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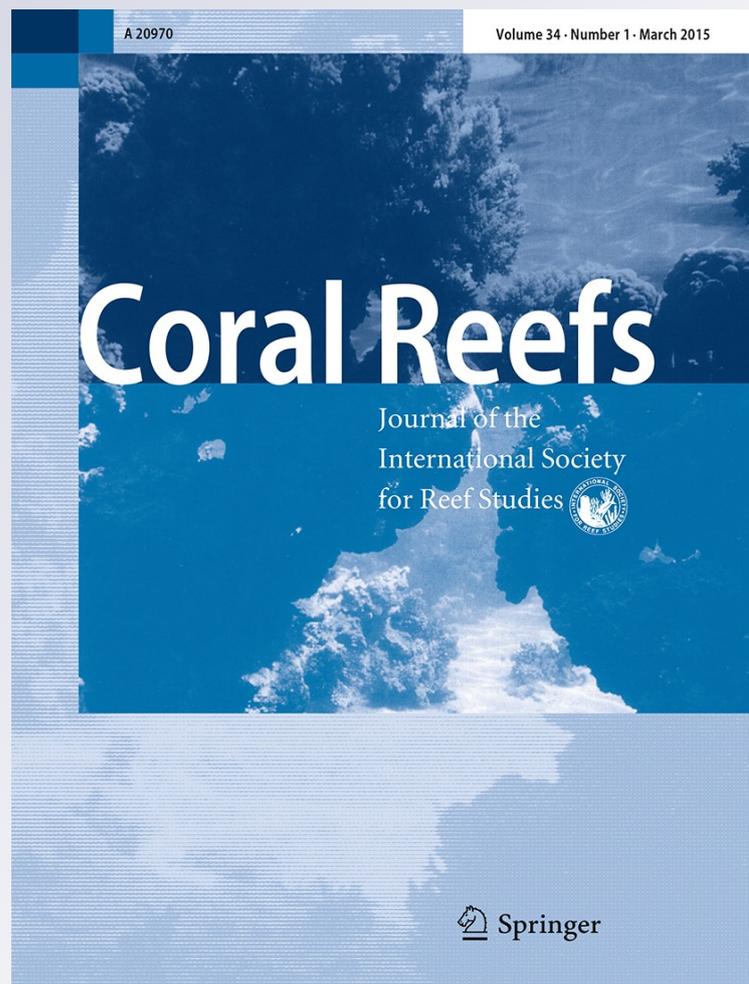
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Hot moments in spawning aggregations: implications for ecosystem-scale nutrient cycling

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Abstract Biogeochemical hot moments occur when a temporary increase in availability of one or more limiting reactants results in elevated rates of biogeochemical reactions. Many marine fish form transient spawning aggregations, temporarily increasing their local abundance and thus nutrients supplied via excretion at the aggregation site. In this way, nutrients released by aggregating fish could create a biogeochemical hot moment. Using a combination of empirical and modeling approaches, we estimate nitrogen and phosphorus supplied by aggregating Nassau grouper (*Epinephelus striatus*). Data suggest aggregating grouper supply up to an order-of-magnitude more nitrogen and phosphorus than daily consumer-derived nutrient supply on coral reefs without aggregating fish. Comparing current and historic aggregation-level excretion estimates shows that overfishing reduced nutrients supplied by aggregating

fish by up to 87 %. Our study illustrates a previously unrecognized ecosystem viewpoint regarding fish spawning aggregations and provides an additional perspective on the repercussions of their overexploitation.

Keywords Spawning aggregation · Nitrogen · Phosphorus · Nassau grouper · *Epinephelus striatus* · Biogeochemical hot moments

Introduction

Hot spots and hot moments are defined by the intensification of biogeochemical reactions spatially and temporally, respectively (McClain et al. 2003). Hot moments are typically associated with physical disturbances such as hurricanes or floods that temporarily increase the abundance of one or more limiting reactants (McClain et al. 2003). Hot moments, similar to resource pulses, are characterized by intense but brief increases in a limiting resource. However, unlike resource pulses, hot moments need not be rare or unpredictable (McClain et al. 2003; Yang et al. 2008).

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Recently, increasing attention has been given to the role of consumers in facilitating hot spots via nutrients released as excretion (Powell et al. 1989; Frank et al. 1994; McIntyre et al. 2008; Bouletreau et al. 2011; Ruhl et al. 2011; Allgeier et al. 2013; Peterson et al. 2013), but less attention has been given to their role in creating potential hot moments (but see Post et al. 1998; Glud et al. 2008).

