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Mechanistic support for increased primary production around artificial reefs

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Abstract

Understanding factors controlling primary production is fundamental for the protection, management, and restoration of ecosystems. Tropical seagrass ecosystems are among the most productive ecosystems worldwide, yielding tremendous services for society. Yet they are also among the most impaired from anthropogenic stressors prompting calls for ecosystem-based restoration approaches. Artificial reefs are commonly applied in coastal marine ecosystems to rebuild failing fisheries and have recently gained attention for their potential to promote carbon sequestration. Nutrient hotspots formed via excretion from aggregating fishes have been empirically shown to enhance local primary production around artificial reefs in seagrass systems. Yet, if and how increased local production affects primary production at ecosystem-scale remains unclear, and empirical tests are challenging. We used a spatially explicit individual-based simulation model that combined a data-rich single-nutrient primary production model for seagrass and bioenergetics models for fish to test how aggregating fish on artificial reefs affect seagrass primary production at patch- and ecosystem-scales. Specifically, we tested how the aggregation of fish alters: *(i)* ecosystem seagrass primary production at varying fish densities and levels of ambient nutrient availability and *(ii)* the spatial distribution of seagrass primary production. Comparing model ecosystems with equivalent nutrient levels, we found that when fish aggregate around artificial reefs ecosystem-scale primary production is enhanced synergistically. This synergistic increase in production was caused by non-linear dynamics associated with nutrient uptake and biomass allocation that enhances aboveground primary production more than belowground production. Seagrass production increased near the artificial reef and decreased in areas away from the artificial reef despite marginal reductions in seagrass biomass at the ecosystem level. Our simulation's findings that artificial reefs can increase ecosystem production provide

novel support for artificial reefs in seagrass ecosystems as an effective means to promote: *(i)* fisheries restoration – increased primary production can increase energy input into the food web, and *(ii)* carbon sequestration – via higher rates of primary production. Although our model represents a simplified, closed seagrass system without complex trophic interactions, it nonetheless provides an important first step in quantifying ecosystem-level implications of artificial reefs as a tool for ecological restoration.

Introduction

Predicting ecosystem productivity is a fundamental challenge in ecology and is necessary for effective management of ecosystem services. Essential to this is understanding the controls on primary production as it represents an important ecosystem service in of itself through the sequestration of carbon, and provides the energetic basis for secondary production, e.g., fisheries (Ryther 1969). Coastal marine ecosystems are among the most productive ecosystems on the planet and have long provided an essential source of protein for coastal societies. More recently, coastal ecosystems are being acknowledged for the role they play in carbon sequestration. Mangroves and seagrass beds can sequester more carbon per unit area than any other ecosystem type (Mcleod et al., 2011), though seagrass carbon dynamics are complex and carbon emissions can exceed sequestration under specific conditions (Van Dam et al. 2021). Yet coastal ecosystems are also among the most globally degraded due to habitat degradation, over exploitation, and climate change (Lotze 2006; Halpern et al. 2008; 2012; Sale 2008). Ecosystem-based management approaches (Arkema, Abramson, and Dewsbury 2006), which seek to simultaneously restore coastal ecosystem structure and function are therefore emerging as promising avenues for holistic ecosystem restoration.

Artificial reefs (ARs), defined as structures on the seafloor that mimic some aspect of natural reefs, are widely touted as useful tools for restoring and rebuilding depleted fisheries (Carr and Hixon 1997), and more recently to promote increase carbon sequestration via increased seagrass primary production (Layman and Allgeier 2020) or increased coral growth rates (Allgeier et al., 2020; Shantz et al., 2015). From a more traditional perspective, ARs are a fisheries-centric management tool, and have been widely utilized because they promote dense aggregations of fish

(Bohnsack, Johnson, and Ambrose 1991; Stone et al. 1991; Carr and Hixon 1997; Baine 2001; Seaman 2019). For example, Claisse et al. (2014) demonstrated that abandoned oil rigs off the coast of California have the highest rate of fish production of any system globally. Yet, despite their widespread use, and consistent evidence of high densities of fishes, it remains unresolved whether fish are simply attracted to the ARs or if the ARs increase local fish production. Two hypotheses frame the on-going debate: *(i)* ARs act as attractors of fish, moving fish that already exist in the system to a single location, and therefore potentially increasing the risk of overfishing, or *(ii)* ARs alter ecosystem dynamics such that they facilitate increased secondary production via mechanisms that may not otherwise occur in a structure-free environment (Bohnsack 1989; Grossman, Jones, and Seaman 1997; Wilson et al. 2001; Osenberg 2002; Powers et al. 2003; Sadovy and Domeier 2005). These competing hypotheses, dubbed the "attraction-production debate," have been at the center of decades of research that has largely used population- or community-level measures to quantify secondary production (e.g., Powers et al. 2003; Claisse et al. 2014). However, these methods do not disentangle the mechanisms by which production may be enhanced – either by increasing fishes access to basal resources, or by increasing the basal resources themselves. A complementary approach to understanding the extent to which ARs can enhance local fish production is to quantify if ARs increase the energy base of the local ecosystem via primary production that in turn can support increased production at higher trophic levels (Lindeman 1942; Ryther 1969; Layman and Allgeier 2020). Importantly, this approach also provides additional means to understand how ARs may promote other services such as carbon sequestration.

ARs in shallow seagrass beds (dominated by *Thalassia testudinum*) have been shown to increase localized primary production through fertilization via nutrient excretion from aggregating

fishes (Bohnsack, Johnson, and Ambrose 1991; J.E. Allgeier, Yeager, and Layman 2013; J.E. Allgeier et al. 2018; Layman, Allgeier, and Montaña 2016), similar to consumer-mediated biogeochemical hotspots found in other systems (e.g., McIntyre et al. 2008; Atkinson et al. 2013). The proposed mechanism for increased production is that under ambient, low-nutrient conditions, seagrasses allocate most nutrients and energy to storage in their root structures, whereas, under high levels of enrichment from fish excretion, seagrasses shift resource allocation to aboveground primary production (Layman, Allgeier, and Montaña 2016). This allocation mechanism is also common among terrestrial plants (Chapin 1980; Shipley and Meziane 2002; Poorter et al. 2012), and has been demonstrated empirically in seagrass beds where local seagrass production adjacent to an AR with aggregating fish was shown to have enhanced seagrass growth rates ~200% higher than nonadjacent seagrass (J.E. Allgeier, Yeager, and Layman 2013). Because ambient nutrients must exceed a certain threshold to trigger aboveground production, this proposed mechanism also suggests that the loss of fishes from the open seagrass bed will not result in subsequent reductions of seagrass production because fishes in the open seagrass do not aggregate in densities sufficient to sustain prolonged increases in nutrient availability and thus production. While this mechanism has been empirically supported through increased local production relative to production in open seagrass beds (J.E. Allgeier, Yeager, and Layman 2013; J.E. Allgeier et al. 2018; Layman, Allgeier, and Montaña 2016), discerning if total ecosystem production is enhanced due to the attraction of fishes remains challenging because it must be demonstrated that production is not declining in areas peripheral to the artificial structures.

Here we create a model seagrass ecosystem to explicitly test the mechanisms by which ARs increase seagrass primary production around the AR, and at the scale of the entire ecosystem. To do so, we use an individual-based simulation framework that couples a single-nutrient primary

production model (DeAngelis 1992) and a fish bioenergetics model (Hanson et al. 1997; Deslauriers et al. 2017). The model is parameterized by substantial empirical data from ARs constructed in shallow seagrass beds in The Bahamas (J.E. Allgeier, Yeager, and Layman 2013; J.E. Allgeier et al. 2018; Layman et al. 2013; Layman, Allgeier, and Montaña 2016), and fish energetics of common species found on ARs in this region (J.E. Allgeier et al. 2015; 2020). We test whether increased production is possible at both the patch and ecosystem-scales by answering two interrelated questions:

1) How do varying fish densities and initial seagrass biomass impact aboveground and belowground seagrass production in a system with or without an AR?

2) How do aggregating fishes alter both the levels and spatial distribution of seagrass production around the AR?

We address these questions by running simulations and altering three model components: *(i)* fish movement behavior, i.e., fish are either attracted to the AR or move randomly about the model environment *(ii)* the number of fish within the system, i.e., fish population size, and *(iii)* the initial seagrass biomass capacities in the system. Our model represents a simplified seagrass ecosystem in which the model environment is closed to maintain equal nutrient levels across simulations. This allows us to isolate the importance of ARs and fish aggregation for ecosystem primary production. Additionally, the model does not incorporate fish population dynamics or complex trophic dynamics. While these simplifications mean that our model does not precisely represent the reality of these complex ecosystems, they allowed us to specifically test for mechanisms by which fish aggregations may or may not alter primary production around artificial reefs.

