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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 (ARs) 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 ARs 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 ARs 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 ARs, ecosystem-scale primary production is enhanced synergistically. This synergistic increase in production was caused by nonlinear dynamics associated with nutrient uptake and biomass allocation that enhances aboveground primary production more than belowground production. Seagrass production increased near the AR and decreased in areas away from the AR, despite marginal reductions in seagrass biomass at the ecosystem level. Our simulation's findings that ARs can increase ecosystem production provide novel support for ARs in seagrass ecosystems as an effective means to promote (i) fishery restoration (increased primary production can increase energy input to 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 ARs as a tool for ecological restoration.

INTRODUCTION

Predicting ecosystem productivity is a fundamental challenge in ecology and is necessary for the effective management of ecosystem services. Essential to this is understanding the controls on primary production because it represents an important ecosystem service in and of itself through the sequestration of carbon and provides the energetic basis for secondary production, for example, 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, overexploitation, and climate change (Halpern et al., 2008, 2012; Lotze, 2006; Sale, 2008). Ecosystem-based management approaches (Arkema et al., 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 & Hixon, 1997) and, more recently, to promoting increased carbon sequestration via increased seagrass primary production (Layman & Allgeier, 2020) or increased coral growth rates (Allgeier, Andskog, et al., 2020; Shantz et al., 2015). From a more traditional perspective, ARs are a fishery-centric management tool and have been widely utilized because they promote dense aggregations of fish (Baine, 2001; Bohnsack et al., 1991; Carr & Hixon, 1997; Seaman, 2019; Stone et al., 1991). 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 ongoing debate: (i) ARs act as attractors of fish, moving fish that already exist in a 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 et al., 1997; Osenberg, 2002; Powers et al., 2003; Sadovy & Domeier, 2005; Wilson et al., 2001). 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., Claisse et al., 2014; Powers et al., 2003). 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 (Layman & Allgeier, 2020; Lindeman, 1942; Ryther, 1969). 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 et al., 1991; Allgeier et al., 2013, 2018; Layman et al., 2016), similar to consumer-mediated biogeochemical hotspots found in other systems (e.g., Atkinson et al., 2013; McIntyre et al., 2008). 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 (AG) primary production (Layman et al., 2016). This allocation mechanism is also

common among terrestrial plants (Chapin, 1980; Poorter et al., 2012; Shipley & Meziane, 2002) 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 (Allgeier et al., 2013). Because ambient nutrients must exceed a certain threshold to trigger AG production, this proposed mechanism also suggests that the loss of fishes from open seagrass beds will not result in subsequent reductions of seagrass production because fishes in 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 (Allgeier et al., 2013, 2018; Layman et al., 2016), discerning whether 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 (Deslauriers et al., 2017; Hanson et al., 1997). The model is parameterized by substantial empirical data from ARs constructed in shallow seagrass beds in The Bahamas (Allgeier et al., 2013, 2018; Layman et al., 2013, 2016) and fish energetics of common species found on ARs in this region (Allgeier et al., 2015, Allgeier, Cline, et al., 2020). We test whether increased production is possible at both the patch and ecosystem scales by answering two interrelated questions. First, how do varying fish densities and initial seagrass biomass impact AG and belowground (BG) seagrass production in a system with or without an AR? Second, 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, that is, fish either are attracted to the AR or move randomly about the model environment; (ii) the number of fish within the system, that is, 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 ARs.

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 given in what follows) 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 parameterization and initialization of the IBM.

