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RESEARCH ARTICLE

Demography alters carbon flux for a dominant benthic suspension feeder, the giant barrel sponge, on Conch Reef, Florida Keys

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Abstract

1. A challenge to understanding ecosystem processes is that the functional roles of species are linked with the demography of populations. In many systems, and particularly on coral reefs, the dynamics and structure of populations of many functionally important species has significantly changed over recent decades due to a variety of disturbances, and the changes in the ecological processes mediated by them are poorly understood.
2. Benthic suspension feeders are allogenic ecosystem engineers that contribute to the flow of materials and energy in aquatic systems. There is increasing evidence that sponges dominate this functional group on Caribbean reefs. Using demographic data from 2000 to 2012 and measurements of filtration rates of particulate and dissolved organic carbon, we parameterized a stage-based matrix model of population-mediated carbon flux for the Caribbean giant barrel sponge *Xestospongia muta* on Conch Reef, Florida Keys, to investigate the demographic mechanisms that mediate changes in benthic-pelagic coupling.
3. Population-mediated carbon flux increased over time with increasing sponge density and volume, with the largest individuals making the greatest contribution. Elasticity analysis revealed that the growth of sponges in all stages, the survival of sponges in the two largest stages, and the production of new recruits by the largest sponges had the greatest influence on changes in population-mediated carbon flux. We estimate the mean carbon flux over 2000–2012 for *X. muta* at Conch Reef was 1575 mg C days^{-1} m^{-2}, a value that exceeds that of any other single-species rate.
4. Projections indicated that population-mediated carbon flux will continue to increase under present conditions; thus, *X. muta* is expected to play an even larger role in the transfer of carbon from the water column to the benthos on Caribbean coral reefs.
5. Rather than being fixed, the functional role of species within a community are often dynamic and influenced by the demography of populations. The general framework developed here, a conversion of the basic unit of measurement for population models (i.e. the individual) into quantifiable metrics of species traits or activities, may be more broadly applied by further efforts to examine interrelationships between population and ecosystem processes.

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KEYWORDS

benthic pelagic coupling, benthic suspension feeding, demography, dissolved organic carbon, particulate organic carbon, Porifera

1 | INTRODUCTION

A challenge to understanding ecosystem processes is that the functional roles of species are coupled with the demography of populations (Jones & Lawton, 1995; Piraino, Fanelli, & Boero, 2002; Rudolf & Rasmussen, 2013). For example differences in herbivory, bioerosion and coral predation between parrotfish populations have been directly attributed to differences in parrotfish abundance and size (Bellwood, Hoey, & Hughes, 2012; Bonaldo & Bellwood, 2008). While relationships between population structure and size and ecosystem function have been informed by a number of natural and field manipulations (Bellwood et al., 2012; Burkepile & Hay, 2008), much less attention has been given to the dynamics of ecological processes and the demographic mechanisms that mediate changes in the functional role of species.

The role of benthic suspension feeders in aquatic ecosystems has been described as “paramount,” as they mediate benthic-pelagic coupling and the flow of energy and nutrients (Gili & Coma, 1998). Suspension feeding has a direct effect on plankton communities, which may indirectly effect benthic autotrophs (Peterson, Chester, Jochem, & Fourqurean, 2006). Moreover, benthic suspension feeders modify the abiotic properties of seawater (de Goeij et al., 2013; Southwell, Weisz, Martens, & Lindquist, 2008) and thus may be considered allogenic ecosystem engineers (Jones, Lawton, & Shachak, 1994).

There is increasing evidence that sponges are particularly important benthic suspension feeders in aquatic systems and especially on Caribbean coral reefs (Colman, 2015; Maldonado, Ribes, & van Duyl, 2012; Pawlik, Burkepile, & Thurber, 2016), where their biomass surpasses that of any other benthic group (Diaz & Rützler, 2001). Sponge populations efficiently process large volumes of seawater (McMurray, Pawlik, & Finelli, 2014; Reiswig, 1974) and represent an important trophic link between pelagic and benthic systems (Perea-Blázquez, Davy, & Bell, 2012; Pile, Patterson, Savarese, Chernykh, & Fialkov, 1997). Sponges significantly influence the cycling of phosphorous and nitrogen and thus may influence levels of primary production on coral reefs (Southwell et al., 2008; Zhang et al., 2015). In a recently described pathway analogous to the pelagic microbial loop, sponges may sustain fish biomass (Silveira et al., 2015) and the high productivity of coral reef systems through the “sponge loop” (de Goeij et al., 2013), whereby sponges transform dissolved organic matter into a form (detritus) biologically available to other trophic levels (Alexander et al., 2014; de Goeij et al., 2013).

Given significant recent and predicted changes in populations of benthic suspension feeders on coral reefs and in other aquatic systems (Bell, Davy, Jones, Taylor, & Webster, 2013; Ruzicka et al., 2013), there is a need for a greater understanding of the dynamics of the ecological processes mediated by benthic suspension feeders through their interactions with the water column. Here we investigated the dynamics of carbon flux mediated by populations of the Caribbean giant barrel sponge *Xestospongia muta* and the relative sensitivity of carbon flux to changes in demographic vital rates (i.e. growth, mortality, recruitment). A stage-based carbon flux matrix model that considers population dynamics and size structure was parameterized using in situ measurements of sponge filtration rates of organic carbon and demographic data for *X. muta* from 2000 to 2012. *Xestospongia muta* is arguably the largest member of the Porifera (McClain et al., 2015), populations are abundant across the Caribbean and constitute a large proportion of sponge community biomass (Loh & Pawlik, 2014; Southwell et al., 2008), and populations can filter the water-column in as little as 2.3 days (McMurray et al., 2014); thus, *X. muta* is expected to have a relatively large influence on carbon cycling on Caribbean coral reefs (Walker, Kinzig, & Langridge, 1999). Moreover, the density of *X. muta* on reefs off Key Largo, Florida has more than doubled since 2000 (McMurray, Finelli, & Pawlik, 2015). The general framework developed here should be applicable for further studies of the dynamics of material fluxes mediated by active suspension feeders in aquatic systems and may be more broadly applied to better understand the dynamics of interactions between organisms and ecosystem function.

