loss threshold below which habitat fragmentation has primarily negative effects on species persistence could be an important conservation tool.

Marine and terrestrial systems may be expected to differ in their responses to habitat fragmentation. In contrast to most terrestrial species, many marine species are characterized by relatively open population structure due to the large dispersal distances of marine organisms during their larval life stage [27]. Thus, habitat fragmentation may have relatively weak effects on meta-population structure or persistence when compared to terrestrial species where sub-populations may be separated among habitat fragments and crossing habitat matrix may represent a major dispersal barrier. Similarly, the nature of material movement differs fundamentally in marine systems as energy and nutrients may be readily carried across habitat boundaries by water flow. Additionally, the relative extent of many marine habitats is relatively limited compared to many terrestrial habitats, as the most productive marine habitats are typically depth-limited and exist only along shallow coastal margins. Thus, habitat fragmentation occurring over comparatively small spatial scales may have more significant impacts on overall habitat function. Finally, matrix quality may be fundamentally different between marine and terrestrial realms. Although not universal, many structured marine habitats exist in unstructured matrices (e.g., sand or mud bottom). These unstructured bottoms differ greatly from structured habitats in terms of primary production or refuge availability and thus may better represent a binary habitat/non-habitat matrix model. Thus, responses to habitat fragmentation in marine ecosystems may not necessarily follow similar patterns to those observed in terrestrial ecosystems, yet marine studies have been grossly under-represented in habitat fragmentation syntheses. For instance, less than 10% of the studies reviewed in Fahrig [11••] were from marine environments.

Our overall objective was to review the literature and synthesize past research on the effects of habitat fragmentation in marine systems. We reviewed findings on the proportion of studies which found significant impacts of fragmentation on ecological response variables, the strength of these effects relative to habitat area, and the sign (positive or negative) of these effects. We also conducted a meta-analysis on the effects of habitat fragmentation on ecological response variables for studies in which sufficient data were reported to do so. We examined variation in the effect of habitat fragmentation across habitat types, ecological responses, and aspects of study design. We tested whether taxa body size and mobility were important in mediating the response. Finally, we tested the fragmentation threshold hypothesis by examining the strength of fragmentation effects across a gradient of habitat cover within the landscape.

Methods

Literature Search

We conducted a systematic literature search of all databases in the Institute of Scientific Information's Web of Science on November 9, 2018 to identify primary literature examining habitat fragmentation in marine ecosystems. We used the following set of search terms: (Fragmentation OR SLOSS) AND (seagrass OR coral OR mangrove OR reef OR wetland OR oyster OR salt marsh OR kelp OR marine OR intertidal OR tide pool). All returned results were subject to an initial screening by one of the authors of the current study for relevance to ecology and to ensure the focal habitat was marine. After the initial screening, all remaining articles were assessed by one of the study authors to determine whether each met the following four inclusion criteria: (1) the study analyzed empirical data; (2) the study was conducted at the landscape scale, not the patch scale (sensu [6]); (3) habitat fragmentation was measured independently from habitat area; and (4) the effects of habitat fragmentation on an ecological response variable (e.g., community structure or a type of ecosystem function) were reported. For criteria (3), the study needed to measure habitat fragmentation independently from the area (e.g., number habitat patches, fractal dimension, mean patch isolation, connectivity), although habitat fragmentation was not always statistically independent from habitat area across landscapes within all studies. If a reviewer was unsure whether an article should be retained, they obtained the opinion of a second reviewer. In many cases, there were multiple tests of links between habitat fragmentation and ecological responses within an individual published article (e.g., responses of different species). For the purpose of the current paper, we termed each independent test a "study" in contrast to an "article" which is used to refer to each published unit.