General model purpose

We used an IBM (DeAngelis & Grimm, 2014) to understand the influence of fish aggregations around a single AR on standing seagrass biomass and production (both AG and BG). The model environment simulates a shallow seagrass bed (~3 m depth), similar to those of previous empirical studies (Allgeier et al., 2013, 2018; Layman et al., 2013, 2016). Seagrass production is based on a single nutrient primary production model following DeAngelis (1992), detailed in what follows. 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 common throughout shallow coastal ecosystems in the Caribbean and frequently found to aggregate on ARs (Appeldoorn et al., 2009). In the IBM, fish movement, consumption of biomass, and excretion of nutrients are governed by principles of bioenergetics (Deslauriers et al., 2017; Hanson et al., 1997; Schreck & Moyle, 1990), detailed in what follows. Individual fish 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 to 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
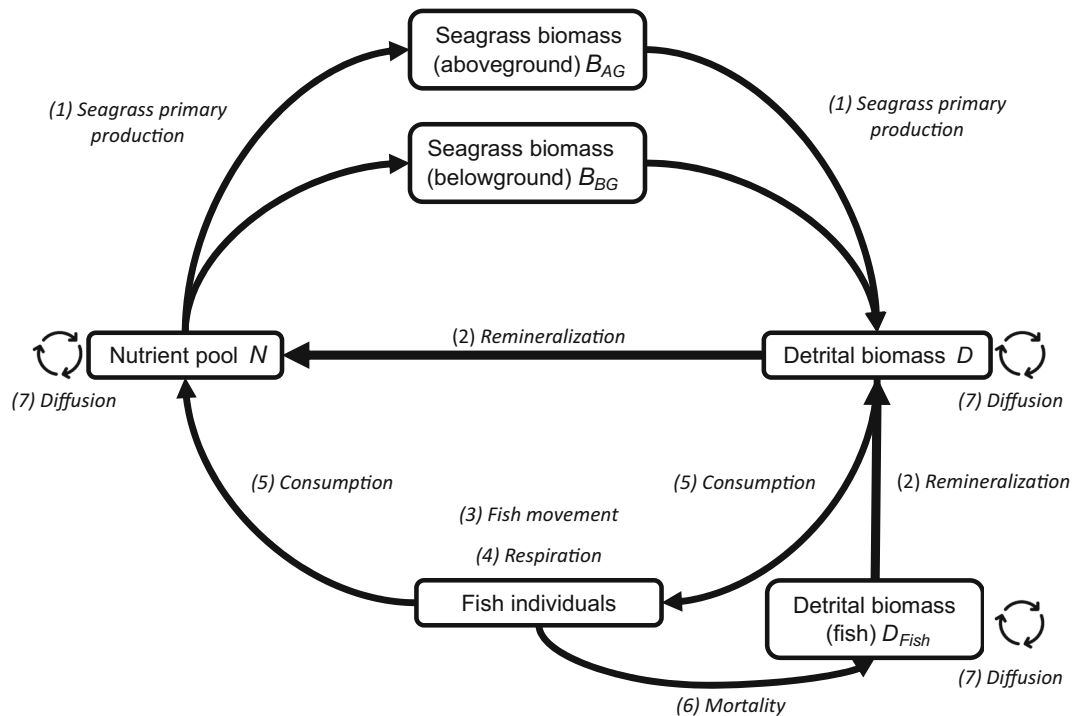
FIGURE 1 Overview of all model subprocesses and their scheduling (adapted from DeAngelis [1992]). Seagrass primary production is calculated based on available nutrients in water column, and simultaneously seagrass biomass is sloughed to detrital biomass. The detrital biomass is remineralized to water column nutrients. Individual fish 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

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 scales: (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 the R programming language (R Core Team, 2019). Model code and analysis scripts can be found at https://doi.org/10.5281/zenodo.5889083 and https://doi.org/10.5281/zenodo.5847402, respectively.

State variables and scales

The seagrass bed model environment was simulated using a 100×100 cell grid (spatial extent) with a cell resolution of 1×1 m (spatial grain). Each grid cell contains seagrass biomass (separated into AG and BG), a water column nutrient pool, and detrital biomass. Individual fish 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 individual fish 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 min (one iteration, temporal grain) for a total of 50 years (219,000 iterations, temporal extent). All seagrass-related processes (Processes 1 and 2 in what follows) were simulated every 24 h (i.e., 12 iterations). The temporal extent of 50 years was chosen because it represents sufficient time beyond which no major changes in 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 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 the biomass of dead individual fish decomposes to detrital biomass.

3. Individual fish move around the seagrass bed. For the random movement scenario, the direction of movement is completely random, and for the attracted movement scenario, individual fish tend to move toward the AR.

4. A bioenergetics model is used to calculate respiration for individual fish based on water temperature (homogeneous in model environment), body mass, and movement activity.

5. The energetic demand for growth is calculated based on demands for respiration, and individual fish consume detrital biomass according to this demand, resulting in body mass accumulation (growth). During consumption and subsequent growth, individual fish also excrete nutrients on the grid cell they occupy. If the available detrital biomass (the energetic resource for fishes in our model environment) is less than the energetic demand for growth and individual fish do not have sufficient stored energetic reserves, then the individual fish die and the biomass of dead individuals is added to the fish detrital biomass.

6. Background mortality occurs where 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 individual fish were also tracked including body length and mass, mortality, and spatial location within the model environment. Individual fish do not interact with each other. For the attracted movement scenario, individual fish 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, fish movement (aforementioned Process 3) and background mortality (aforementioned Process 6) include stochasticity, that is, 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 Tables 1 and 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 includes three subprocesses: biomass sloughing, nutrient uptake, and plant growth.