2 | MATERIALS AND METHODS

2.1 | Sponge feeding rates

Suspension feeding by *X. muta* was investigated in situ on Conch Reef (24°56′59″N; 80°27′13″W), Key Largo, Florida in June of 2013. Food availability is known to vary temporally on Conch Reef (e.g. McMurray, Johnson, Hunt, Pawlik, & Finelli, 2016); therefore, a total of 32 individuals were haphazardly selected for study at 20 m depth over the course of 6 days (5–6 sponges/day) to quantify feeding rates over a large natural range of food abundances. Individuals spanned a broad range of sizes, however, only individuals with a single osculum were included.

A total of 1 L of both incurrent (ambient) and excurrent seawater was collected from each sponge over a 5-min sampling interval with paired 100 ml syringes as previously described (McMurray et al., 2016). Following seawater sample collection, the dimensions of each sponge were measured and the morphology of *X. muta* was approximated as a frustum of a cone to obtain sponge volume estimates (McMurray, Blum, & Pawlik, 2008). Estimates of sponge pumping rates were derived from the equation $Q = 0.02\ V^{1.1}$ ($p < .001$, $R^2 = .78$; McMurray et al., 2014), where Q is the pumping rate (ml/s) and V is sponge volume (cm^3)

Particulate and dissolved organic carbon (POC and DOC respectively) in incurrent and excurrent seawater was quantified as previously described (McMurray et al., 2016). Briefly, each sample was filtered through a 100 μm mesh and subsequently through a pre-combusted GF/F glass fibre filter. In the laboratory, POC on filters was measured using a CE Elantech NC2100 elemental analyser; DOC in filtrate samples was measured using high-temperature catalytic oxidation with a Shimadzu TOC 5050 analyser. *Xestospongia muta* hosts symbiotic microbes which may contribute to DOC retention rates (Maldonado et al., 2012); therefore carbon flux estimates reported here consider the sponge as a holobiont.

To assess the effects of sponge feeding on POC and DOC, differences in the concentration of each food type between incurrent and excurrent seawater were analysed using paired *t*-tests. For each sponge, POC and DOC consumed were calculated as the difference between the quantities of each food resource in incurrent and excurrent seawater samples. To investigate selective feeding on food resource types, and if relative foraging effort between food resources varied as a function of relative food availability (McMurray et al., 2016), the $\log_{10}$-transformed ratio of POC:DOC consumed was regressed against the $\log_{10}$-transformed ratio of incurrent POC:DOC concentration (van Leeuwen, Brännström, Jansen, Dieckmann, & Rossberg, 2013). A one-tailed *t*-test was used to test if the slope of this regression was greater than a slope of 1 to examine frequency-dependent food consumption.

Retention efficiency of each food resource was calculated as:

$$\mathrm{RE} = \left(\frac{C_{\mathrm{in}} - C_{\mathrm{ex}}}{C_{\mathrm{in}}}\right) \times 100$$

where RE is the retention efficiency (%), and C_{in} and C_{ex} are the incurrent and excurrent quantities of each food resource (μM) respectively. The filtration rate for each food resource was calculated as:

$$\mathrm{FR} = (C_{\mathrm{in}} - C_{\mathrm{ex}}) \times Q$$

where FR is the filtration rate (μmol C s^{-1}). Ordinary least squares regression was used to examine how filtration rates for each food resource scaled with sponge size. Filtration rates were standardized by sponge volume to obtain specific filtration rates (μmol C s^{-1} l^{-1}). The relationship between specific filtration rate and $\log_e$-transformed incurrent food abundance for each food resource was described by ordinary least squares regression.

2.2 | Model of carbon flux

Stage-based matrix population models were used to examine how the demographics of *X. muta* influence population-mediated carbon flux. Models were parameterized by monitoring the fate of individuals in permanent 16 m diameter circular plots on Conch Reef, Florida from 2000 to 2012 as described by (McMurray et al., 2015). Briefly, all sponges within a total of nine plots, three each at 15, 20 and 30 m, were tagged and surveyed up to twice-yearly beginning in the spring of 2000. During each survey, the fate of all sponges was assessed and new recruits were identified and tagged. Each sponge was additionally photographed from above and in profile with a 16 cm scale.

We first parameterized a traditional stage-based matrix population model to describe the dynamics of *X. muta* on Conch Reef. To model the average trajectory of the Conch Reef population over 2000 to 2012, the time series was divided into two equal 6-year intervals, May 2000 to May 2006 and May 2006 to May 2012, and a summary matrix, ***A***, was constructed with transition probabilities calculated by pooling transitions over both 6-year intervals. At the beginning and end of each interval, sponges were assigned to one of six stages following McMurray, Henkel, and Pawlik (2010). For all sponges with typical cylindrical-like morphologies, UTHSCA Image Tool image analysis software was used to obtain two perpendicular measurements of the osculum diameter (OD) of each sponge and individuals were assigned to stages I–V based on estimates of sponge volume derived from the equation $V = 28.514 \times \mathrm{OD}^{2.1}$ ($p < .001$, $R^2 = .90$; McMurray et al., 2010): stage I (≤143.13 cm^3), stage II (>143.13 cm^3 but ≤1,077.13 cm^3), stage III (>1,077.13 cm^3 but ≤5,666.32 cm^3), stage IV (>5666.32 cm^3 but ≤17,383.97 cm^3) and stage V (>17,393.97 cm^3). Size classes were chosen to encompass the range of sponge sizes found in the population while minimizing sample and distribution errors (Caswell, 2001). All individuals with remnant-like morphologies, typically consisting of a thin ring of multi-oscule remnants, were assigned to the base stage. Individuals transition to the base stage after suffering partial mortality, but may subsequently transition to stages I–V after growth and fusion of oscules restores a cylindrical-like morphology (McMurray et al., 2010).