Literature Review

From each study retained for our final literature review, we extracted metadata and results related to our primary research question. Specifically, we extracted data related to experimental design, study location, landscape size, metric of habitat fragmentation measured, and data analysis approach employed (full list of metadata extracted included in Table S1). For the literature review, we summarized the characteristics of all included studies. We also summarized results of each study by answering the following questions: (1) Was habitat fragmentation determined to be important in affecting the given response variable (e.g., was the fragmentation effect statistically significant or retained in the final model under model selection approaches)? (2) Did habitat fragmentation have a positive, neutral, or negative effect on the response variable? and (3) Was the effect of habitat fragmentation more important, equally important, or less important than the effect of landscape habitat area if they were both evaluated? To answer these questions, we relied on the results reported in the study based on the analysis approach selected by the authors. In some cases, habitat fragmentation was one of multiple predictor variables in the model and its importance in affecting the ecological response variable could have been evaluated by frequentist statistics or model selection techniques. We compared our results from question (1) based on vote counting to another method to assess the frequency of significant effects on habitat fragmentation following Fahrig [11••]. Specifically, to reduce the probability of Type I error based on the bias against publishing non-significant results, we summarized the frequency of significant results reported in articles that made multiple contrasts (≥ 10 tests of habitat fragmentation effects). These typically included responses of multiple species or measures of community structure and function within the same system. We then averaged the mean proportion of significant results across articles.

Quantitative Meta-analysis

In addition to our literature review, we conducted a meta-analysis on the effects of habitat fragmentation (independent of area) for all studies where sufficient data was reported to do so. For this meta-analysis, we used Hedge's d (corrected for small sample sizes, [28]) as our effect size to compare the standardized mean difference between high and low (or no) fragmentation treatments/groups. We chose Hedge's d as our effect size measure as most studies compared ecological responses between two fragmentation treatments and it allows for the comparison of means that differ in sign (as opposed to the Log response ratio, LRR [29]). Hedge's d ranges from $-\infty$ to ∞ and a value of $d = 1$ would indicate the mean for the high fragmentation group was one standard deviation higher than the mean of the low fragmentation group. For studies in which landscapes across multiple fragmentation levels were analyzed, we compared only the most fragmented and least fragmented treatments. Mean (and variance) in ecological response variables was extracted directly from the text or data tables or extracted from digitized figures using online tool WebPlot Digitizer (https://automeris.io/WebPlotDigitizer/).

To assess whether the overall mean effect of fragmentation differed from zero, we conducted a meta-analytic random-effect regression model using the rma.mv function in the metaphor package in R [30, 31]. We weighted effect sizes from individual studies by the within-study variance and we report the mean (model intercept) and 95% confidence interval across all studies. To account for non-independence of effect sizes taken from the same article, we used a random intercept based on article identifier.

In addition to calculating the overall effect of habitat fragmentation of ecological responses, we were also interested in how the effects varied across habitats and various aspects of study design. Specifically, we focused on how (1) focal habitat, (2) matrix type (land, unstructured bottom, and structured bottom), (3) metric of habitat fragmentation used (patch number, connectivity, patch isolation, or other metric), (4) study design (observational vs. experimental), and (5) type of response metric (e.g., movement/habitat use, growth, survival, abundance/biomass, biodiversity, stability, or ecosystem function) affected the effect size of fragmentation on ecological responses. We ran a meta-analytic mixed effects regression model with all the above listed predictor variables as fixed effects and article identifier as a random effect. To explore which predictor variables were most important in mediating the effect of fragmentation on the ecological response, we used model selection based on Akaike's information criterion with a small sample size correction (AICc) and compared all possible model subsets using the dredge function in the MuMIn package [32]. To calculate the mean effects (± 95% CI) across different levels for each of these predictor variables, we also ran individual meta-analytic mixed effects regression models with a single predictor as the fixed effect and article identifier as a random effect.

Next, we were interested in how species traits may mediate their response to habitat fragmentation. For the subset of studies in which responses of individual species or taxonomic families were considered, we extracted information on species body size (maximum body size for the species) and post-settlement mobility (sessile, sedentary, or mobile). Body size information was extracted from the online databases Fishbase.org [33] or Sealifebase.org [34]. We then performed similar meta-analytic mixed effects regression models as above with either species maximum body size or species mobility as the fixed effect.