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Methods

Our description of the individual-based simulation model (IBM) follows the Overview, Design, and Details (ODD) protocol (Grimm et al. 2020) and includes (denoted by subheadings below): a description of the general model purpose, state variables and scales, an overview of all processes and their scheduling (Figure 1), details about the design concept, a detailed description of all processes, and parametrization and initialization of the individual-based model.

General Model Purpose

We used an individual-based simulation model (DeAngelis and Grimm 2014) to understand the influence of fish aggregations around a single AR on standing seagrass biomass and production (both above- and belowground; AG and BG). The model environment simulates a shallow seagrass bed (~3m depth), similar to those of previous empirical studies (J.E. Allgeier, Yeager, and Layman 2013; J.E. Allgeier et al. 2018; Layman et al. 2013; Layman, Allgeier, and Montaña 2016). Seagrass production is based on a single nutrient primary production model following DeAngelis (1992; detailed below). The primary production model allows seagrass to slough (or lose) biomass, take up nutrients from the water column, and grow biomass (in both the AG and BG tissues). The seagrass bed is populated with a single species of fish parameterized to resemble *Haemulon plumerii*, an abundant and common generalist species that are common throughout shallow coastal ecosystems in the Caribbean and that are frequently found to aggregate on ARs (Appeldoorn et al. 2009). In the IBM, fish movement, consumption of biomass, and excretion of nutrients, is governed by principles of bioenergetics (Deslauriers et al. 2017; Hanson et al. 1997; Schreck and Moyle 1990; detailed below). Fish individuals perform two primary processes within our model: (*i*) they acquire nutrients through feeding, and (*ii*) they supply and move nutrients in the system

through excretion. Fish movement is simulated such that they either move randomly throughout the model environment, functioning as our control scenario by simulating no influence of the AR (herein *random movement scenario*) or are attracted towards and thus aggregate around the AR (herein *attracted movement scenario*). We did not incorporate any fish population dynamics or secondary production because we were primarily interested in testing the implications of ARs for primary production in the model environment. Thus, processes like mortality were simulated to maintain relatively consistent fish population size and body size distribution through time while allowing fish to grow according to their bioenergetics. In sum, this IBM framework allowed us to specifically test the influence of two treatments on primary production at the patch and ecosystem-scale: (*i*) a continuous treatment of fish population size (herein *fish density treatment*), and *(ii)* a continuous treatment of different initial biomass values (herein *biomass capacity treatment*) under the *random movement* and *attracted movement scenario* to test the importance of fish aggregations around ARs.

The model was constructed and analyzed in R programming language (R Core Team 2019). Model code and analysis scripts can be found *https://doi.org/10.5281/zenodo.5889083* and *https://doi.org/10.5281/zenodo.5847402,* respectively.

<u>*State variables and scales*</u>

The seagrass bed model environment is simulated using a 100 x 100 cell grid (spatial extent) with a cell resolution of 1 x 1 m (spatial grain). Each grid cell contains seagrass biomass (separated into AG and BG), the water column nutrients pool, and detrital biomass. Fish individuals are described by their location (x-, and y-coordinates), body dimensions (length and weight), and nutrient reserves stored in their body. The x- and y-location of each fish individual allows us to

place each individual within a single cell, however several individuals can be present in a cell at the same time.

The IBM simulates most processes every 120 minutes (1 iterations; temporal grain) for a total of 50 years (219000 iterations; temporal extent). All seagrass related processes (Processes (1) and (2) below) were simulated every 24 hours (i.e., 12 iterations). The temporal extent of 50 years was chosen because it represents sufficient time beyond which no major changes of the overall system were observed.

Process overview and scheduling

All processes are simulated in the model in the following order (Figure 1): (*1*) A fraction of the standing biomass sloughs to the detrital biomass – the exact amount is determined by the size of seagrass at that time step relative to minimum and maximum biomass values. Nutrient uptake is then calculated based on Michaelis-Menten uptake dynamics using seagrass biomass (post slough) and the concentration of available nutrients in the water column and nutrients are allocated as either BG or AG biomass; (*2*) A fraction of the total sloughed detrital biomass remineralizes to water column nutrients and biomass of dead fish individuals decomposes to the detrital biomass. (*3*) Fish individuals move around the seagrass bed. For the *random movement scenario*, the direction of movement is completely random and for the *attracted movement scenario*, fish individuals tend to move towards the AR; (*4*) A bioenergetics model is used to calculate respiration for fish individuals based on: water temperature (homogenous in model environment), body mass, and movement activity; (*5*) The energetic demand for growth is calculated based on demands for respiration, and fish individuals consume detrital biomass according to this demand, resulting in body mass accumulation (growth). During consumption and subsequent growth, fish individuals also excrete nutrients on the grid cell they occupy. If the available detrital biomass (the energetic

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resource for fishes in our model environment) is less than energetic demand for growth and fish individuals do not have sufficient stored energetic reserves the fish individuals die and the biomass of dead individuals is added to the fish detrital biomass; (*6*) Background mortality occurs whereby the probability of dying increased with increasing body mass (biomass of dead individuals is added to the fish detrital biomass as well); (*7*) Lastly, nutrients and detrital biomass diffuse among neighboring grid cells.

Design concept

The IBM design allowed us to track standing seagrass biomass and seagrass production (our two primary response variables), the water column nutrient pool, and detrital biomass in a spatially explicit manner across the whole model environment. Characteristics of the fish individuals were also tracked including body length and mass, mortality, and spatial location within the model environment. Fish individuals do not interact with each other. For the *attracted movement scenario*, fish individuals are "aware" of the distance to the AR in their direct surrounding and minimized this distance. While most processes are deterministic after the initialization of the model environment, the fish movement (Process (3) above) and background mortality (Process (6) above) include stochasticity, i.e., distances and directions are sampled from log normal and uniform distributions, respectively, for fish movement, and background mortality is based on a body-size dependent mortality probability.

Processes

The formulas and parameters, including references, of all processes can be found in Table 1 and Table 2, respectively. Starting parameter values for simulations are reported in Table 3.

(1) Seagrass primary production: Seagrass primary production is determined using a single-nutrient, autotrophic model and included three subprocesses: biomass slough, nutrient uptake, and plant growth.

(1.a) Biomass slough: Sloughed biomass (S_i) represents the proportion ($\alpha_i; 0 < \alpha_i < 1$) of BG and AG biomass sloughed at each iteration (Table 1, Formula 1.1). A modifier (β_i; Table 1, Formula 1.2) decreases the fraction α_i as the biomass approaches the minimum possible biomass, allowing the plant to grow more by sloughing less. In contrast, the modifier (β_i) increases as biomass approaches the maximum possible biomass, thus increasing slough and stabilizing biomass to be maintained roughly at its maximum under high nutrient conditions. Sloughed biomass is added to the detrital biomass (D) in each iteration (Table 1, Formula 1.3).

(1.b) Nutrient uptake: Nutrient uptake from the water column follows Michaelis-Menten uptake dynamics and occurs in belowground- and aboveground biomass (B_{BG}; B_{AG}) separately as a function of total plant biomass and water column nutrient availability (N; Table 1, Formula 1.4). The sum of AG and BG uptake (total nutrient uptake; U_{total}) is removed from the water column nutrients in each iteration (Table 1, Formula 1.5).

(1.c) Plant growth: Plant growth is determined by converting the total uptake to biomass using the nitrogen content (percent dry weight) of belowground and aboveground biomass. Nutrient allocation to growth follows basic plant allocation rules such that maintaining BG biomass is prioritized over AG biomass (Appendix S1: Figure S1, S2). Specifically, if total nutrient uptake (converted to biomass equivalent using the nutrient content percent per dry weight) is smaller than

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the sloughed BG biomass, all nutrients are allocated to BG biomass to minimize BG biomass loss (Table 1, Formula 1.6). If the total nutrient uptake is larger than the sloughed BG biomass, BG biomass is kept stable by allocating nutrients equivalent to the sloughed biomass. The remaining uptake has two fates: *(i)* if it is smaller than the sloughed AG biomass, all remaining nutrients are allocated to the AG biomass to minimize AG biomass loss (Table 1, Formula 1.6), *(ii)* if it is larger than the sloughed AG biomass, biomass is kept stable by allocating nutrients equivalent to the sloughed biomass. Finally, if any nutrients from uptake remain, they are shared between BG and AG biomass (Table 1, Formula 1.7, 1.8) based on a predetermined sigmoid function (described by a slope m and midpoint τ; Table 1, Formula 1.7, Appendix S1: Figure S2) that determines the ratios of the remaining nutrients allocated in AG or BG biomass (δ_{BG}). Lastly, if the biomass of either AG or BG exceeds the maximum biomass in a cell after the nutrient allocation, it is reduced back to the maximum biomass value (B_i^{max}) and the excess is added to the sloughed biomass.

