

1 **Hot moments in spawning aggregations:**
2 **Implications for ecosystem-scale nutrient**
3 **cycling**

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26 **Abstract**

27 Biogeochemical hot moments occur when a temporary increase in availability of one or more
28 limiting reactants results in elevated rates of biogeochemical reactions. Many marine fish form
29 transient spawning aggregations, temporarily increasing their local abundance and thus nutrients
30 supplied via excretion at the aggregation site. In this way, nutrients released by aggregating fish
31 could create a biogeochemical hot moment. Using a combination of empirical and modeling
32 approaches, we estimate nitrogen and phosphorus supplied by aggregating Nassau grouper
33 (*Epinephelus striatus*). Data suggest aggregating grouper supply up to an order-of-magnitude more
34 nitrogen and phosphorus than daily consumer-derived nutrient supply on coral reefs without
35 aggregating fish. Comparing current and historic aggregation-level excretion estimates shows that
36 overfishing reduced nutrients supplied by aggregating fish by up to 87%. Our study illustrates a
37 previously unrecognized ecosystem viewpoint regarding fish spawning aggregations, and provides
38 an additional perspective on the repercussions of their overexploitation.

39 **Introduction**

40 Hot spots and hot moments are defined by the intensification of
41 biogeochemical reactions spatially and temporally, respectively (McClain et al.
42 2003). Hot moments are typically associated with physical disturbances such as
43 hurricanes or floods that temporarily increase the abundance of one or more
44 limiting reactants (McClain et al. 2003). Hot moments, similar to resource pulses,
45 are characterized by intense but brief increases in a limiting resource. However,
46 unlike resource pulses, hot moments need not be rare or unpredictable (McClain
47 et al. 2003; Yang et al. 2008). Recently, increasing attention has been given to the
48 role of consumers in facilitating hot spots via nutrients released as excretion
49 (Powell et al. 1989; Frank et al. 1994; McIntyre et al. 2008; Bouletreau et al.
50 2011; Ruhl et al. 2011; Allgeier et al. 2013; Peterson et al. 2013), but less
51 attention has been given to their role in creating potential hot moments (but see
52 Post et al. 1998; Glud et al. 2008).

53 The formation of fish spawning aggregations (FSAs) is common in
54 tropical reef fish species (Sadovy de Mitcheson et al. 2008). FSAs are either

55 resident, occurring when fish convene at a central location on a home reef, or
56 transient, when fish travel from surrounding reefs to a fixed location at a specific
57 time of year (Domeier and Colin 1997). By temporarily increasing fish abundance
58 at specific sites, transient FSAs may create hot moments through excretion of
59 nitrogen (N) and phosphorus (P). This process could have important implications
60 for ecosystem processes (e.g., enhanced primary, microbial, or coral production),
61 particularly in oligotrophic waters that are common in tropical regions.

62 Nassau grouper (*Epinephelus striatus*; hereinafter grouper) is one of the
63 most well-known aggregating species, with >50 known FSAs throughout the
64 Caribbean, although the majority of these have been heavily overfished such that
65 many no longer form (Sadovy and Eklund 1999). To investigate the potential for
66 transient FSAs to create biogeochemical hot moments through supply of N and P,
67 we use empirically-derived excretion models for N and P, along with recent visual
68 survey estimates of aggregation sizes. In addition, we estimate the effect of
69 fishing pressure on nutrients supplied by aggregating grouper by comparing
70 estimates of nutrient supply on current and historic aggregations.

71 **Materials and Methods**

72 **Nitrogen and Phosphorus Excretion Models**

73 Using experimental and bioenergetics approaches, two linear models were
74 constructed to predict excretion rates (i.e., a pair of models for both N and P) for a
75 given mass of an individual grouper. Empirical *in situ* excretion rates of dissolved
76 forms of N and P were measured as the difference in nutrients before and after
77 fish were incubated in a bag of prefiltered water (Allgeier et al. 2014).