Test of the Fragmentation Threshold Hypothesis

We conducted a second meta-analysis to test the fragmentation threshold hypothesis and to determine whether the effects of habitat fragmentation were dependent upon habitat area in the landscape. Specifically, we estimated the strength of the habitat fragmentation effect at varying amounts of landscape habitat cover across studies. To do this, we compared the difference in ecological response between high habitat fragmentation and low habitat fragmentation landscapes with a similar total habitat percent cover (within a 5% cover bin) within a given study. Only a small number of studies reported percent cover information and made measurements on high and low habitat fragmentation landscapes within comparable percent habitat cover landscapes. Because some contrasts were unreplicated within a given percent habitat cover bin (e.g., there was only one low fragmentation and one high fragmentation landscape at a given percent cover within a study), we could not calculate within study variance and hence could not use Hedge's d for this meta-analysis. We therefore used the LRR as our measure of effect size as it can be estimated without knowledge of the sample size or within study variance [29]. The LRR is calculated as the natural log of the mean high fragmentation group divided by the mean of the low fragmentation group. We ran a linear regression model to determine whether the habitat percent cover within the landscape predicted the habitat fragmentation effect size (LRR). We also explored non-linear models to capture the predicted threshold effect, but these models had poorer fits to the data.

Results

Literature Search

Our initial literature searched yielded 3057 articles (Fig. 1). Of these, 585 articles passed our first screening, while only 28 passed the second screening and met all four of our search criteria [24, 35–61]. From these 28 articles, we extracted data from 180 studies that represented individual tests of habitat fragmentation on ecological response variables.

Literature Review

Studies of habitat fragmentation were conducted in diverse temperate and tropical marine habitats and spanned the coastal margins of four continents (Asia, Australia, Europe, and North America; Table S1). Most studies were conducted in the Northern Hemisphere. Matrix habitat varied and included land, unstructured bottom (e.g., mud flat, bare rock), and structured habitats (e.g., seagrass, saltmarsh). Studies employed both experimental (56%, 101/180 studies) and observational (44%, 79/180 studies) approaches. Most were conducted in the field (89% of studies), although some mesocosm studies where habitat configuration was manipulated in tanks were also included (11%). The majority of studies used a measure of patch number (76%) alone or in conjunction with another landscape metric as a measure of habitat fragmentation. Other metrics included measures of habitat patchiness (e.g., largest patch index, fractal dimension; 4%), patch isolation (6%), and connectivity (hydrologic or physical; 13%). Landscape size varied widely across studies (0.03 m^2 to > 3 km^2) and was larger for observational studies (mean ± SD = 197,000 ± 725,000 m^2) than for experimental studies

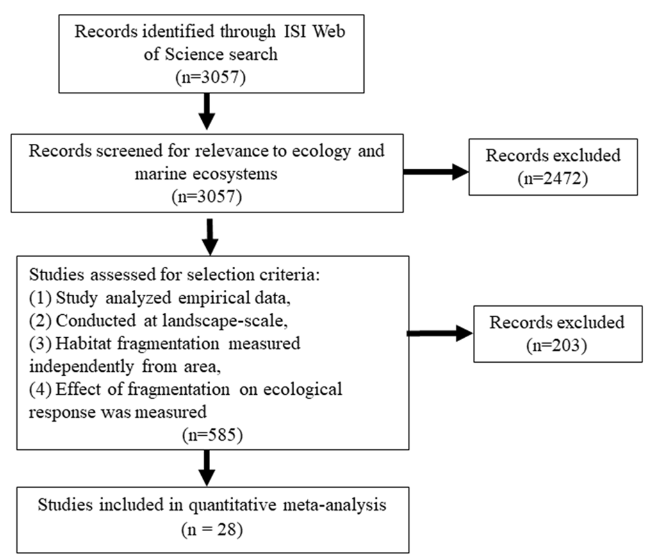


Fig. 1 Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) diagram for current review of habitat fragmentation effects in marine ecosystems

(7.1 ± 9.5 m^2). The effects of habitat fragmentation were measured on a suite of ecological responses ranging from individual- and population-level responses to metrics of community structure and ecosystem function. Response taxa included plants, invertebrates, and vertebrates (i.e., fishes) and 39% of studies measured response of macrofaunal assemblages rather than those of individual taxa.