1.a. Biomass sloughing: 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

TABLE 1 Overview of all functions used in individual-based simulation model ordered by subprocesses they are used in

Formula no.	Function	Subprocess	Formula	Reference
1.1	*Seagrass primary production*	Slough proportion of biomass	$S_i = B_i \times (\alpha \times (1-\beta_i))$	DeAngelis (1992)[a]
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)[a]
1.4	*Seagrass primary production*	Ambient nutrient uptake	$U_i = (B_i \times v_i^{max} \times N)/(k_i^m + N)$	DeAngelis (1992)
1.5	*Seagrass primary production*	Total nutrient uptake	$N = N-U_{BG}+U_{AG}$	DeAngelis (1992)

(Continues)

TABLE 1 (Continued)

Formula no.	Function	Subprocess	Formula	Reference
1.6	*Seagrass primary production*	Stabilize biomass	IF $U_{total} < (S_{BG} \times \gamma_{BG}) \rightarrow B_{BG} =$ $B_{BG} + U_{total}/\gamma_{BG}$ IF $U_{total} - (S_{BG} \times \gamma_{BG}) < (S_{AG} \times \gamma_{AG})$ $\rightarrow B_{AG} = B_{AG} + (U_{total} - S_{BG} \times \gamma_{BG})/\gamma_{AG}$	–
1.7	*Seagrass primary production*	Sigmoid function biomass allocation	$\delta_{BG} = \dfrac{1}{1 + \left(\frac{B_{BG}m}{1-B_{BG}m}\right)^{-\upsilon}}; m = \dfrac{-\log(2)}{\log(\tau)}$	–
1.8	*Seagrass primary production*	Biomass growth	$B_{BG} = B_{BG} + S_{BG} +$ $(U_{total} - (S_{BG} \times \gamma_{BG} + S_{AG} \times \gamma_{AG})) \times \delta/\gamma_{BG}$ $B_{AG} = B_{AG} + S_{AG} +$ $(U_{total} - (S_{BG} \times \gamma_{BG} + S_{AG} \times \gamma_{AG}))$ $\times (1-\delta)/\gamma_{AG}$	–
2.1	*Remineralization*	Remineralization of detritus to nutrients	$N = N + D \times \epsilon_i; D = D - D \times \epsilon_i$	DeAngelis, (1992)[a]
2.2	*Remineralization*	Decompose fish detritus to detritus	$D = D + D_{fish} \times \epsilon_i$ $D_{fish} = D_{fish} - D_{fish} \times \epsilon_i$	–
3.1	*Fish movement*	Activity for respiration	$ACT = (1/(\lambda_{max} + 1)) \times dist + 1$	Allgeier, Cline, et al. (2020)
4.1	*Fish respiration*	Respiration of individual	$R(T) = V^x \times e^{(X \times (1-V))}$	Hanson et al. (1997)
4.2	*Fish respiration*	Temperature dependence of respiration	$V = (temp_{max} - temp)/\left(temp_{max} - temp_{optim}\right)$	Hanson et al. (1997)
4.3	*Fish respiration*	Temperature dependence of respiration	$X = \left(Z^2 \times \left(1 + (1 + 40/Y)^{0.5}\right)^2\right)/400$	Hanson et al. (1997)
4.4	*Fish respiration*	Temperature dependence of respiration	$Z = \log\left(temp_{Q10}\right) \times \left(temp_{max} - temp_{optim}\right)$	Hanson et al. (1997)
4.5	*Fish respiration*	Temperature dependence of respiration	$Y = \log\left(temp_{Q10}\right) \times \left(temp_{max} - temp_{optim} + 2\right)$	Hanson et al. (1997)
5.1	*Fish consumption, growth, mortality*	Length growth of individual	$G = L_{inf}\left(1 - e^{-K(t-t_0)}\right)$	Allgeier et al. (2015), Froese & Pauly (2019)
5.2	*Fish consumption, growth, mortality*	Length–weight conversion	$W = a \times L^b$	Froese & Pauly (2019)
5.3	*Fish consumption, growth, mortality*	Consumption requirements	$C = \frac{G+R(A)}{0.55}$	Allgeier et al. (2015)
5.4	*Fish consumption, growth, mortality*	Nutrient excretion	$E = C - G$	Allgeier et al. (2015)
5.5	*Fish background mortality*	Mortality probability	$P = e^{L - L_{inf}}$	Froese & Pauly (2019)

[a]The formula used is modified from that in the reference.

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, thereby 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 BG and AG 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).

TABLE 2 Values and references for all parameters used in the individual-based simulation model