78 Bioenergetics models, i.e., a mass-balance approach to estimate excretion
79 (Schreck and Moyle 1990), were generated from stoichiometric values for grouper

80 and their diet and published physiological data (Allgeier et al. 2013, 2014; see
81 Electronic Supplementary Materials, ESM, for details). Estimates of bioenergetic
82 model coefficients were then used as priors to inform the empirical data in a linear
83 Bayesian model, providing robust posterior distributions for the slope and
84 intercept (Allgeier et al. 2014). These posterior distributions were used to predict
85 estimates of nutrient supply for a given size of grouper. We acknowledge that
86 many factors can affect nutrient excretion (e.g., temperature, feeding, activity
87 levels). For this reason, in all cases, simulation by means of Monte Carlo draws
88 was used to propagate uncertainty into our estimates of aggregate fish nutrient
89 supply.

90 **Aggregation Loading Models**

91 *Current Aggregation*

92 Estimates of grouper abundance, length frequency distributions, and the
93 yearly durations for current FSAs were collected from the Little Cayman FSA
94 (2004 through 2009), as described in Heppell et al. (2012). The Little Cayman
95 FSA, located off of the island of Little Cayman, British West Indies, has been
96 monitored since 2003 (Whaylen et al. 2004, 2006; Heppell et al. 2012). The N and
97 P loading rates for the aggregation were estimated separately for each year using a
98 Monte Carlo simulation (see ESM for model details). While the aggregation
99 occurs at depths of 24-33 m, when not spawning, aggregating fish typically stay
100 within 6 m of the bottom over an area of approximately 5,000 m² (Whaylen et al.
101 2004). Therefore, to facilitate comparisons with other published estimates of
102 consumer-derived nutrient loading, we present N and P nutrient load estimates in
103 g m⁻² day⁻¹ (Allgeier et al. 2013).

104 *Historic Aggregation*

105 Smith (1972) recorded the first description of a grouper spawning
106 aggregation. The aggregation, first discovered by fishermen, occurred in January
107 of 1971 off of Cat Cay, Bahamas. Smith (1972) did not provide daily estimates of
108 fish abundance in his description; however, observations from the current Little
109 Cayman aggregation suggest that abundance of fish on an aggregation can vary
110 widely from day to day (Table 1). The data collected on the Little Cayman
111 aggregation site (described above) show a strong correlation between the standard
112 deviation in daily abundance of grouper and the peak abundance estimate for each
113 year ($R^2 = 0.85$). We used the relationship between variance and peak abundance
114 to generate estimates of daily fish abundance at the historic aggregation for both
115 the conservative (30,000 fish) and upper-end (100,000 fish) estimates of fish
116 abundance provided by Smith (1972; also see ESM Methods). The length
117 frequency distribution from the Little Cayman FSA in 2009 was used for the
118 historic models, as this distribution most closely approximates a length
119 distribution on an unfished aggregation (Heppell et al. 2012). The N and P loading
120 rates for both the conservative and upper end estimates were generated using the
121 same Monte Carlo simulations as described in the ESM.

122 **Results and Discussion**

123 Our estimates suggest that aggregating grouper excrete between 1.54 - 4.61 g N
124 m^{-2} and 0.75 - 2.27 g P m^{-2} over the course of a FSA (5-10 d; Table 1). Estimated
125 nutrient loading by aggregating grouper is higher than daily areal-based loading
126 rates of many other nutrient inputs in a wide variety of ecosystems despite the
127 exclusion of nutrients supplied via gametes from our estimates (Figure 1). For
128 example, aggregating grouper excreted ~3.4 times more N and ~26 times more P

129 per area per day than juvenile grunts schooling over a single coral head (Meyer et
130 al. 1983), and ~8 times more N and ~32 times more P per area per day than the
131 fish communities on artificial reefs in seagrass beds in the Bahamas (Allgeier et
132 al. 2013). In both of these previous studies, important ecological effects were
133 demonstrated as a result of the concentrated nutrient supply (i.e., enhanced coral
134 and seagrass growth, respectively), suggesting that the quantity of nutrients
135 supplied by FSAs may have ecological repercussions.