Xestospongia muta reproduces during sporadic mass broadcast spawning events (Ritson-Williams, Becerro, & Paul, 2004). While the genetic structure of populations across the Caribbean suggest that larval dispersal is influenced by ocean currents (López-Legentil & Pawlik, 2008), the degree of local connectivity remains unknown. Larval dispersal distance estimates of 60–140 m for *Xestospongia* species from the Indo-Pacific (Bell et al., 2014) suggest that the population of *X. muta* on Conch Reef may be demographically open; nonetheless, there is a possibility of self-recruitment, as eggs are negatively buoyant (Ritson-Williams et al., 2004). Given this uncertainty, we modelled both an open and demographically closed population.

The population dynamics of a demographically open population were described as $\boldsymbol{n}_{t+\Delta t} = \boldsymbol{A}\boldsymbol{n}_t + \boldsymbol{r}$, where $\boldsymbol{A}$ is a 6 × 6 population projection matrix that gives the transitions of individuals between stages through the processes of survivorship, survivorship and growth, and survivorship and shrinkage or partial mortality, $\boldsymbol{n}_t$ is a 6 × 1 vector of the number of individuals in each stage at time t, Δt is an interval of 6 years and $\mathbf{r}$ is a 6 × 1 vector with the number of new sponges that recruited to each stage and survived to the end of the 6-year interval.

In the case of a closed population, population dynamics were described as $\mathbf{n}_{t+\Delta t} = \mathbf{A}\mathbf{n}_t$, where $\mathbf{A}$ now accounts for per-capita fertility, defined as the number of new sponges in stage i, that recruited and survived to the end of each 6-year interval, produced per individual in stage j at the beginning of each time interval (Caswell, 2001). Evidence suggests that there is a minimum size (≈176–200 cm^3) of reproduction for sponges (Reiswig, 1973; Whalan, Battershill, & de Nys, 2007) and that reproductive output is proportional to body size (Uriz, Turon, Becerro, Galera, & Lozano, 1995; Whalan et al., 2007), but see (Fromont, 1994). Therefore, we assumed that stages II–V were reproductively active and that relative fertility was proportional to the size of sponges in each stage (Cropper & DiResta, 1999; Mercado-Molina, Sabat, & Yoshioka, 2011). Fertilities were then calculated following Caswell (2001) so that they satisfy the equation:

$$r_i(t+\Delta t) = \sum_{j=1} F_{ij} n_j(t)$$

where *r* is the number of new recruits and Δ*t* is an interval of 6 years.

Given knowledge of the transition of individuals between stages described by the summary matrix, ***A***, and estimates of the carbon flux through each sponge at the beginning and end of each 6 year interval (*t* and Δ*t*), a summary population-mediated carbon flux projection matrix, $\boldsymbol{A}^c$, was subsequently parameterized. The (*i*, *j*) entry of $\boldsymbol{A}^c$ describes the quantity of carbon consumed by stage *i* after 6 years, per the quantity of carbon consumed by stage *j* in year *t*. Based on our findings for the relationship between sponge specific filtration rates of total organic carbon (TOC) and incurrent TOC available (see Results), we assumed that the median incurrent TOC measured over our study was available (i.e. 80.94 μM); hence sponges consumed carbon at rates of 0.93 μmol C s^{-1} L $sponge^{-1}$. Because the volumes, and thus carbon consumption rates, of individuals in the base stage could not accurately be computed, they were omitted from analysis and $\boldsymbol{A}^c$ is therefore a 5 × 5 matrix. Prior work found that bases have a relatively small influence on population growth rates (McMurray et al., 2010) and bases have become an increasingly smaller proportion of the population of *X. muta* on Conch Reef over time (McMurray et al., 2015). Nonetheless, population-scale carbon flux estimates derived by this study should be viewed as conservative given the omission of the base stage. As stated earlier, we modelled both an open and demographically closed population.

To examine the dynamics of the population of *X. muta* and the effect of demography on population-mediated carbon flux, projections of **A** and $\mathbf{A}^c$ over 24 years were conducted using population vectors describing the initial population structure and quantity of carbon consumed by each stage in 2000, respectively, and a 6-year projection interval. The population growth rate (λ per 6 years) and elasticities were calculated using MATLAB (version 8.2.0.701 (R2013b); The MathWorks, Inc.) and bootstrap calculations were used to generate 95% confidence intervals for λ. For **A**, the dominant eigenvalue, λ, describes the population growth rate, with values <1 indicating population decline and values >1 indicating geometric growth. In the case of $\mathbf{A}^c$, λ describes the rate at which population-mediated carbon flux changes. For **A**, elasticities are the relative contribution of vital rates to the population growth rate (Caswell, 2001). In the case of $\mathbf{A}^c$, elasticities describe the relative importance of vital rates to changes in population-mediated carbon flux.

3 | RESULTS

3.1 | Sponge feeding rates

Over 6 days of sampling, ambient concentrations of POC and DOC ranged from 7.5 to 18.4 and 58.7–123.7 μM respectively. Sponges consumed significant quantities of both food resource types (POC: $t = 11.7$, $p < .001$; DOC: $t = 4.0$, $p < .001$; $df = 31$ for both tests).