Parameter	Formula no. 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	Allgeier et al. (2013), Layman et al. (2016), Shayka (unpublished)
B_i^{max}	1.2	Maximum standing biomass	933.03/193.01	Allgeier et al. (2013), Layman et al. (2016), Shayka (unpublished)
v_i^{max}	1.4	Maximum nutrient uptake rate	28.8125/12.825	Lee & Dunton (1999)
k_i^m	1.4	Half-saturation value of nutrient uptake	366.0125/12.05	Lee & Dunton (1999)
γ_i	1.6, 1.8	Nutrient content percentage of standing biomass per dry weight	0.0082/0.0144	Layman et al. (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
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), Allgeier et al. (2015)
$temp_{optim}$	4.2, 4.4, 4.5	Optimum water temperature for respiration	36	Hanson et al. (1997), 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), Allgeier et al. (2015)
L_{inf}	5.1	Maximum length of individual fish	41.6	Froese & Pauly (2019)
K	5.1	Growth coefficient	0.2	Froese & Pauly (2019)
a	5.2	Length–weight relationship	0.02566176	Froese & Pauly (2019)
b	5.2	Length–weight relationship	2.956776	Froese & Pauly (2019)
...	Various	Proportion of individuals' body mass that can be stored as reserves	0.05	–
...	Various	Nutrient proportion of individuals' body mass	0.02999	–
...	Various	Proportion of nutrients diffused across neighboring cells	2/3	–
...	Various	Proportion of detrital biomass diffused across neighboring cells	1/3	–
...	Various	Proportion of fish detrital biomass diffused across neighboring cells	1/3	–

Note: Values related to belowground biomass are abbreviated by BG, those related to aboveground biomass by AG. If parameters differed between BG and AG or nutrients and (fish) detrital biomass, values are separated by a slash (/).

1.c. Plant growth: Plant growth is determined by converting the total uptake to biomass using the nitrogen content (percent dry weight) of BG and AG biomass. Nutrient allocation to growth follows basic plant allocation rules such that maintaining BG biomass is prioritized over AG biomass (Appendix S1: Figures S1 and S2).

T A B L E 3 Starting values used in individual-based simulation model

Name	Description	Value	Reference
bg_biomass	Starting value of belowground seagrass biomass	440.175, 604.46, 768.745	Allgeier et al. (2013), Layman et al. (2016), Shayka (unpublished)
ag_biomass	Starting value of aboveground seagrass biomass	54.905, 100.94, 146.975	Allgeier et al. (2013), Layman et al. (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	No. individual fish	1, 2, 4, 8, 16, 32	–
pop_mean_size	Mean length of individual fish	9	–
pop_mean_var	Variation of mean length	3	–
water_temp	Mean water temperature	26	Allgeier (unpublished)

Note: Values related to belowground biomass are abbreviated by BG, those related to aboveground biomass by AG.

Specifically, if total nutrient uptake (converted to biomass equivalent using the nutrient content percentage per dry weight) is smaller than 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, then the 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), whereas (ii) if it is larger than the sloughed AG biomass, the 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 nutrient pool (N) at 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 at 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 individual fish 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, individual fish perceive the relative distance to the AR and always move toward 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 individual fish move depends on the original random orientation, they do not move straight toward the AR but nevertheless are attracted toward 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 (so-called torus translation). How far an individual fish 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 a million 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 individual fish (Table 1, Formulas 4.1, 4.2, 4.3, 4.4).
5. *Fish consumption, growth, and mortality*: Individual fish 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 an 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). Individual fish 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 consume up to 5% of body mass extra nutrients and store these nutrients as a nutrient "reserve" that could be used in situations in which insufficient detrital biomass is encountered in a given cell. This reserve capacity is consistent with fish foraging behavior (Armstrong & 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 individual fish excrete nutrients in the grid cell they are located in. If an individual fish cannot meet its requirements from the detrital biomass or its reserves, it dies (referred to here as consumption mortality; for more details on mortality see Process 6). We acknowledge that 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, so 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, individual fish 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 an individual fish 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), thereby preventing large nutrient pulses in the grid cell on which they died. Lastly, after an individual fish dies, a new individual is created with the same initial body size as the recently dead individual fish 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.

Parameterization 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 (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 AG 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. To use representative values for the minimum and maximum BG and AG seagrass biomass, we pooled several data sets (Allgeier et al., 2013, 2018; Layman et al., 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 & Dunton, 1999). Parameters for which no literature values were available ($\alpha_i, \epsilon_i, \tau, m$) 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 & Pauly, 2019) and previously published research from this same Bahamian ecosystem (Allgeier et al., 2013, 2015) for *H. plumerii*.

The initialization of AG and BG biomass was part of the simulation study (see section "*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 (J. E. Allgeier, unpublished).