136 However our approach likely oversimplifies the nutrient dynamics
137 associated with FSAs. For example, because grouper likely feed while on the
138 aggregation site, they remove prey fish from the local community. Consequently,
139 further research is needed to determine the effect of predation by grouper on
140 consumer driven nutrient cycling during non-aggregation periods. Additionally,
141 because we only estimate supply rates of N and P via grouper excretion in our
142 study, our data do not allow us to differentiate between import, recycling, and
143 export of N and P to/from the aggregation site.

144 Additionally, physical conditions, such as currents and upwelling, are
145 important to consider with respect to the ecological repercussions of grouper-
146 supplied nutrients for the local ecosystem, as currents could transport a significant
147 portion of the excreted nutrients away from the site and upwelling could decrease
148 nutrient limitation at the aggregation site. The behavior of grouper, which rest
149 amongst or just above the reef during non-spawning periods (Whaylen et al. 2004)
150 where current speed is the slowest (Cherubin et al. 2011), potentially increases the
151 retention of excreted nutrients. Further, nutrient demand from abundant primary
152 producers (e.g., zooxanthellae, macroalgae) and filter feeding organisms (i.e.,
153 sponges) typically found on the shallow mesophotic reefs where aggregations

154 typically occur may retain a large fraction of the excreted nutrients within the area
155 (Lesser et al. 2009).

156 A defining requirement for the formation of a biogeochemical hot moment
157 is the sudden increase in one or more limiting reactants. Mesophotic reefs are
158 characterized by higher ambient nutrient availability as a consequence of
159 upwelling and internal waves (Lesser et al. 2009). Leichter et al. (2003) found that
160 internal bores significantly increase N and P availability on mesophotic reefs in
161 the Florida Keys. However, to our knowledge it is unknown whether the nutrients
162 delivered by these bores are sufficient to alleviate N and P limitation on
163 aggregation sites. Our estimates of nutrient supplied FSAs represent 2-97% of the
164 N and 7-216% of the P supplied per square meter of reef by an internal bore,
165 suggesting that N and P loading by FSAs may still represent a significant pulse of
166 these nutrients. Future research is needed to determine the degree to which
167 primary production is limited by N and P at aggregation sites, the proportion of
168 nutrients supplied by grouper retained within local environment around the
169 aggregation site and how this pulse of nutrients compares to the delivery of
170 nutrients via upwelling at aggregation sites.

171 Previous studies of nutrients supplied via consumer excretion typically
172 focus on a constant press of nutrients resulting in biogeochemical hot spots which
173 are relatively stable over space and time (Meyer et al. 1983; Allgeier et al. 2013;
174 Capps and Flecker 2013; Layman et al. 2013; Peterson et al. 2013). Pulses of
175 nutrients can result in biogeochemical hot moments that are temporally and
176 spatially variable. For example, a hot moment generated by a Gobi Desert dust
177 cloud doubled biomass and increased chlorophyll uptake efficiency in the North
178 Pacific for two weeks (Bishop et al. 2002). Mass coral spawning creates a hot
179 moment indicated by increased biological oxygen demand and subsequent

180 increased rates of nutrient cycling on reefs that persist for approximately one
181 week (Eyre et al. 2008; Glud et al. 2008; Guest 2008). Our results suggest that
182 transient FSAs may result in the formation of a biogeochemical hot moment as a
183 consequence of the N and P excreted by aggregating fish. As such, further
184 research should be directed towards understanding the biogeochemical response
185 to nutrients supplied during FSAs and the importance of these nutrients in the N
186 and P budgets at aggregation sites.