(2) Remineralization: A proportion ($\epsilon_i; 0 < \epsilon_i < 1$) of detrital biomass ($D$) is remineralized and added to the nutrients pool (N) each iteration (Table 1, Formula 2.1). Also, a fraction of the fish detrital biomass (D_{fish}) is decomposed and added to the detrital biomass each iteration (Table 1, Formula 2.2).

(3) Fish movement: Fish movement is based on randomly generated values for movement distance and direction. For each fish individual at each iteration, a distance is sampled from a log-normal distribution (with a mean λ and standard deviation σ), and a direction is sampled from a uniform distribution with a range of 0°-360°. In the *attracted movement scenario,* fish individuals perceive the relative distance to the AR and always move towards the AR as is determined by the shortest

distance based on one of three directions of movement from their current orientation (-45°,0° and 45°). Because the direction in which fish individuals move depends on the original random orientation, they do not move straight towards the AR, but nevertheless are attracted towards the general orientation of the AR (Appendix S1: Figure S3). If an individual fish moves outside the model environment, it enters it on the opposite side again ("torus translation"). How far a fish individual moves in each iteration in relation to the maximum possible travel distance is used to calculate the movement activity, which in turn is used to calculate respiration in the bioenergetics model. The maximum possible travel distance was determined by sampling 1,000,000 values from the corresponding log-normal distribution and setting the 95% percentile as maximum travel distance.

(4) Fish respiration: Respiration (*R*), following assumptions of fish bioenergetics, depends on the water temperature and movement activity by fish individuals (Table 1, Formula 4.1, 4.2, 4.3, 4.4):

(5) Fish consumption, growth, and mortality: Fish individuals grow in body length (*G*) at every iteration governed by the von Bertalanffy growth curve (Table 1, Formula 5.1). Length is then converted to weight using species-specific parameters *a* and *b* (Table 1, Formula 5.2). The amount that a fish must consume (*C*) to maintain energetic mass balance per iteration is then determined by back-calculating the consumption required to meet the demand for growth (Table 1, Formula 5.3). Fish individuals feed directly from the detrital biomass (converted to nutrients) of the grid cell they are located in. If there is more than sufficient detrital biomass available, fish consumed up to 5% of body mass extra nutrients and stored these nutrients as a nutrient "reserve" that could be used in situations in which fishes did not encounter sufficient detrital biomass in a

given cell. This reserve capacity is consistent with fish foraging behavior (Armstrong and Schindler 2011). Once a fish has consumed its required nutrients from the detrital biomass, excretion is calculated as the remaining nutrients assimilated but not used for other processes (Table 1, Formula 5.4) and fish individuals excrete nutrients in the grid cell they are located in. If a fish individual cannot meet its requirements from the detrital biomass or its reserves, it dies (herein "consumption mortality"; for more details on mortality see Process (6)).

We acknowledge that the feeding directly from the detrital pool is an oversimplification but given that primary production is the energetic base of these food webs (Ryther 1969), and quantifying secondary production is not a goal of our study, we opted for the most simplistic trophic interactions possible that would still allow us to test our underlying questions.

(6) Fish background mortality: In addition to consumption mortality, fish individuals can also die through aging, which is determined by a mortality probability that increases as individuals get closer to their maximum mass (Table 1, Formula 5.5). When a fish individual dies, its nutrients are initially fed into a separate detrital biomass pool (D_{fish}), which allows these nutrients to diffuse through the environment before entering the regular detrital biomass through decomposition (Table 1, Formula 2.2), thus preventing large nutrient pulses in the grid cell on which they died. Lastly, after a fish individual dies, a new individual is created with the same initial body size as the recently dead fish individual at the beginning of its life span. The mortality probability is low, especially for smaller individuals. The main purpose of the background mortality is to maintain a relatively consistent fish population size and body size distribution rather than simulating fish population dynamics.

(7) Diffusion: Diffusion of nutrients and detrital biomass occurs throughout the model environment at every iteration. Diffusion occurs by each grid cell sharing a proportion of the nutrients and detrital biomass with the surrounding eight grid cells equally.

Parametrization and Initialization

The model is constructed to simulate a shallow seagrass bed (~3 m depth) in The Bahamas, or any comparable subtropical or tropical seagrass ecosystems dominated by *T. testudinum*. The model was parameterized with data from over a decade of research in Bahamian seagrass ecosystems, and primarily from a single embayment (The Bight of Old Robinson, Abaco Island; Table 1).

All seagrass processes were parameterized for a single seagrass species, *T. testudinum*. The species accounts for a majority of the aboveground biomass in seagrass beds of the Caribbean (Buesa 1974; Heck 1979), and, in particular, The Bahamas (Buchan 2000). Even though the model was designed to be flexible as to which nutrient drives production dynamics, processes are parameterized based on nitrogen (N) dynamics in the system. In order to use representative values for the minimum and maximum belowground- and aboveground seagrass biomass, we pooled several datasets (J.E. Allgeier, Yeager, and Layman 2013; J.E. Allgeier et al. 2018; Layman, Allgeier, and Montaña 2016, Shayka unpublished). In cases where parameters were not available from previous research from the authors, we used literature values from studies in comparable systems. For example, the most important literature-derived parameters were for seagrass AG and BG uptake dynamics (Michaelis-Menten), which were generated from a study of *T. testudinum* in the Gulf of Mexico (Lee and Dunton 1999). Parameters for which no literature values were available (α_i; ϵ_i; τ; m) were determined by running the IBM systematically for a range of values and eliminating all values that led to unrealistic results. For all fish growth processes using, we

used values from Fishbase (Froese and Pauly 2019) and previously published research from this same Bahamian ecosystem (J.E. Allgeier, Yeager, and Layman 2013; J.E. Allgeier et al. 2015) for *H. plumerii.*

The initialization of AG and BG biomass were part of the simulation study (see Simulation experiment). The water column nutrient pool and detrital biomass were initialized at levels that were predetermined to maintain stable biomass of AG and BG biomass without fish in the model environment (i.e., growth equaled slough). Initial individual fish length was simulated randomly using a log-normal distribution. All temperature dependent processes operated at 26 °C, the approximate annual average water temperature in the Bight of Old Robinson, The Bahamas (Allgeier *unpublished*).

Sensitivity analysis

Sensitivity analysis explores how changes of model parameters result in changes of the model output and thus give insights into the importance of parameters (Pianosi et al. 2016; Thiele, Kurth, and Grimm 2014). First, we used a local, one-at-a-time sensitivity analysis in which each parameter was decreased and increased individually by 5% and 10%, respectively, and the BG and AG standing biomass and production were then compared to the unchanged parameters. For each changed parameter, we ran the model 25 times. Second, we ran a Sobol global sensitivity analysis (Sobol et al., 2007) using all parameters for which the relative output from the one-at-a-time analysis exceeded 5% change in relation to the unchanged parameters. This second test allowed us to explore interactions between parameters and the parameter space by using Latin hypercube sampling (n = 250 McKay, Beckman, and Conover 1979). For each parameter, the Sobol method generates a main effect S_i and total effect S_{Ti} (main effect and interaction effect). While the sum

of all main effects cannot exceed one ($S_i \leq 1$), the sum of total effects can be greater than one ($S_{Ti} > 1$) if interactions between parameters are present.

The midpoint τ of the sigmoid function that determines how nutrients are shared between BG and AG biomass is a key parameter of the IBM (Appendix S1: Figure S2). Thus, to determine whether τ heavily impacts the results, we ran the model for two additional values of $\tau = \frac{1}{2}$ (Appendix S1: Figure S5) and $\tau = \frac{2}{3}$ (Appendix S1: Figure S6).

Simulation experiment

To test how the AR influences BG and AG seagrass primary production and biomass, we compared outcomes from models under two fish-behavior scenarios: *(i)* fish moved randomly about the model environment (*random movement scenario*), and *(ii)* fish were attracted to the AR (*attracted movement scenario)*. Under each fish behavior scenario, we included two additional factorial treatments: (*i*) *fish density treatment* – fish population sizes were either 1, 2, 4, 8, 16, or 32 individuals, and (*ii*) initial seagrass *biomass capacity treatment* – models were initialized under conditions in which both the AG and BG biomass started at either 25%, 50%, or 75% of their maximum capacity. Variation in fish densities allowed us to test how the absolute number of fish, and thus amount of excretion in the system, would affect primary production. Because the water column nutrient pool was initialized at levels that maintain table AG and BG biomasses, variation in initial seagrass biomass capacity allowed us to test how the initial water column nutrient pool of the system affected primary production. Fish densities were chosen to reflect a broad range of densities that occur in seagrass ecosystems throughout The Bahamas (J.E. Allgeier et al. 2015). For each combination of the two treatments (36 total), separate fish behavior scenarios (*random*

movement or *attracted movement scenario*) were simulated 25 times to capture the effects of stochasticity in the model.