Sensitivity analysis

Sensitivity analysis explores how changes in model parameters result in changes in the model output and thus give insights into the importance of parameters (Pianosi et al., 2016; Thiele et al., 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 using Latin hypercube sampling ($n = 250$ McKay et al., 1979). For each parameter, the Sobol method generated a main effect S_i and total effect S_{Ti} (main effect and interaction effect). Though 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 $\tau = 1/2$ (Appendix S1: Figure S5) and $\tau = 2/3$ (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, in which fish population sizes were either 1, 2, 4, 8, 16, or 32 individuals and (ii) initial seagrass *biomass capacity treatment*, where models were initialized under conditions in which both the AG and BG biomass started at 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 (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 (RRs) (Hedges et al., 1999) to evaluate the model outcomes between the random movement and attracted movement scenarios under all combinations of the two treatments (fish density and biomass capacity treatments). The log RR describes the proportional effect of an experimental scenario (here the attracted movement scenario) in comparison to a control (here the random movement scenario) $RR = \log(\bar{x}_{\text{attraction}}) - \log(\bar{x}_{\text{random}})$. To calculate uncertainties related to the RR we used bootstrapping to generate 95% confidence intervals (CIs) (1000 bootstrap replicates) (Efron & Tibshirani, 1986) using the *boot* packages in R (Davison & 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 AG production larger than 5%. AG and BG biomasses showed a relative change in 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 the fact that the total effects S_{Ti} were not larger than the main effects S_i. The AG biomass was primarily sensitive to the maximum AG and BG biomasses. 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 was to a lesser degree sensitive to the length–weight relationship parameters and the maximum fish length. BG production was sensitive to just two parameters: maximum BG biomass and, to a much lesser degree, slough proportion (Appendix S1: Figure S4).

In general, results were similar for the two midpoint τ parameter values $\tau = 1/2$ (Appendix S1: Figure S6) and $\tau = 2/3$ (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, the

relative decrease in BG production for the attracted movement scenario also increased. Thus, the increase in total production decreased as well.

Comparisons between model environments for random movement and attracted movement scenarios

Under the random movement scenario (which we consider our control treatment), fish excretion was randomly distributed throughout the simulation environment, whereas for the 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 were comparable between the random movement and attracted movement scenarios across all fish density and biomass capacity treatments (Figure 2). However, there were two exceptions: for low seagrass biomass capacity (25%) and for the highest fish densities (16 and 32 individuals), for which nutrient excretion was significantly lower in the random movement scenario owing 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 AR exceeded the increased demand in fish consumption from the higher fish densities.

How do varying fish densities and initial seagrass biomass capacity impact total AG and BG 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 the exception of fish densities with one individual fish and initial biomass capacities of 25% or 50%. For lower fish densities (two or four individual fish), the standing AG biomass decreased only marginally. For higher fish densities (8, 16, 32 individual fish), 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 AG 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 was synergistic because, despite having the same total nutrients within the system as the random movement scenario, the aggregating behavior of the fish promoted nonlinear dynamics that allowed AG production to increase disproportionately relative to BG production, thus generating a net increase in production at the ecosystem scale. This contrast to the alternative outcome not supported by our study whereby a change in the availability of nutrients around the AR would have meant a simple spatial reallocation of seagrass production, but it 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 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 square meter increased by 325% (for 1 individual) up to 18,996%
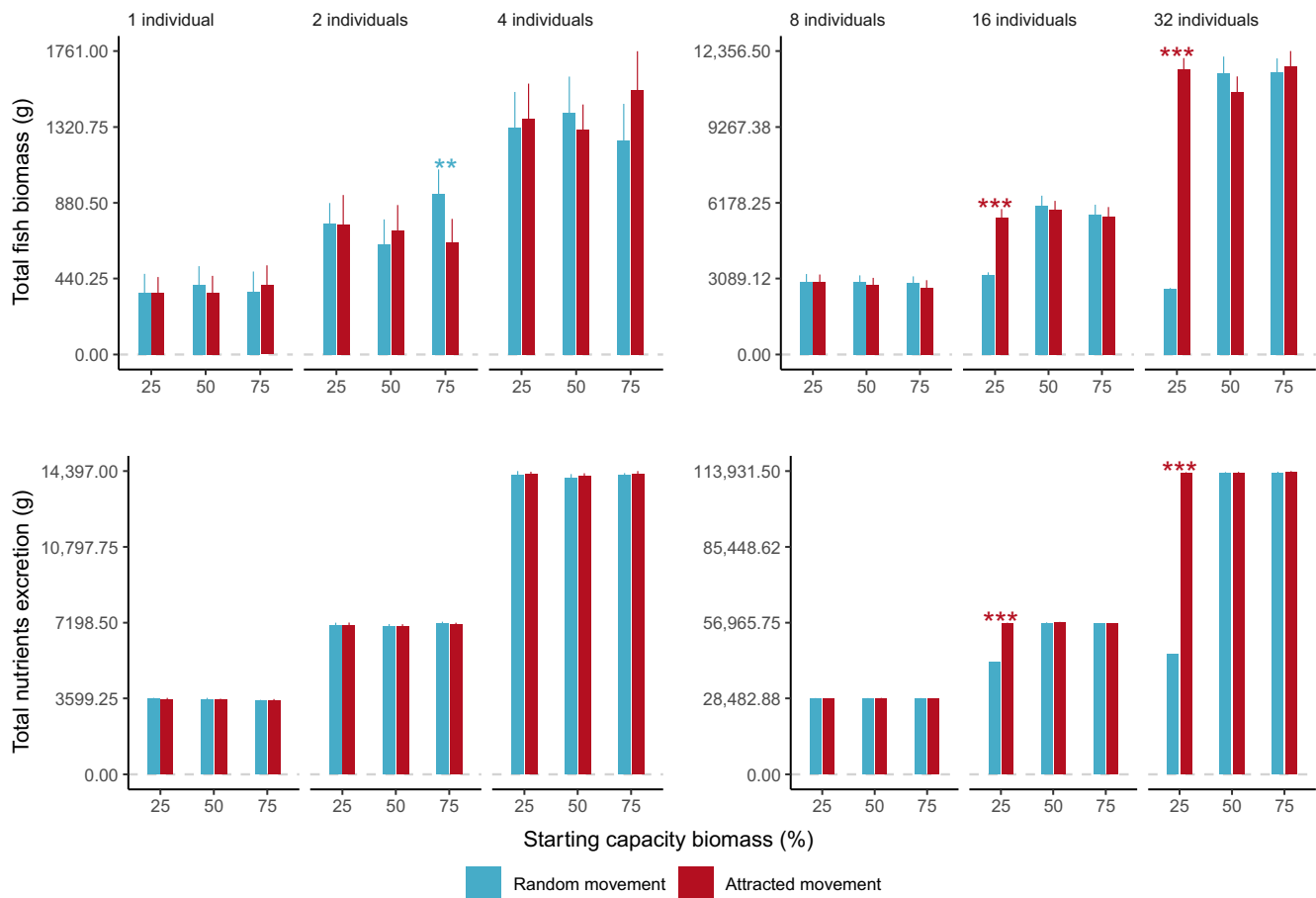
FIGURE 2 Total fish biomass (upper panel) and total nutrient excretion by individual fish (lower panel) after 50 simulation years. Colors indicate random movement scenario (blue) and attracted movement scenario (red). Initial biomass capacities increase on the x-axis and fish densities across panels from left to right. Error bars represent the standard error of the 25 repetitions for each treatment level. Asterisks indicate significant differences between values based on a t-test (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$)