187 The number of grouper that gather at FSAs has been significantly reduced
188 by direct fishing pressure, and many FSAs have ceased to form entirely (Sadovy
189 1997; Sadovy and Domeier 2005). We estimate the historic FSA supplied a total
190 of 3.58-11.94 g N m⁻² and 1.75-5.85 g P m⁻² (Table 1). Assuming the aggregation
191 described by Smith (1972) was representative of other grouper aggregations
192 throughout the Caribbean, these estimates suggest that fishing has reduced the
193 input of N and P by up to 87%. The active Little Cayman aggregation is
194 estimated to cover ~5,000 m² compared to the estimated 50,000 m² covered by the
195 historic aggregation. Therefore, both the total input and spatial extent of N and P
196 inputs has diminished. Our results imply that, in addition to altering grouper
197 population dynamics, heavy fishing pressure at FSA sites may have important
198 biogeochemical consequences that have previously been overlooked.

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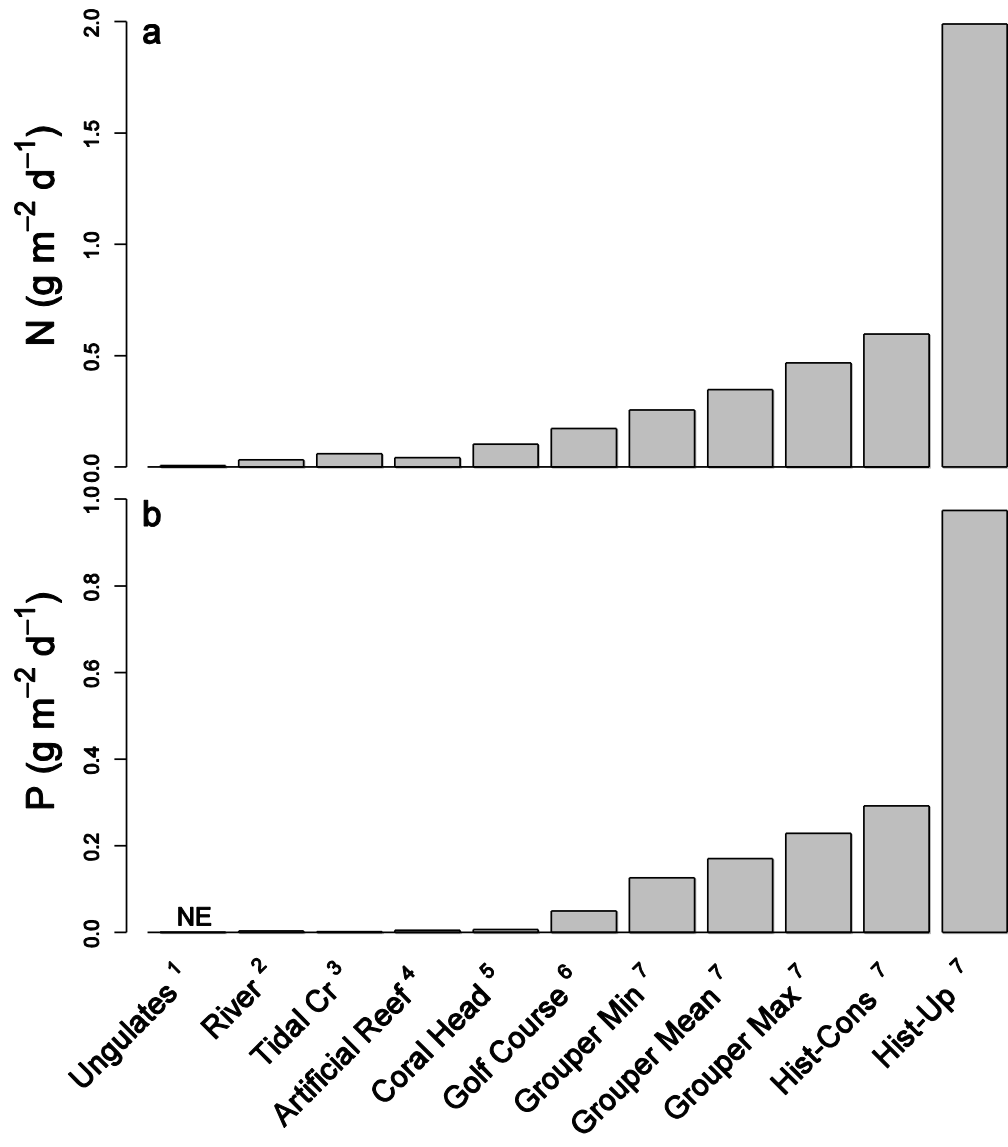
299 **Figure Legends**