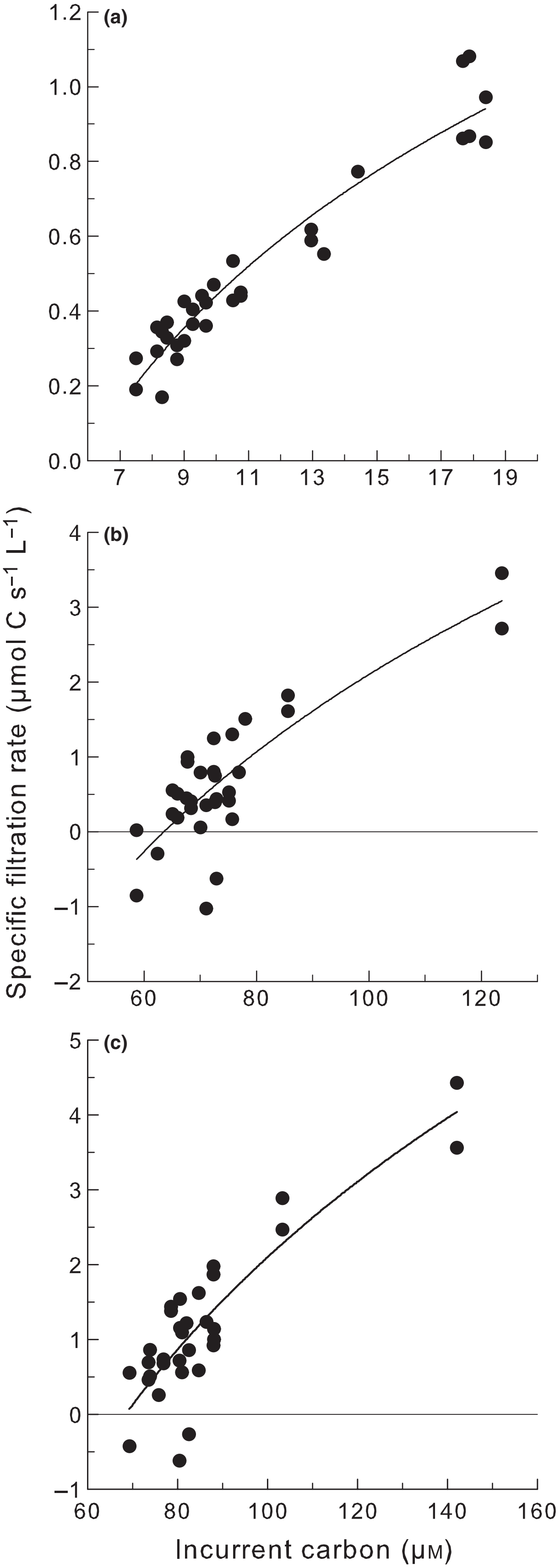

FIGURE 1 Relationship between specific filtration rate and food resource abundance for (a) particulate organic carbon (POC), (b) dissolved organic carbon (DOC) and (c) total organic carbon (TOC). $n = 32$

TABLE 1 Vectors describing the number of individuals (***n***) and the number of recruits (***r***) in each stage at time ***t***

	n_t			r_t	
Stage	**2000**	**2006**	**2012**	**2006**	**2012**
Base	33	23	22	2	4
I	23	101	207	94	184
II	38	68	114	46	56
III	55	46	65	5	17
IV	42	46	60	1	0
V	48	51	63	0	0

Filtration rates increased linearly with sponge volume for POC ($r^2 = .54$, $p < .001$), DOC ($r^2 = .21$, $p = .009$) and TOC ($r^2 = .36$, $p < .001$; see Figure S1).

Although a large proportion of the carbon available in incurrent seawater was in the form of DOC, sponges consistently preferred POC relative to DOC (Figure S2). There was a direct relationship between the $\log_{10}$ ratio of POC:DOC consumed versus the $\log_{10}$ ratio of incurrent POC:DOC ($r^2 = .23$, $p = .010$; Figure S2). The slope (±*SE*) of this relationship was 2.13 (±0.76), indicating that consumption is frequency-dependent; however, it was only marginally greater than a slope of 1 ($t = 1.49$, $df = 26$, $p = .074$; Figure S2). POC was generally retained with greater efficiency (mean ± *SD* = 68 ± 13%) relative to DOC (mean ± *SD* = 12 ± 16%), however, retention of both food types and TOC increased and approached an asymptote with incurrent food abundance (Figure S3). Similarly, there was a positive, logarithmic relationship between the concentration of each food resource in incurrent seawater and specific filtration rates (POC: $r^2 = .92$, $p < .001$; DOC: $r^2 = .68$, $p < .001$; TOC: $r^2 = .74$, $p < .001$; Figure 1).

3.2 | Demography and population-mediated carbon flux

The number of individuals in each stage, with the exception of the base stage, increased from 2000 to 2012 and stages I and II experienced the largest increases in sponges (Table 1). The fate of a total of 239 sponges was monitored from 2000 to 2006, 335 sponges were monitored from 2006 to 2012, and the population was comprised of 531 sponges in 2012. For stages I–V, the proportion of sponges that survived and remained in a particular stage (stasis) increased with sponge size while mortality was generally inversely related to sponge size (Table 2). Small proportions (0%–6%) of sponges in each stage were observed to shrink to smaller stages or suffer partial mortality and transition into the base stage. Sponge growth decreased with increasing sponge size and bases grew and contributed to all stages (Table 2). Mean sponge volumes of stages I–V increased over time and stages IV and V comprised approximately 18% and 76% of the total population volume respectively (Figure S4).