The formation of fish spawning aggregations (FSAs) is common in tropical reef fish species (Sadovy de Mitcheson et al. 2008). FSAs are either resident, occurring when fish convene at a central location on a home reef, or transient, when fish travel from surrounding reefs to a fixed location at a specific time of year (Domeier and Colin 1997). By temporarily increasing fish abundance at specific sites, transient FSAs may create hot moments through excretion of nitrogen (N) and phosphorus (P). This process could have important implications for ecosystem processes (e.g., enhanced primary, microbial, or coral production), particularly in oligotrophic waters that are common in tropical regions.

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

Materials and methods

Nitrogen and phosphorus excretion models

Using experimental and bioenergetics approaches, two linear models were constructed to predict excretion rates (i.e., a pair of models for both N and P) for a given mass of an individual grouper. Empirical in situ excretion rates of dissolved forms of N and P were measured as the difference in nutrients before and after fish were incubated in a bag of prefiltered water (Allgeier et al. 2014). Bioenergetics models, i.e., a mass-balance approach to estimating excretion (Schreck and Moyle 1990), were generated from stoichiometric values for grouper and their diet and published physiological data (Allgeier et al. 2013, 2014; see Electronic Supplementary Materials, ESM, for details). Estimates of bioenergetic model coefficients were then used as priors to inform the empirical data in a linear Bayesian model, providing robust posterior distributions for the slope and intercept (Allgeier et al. 2014). These

posterior distributions were used to predict estimates of nutrient supply for a given size of grouper. We acknowledge that many factors can affect nutrient excretion (e.g., temperature, feeding, activity levels). For this reason, in all cases, simulation by means of Monte Carlo draws was used to propagate uncertainty into our estimates of aggregate fish nutrient supply.

Aggregation loading models

Current aggregation

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

Historic aggregation

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

Table 1 Summary of the estimated nitrogen (N) and phosphorus (P) excretion from the Little Cayman Nassau Grouper (*Epinephelus striatus*) aggregation from 2004 to 2009 and the historic aggregation described by Smith (1972)

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})
Little Cayman aggregation							
2004	8	1,108 (844)	631 (90)	0.27 (0.20)	0.13 (0.10)	2.15 (1.38)	1.06 (0.67)
2005	10	1,042 (650)	636 (80)	0.26 (0.16)	0.13 (0.08)	2.56 (1.65)	1.26 (0.80)
2006	6	1,300 (457)	640 (79)	0.32 (0.11)	0.16 (0.06)	1.94 (1.25)	0.96 (0.60)
2007	5	1,431 (145)	608 (75)	0.31 (0.03)	0.15 (0.02)	1.54 (0.98)	0.75 (0.48)
2008	10	2,000 (922)	623 (77)	0.46 (0.21)	0.23 (0.10)	4.61 (2.96)	2.27 (1.43)
2009	6	2,350 (1,129)	591 (77)	0.47 (0.22)	0.23 (0.11)	2.81 (1.79)	1.37 (0.87)
Historic aggregation							
Conservative	6	30,000 (3,498)	591 (77)	0.60 (0.37)	0.29 (0.18)	3.58 (2.29)	1.75 (1.11)
Upper end	6	1,000,000 (4,826)	591 (77)	1.99 (1.27)	0.97 (0.61)	11.94 (7.61)	5.85 (3.68)

The numbers reported for each year are the duration of the aggregation in days, the number of fish at the aggregation site, the length of a subset of fish on the aggregation site in mm, the daily loading of nitrogen (N) and phosphorus (P) in g m^{-2} , and the total input of N and P over the entire aggregation in g m^{-2} . All numbers reported are means (SD). All estimates of grouper nutrient loading exclude any contribution of nutrients contained in feces and gametes

upper end estimates were generated using the same Monte Carlo simulations as described in the ESM.

Results and discussion

Our estimates suggest that aggregating grouper excrete between 1.54–4.61 g N m^{-2} and 0.75–2.27 g P m^{-2} over the course of a FSA (5–10 d; Table 1). Estimated nutrient loading by aggregating grouper is higher than daily areal-based loading rates of many other nutrient inputs in a wide variety of ecosystems despite the exclusion of nutrients supplied via gametes from our estimates (Fig. 1). For example, aggregating grouper excreted ~ 3.4 times more N and ~ 26 times more P per area per day than juvenile grunts schooling over a single coral head (Meyer et al. 1983), and ~ 8 times more N and ~ 32 times more P per area per day than the fish communities on artificial reefs in seagrass beds in the Bahamas (Allgeier et al. 2013). In both of these previous studies, important ecological effects were demonstrated as a result of the concentrated nutrient supply (i.e., enhanced coral and seagrass growth, respectively), suggesting that the quantity of nutrients supplied by FSAs may have ecological repercussions.

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

between import, recycling, and export of N and P to/from the aggregation site.