We used log response ratios (RR; Hedges, Gurevitch, and Curtis 1999) to evaluate the model outcomes between the *rand movement* and *attracted movement scenario* under all combinations of the two treatments (*fish density* and *biomass capacity treatment*). The log response ratio describes the proportional effect of an experimental scenario (here the *attracted movement scenario*) in comparison to a control (here the *random movement scenario*) $RR = \log(x_{attraction}) - \log(x_{random})$. To calculate uncertainties related to the *RR* we used bootstrapping to generate 95% confidence intervals (CI; 1000 bootstrap replicates; Efron and Tibshirani 1986) using the *boot* packages in R (Davison and Hinkley 1997), whereby $RR > 0$ indicates a positive effect of the experimental scenario (i.e., *attracted movement scenario*), $RR < 0$ indicates a negative effect, and statistical significance is indicated when the 95% CIs do not overlap zero.

Results

Sensitivity analysis

The local, one-at-a-time sensitivity analysis showed that AG and BG production were sensitive to nine and two parameters, respectively, whereby a relative increase or decrease of 5% and 10% resulted in relative changes in aboveground production larger than 5%. AG and BG biomass showed a relative change of model output of more than 5% for one parameter each (Appendix S1: Table S1).

The Sobol sensitivity analysis revealed no strong interactions between the 12 sensitive parameters of the local, one-at-a-time analysis as shown by total effects S_{Ti} being not larger than

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the main effects S_i. The AG biomass was primarily sensitive to the maximum AG and BG biomass. AG production was mainly sensitive to parameters related to fish consumption and growth processes: the length-weight relationship parameters and the maximum fish length. BG biomass was most sensitive to maximum BG biomass and to a lesser degree was sensitive to the length-weight relationship parameters and the maximum fish length. BG production was sensitive to just two parameters: the maximum BG biomass and to a much lesser degree to the slough proportion (Appendix S1: Figure S4).

In general, results were similar for the two midpoint τ parameter values $\tau = \frac{1}{2}$ (Appendix S1: Figure S6) and $\tau = \frac{2}{3}$ (Appendix S1: Figure S7), particularly with respect to the patterns across all treatments. However, with increasing τ (i.e., higher BG biomass is required before AG receives a greater proportion of the excess nutrients taken up from the water column), the *RR* for AG production also increased. Simultaneously, also the relative decrease of BG production for the *attracted movement scenario* increased. Thus, the increase in total production decreased as well.

Comparisons between model environments for random movement and attracted movement scenario

Under the *random movement scenario* (which we consider our control treatment), fish excretion was randomly distributed throughout the simulation environment, while for *attracted movement scenario*, excretion was greater in cells near the AR creating a biogeochemical hotspot (Appendix S1: Figure S3). In all cases higher fish densities resulted in greater amounts of nutrient excretion in the model environment. The total fish biomasses and total excretion amount was comparable between the *random movement* and *attracted movement scenario* across all *fish density*

and *biomass capacity treatments* (Figure 2). However, there were two exceptions: (*i*) for low seagrass biomass capacity (25%) and, (*ii*) for the highest fish densities (16, 32 individuals), for which nutrient excretion was significantly lower in the *random movement scenario* due to an increased mortality driven by less available detrital biomass. This increased mortality was not present for the *attracted movement scenario* because the increase in seagrass production from aggregated fish excretion and resultant increases in sloughed detrital material near the artificial reef exceeded the increased demand in fish consumption from the higher fish densities.

How do varying fish densities, and initial seagrass biomass capacity impact total aboveground and belowground seagrass biomass and production?

The *attracted movement scenario* decreased the standing AG biomass relative to the *random movement scenario* for almost all *fish density* and *biomass capacity treatments* (*RR* < 0; Figure 3, Appendix S1: Table S2) with exception of the fish densities with 1 fish individual and initial biomass capacities of 25% or 50%. For lower fish densities (2, 4 fish individuals), the standing AG biomass decreased only marginally. For higher fish densities (8, 16, 32 fish individuals), standing AG biomass decreased for all biomass capacities and differences were more pronounced.

Standing BG biomass was less influenced by the different movement scenarios (*RR* < 0, Figure 3, Appendix S1: Table S2). The relative decrease in standing BG biomass was minimal for all *biomass capacity treatments*. Because BG biomass exceeded AG biomass by roughly two orders of magnitude, total biomass (AG + BG) was primarily driven by BG biomass with only minor decreases for 1,2, and 4 individuals and slightly higher decreases for 8, 16, and 32 individuals for the *attracted movement scenario*.

In contrast to standing biomass, AG production increased under the *attracted movement scenario* for all fish densities ($RR > 0$, Figure 3, Appendix S1: Table S2). The relative increase in production increased especially for fish densities of 16 or more individuals and low initial biomass capacities. Generally, the relative change was higher for low initial biomass capacities and high fish densities.

Belowground production decreased in the *attracted movement scenario* for almost all *fish density* and *biomass capacity treatments* ($RR < 0$; Figure 3, Appendix S1: Table S2). The decrease was far less pronounced than the increase in aboveground production - never exceeding -6%. Total production (AG + BG) largely reflected BG production at lower fish densities but reflected AG production at higher fish densities. The ecosystem-level increase in total production in the *attracted movement scenario* is synergistic because, despite having the same total nutrients within the system as the *random movement scenarios*, the aggregating behavior of the fish promoted non-linear dynamics that allowed aboveground production to increase disproportionately relative to belowground production – thus generating a net increase in production at the ecosystem-scale. This contrast to the alternative outcome not supported by our study whereby by changing the availability of nutrients around the AR, seagrass production would have simply been reallocated spatially, but would not have changed at the ecosystem-scale.

How does the presence of an AR alter both the levels and spatial distribution of seagrass production around the AR?

For the *attracted movement scenario,* increased production was highest near the AR and decreased with distance from the AR for both AG and BG production (Figure 4). This trend was more pronounced for AG production and high *fish density treatments* (8, 16, 32 individuals). For cells further from the AR (> 30 m) the AR either had no influence or decreased production

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regardless of the fish density. Standing AG biomass followed similar trends as AG production (Appendix S1: Figure S5).

Within 3 m of the AR, mean AG production per m^2 increased by 325% (for 1 individual) up to 18996% (for 32 individuals), thus near the AR production was increased for all *fish density* and *biomass capacity treatments* under the *attracted movement* relative to the *random movement scenario* (Appendix S1: Table S3). Similarly, BG production per m^2 within 3 m of the AR was increased under the *attracted movement* relative to the *random movement scenario* for all *fish density* and *biomass capacity treatments*. Values ranged between 8% (1 individual) to 456% (32 individuals).

At the same time, mean AG production per m^2 30 m away from the AR decreased under the *attracted movement* compared to the *random movement scenario* with values ranging from -87% for 32 individuals to -9% for 1 individual (Appendix S1: Table S3). There were also decreases of BG production 30 m^2 away from the AR under the *attracted movement scenario*, however, to a lesser degree with a maximum decrease of -41% for 32 individuals and no relative change for 1 individual.

Differences in standing biomass under the *random movement* and the *attracted movement scenario* followed similar trends as production for both AG and BG (Appendix S1: Table S3). Within 3 m of the AR, both AG and BG biomass was increased, whereas increases were more pronounced for AG than for BG biomass. Simultaneously, 30 m away from the AR, both AG and BG biomass decreased under the *attracted movement scenario*. However, biomass increases close to the AR under *attracted movement scenario* close to the AR were less pronounced than production increases.