A total of 148 new sponges recruited between 2000 and 2006 and survived to the end of the interval, whereas a total of 261 recruited between 2006 and 2012 and survived to 2012. New recruits at the end of each 6-year interval mostly contributed to stages I and II,

TABLE 2 Population projection matrix (**A**) decomposed into transition (**T**) and fertility (**F**) matrices

		Stage					
Matrix	**Stage**	**Base**	**I**	**II**	**III**	**IV**	**V**
T	Base	0.4464	0.0081	0.0566	0.0396	0.0227	0.0101
	I	0.0714	0.1774	0.0283	0.0099	0	0
	II	0.1071	0.3710	0.2453	0.0198	0	0
	III	0.0357	0.1452	0.3585	0.2772	0.0341	0
	IV	0.0714	0	0.1321	0.4356	0.4432	0.0404
	V	0.0357	0	0	0.0495	0.3636	0.7576
	q_x	0.2321	0.2984	0.1792	0.1683	0.1364	0.1919
F	Base	0	0	0.0005	0.0032	0.0116	0.0465
	I	0	0	0.0217	0.1493	0.5381	2.154
	II	0	0	0.0080	0.0548	0.1974	0.7904
	III	0	0	0.0017	0.0118	0.0426	0.1705
	IV	0	0	0.0001	0.0005	0.0019	0.0077
	V	0	0	0	0	0	0
A	Base	0.4464	0.0081	0.0571	0.0428	0.0343	0.0566
	I	0.0714	0.1774	0.0500	0.1592	0.5381	2.154
	II	0.1071	0.3710	0.2532	0.0746	0.1974	0.7904
	III	0.0357	0.1452	0.3602	0.2890	0.0767	0.1705
	IV	0.0714	0	0.1322	0.4362	0.4451	0.0482
	V	0.0357	0	0	0.0495	0.3636	0.7576

q_x is the stage-specific mortality rate.

TABLE 3 Vectors describing the total carbon consumed (μM) by individuals (***n***) and recruits (***r***) in each stage at time ***t***

	n_t			r_t	
Stage	**2000**	**2006**	**2012**	**2006**	**2012**
I	1.06	4.59	9.36	4.31	8.44
II	14.0	24.9	44.0	17.9	21.8
III	139	120	169	13.4	45.6
IV	386	444	570	9.7	0
V	1820	1972	2398	0	0

but also contributed to stages III and IV and the base stage (Table 1). Assuming that fertility is proportional to sponge size, stages IV and V contributed the largest proportion of new individuals to the population, with each stage IV and V individual producing 0.79 and 3.2 surviving recruits over a 6-year interval respectively (Table 2; Figure S5).

Carbon flux estimates for each stage increased over time and total carbon flux for the population was largely contributed by the largest stages (Table 3). Growth of sponges was responsible for a large proportion of the change in carbon consumed by each stage; for example transition of stage I to stages II and III resulted in 317 and 854% more carbon consumed, respectively, after 6 years relative to carbon consumed by stage I individuals at time *t* (Table 4). Although recruitment was highest into stage I (Table 1) recruitment into stages II and III was responsible for larger contributions to carbon flux relative to stage I (Table 3). For all stages, contributions to carbon flux after 6 years due to the production of new individuals were much lower than those resulting from sponge survival and growth (Table 4).

Projecting forward over 24 years, there was a relatively small difference (2.5%) in carbon flux predicted by models that assume that the population is demographically open vs. closed (Figure 2). Density estimates from the open and closed models after 24 years differed by 26.7%, but this was due to differences in the number of new recruits which have a minimal effect on carbon flux. Therefore, for the purpose of further examining the effect of demography on population-mediated carbon flux, all subsequent analyses were conducted by assuming that the population was demographically closed and projections were limited to 24 years.

Population density increased under the conditions of **A** and the projected population structure was found to become increasingly dominated by small sponges through time (Figure 3). Projections of sponge density overestimated the actual density of *X. muta* on Conch Reef in 2006, but closely approximated the actual density of sponges observed in 2012. Similarly, population-mediated carbon flux was projected to increase over time and closely approximated estimates of flux derived from estimates of total sponge volume on Conch Reef in 2006 and 2012 (Figure 4). Projected flux estimates in 2000, 2012 and 2024 were 1.30, 1.74 and 2.77 $\mu\text{mol C s}^{-1}\,\text{m}^{-2}$ respectively. Population-mediated carbon flux was largely contributed by stages IV and V over time, whereas stages I–III accounted for only ≈8% of total carbon flux (Figure 4).

The rate of population growth, λ, for the Conch Reef population of *X. muta* was 1.28 (CI = 1.22, 1.34) and population-mediated carbon flux increased at a rate of 1.28 (CI = 1.21, 1.35). Elasticities of $\mathbf{A}^c$ indicated that sponge survival had a greater proportional influence on changes in population-mediated carbon flux than the production of new recruits (Table 5). Transitions responsible for the largest influence on changes in carbon flux included the survival and growth of sponges in stages I–IV, the stasis of stages IV and V and the production of new stage I and II individuals by the largest sponges (V). Total elasticities increased with increasing sponge size, indicating that the largest sponges had the greatest influence on changes in carbon flux (Table 5).

TABLE 4 Population-mediated carbon flux projection matrix ($\mathbf{A}^c$) decomposed into transition ($\mathbf{T}^c$) and fertility ($\mathbf{F}^c$) matrices

		Stage				
Matrix	**Stage**	**I**	**II**	**III**	**IV**	**V**
$\mathbf{T}^c$	I	0.1789	0.0035	0.0002	0	0
	II	3.170	0.2600	0.0030	0	0
	III	8.545	2.618	0.2887	0.0097	0
	IV	0	3.477	1.635	0.4535	0.0102
	V	0	0	0.7440	1.490	0.7653
$\mathbf{F}^c$	I	0	0.0000	0.0002	0.0008	0.0032
	II	0	0.0001	0.0007	0.0025	0.0099
	III	0	0.0001	0.0010	0.0037	0.0147
	IV	0	0.0000	0.0002	0.0006	0.0024
	V	0	0	0	0	0
$\mathbf{A}^c$	I	0.1789	0.0036	0.0004	0.0008	0.0032
	II	3.170	0.2601	0.0037	0.0025	0.0099
	III	8.545	2.618	0.2897	0.0133	0.0147
	IV	0	3.477	1.635	0.4541	0.0126
	V	0	0	0.7440	1.490	0.7653