(for 32 individuals); therefore, 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 square meter 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) and 456% (32 individuals).

At the same time, mean AG production per square meter 30 m 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 in BG production 30 m² 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 scenarios

followed trends similar to those of 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 from the AR, both AG and BG biomasses decreased under the attracted movement scenario. However, biomass increases close to the AR under the 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, ARs can synergistically enhance total ecosystem primary production, but not necessarily total standing seagrass biomass, in a closed seagrass ecosystem. This finding contrasts with the alternative, whereby the aggregating behavior and ensuing biogeochemical hotspot would have simply reallocated
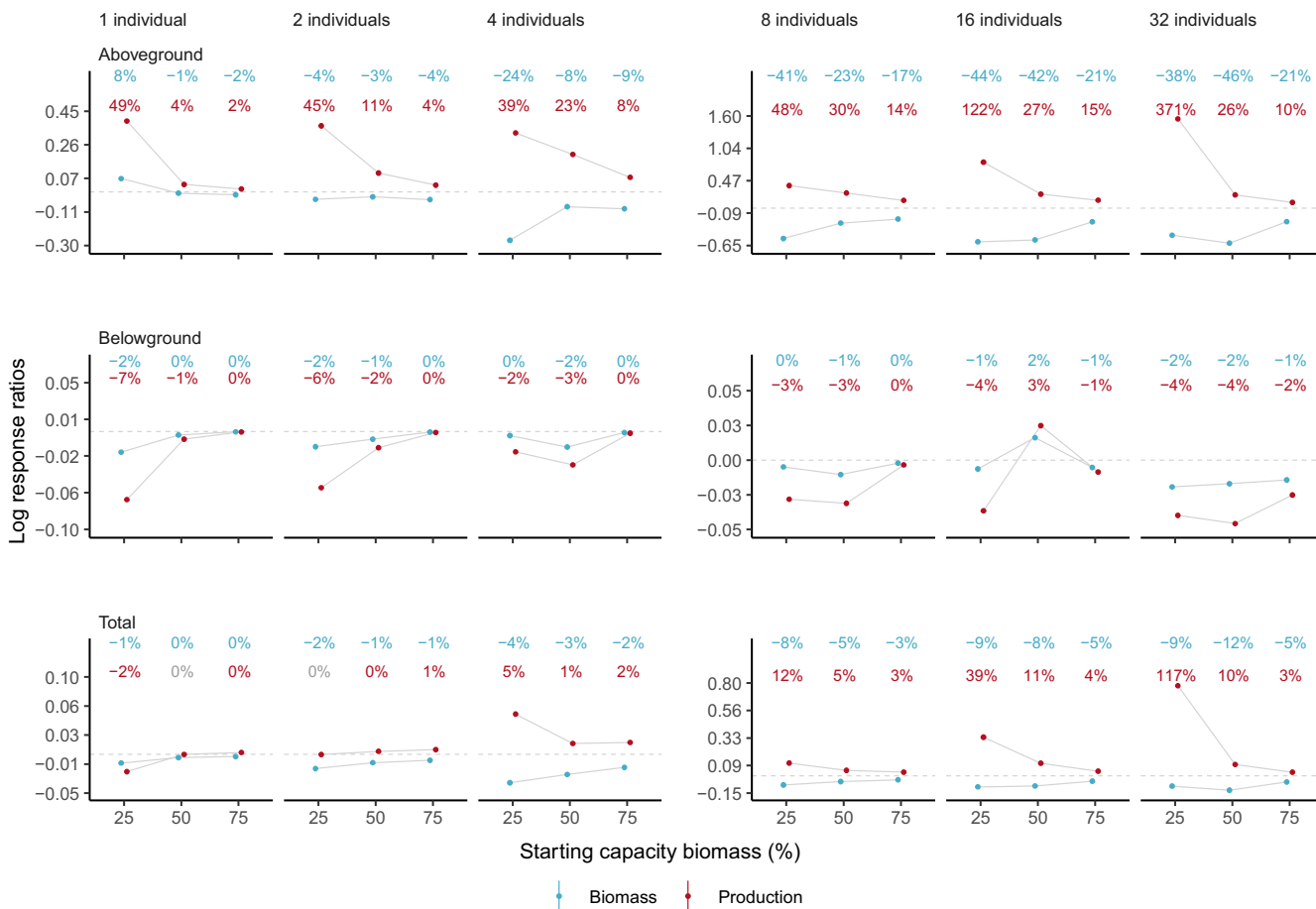
FIGURE 3 Log response ratios of random movement and attracted movement scenario for aboveground, belowground, and total standing biomass (blue) and production (red). Initial biomass capacities increase along the *x*-axis and fish densities increase across panels from left to right. The percentage value describes the relative difference between the random movement and attracted movement scenario of biomass (blue) and production (red). If percentage values are written in gray, the log response ratios overlapped zero, that is, no significant difference was present