Based on results reported in the original studies, the effects of fragmentation were reported to be significant 48% of the time (87/180 studies; Fig. 2a). The percentage of significant effects was lower when considering only articles with ≥ 10 tests (mean ± SD = 38% ± 29%), suggesting that bias against publication of non-significant results may have led to inflation of the percentage of studies detecting a fragmentation effect. Of the studies that reported significant effects of fragmentation (and a sign could be determined), fragmentation was more likely to have a negative effect (60% of studies) than a positive one (40%; Fig. 2b). For studies that compared the relative strength of changes in habitat area and habitat fragmentation on ecological responses ($n = 74$ studies), most studies found neither to be a strong predictor (69%; Fig. 2c). These were largely small-scale experimental studies that manipulated patch size and arrangement. Of the remaining studies, most found habitat fragmentation to be more important (16%) or equally important (8%) to habitat area in predicting ecological responses, as compared to only 7% of studies that found area to be more important than habitat fragmentation.

Meta-analysis of Effects of Habitat Fragmentation

Eighty-six of the 180 studies reported sufficient data to calculate Hedge's d. The effect size for habitat fragmentation on ecological responses was highly variable across studies, ranging from − 17.07 to 35.07. The overall mean effect estimated from the meta-analytic random-effect regression model was negative at − 0.84 indicating that on average, ecological response metrics were lower in more fragmented landscapes, but the 95% CI overlapped zero (− 2.03, 0.33). There was significant heterogeneity in effect sizes across studies, however, suggesting that observed variation in effect sizes is larger than one would expect based on sample variability alone (Cochran's Q = 983.9, df = 85, $P < 0.0001$).

Including predictors related to landscape characteristics and study design improved the overall model fit (full model AICc = 663.0 vs. 950.0 for the random intercept only model, Omnibus test for fixed effects, $Q_m = 260.7$, df = 18, $P < 0.001$). The full model with all five predictor variables performed better than models with all possible subsets of predictors (ΔAICc relative to next best model = 3.15), indicating each was important in mediating the effect size. Studies that used measures of connectivity found an overall negative effect of habitat fragmentation on ecological responses; those using patch isolation and patch number did not have a mean effect that differed from zero (Fig. 3a). Studies that employed observational study designs had a negative mean effect size; the mean effect size for experimental studies was near zero (Fig. 3c). Interestingly, the mean effect size varied greatly among types of response variables (Fig. 3b). The mean responses were negative when considering ecosystem function and individual-level responses (survival and growth), but were positive when the ecological response was measured at the population or community level (abundance, biodiversity, population stability). All the mean effect sizes for focal habitat types had 95% CIs that overlapped zero and the mean effect was lowest for tidal creeks (Fig. 3d). There were also differences in mean effect sizes across landscapes within different types of habitat matrices (Fig. 3e). The mean effect was negative for marine habitats embedded within a matrix of land, but did not differ from zero when the matrix habitat was a submerged unstructured or structured bottom.

There were 36 studies for which we were able to assign a mobility trait value to focal taxa. Only the mean effect size for