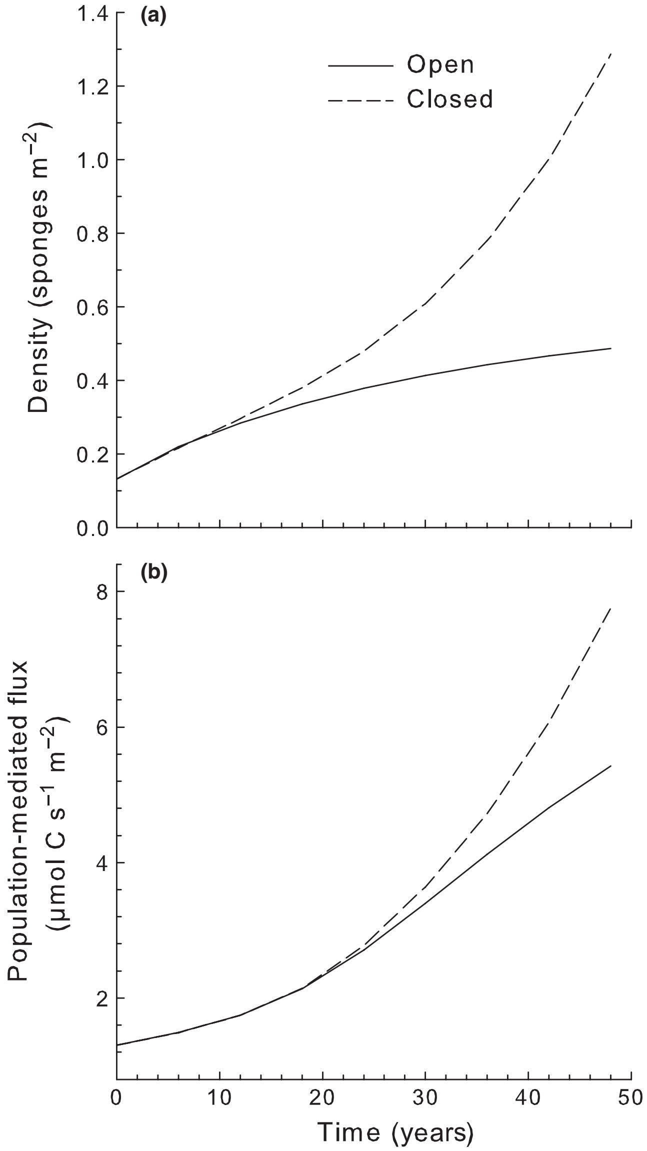

FIGURE 2 Projections of (a) sponge density and (b) population-mediated carbon flux over 48 years for demographically closed and open populations

4 | DISCUSSION

The significant changes in the dynamics and structure of coral reef benthic communities observed over recent decades (Ruzicka et al., 2013; Schutte, Selig, & Bruno, 2010) have highlighted the need for ecosystem-based approaches to management (NOAA, 2007). Despite the roles of benthic suspension feeders in mediating water-column processes on coral reefs (Colman, 2015; Maldonado et al., 2012), there has been little effort to quantify benthic suspension feeder-mediated fluxes in a way that is applicable to management needs. Estimates of material fluxes on the scales of populations and communities provide important insight into the magnitude of the influence of benthic suspension feeders on benthic-pelagic processes (Perea-Blázquez et al., 2012; Pile, Patterson, & Witman, 1996; Pile et al., 1997), but do not consider the dynamics and underlying demographic rates that mediate such processes. Our results for population-mediated carbon flux by *X. muta* indicate that population and ecosystem processes are not only tightly coupled, but also remarkably dynamic.

The population model presented here closely approximated changes in sponge demographics on Conch Reef over 2000–2012 (McMurray et al., 2015). Concurrent with increases in sponge density and biomass, sponge-mediated carbon flux was found to have increased over 2000–2012 and there was close agreement between carbon flux estimates and model projections. Although the degree of local connectivity for *X. muta* is presently unknown, there was little difference in projections of population-mediated carbon flux over the temporal scale considered (24 years) by assuming that the population was demographically open vs. closed. After 24 years, differences between the models increased as sponge density and carbon flux increased exponentially for closed models due to a lack of density dependence, but approached an asymptote for open models as per capita recruitment decreased with increasing population density, becoming effectively density-dependent (Caley et al., 1996). Under current conditions, projections indicate that both the density of *X. muta* and population-mediated carbon flux will continue to increase.

Elasticity analysis indicated that population-mediated carbon flux is mostly influenced by demographic processes that have a large effect on changes in population biomass. Specifically, changes in carbon flux are primarily influenced by three processes: (1) the growth of sponges in all stages, (2) the survival of the largest sponges (stages IV and V), and (3) the input of new recruits by the largest sponges (stage V). Given their size, which can exceed 1 m in height and diameter (McClain et al., 2015), the largest sponges have a proportionally high contribution to total population biomass, and hence, carbon flux, through the processes of reproduction and survival. These results highlight the need for increased conservation of the largest *X. muta*, as they are particularly susceptible to mortality from vessel groundings, dredging and marine debris (McMurray & Pawlik, 2009).