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 biomasses under increasing nutrient availability and the underlying nonlinear dynamics of the nutrient uptake and allocation thresholds that drive production. Though our IBM 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), thereby allowing us to disentangle the complex dynamics that led 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) nonlinear dynamics associated with nutrient uptake rates, and sloughing, largely in the AG biomass. Under the attracted movement scenario, fish redistribute and concentrate nutrients by forming a biogeochemical hotspot around the AR. In nutrient-poor environments, seagrass, like most plants, prioritizes 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 that BG growth is always prioritized (Layman et al., 2016).
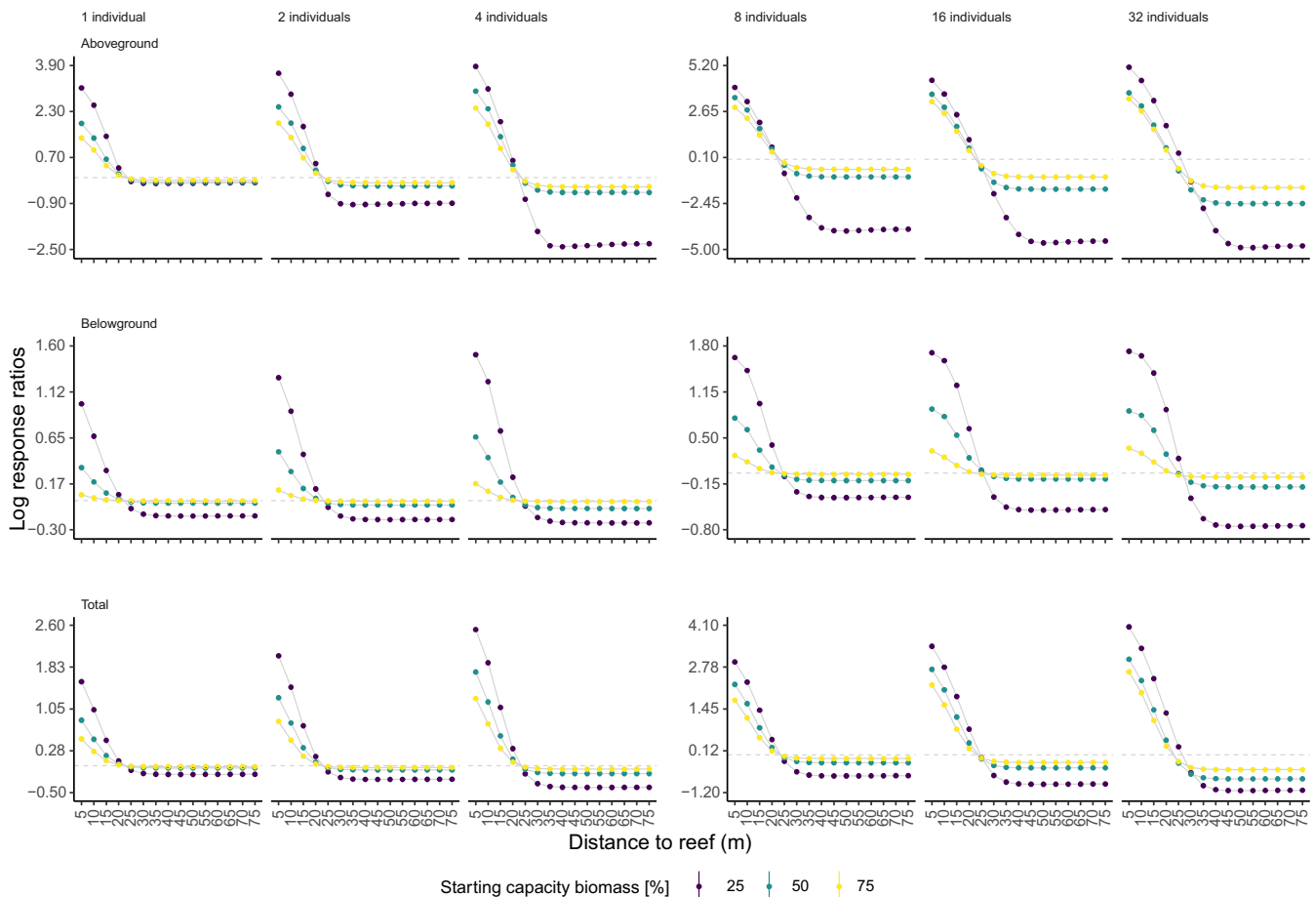
FIGURE 4 Log response ratios of random movement and attracted movement scenario for aboveground, belowground, and total production in distance to artificial reef. Distances were classified into 5-m classes. Initial biomass capacities are indicated by colors, and fish densities increase across panels from left to right