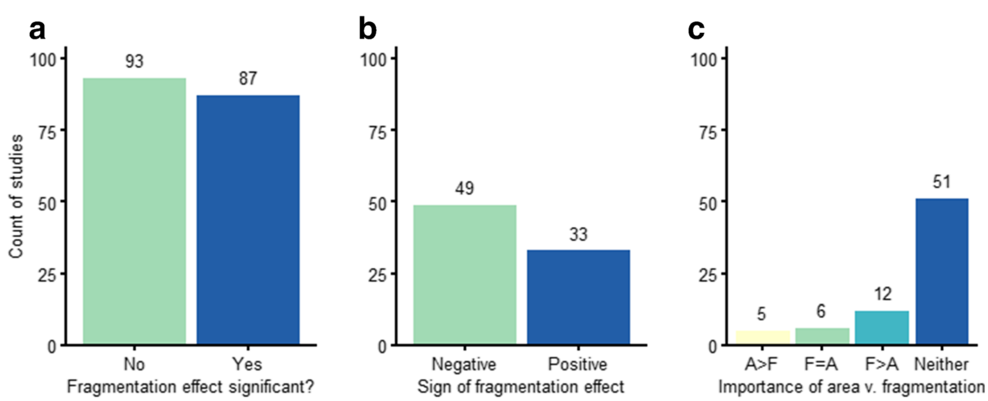
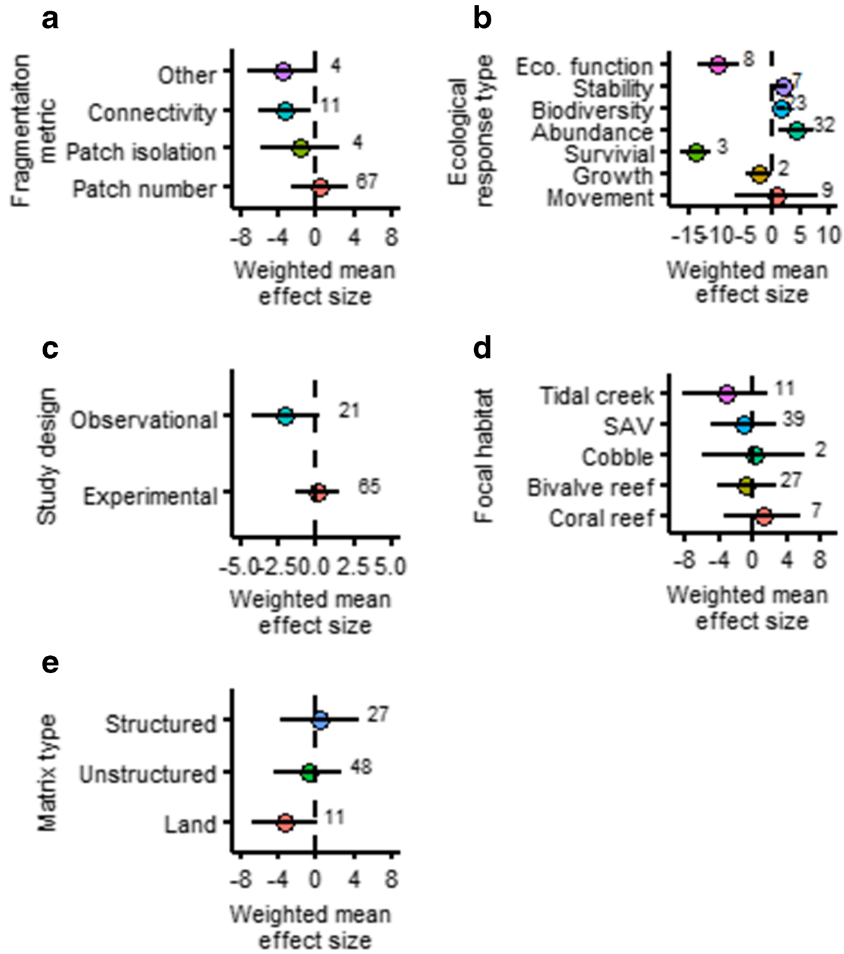


Fig. 2 Count of studies reporting. **a** Non-significant vs. significant effects of habitat fragmentation; **b** of significant effects, those reporting negative vs. positive effects of fragmentation on ecological response variables; and **c** of studies assessing independent effects of habitat fragmentation and habitat area on ecological responses, the relative strength of the two effects. F = habitat fragmentation, A = habitat area, Neither = neither habitat fragmentation, or area were important in predicating the response