Sponge carbon flux estimates range from 0.5–3.5 mg C days^{-1} m^{-2} for the sponge *Callyspongia* sp. off southwestern Australia (Hanson, McLaughlin, Hyndes, & Strzelecki, 2009), 29 mg C days^{-1} m^{-2} for the sponge *Mycale lingua* in the northwest Atlantic (Pile et al., 1996), 1870 mg C days^{-1} m^{-2} for the sponges *Baikalospongia bacillifera* and *B. intermedia* occupying Lake Baikal (Pile et al., 1997), 70–3,500 mg C days^{-1} m^{-2} for a sponge assemblage off southern New Zealand (Perea-Blázquez et al., 2012), and 1,800–4,100 mg C days^{-1} m^{-2} for glass sponge assemblages in the northeastern Pacific (Kahn, Yahel, Chu, Tunnicliffe, & Leys, 2015). Using data on sponge biomass, carbon consumption and specific filtration rates from Reiswig (1971, 1973, 1974) we estimate the carbon fluxes for populations of the Caribbean sponges *Mycale laxissima*, *Verongula reiswigi* and *Tectitethya crypta* off Jamaica to be 2.1, 26.6 and 99.4 mg C days^{-1} m^{-2} respectively. Assuming the median incurrent TOC measured over our study was available for consumption by sponges, the mean carbon flux over 2000–2012 for *X. muta* was 1575 mg C days^{-1} m^{-2}. This estimate of carbon flux is greater than any other single-species rate and is likely partly because previous investigations only considered the flux of POC. Consistent with recent work

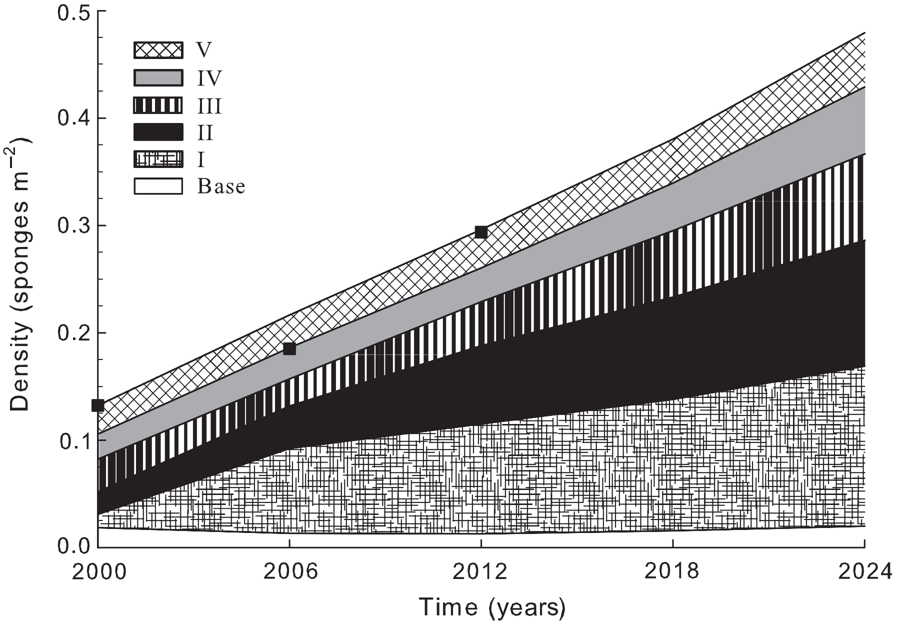

FIGURE 3 Projection of the closed population model, **A**, over 24 years from the initial population structure in 2000. Symbols (■) denote the actual densities of *Xestospongia muta* on Conch Reef in 2000, 2006 and 2012

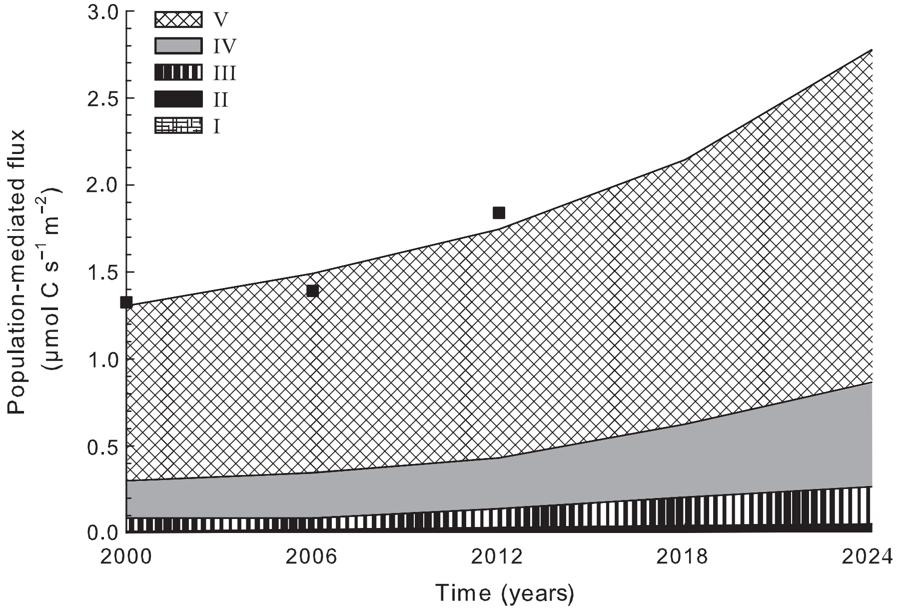

FIGURE 4 Projection of the closed population-mediated carbon flux model, $\mathbf{A}^c$, over 24 years from the initial carbon flux mediated by each stage in 2000. Symbols (■) denote estimates of population-mediated carbon flux by *Xestospongia muta* on Conch Reef in 2000, 2006 and 2012. Note that the carbon flux mediated by size class I is negligible and therefore is not visible as plotted

on DOC retention by sponges (de Goeij, van den Berg, van Oostveen, Epping, & van Duyl, 2008; Mueller et al., 2014; Yahel, Sharp, Marie, Häse, & Genin, 2003), DOC was found to generally account for a large proportion of TOC available in seawater (mean ± *SD* = 87 ± 3.0%) and a large proportion of the diet of *X. muta* (55 ± 20%). Nonetheless, such comparisons should be interpreted cautiously, as carbon flux can vary due to variability in available food resources and sponge diet selection (Hanson et al., 2009; McMurray et al., 2016; Rix et al., 2016). For example *X. muta* was found to selectively consume POC relative to DOC, and results support the hypothesis that consumption of POC relative to DOC is frequency-dependent (McMurray et al., 2016). Moreover, as shown here, the magnitude of carbon flux estimates is closely linked with sponge demographics. For example the mean volume of *X. muta* over the study interval, 1627 ± 300 cm^3/m^2, is 1–2 orders of magnitude greater than the volume of *M. laxissima* (5.0 cm^3/m^2), *V. reiswigi* (141 cm^3/m^2) and *T. crypta* (210 cm^3/m^2) (Reiswig, 1973). In addition, the biomass (as estimated tissue volume) of *X. muta*, and thus population-mediated carbon flux, increased by 39% from 2000 to 2012.