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 and 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 nonlinear than in BG biomass (Lee & Dunton, 1999), such that, when allocation of nutrients shifts to promote AG 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 nonlinearly per unit biomass such that with greater biomass, there is proportionally more slough, which means greater biomass turnover and, thus, greater production. Hence, 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 there being no change in absolute ecosystem nutrients—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 biomasses both decrease marginally at the ecosystem level. This decrease is in part due to the aforementioned 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 seldom 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 more patches 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 individual fish 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 individual fish relative to exogenous nutrients. While we acknowledge that 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), 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 to restore multiple ecosystem functions in the face of increased and simultaneous anthropogenic stressors (Holsman et al., 2020; Howell et al., 2021; Smith et al., 2007). Our findings have important implications for the use of ARs to 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 & 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 in promoting carbon sequestration because of the increased demand for C in photosynthesis. Interestingly, while heightened 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 (Fourqurean et al., 2012; Kennedy et al., 2010; 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 in total ecosystem primary production is encouraging for the application of ARs as a tool of conservation, but the extent to which this may occur requires further investigation.

We acknowledge that our model is an overly simplistic 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 (Green & Short, 2003), and in particular the Bahamas (Allgeier et al., 2013, 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*, suggesting that the physiological mechanisms of *T. testudinum* that led 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 & Rose, 2013). Because the simple aggregation of fish leads to increased production, we also expect fish movement behavior, both among (Green et al., 2015; Allgeier et al., 2017) and within species (Allgeier, Cline, 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

would require integrating fish and invertebrate population dynamics, their foraging behaviors, and their predator–prey interactions. The spatial dynamics of fishes could also be important in translocating nutrients both into and out of the modeled environment via movement (Harborne et al., 2016; 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 & 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, provides an important first step toward 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 nonlinear dynamics for ecosystem-level properties and (ii) the potential application of ARs for ecosystem restoration and management. Despite their increasing prevalence worldwide, there remains 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.

CONFLICT OF INTEREST
The authors declare that there is no conflict of interest.

AUTHOR CONTRIBUTIONS
Kenzo E. Esquivel and Jacob E. Allgeier designed the initial research. Maximilian H. K. Hesselbarth programmed the model and conducted the analysis with input from Kenzo E. Esquivel and Jacob E. Allgeier. The manuscript was drafted by Kenzo E. Esquivel, with substantial contributions from Jacob E. Allgeier and Maximilian H. K. Hesselbarth. Kenzo E. Esquivel and Maximilian H. K. Hesselbarth contributed equally to the manuscript. All authors gave final approval for publication.

DATA AVAILABILITY STATEMENT
Model code (Hesselbarth et al., 2022) is available on Zenodo at https://doi.org/10.5281/zenodo.5889083. Data and analysis scripts (Hesselbarth, 2022) are available on Zenodo at https://doi.org/10.5281/zenodo.5847402.

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