Discussion

Our study shows that by initiating aggregating behavior of fish and thus a biogeochemical hotspot, artificial reefs (ARs) can synergistically enhance total ecosystem primary production, but not necessarily total standing seagrass biomass, in a closed seagrass ecosystem. This finding contrasts the alternative, whereby the aggregating behavior and ensuing biogeochemical hotspot would have simply reallocated primary production with no net change in ecosystem-level primary production. Importantly, because we tested our hypotheses in closed systems, and the amount of total nutrients were identical across *random movement* and *attracted movement scenarios*, we can specifically identify the aggregation behavior of the fish around the AR as the primary driver of increased ecosystem primary production. However, the ultimate mechanisms that underpin the synergistic increase in production are associated with how nutrients are allocated to AG and BG biomass under increasing nutrient availability, and the underlying non-linear dynamics of the nutrient uptake and allocation thresholds that drive production. While our individual-based simulation model does not account for real-world trophic dynamics and does not quantify secondary production, it is mechanistic, structurally realistic, and spatially explicit (Grimm et al. 2005) thus allowing us to disentangle the complex dynamics that lead to the synergistic primary production we found. As such, our findings provide novel evidence that ARs (within the bounds of the environment in which we model them) can enhance production via previously unrecognized bottom-up mechanisms, and therefore may be a useful tool for ecosystem-based conservation efforts targeting both fisheries and carbon sequestration in tropical coastal ecosystems.

The two primary mechanisms that lead to synergistic ecosystem production are: (*i*) nutrient allocation rules for BG and AG production, and (*ii*) non-linear dynamics associated with nutrient uptake rates, and sloughing, largely in the AG biomass. Under the *attracted movement scenario*,

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fish redistribute and concentrate nutrients by forming a biogeochemical hotspot around the AR. In nutrient-poor environments, seagrass, like most plants, prioritize BG production because this represents a more stable, long-term investment (Chapin 1980). As such, under conditions in which fish are not aggregating around the AR, nutrient availability is low enough such that BG growth is always prioritized (Layman, Allgeier, and Montaña 2016). For this reason, we see a slight reduction in BG production when fish aggregate around the AR (especially at higher fish densities), because the loss of fish from the open seagrass reduces the availability of nutrients for BG production in this part of the model environment. However, when environmental availability of nutrients becomes greater, seagrasses shift allocation from BG to AG production (Appendix S1: Figure S1). Therefore, the biogeochemical hotspot that results from fish aggregation around the AR ultimately drives a shift in nutrient allocation to AG production. Yet, under circumstances where all dynamics are linear and similar between AG an BG processes, seagrasses would simply reallocate (additively) where production was occurring both spatially within the model environment and within the seagrass itself (i.e., to AG production), and the expectation would be no net change to ecosystem-level production. However, nutrient uptake rates in AG biomass are both greater, and more non-linear than in BG biomass (Lee and Dunton 1999), such that, when allocation of nutrients shifts to promote aboveground production (i.e., when fish are aggregating around the AR), AG biomass can take up more nutrients per incremental increase in nutrient availability. Greater uptake rates lead to increased primary production. Further, the rate of sloughed biomass increases non-linearly per unit biomass such that with greater biomass, there is proportionally more slough, which means greater biomass turnover, and thus greater production. Thus, the shift from BG to AG production and the fact that AG biomass, relative to BG biomass, can essentially have higher rates of biomass turnover per unit nutrient are the features of

T. testudinum dominated seagrass ecosystems that enable higher ecosystem production despite no change in absolute ecosystem nutrients – i.e., a synergistic ecosystem-level effect.

Another important outcome of our model is that despite the ecosystem-level increase in primary production, we found that standing AG and BG biomass both decrease marginally at the ecosystem level. This decrease is in part due to the abovementioned turnover that is heightened near the reef which keeps standing biomass relatively low at any given time, along with the spatial composition and configuration of the model environment whereby there is simply more seagrass that is non-adjacent to the AR, than near the reef. While all patches are visited equally by fish in the *random movement scenario*, patches further away from the reef are seldomly visited in the *attracted movement scenario* (Appendix S1: Figure S2). In patches near the reef, we see significant increases in both AG and BG biomass, and for patches further from the reef, we generally see relatively smaller decreases (Figure 4). However, because there are more patches that experience these marginal decreases, the net effect at the ecosystem scale is a decrease in biomass.

The fact that our model environment is closed is particularly relevant to the changes we found in both AG and BG biomass. In a closed environment, if fish are attracted to the AR the open seagrass becomes relatively void of nutrient input beyond what is remineralized from the detrital biomass. This is in sharp contrast to real-world seagrass ecosystems that are open and receive exogenous nutrient inputs from oceanic and terrestrial sources (Boyer et al., 2006) that can replenish nutrients as they are lost from the system. Therefore, if we open our model environment (i.e., to have exogenous inputs and losses to and from the whole model environment), exogenous nutrients to the system could, to some extent, mitigate this loss of fish individuals in the open seagrass. Further, opening the model environment and incorporating factors such as water currents at varying velocity could allow us to test the relative importance of nutrient redistribution and

concentration by fish individuals relative to exogenous nutrients. While we acknowledge the closed nature of our model environment is unrealistic (and that there are myriad other factors we did not include in our model – e.g., currents, AR location, AR size, etc.), the simplicity was intentional because it allowed us to hold absolute ecosystem nutrient concentrations constant among fish movement scenarios and thus was the most effective way to isolate the importance of the fish-mediated biogeochemical hotspot for ecosystem primary production.

Ecosystem-based restoration and management is gaining substantial traction as an effective conservation strategy because of the increasing need restore multiple ecosystem functions in the face of increased and simultaneous anthropogenic stressors (Smith et al. 2007; Holsman et al. 2020; Howell et al. 2021). Our findings have important implications for the use of ARs towards this end. ARs have long been touted as a potential tool to augment failing fisheries, but their application has been mired by concerns about whether they are simply attracting fishes, or actually increasing fish productivity – the attraction-production debate (Pickering and Whitmarsh 1997). While our models do not quantify secondary production, our results still provide good evidence that through bottom-up mechanisms, ARs should facilitate enhanced fish production in seagrass beds. Specifically, increased primary production will also facilitate increased secondary production via the increased energetic base of the whole ecosystem (Ryther 1969). Importantly, our findings of increased total primary production also suggest that ARs may be useful to help promote carbon sequestration because of the increased demand for C in photosynthesis. Interestingly, while heighted total primary production should increase the amount of C taken up by plants, it is the burial of the C in sediments, which occurs at the root-sediment interface, that is most important for mitigating climate change (Kennedy et al. 2010; Fourqurean et al. 2012; Marbà et al. 2015). In this sense, because we did find a slight reduction in BG production in the open

seagrass (non-adjacent to the reef), this indicates there could also be tradeoffs associated with ARs. However, without having simulated an open ecosystem, the extent to which this is ultimately a tradeoff or not, is difficult to discern. Nonetheless, the finding of a synergistic increase to total ecosystem primary production is encouraging for the application of ARs as a tool for conservation, but the extent to which this may occur requires further investigation.

We acknowledge that our model is an oversimplistic representation of a seagrass ecosystem. Besides being a closed system, there are three primary ways our model deviates from the real-world. First, the seagrass community in our model environment is exclusively one species – *T. testudinum*. This species makes up the vast majority of biomass in Caribbean seagrass ecosystems (E. P. Green and Short 2003), and in particular The Bahamas (J.E. Allgeier, Yeager, and Layman 2013; J.E. Allgeier et al. 2018), but two other seagrass species and dozens of macroalgae species also thrive in these environments. While we acknowledge that these species could respond differentially to increased nutrients from aggregating fish, empirical evidence from Allgeier et al. (2018) showed that AR reduced seagrass community diversity and increased the dominance of *T. testudinum*, thus suggesting that the physiological mechanism of *T. testudinum* that lead to increased ecosystem production in our model environment are also likely occurring in the real world. Second, the movement behavior of the fish in our model is very simplistic (Watkins and Rose 2013). Because the simple aggregation of fish leads to increased production, we also expect fish movement behavior, both among- (A. L. Green et al. 2015; J.E. Allgeier, Adam, and Burkepile 2017) and within species (J.E. Allgeier et al. 2020) to have important ramifications for nutrient dynamics in these ecosystems. Future research should seek to test the importance of different fish behaviors. A third limitation of our model is that it does not generate estimates of secondary production or associated dynamics such as herbivory from fish and their prey. To do so

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would require integrating fish and invertebrate population dynamics, their foraging behaviors, and their predator-prey interactions. Spatial dynamics of fishes could also be important in translocating nutrients both into and out of the modeled environment via movement (Harborne et al., 2017; Williams et al., 2018) or larvae (Allgeier et al., 2018). Currently, recruitment and mortality processes only ensure that total fish biomass is maintained throughout model runs, occluding the ability to realistically estimate secondary production. Further, in our model, fish directly consume seagrass detritus as their sole food source. While seagrass is both a food resource and an important habitat for invertebrates (Boström and Mattila 1999), how changes in seagrass production influences invertebrate secondary production is not well understood (de la Morinière et al. 2003). Relatedly, while mortality is based partly on consumption, fish growth is simulated to be constant following the von Bertalanffy growth curve whereby mortality occurs if consumption does not meet these requirements. Future research efforts should focus on incorporating food-dependent growth to explore potential feedbacks on ecosystem primary and secondary production. Integrating greater complexity into the food webs and fish population dynamics will be required to assess the potential of ARs to influence secondary production.