Increases in the sponge-mediated transfer of carbon from the pelagic to the benthos may have several implications for Caribbean coral reefs. The carbon incorporated into sponge biomass likely fuels higher trophic levels via predation by spongivorous fishes and turtles (Dunlap & Pawlik, 1998). *Xestospongia muta* is also long-lived (McMurray et al., 2008) and populations may buffer climate change as carbon is sequestered and stored as sponge biomass (Kahn et al., 2015). Furthermore, although the production of detritus by *X. muta* has yet to be directly quantified (McMurray et al., 2016), the transformation of dissolved

TABLE 5 Elasticity matrices of the population-mediated carbon flux projection matrix decomposed into transition and fertility matrices

		Stage				
Matrix	Stage	I	II	III	IV	V
$\mathbf{T}^{c}$	I	0.0139	0.0018	0.0004	0	0
	II	**0.0526**	0.0278	0.0015	0	0
	III	0.0333	**0.0656**	0.0353	0.0035	0
	IV	0	0.0422	**0.0966**	**0.0797**	0.0060
	V	0	0	0.0221	**0.1317**	**0.2261**
$\mathbf{F}^{c}$	I	0	0.0000	0.0006	0.0058	**0.0774**
	II	0	0.0000	0.0004	0.0039	**0.0512**
	III	0	0.0000	0.0001	0.0013	0.0178
	IV	0	0.0000	0.0000	0.0001	0.0014
	V	0	0	0	0	0
A^{c}	I	0.0139	0.0018	0.0010	0.0058	**0.0774**
	II	**0.0526**	0.0278	0.0019	0.0039	**0.0512**
	III	0.0333	**0.0656**	0.0354	0.0048	0.0178
	IV	0	0.0422	**0.0966**	**0.0798**	0.0074
	V	0	0	0.0221	**0.1317**	**0.2261**
Total		0.0998	0.1374	0.1570	0.2260	0.3799

Elasticities >0.05 are indicated in bold.

organic matter into detritus may be important for sustaining microbial, detritivore and benthic suspension feeder communities on coral reefs (de Goeij et al., 2013). More recently, it has been proposed that the growth of sponges and macroalgae is enhanced through a reciprocal positive interaction whereby sponges release nutrients that fertilize macroalgae and in return benefit from enhanced levels of macroalgal-derived labile DOC, all to the detriment of reef-building corals; a process termed the "vicious circle hypothesis," which may explain the lower resilience of Caribbean reefs relative to those in other parts of the tropics (Pawlik et al., 2016).

Coral reefs and other aquatic systems have experienced significant changes in ecosystem function over recent decades and are increasingly threatened by a number of anthropogenic and natural disturbances (Hoegh-Guldberg & Bruno, 2010). Benthic suspension feeders play a number of important functional roles in aquatic systems and there is increasing need to link population and ecosystem processes, as changes in benthic suspension feeder populations can result in large changes in ecosystem function. For example a reduction in stocks of the American oyster has been implicated in numerous ecological changes in the Chesapeake Bay, (Newell, 1988) and mortality of sponges in Florida Bay resulted in an increased prevalence of algal blooms and a concurrent decrease in light availability to benthic plant communities (Peterson et al., 2006). Stage-based matrix models have traditionally been used to investigate how biotic and abiotic factors affect population processes (Caswell, 2001); more recently, such models have been applied to examine the influence of populations on ecosystems, including changes in the carbon dynamics of forests (Hu, Wang, Guo, Xu, & Fang, 2015; Kruys, Jonsson, & Stahl, 2002; Liang & Zhou, 2014). To our knowledge, this is the first attempt to apply similar methods to marine systems; and given the important roles of benthic suspension feeders in the cycling of carbon and other nutrients, including phosphorous and nitrogen (Southwell et al., 2008; Zhang et al., 2015), we anticipate that the framework developed here should serve as a foundation for further work investigating the dynamics of population-mediated material fluxes and the consequences of those dynamics in aquatic systems. Moreover, this approach, a conversion of the basic unit of measurement for population models (i.e. the individual) into quantifiable metrics of species traits or activities, may be more broadly applied to better understand the dynamics of interactions between organisms and ecosystem function. For example it would allow management and conservation efforts to identify and target the particular life stages of species that have the largest influence on ecosystem processes. Furthermore, functional variation within species can exceed functional variation among species, highlighting the need to consider population demography in studies of community structure and ecosystem function (Rudolf & Rasmussen, 2013). Considering the recent and predicted changes in the demographics of populations of aquatic and terrestrial organisms due to the global changes that characterize the Anthropocene (Boyce, Haridas, & Lee, 2006), there is increasing need to better understand and consider links between population and ecosystem processes.

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AUTHORS' CONTRIBUTIONS

S.E.M. conceived the ideas, designed methodology, collected the data, analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data deposited in The Biological and Chemical Oceanography Data Management Office (BCO-DMO): http://dx.doi.org/10.1575/1912/bco-dmo.685952 (http://darchive.mblwhoilibrary.org/handle/1912/8835) (McMurray, Pawlik, & Finelli, 2017).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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