Fig. 3 Mean effect size (± 95% CI) derived from meta-analytic mixed effects regression model for groups of studies based on **a** the type of fragmentation metric used, **b** the type of ecological response variable considered, **c** the design of the study, **d** the focal habitat type, **e** the relationship between landscape habitat area and fragmentation (area was held constant among levels or fragmentation or may have varied with fragmentation), and **f** the matrix type. SAV = submerged aquatic vegetation and includes seagrass and macroalgae habitats



sessile taxa had a 95% CI that did not overlap zero, and counter to our hypothesis, this effect was on average positive rather than negative, although the sample size for sessile taxa was small ($n = 4$, Fig. 4a). There were 29 studies for which we could assign a maximum body size to focal taxa. There was a weak negative relationship between species body size and Hedge's *d* predicted by the mixed effects meta-regression model (slope = − 1.1, $Q_m = 17.0$, df = 1, $p < 0.0001$), although

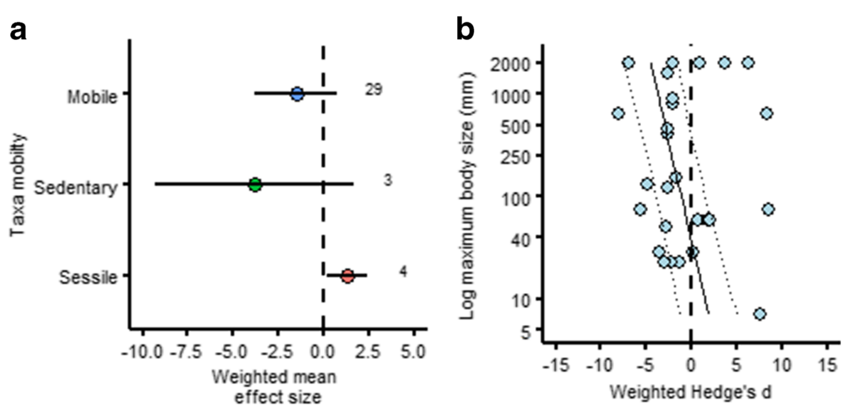


Fig. 4 **a** Mean effect size (± 95% CI) derived from meta-analytic mixed effects regression model for groups of taxa based on post-settlement mobility and **b** relationship between taxa maximum body size and weighted Hedge's d across studies. Solid line in **b** displays predicted effect of body size based on meta-regression model. Dotted lines display the 95% confidence interval around the effect. Note maximum body size was log-transformed prior to analysis and *y*-axis labels were back-transformed to aid in interpretation

the examination of the data did not reveal a strong relationship between the two variables (Fig. 4b).

Test of the Fragmentation Threshold Hypothesis

We found 26 estimates across six articles of habitat fragmentation effects at a similar level of habitat percent cover. There was a marginal negative relationship between the effect size and landscape percent cover (i.e., fragmentation effects were on average more negative when landscape habitat cover was low; Wald $X^2 = 3.34$, df = 1, $P = 0.07$, $R^2_{marginal} = 0.12$; Fig. 5). Although we did not find a clear threshold, most effects of fragmentation from landscapes with under 35% habitat cover were negative (89% of effects were negative, 16/18 studies) while those from landscapes with > 35% habitat cover were more mixed (38% of effects were negative, 3/8 studies).

Discussion

Our literature review and meta-analysis found that the effects of fragmentation were highly variable across marine ecosystems. In contrast to a recent review dominated by terrestrial studies [11••], habitat fragmentation effects were more often negative in our review, although the frequency of significant effects was similar (38% in the current review vs. 30% in [11••]). Surprisingly, we did not find clear evidence that habitat area is a stronger driver of