300 Figure 1. A comparison of **(a)** nitrogen, N, and **(b)** phosphorus, P, loading rates ($\text{g m}^2 \text{d}^{-1}$). The
301 values presented are from: 1- ungulate excretion in Yellowstone National Park (P not estimated by
302 the study as indicated by NE; Frank et al. 1994), 2- fish excretion in a tropical river (McIntyre et
303 al. 2008), 3- grey snapper (*Lutjanus griseus*) excretion in Bahamian tidal creeks (Layman et al.
304 2011), 4- excretion from the fish community on artificial reefs in The Bahamas (Allgeier et al.
305 2013), 5- excretion by haemulid fish schooling over a coral head (Meyer et al. 1983), 6- fertilizer
306 inputs to a golf course (King et al. 2007), and 7- from this study the minimum, mean, and
307 maximum (Grouper Min, Grouper Mean, and Grouper Max respectively) excretion estimates from
308 the Nassau grouper (*Epinephelus striatus*) spawning aggregation off of Little Cayman, British
309 West Indies. Also shown is the mean excretion for conservative (Hist-Cons) and upper end (Hist-
310 Up) population estimates by Smith (1972) from the Nassau grouper spawning aggregation off of
311 Cat Cay, Bahamas. All estimates of grouper nutrient loading exclude any contribution of nutrients
312 contained in gametes.

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319 Table 1. Summary of the estimated nitrogen (N) and phosphorus (P) excretion from the Little
 320 Cayman Nassau Grouper (*Epinephelus striatus*) aggregation from 2004 to 2009 and the historic
 321 aggregation described by Smith (1972). The numbers reported for each year are the duration of the
 322 aggregation in days, the number of fish at the aggregation site, the length of a subset of fish on the
 323 aggregation site in mm, the daily loading of nitrogen (N) and phosphorus (P) in g m^{-2} , and the total
 324 input of N and P over the entire aggregation in g m^{-2} . All numbers reported are means (SD). All
 325 estimates of grouper nutrient loading exclude any contribution of nutrients contained in feces and
 326 gametes.

Year	Duration (d)	Fish	Length (mm)	Daily N ($\text{g m}^{-2} \text{d}^{-1}$)	Daily P ($\text{g m}^{-2} \text{d}^{-1}$)	Total N (g m^{-2})	Total P (g m^{-2})
<i>Little Cayman Aggregation</i>							
2004	8	1108 (844)	631 (90)	0.27 (0.20)	0.13 (0.10)	2.15 (1.38)	1.06 (0.67)
2005	10	1042 (650)	636 (80)	0.26 (0.16)	0.13 (0.08)	2.56 (1.65)	1.26 (0.80)
2006	6	1300 (457)	640 (79)	0.32 (0.11)	0.16 (0.06)	1.94 (1.25)	0.96 (0.60)
2007	5	1431 (145)	608 (75)	0.31 (0.03)	0.15 (0.02)	1.54 (0.98)	0.75 (0.48)
2008	10	2000 (922)	623 (77)	0.46 (0.21)	0.23 (0.10)	4.61 (2.96)	2.27 (1.43)
2009	6	2350 (1129)	591 (77)	0.47 (0.22)	0.23 (0.11)	2.81 (1.79)	1.37 (0.87)
<i>Historic Aggregation</i>							
Conservative	6	30000 (3498)	591 (76.87)	0.60 (0.37)	0.29 (0.18)	3.58 (2.29)	1.75 (1.11)
Upper end	6	1000000 (4826)	591 (76.87)	1.99 (1.27)	0.97 (0.61)	11.94 (7.61)	5.85 (3.68)

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