Despite these simplifications, our data-driven model, and the outcomes presented herein, provide an important first step towards a more mechanistic and spatially explicit understanding of how AR can enhance the energetic base of a seagrass ecosystem through altered nutrient dynamics associated with aggregating fishes. Additionally, our findings based on a theoretical simulation model should guide future empirical research (Grainger et al. 2022), such as species-specific movement behavior or larval dispersal dynamics near ARs. Our model and findings have important implications for (*i*) our understanding of the importance of non-linear dynamics for ecosystem-level properties, and (*ii*) the potential application of ARs for ecosystem restoration and

management. Despite their increasing prevalence worldwide, there is still considerable uncertainty as to how AR structures alter both patch and ecosystem-scale dynamics across different types of marine ecosystems. Our simulation model demonstrates how the attraction of fishes to ARs can promote enhanced primary production in a coastal seagrass system. However, it remains to be determined how exactly this may translate to secondary production and AR application in fisheries, and the extent to which this may influence carbon sequestration in seagrass ecosystems. Future empirical and modeling studies will be needed to determine the impact of AR structure on the broader suite of other marine ecosystems in which they are deployed (i.e., coral reefs), and their optimal management for multiple ecosystem services.

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Authorship Statement

K.E.E. and J.E.A. designed the initial research. M.H.K.H. programmed the model and conducted the analysis with input from K.E. and J.E.A. The manuscript was drafted by K.E.E. with substantial contributions from J.E.A. and M.H.K.H. K.E. and M.H.K.H. contributed equally to the manuscript. All authors gave final approval for publication.

Conflict of Interest

The authors declare that there is no conflict of interest.

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Tables

Table 1: Overview of all functions used in the individual-based simulation model ordered by subprocesses they are used in. The * of the "References" column indicates that the used formula is modified from the reference.

Formula #	Description	Formula	Reference
1.1	*Seagrass primary production* Slough proportion of biomass	$S_i = B_i * (\alpha * (1 - \beta_i))$	(DeAngelis 1992)*
1.2	*Seagrass primary production* Slough proportion modifier	$\beta_i = (B_i^{max} - B_i)/(B_i^{max} - B_i^{min})$	-
1.3	*Seagrass primary production* Slough biomass to detritus biomass	$B_i = B_i - S_i; \ D = D + S_{BG} + S_{AG}$	(DeAngelis 1992)*
1.4	*Seagrass primary production* Ambient nutrient uptake	$U_i = (B_i * v_i^{max} * N)/(k_i^m + N)$	(DeAngelis 1992)
1.5	*Seagrass primary production* Total nutrient uptake	$N = N - U_{BG} + U_{AG}$	(DeAngelis 1992)
1.6	*Seagrass primary production* Stabilize biomass	$IF\ U_{total} < (S_{BG} * \gamma_{BG}) \rightarrow B_{BG} = B_{BG} + U_{total}/\gamma_{BG}$ $IF\ U_{total} - (S_{BG} * \gamma_{BG}) < (S_{AG} * \gamma_{AG}) \rightarrow B_{AG} = B_{AG} + (U_{total} - S_{BG} * \gamma_{BG})/\gamma_{AG}$	-
1.7	*Seagrass primary production* Sigmoid function biomass allocation	$\delta_{BG} = \dfrac{1}{1+\left(\frac{B_{BG}{}^m}{1-B_{BG}{}^m}\right)^{-v}}; \ m = \dfrac{-\log(2)}{\log(\tau)}$	-

1.8	*Seagrass primary production* Biomass growth	$B_{BG} = B_{BG} + S_{BG} + (U_{total} - (S_{BG} * \gamma_{BG} + S_{AG} * \gamma_{AG})) * \delta/\gamma_{BG}$ $B_{AG} = B_{AG} + S_{AG} + (U_{total} - (S_{BG} * \gamma_{BG} + S_{AG} * \gamma_{AG})) * (1 - \delta)/\gamma_{AG}$	-
2.1	*Remineralization* Remineralization of detritus to nutrients	$N = N + D * \epsilon_i; \; D = D - D * \epsilon_i$	(DeAngelis 1992)*
2.2	*Remineralization* Decompose fish detritus to detritus	$D = D + D_{fish} * \epsilon_i$ $D_{fish} = D_{fish} - D_{fish} * \epsilon_i$	-
3.1	*Fish movement* Activity for respiration	$ACT = (1/(\lambda_{max} + 1)) * dist + 1$	(J.E. Allgeier et al. 2020)
4.1	*Fish respiration* Respiration of individual	$R(T) = V^x * e^{(X*(1-V))}$	(Hanson et al. 1997)
4.2	*Fish respiration* Temperature dependence of respiration	$V = (temp_{max} - temp)/(temp_{max} - temp_{optim})$	(Hanson et al. 1997)
4.3	*Fish respiration* Temperature dependence of respiration	$X = (Z^2 * (1 + 40/Y)^{0.5})^2)/400$	(Hanson et al. 1997)
4.4	*Fish respiration* Temperature dependence of respiration	$Z = log(temp_{Q10}) * (temp_{max} - temp_{optim})$	(Hanson et al. 1997)
4.5	*Fish respiration* Temperature dependence of respiration	$Y = log(temp_{Q10} * (temp_{max} - temp_{optim} + 2)$	(Hanson et al. 1997)

5.1	*Fish consumption, growth, mortality* Length growth of individual	$G = L_{inf}(1 - e^{-K(t-t_0)})$	(J.E. Allgeier et al. 2015; Froese and Pauly 2019)
5.2	*Fish consumption, growth, mortality* Length-weight conversion	$W = a * L^b$	(Froese and Pauly 2019)
5.3	*Fish consumption, growth, mortality* Consumption requirements	$C = \dfrac{G + R(A)}{0.55}$	(J.E. Allgeier et al. 2015)
5.4	*Fish consumption, growth, mortality* Nutrient excretion	$E = C - G$	(J.E. Allgeier et al. 2015)
5.5	*Fish background mortality* Mortality probability	$P = e^{L - L_{inf}}$	(Froese and Pauly 2019)

Table 2: Values and references for all parameters used in the individual-based simulation model. Values related to the belowground biomass are abbreviated by BG, values related to the aboveground biomass by AG. If parameters differed between BG and AG or nutrients and (fish) detrital biomass, values are separated by a dash (/).

Parameter	Formula # from Table 1	Description	Value (bg / ag)	Reference
α	1.1	Proportion of standing biomass that is sloughed to detrital biomass	0.0001	Systematically explored value range
B_i^{min}	1.2	Minimum standing biomass	275.89 / 8.87	(J.E. Allgeier, Yeager, and Layman 2013; Layman, Allgeier, and Montaña 2016; Shayka unpublished)
B_i^{max}	1.2	Maximum standing biomass	933.03 / 193.01	(J.E. Allgeier, Yeager, and Layman 2013; Layman, Allgeier, and Montaña 2016; Shayka unpublished)
v_i^{max}	1.4	Maximum nutrient uptake rate	28.8125 / 12.825	(Lee and Dunton 1999)
k_i^m	1.4	Half-saturation value of nutrient uptake	366.0125 / 12.05	(Lee and Dunton 1999)
γ_i	1.6, 1.8	Nutrient content percent of standing biomass per dry weight	0.0082 / 0.0144	(Layman, Allgeier, and Montaña 2016)
τ	1.7	Midpoint allocation function	1/4	Systematically explored value range
υ	1.7	Slope of allocation function	2.0	Systematically explored value range
ϵ	2.1, 2.2	Proportion of detrital biomass that is remineralized / Proportion of fish detrital biomass that is decomposed	0.0001 / 0.5	Systematically explored value range

Symbol	Section	Description	Value	Reference
λ	3.1	Mean movement distance of individuals	8	-
-	various	Variance of random movement distance	4.0	-
$temp_{max}$	4.2, 4.4, 4.5	Maximum water temperature for respiration	40	(Hanson et al. 1997; J.E. Allgeier et al. 2015)
$temp_{optim}$	4.2, 4.4, 4.5	Optimum water temperature for respiration	36	(Hanson et al. 1997; J.E. Allgeier et al. 2015)
$temp_{Q10}$	4.4, 4.5	Rate at which respiration increases over low water temp	2.1	(Hanson et al. 1997; J.E. Allgeier et al. 2015)
L_{inf}	5.1	Maximum length of fish individuals	41.6	(Froese and Pauly 2019)
K	5.1	Growth coefficient	0.2	(Froese and Pauly 2019)
a	5.2	Length-weight relationship	0.02566176	(Froese and Pauly 2019)
b	5.2	Length-weight relationship	2.956776	(Froese and Pauly 2019)
-	various	Proportion of individuals' body mass that can be store as reserves	0.05	-
-	various	Nutrient proportion of individuals' body mass	0.02999	-
	various	Proportion of nutrients that is diffused across neighboring cells	2/3	-
-	various	Proportion of detrital biomass that is diffused across neighboring cells	1/3	-

| - | various | Proportion of fish detrital biomass that is diffused across neighboring cells | 1/3 | - |

Table 3: Starting values used in the individual based simulation model. Values related to the belowground biomass are abbreviated by BG, values related to the aboveground biomass by AG.