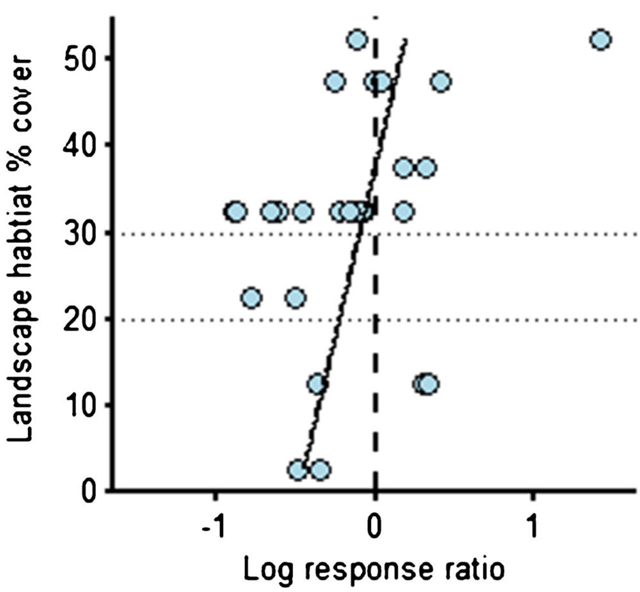


Fig. 5 Relationship with landscape habitat area and observed effect of habitat fragmentation on the predicted response. In this case, the effect size was the Log response ratio. Solid line indicates the predicted relationship between the effect size and landscape percent cover based on the mixed effect model with the random effect excluded. Dotted lines indicate the predicted threshold for an interactive effect based upon the fragmentation threshold hypothesis

ecological responses than habitat fragmentation, although we did not search for studies which varied area alone. Most studies that evaluated both found that neither was important, and habitat fragmentation was more often found to be of greater importance or equal to that of habitat area within the remaining studies. Examining patterns in the mean response across studies varying in design and ecological response variable considered did reveal some sources of variation in the observed effect, which are discussed below.

Although habitat fragmentation has been predicted to have negative effects on biodiversity, we found positive mean effects on organismal abundance, biodiversity, and stability in population size/ecosystem function within marine ecosystems. By decoupling population dynamics in local habitat patches, habitat fragmentation may enhance population stability by reducing extinction risk at the landscape scale through spatial rescue effects [62] or providing structural heterogeneity which stabilizes predator-prey dynamics [63]. As many of the landscapes studied in this review were quite small, however, it seems unlikely that stabilizing mechanisms operating at the meta-population scale for most species would be relevant here. Instead, increasing habitat patchiness may reduce competition among species post-settlement and promote coexistence, especially in diverse ecosystems like coral reefs [39, 40]. Additionally, habitat fragmentation may have positive effects on biodiversity if it serves to enhance habitat heterogeneity across patches and within the matrix, increasing the total diversity of niches available at the landscape scale [64].

Within the meta-analysis, the negative effects of habitat fragmentation within land-matrix types, tidal creek habitats, and when connectivity was the measure of habitat fragmentation came primarily from studies ($n = 20$ studies from articles [37, 60, 61]) conducted within tidal creek ecosystems in The Bahamas fragmented by land bridges/roads. This type of habitat modification resulted in not only the breaking apart of habitat spatially but also reduced hydrologic connectivity. Hydrological connectivity in nearshore ecosystems is vital for maintaining more moderate environmental conditions, preventing the buildup of sediment, and for allowing the free movement of propagules and mobile adult organisms [65]. Thus, it is not surprising that habitat fragmentation that restricts the movement of water could lead to rapid shifts in environmental conditions within remaining fragments. There was one additional set of laboratory studies [43](not included in the meta-analysis because of insufficient data reported) that manipulated connectivity among patches using clear Plexiglas dividers among sediment patches that restricted the movement of organisms but not water flow. Three of the four studies reported in this article found positive effects of fragmentation (i.e., reduced connectivity). These results indicate that habitat fragmentation that restricts water flow may be a major driver of negative habitat fragmentation effects in marine systems.

Study design also appeared to be an important predictor of the strength of the habitat fragmentation effects in our meta-analysis. Notably, many of the marine studies included in our review were experimental and these experimental approaches are ideal for isolating the effects of habitat fragmentation from other factors which may covary with fragmentation in natural landscapes (e.g., habitat area, within patch quality). The mean overall effect for experimental studies was not different from zero, however, while that for observational studies was negative. Landscape sizes for the experimental studies were much smaller than observational ones, which may in part explain the weak effects of habitat fragmentation detected as effects of habitat fragmentation have been shown to be scale-dependent [22]. Diverse response taxa (e.g., fishes, benthic macroinvertebrates) of variable body sizes were included in both experimental and observational studies, thus, it is likely that at least some of the studies were inappropriately scaled to capture landscape-scale responses for focal species. Although there was no relationship between landscape size and effect of habitat fragmentation in our meta-analysis (Pearson's $r = -0.06$, $P = 0.6$), the landscape extents of the majority of the marine studies included in our review were small. Thus, it is not clear whether differences in observational and experimental study results were due to the difference in landscape size or whether other landscape attributes that covaried with habitat fragmentation in natural landscapes were the true drivers of negative responses in ecological variables.

Interestingly, we did find some support for the fragmentation threshold hypothesis as there was a weak negative relationship between the measured effect of habitat fragmentation and habitat percent cover with the effects of habitat fragmentation in landscapes with less than 35% habitat cover being mostly negative. Due in part to the limited sample size, it was not possible to identify a clear threshold from this meta-analysis, but the exact threshold is expected to be higher in some cases and be dependent on the movement ability of focal species [13••]. One article included in this review explicitly tested the fragmentation threshold hypothesis in seagrass habitat and likewise supported the hypothesis [24•]. Studies with increased replication along both habitat area and fragmentation gradients within marine systems may help to elucidate whether such a threshold exists and better inform conservation targets and marine ecosystem management.

Conclusions

This review on habitat fragmentation effects in marine ecosystems is largely consistent with Fahrig's recent review [11••] dominated by terrestrial studies, and lends more evidence to the theory that landscape-scale habitat fragmentation alone does not seem to be consistently "bad" for biodiversity. The exception to this pattern may be when hydrological fragmentation leads to substantial shifts in habitat quality in fragmented landscapes. It was suggested by Fletcher et al. [13••] that Fahrig's review [11••] reporting an overall positive effect of habitat fragmentation may have been biased due in part to narrow search terms used (e.g., "habitat fragmentation per se") and vote-counting technique for synthesis across studies. Our review should not suffer from these same limitations as we used the more general term "habitat fragmentation" in our literature search and we used a meta-analytic technique to increase our statistical power, weighting individual study effects by within-study variance, giving us a more robust estimate of the overall mean effect. Using this approach, we found that the overall effect of fragmentation did not differ from zero, but notably the mean effect was positive when considering organismal abundance and diversity, groupings of the data which had robust sample sizes and replication across systems. In contrast, studies in which response variables measured survival or a type of ecosystem function largely demonstrated negative responses to fragmentation, although low sample sizes within these groups limit the transferability of these observed patterns. The frequent positive effect of habitat fragmentation found at the landscape scale seems to conflict with a review of patch-scale measures of habitat fragmentation reporting consistent negative effect of edge and isolation on biodiversity [66]. A recent review on edge effect in marine ecosystems, however, similarly failed to find a consistent negative effect of habitat edges on ecological response variables [67••]. Future studies employing multi-scale frameworks to assess interactions among fragmentation process across scales may help resolve these patterns and the seeming lack of congruence between patch- and landscape-scale studies.

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Author Contribution Statement Lauren Yeager conceptualized the study. All authors helped to review articles and extract data. Lauren Yeager analyzed the data and wrote the first draft of the manuscript on which all other authors provided feedback.

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Compliance with Ethical Standards

Ethics Statement This article does not contain any studies with human or animal subjects performed by any.
of the authors.

Conflict of Interest Lauren Yeager, Jenelle Estrada, Kylie Holt, Spencer Keyser, and Tobi Oke declare that they have no conflict of interest.

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- • Of importance
- •• Of major importance

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