Name	Description	Value	Reference
bg_biomass	Starting value of belowground seagrass biomass	440.175, 604.46, 768.745	(J.E. Allgeier, Yeager, and Layman 2013; Layman, Allgeier, and Montaña 2016; Shayka unpublished)
ag_biomass	Starting value of aboveground seagrass biomass	54.905, 100.94, 146.975	(J.E. Allgeier, Yeager, and Layman 2013; Layman, Allgeier, and Montaña 2016; Shayka unpublished)
nutrients_pool	Starting value of nutrients	0.0001100017, 0.0003205054, 0.0006315112	-
detritus_pool	Starting value of detrital biomass	1.099907, 3.204733, 6.31448	-
pop_n	Number of fish individuals	1, 2, 4, 8, 16, 32	-
pop_mean_size	Mean length of fish individuals	9	-
pop_mean_var	Variation of mean length	3	-
water_temp	Mean water temperature	26	(Allgeier *unpublished*)

Figure Legends

Figure 1: Overview of all model subprocesses and their scheduling (adapted from DeAngelis 1992). Seagrass primary production is calculated based on the available nutrients in the water column and simultaneously seagrass biomass is sloughed to the detrital biomass. The detrital biomass is remineralized to water column nutrients. Fish individuals move throughout the model environment and their consumption (of the detrital biomass) is determined by their respiration which is largely influenced by body mass and movement activity. If consumption requirements cannot be met, individuals die, adding their body nutrients to the fish detrital biomass. Nutrients and detrital biomass are diffused among neighboring grid cells.

Figure 2: Total fish biomass (upper panel) and total nutrient excretion by fish individuals (lower panel) after 50 simulation years. Colors indicate the *random movement scenario* (blue) and *attracted movement scenario* (red). Initial biomass capacities increase on the x-axis and fish densities across the panels from left to right. Error bars represent the standard error of the 25 repetitions for each treatment level. Stars indicate significant differences between the values based on a t-test (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

Figure 3: Log response ratios of *random movement* and *attracted movement scenario* for aboveground, belowground and total standing biomass (blue) and production (red). Initial biomass capacities increase along the x-axis and fish densities increase across the panels from left to right. The percentage value describes the relative difference between the *random movement* and the *attracted movement scenario* of biomass (blue) and production (red). If percentage values are written in grey, the log response ratios overlapped zero, i.e., no significant difference was present.

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Figure 4: Log response ratios of the *random movement* and *attracted movement scenario* for aboveground, belowground, and total production in distance to the artificial reef. Distances were classified into 5 m classes. Initial biomass capacities are indicated by colors and fish densities increase across the panels from left to right.
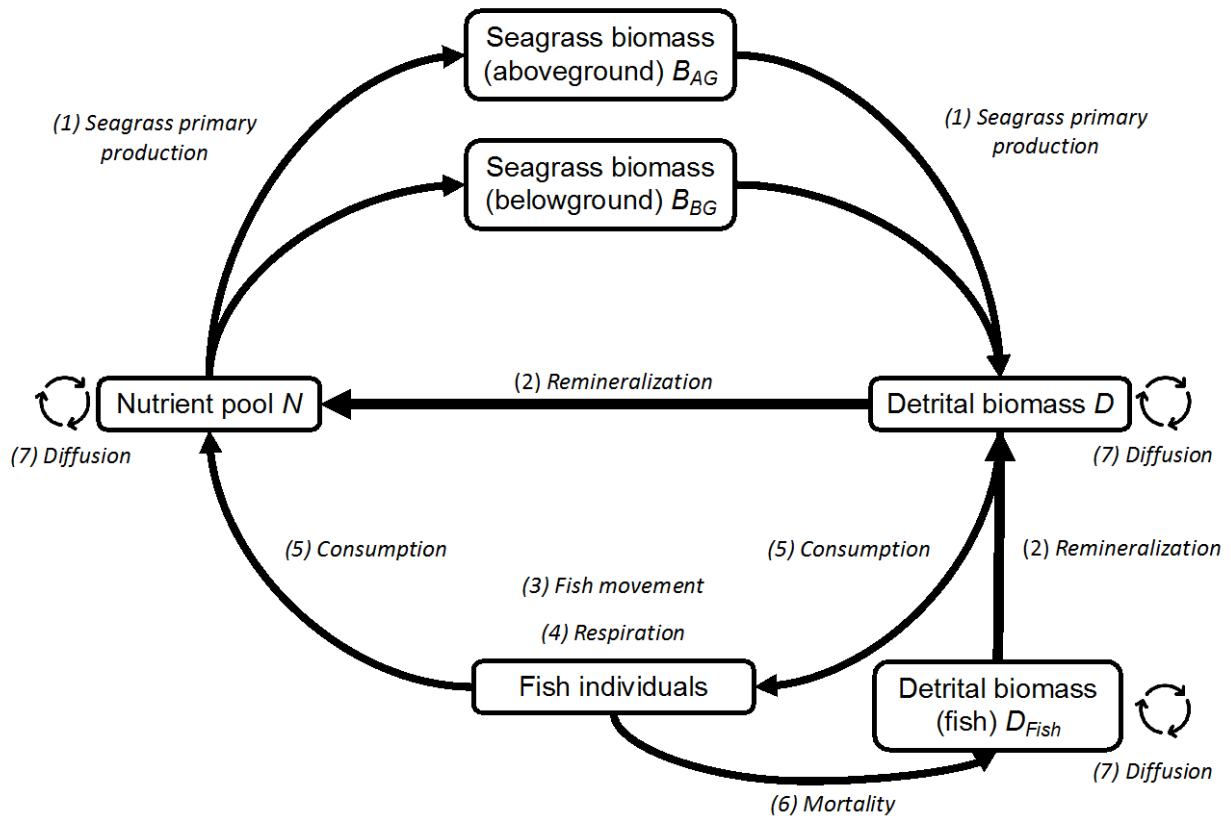
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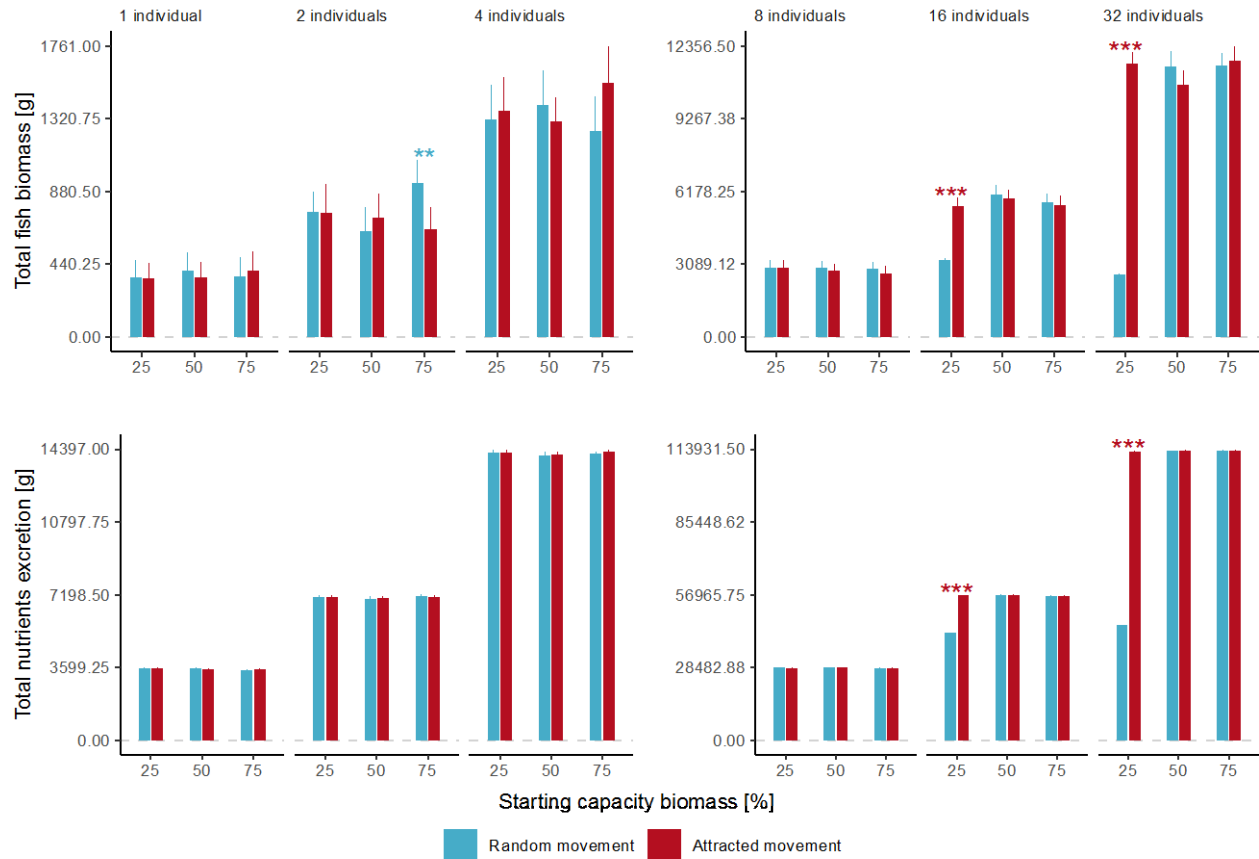
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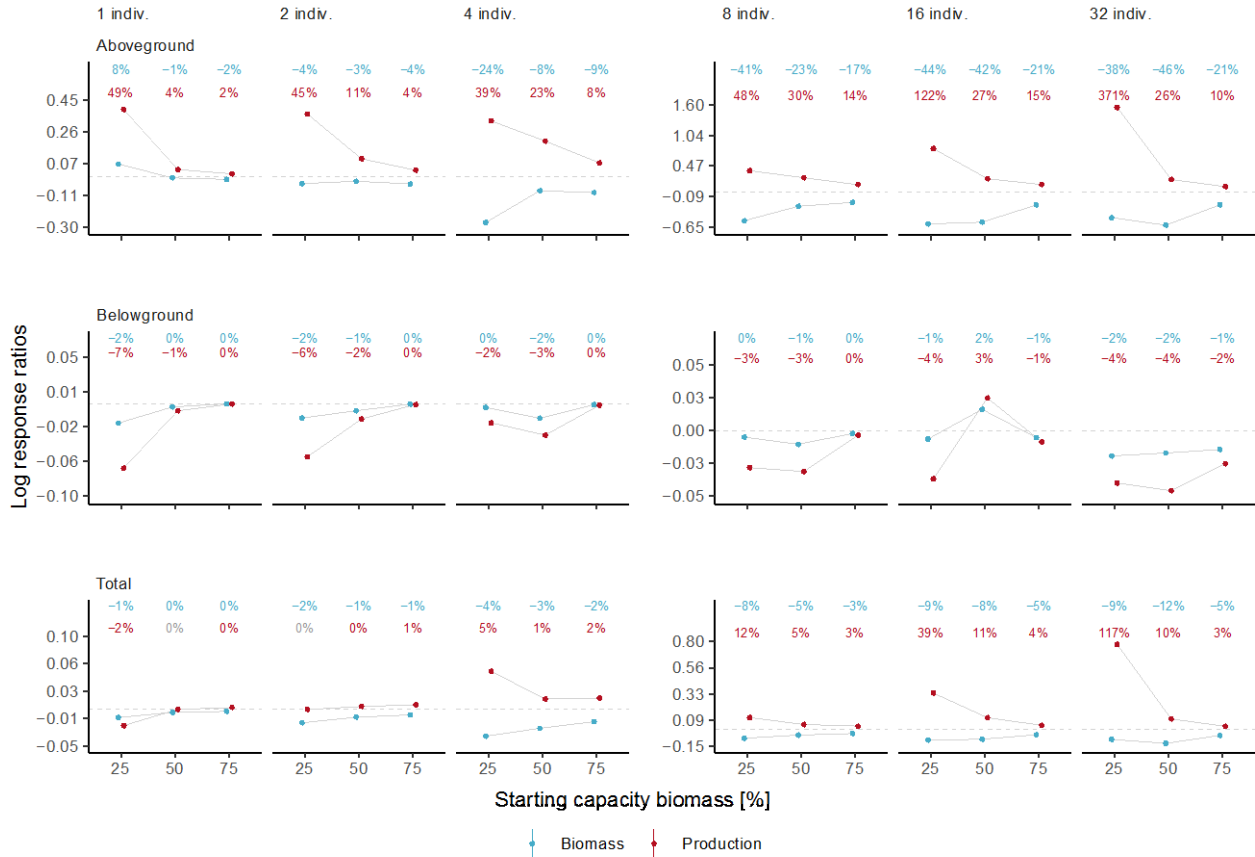
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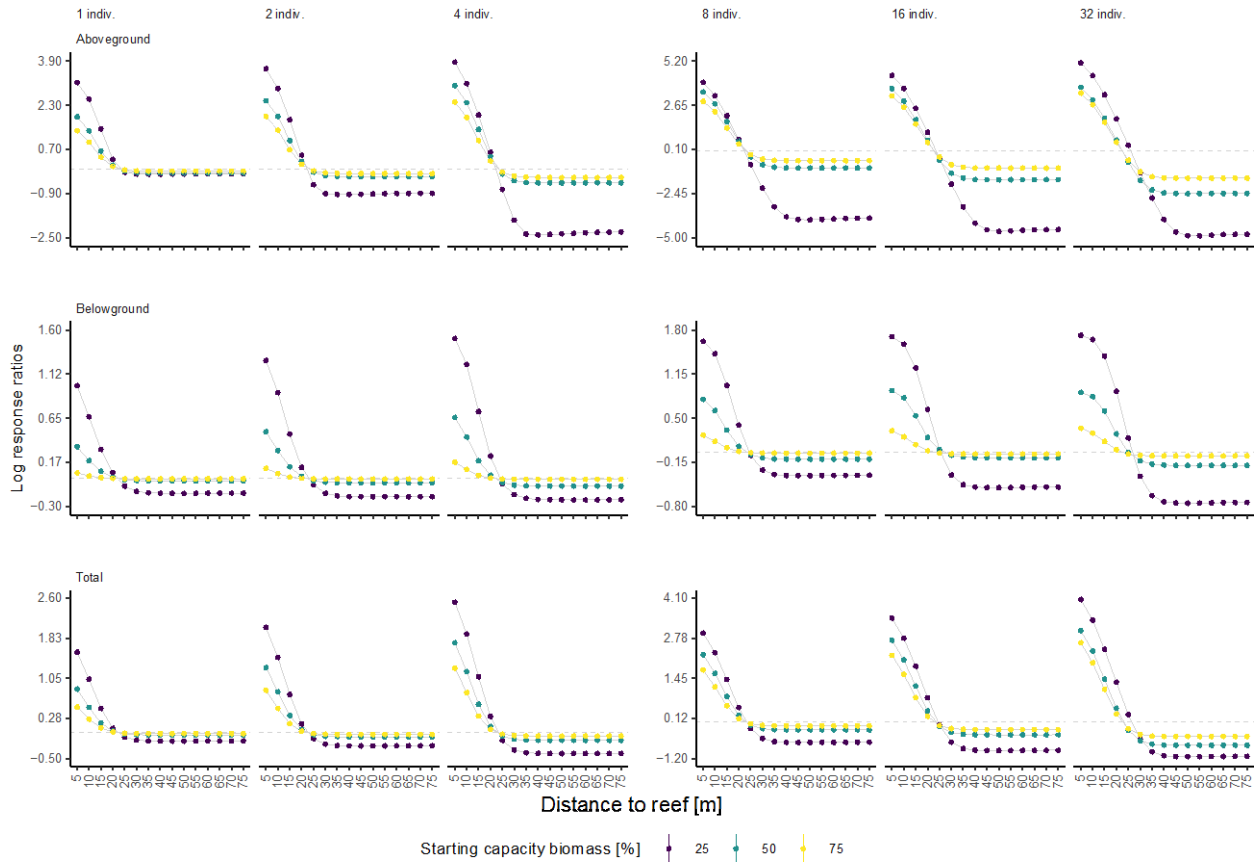
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