Additionally, physical conditions, such as currents and upwelling, are important to consider with respect to the ecological repercussions of grouper-supplied nutrients for the local ecosystem, as currents could transport a significant portion of the excreted nutrients away from the site and upwelling could decrease nutrient limitation at the aggregation site. The behavior of grouper, which rest among or just above the reef during non-spawning periods (Whaylen et al. 2004) where current speed is the slowest (Cherubin et al. 2011), potentially increases the retention of excreted nutrients. Further, nutrient demand from abundant primary producers (e.g., zooxanthellae, macroalgae) and filter feeding organisms (i.e., sponges) typically found on the shallow mesophotic reefs where aggregations typically occur may retain a large fraction of the excreted nutrients within the area (Lesser et al. 2009).

A defining requirement for the formation of a biogeochemical hot moment is the sudden increase in one or more limiting reactants. Mesophotic reefs are characterized by higher ambient nutrient availability as a consequence of upwelling and internal waves (Lesser et al. 2009). Leichter et al. (2003) found that internal bores significantly increase N and P availability on mesophotic reefs in the Florida Keys. However, to our knowledge it is unknown whether the nutrients delivered by these bores are sufficient to alleviate N and P limitation on aggregation sites. Our estimates of nutrient-supplied FSAs represent 2–97 % of the N and 7–216 % of the P supplied per square meter of reef by an internal bore, suggesting that N and P loading by FSAs may still represent a significant pulse of these nutrients. Future research is needed to determine the degree

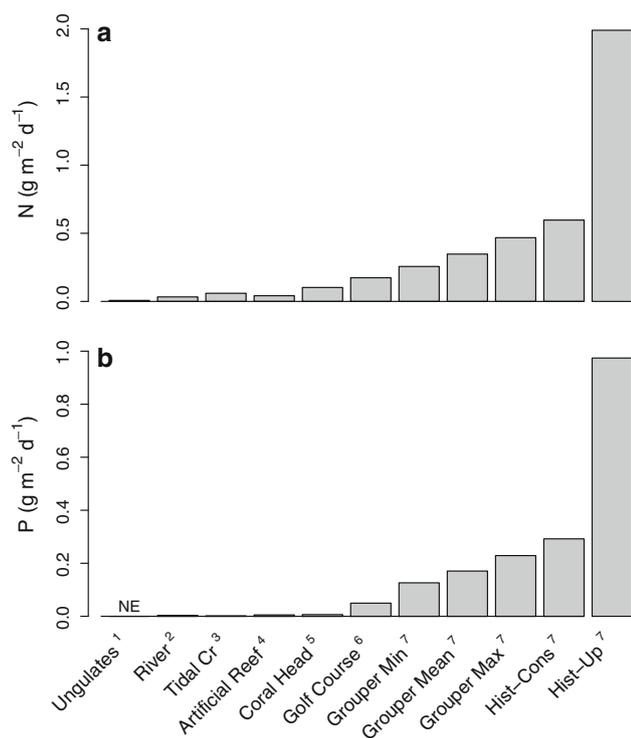


Fig. 1 A comparison of **a** nitrogen, N, and **b** phosphorus, P, loading rates ($\text{g m}^{-2} \text{d}^{-1}$). The values presented are from: 1 ungulate excretion in Yellowstone National Park (P not estimated by the study as indicated by NE; Frank et al. 1994), 2 fish excretion in a tropical river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

to which primary production is limited by N and P at aggregation sites, the proportion of nutrients supplied by grouper retained within the local environment around the aggregation site and how this pulse of nutrients compares to the delivery of nutrients via upwelling at aggregation sites.

Previous studies of nutrients supplied via consumer excretion typically focus on a constant press of nutrients, resulting in biogeochemical hot spots which are relatively stable over space and time (Meyer et al. 1983; Allgeier et al. 2013; Capps and Flecker 2013; Layman et al. 2013; Peterson et al. 2013). Pulses of nutrients can result in biogeochemical hot moments that are temporally and spatially variable. For example, a hot moment generated by

a Gobi Desert dust cloud doubled biomass and increased chlorophyll uptake efficiency in the North Pacific for 2 weeks (Bishop et al. 2002). Mass coral spawning creates a hot moment indicated by increased biological oxygen demand and subsequent increased rates of nutrient cycling on reefs that persist for approximately 1 week (Eyre et al. 2008; Glud et al. 2008; Guest 2008). Our results suggest that transient FSAs may result in the formation of a biogeochemical hot moment as a consequence of the N and P excreted by aggregating fish. As such, further research should be directed toward understanding the biogeochemical response to nutrients supplied during FSAs and the importance of these nutrients in the N and P budgets at aggregation sites.

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

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References

- Allgeier JE, Yeager LA, Layman CA (2013) Consumers regulate nutrient limitation regimes and primary production in seagrass ecosystems. *Ecology* 94:521–529
- Allgeier, JE, Layman, CA, Mumby, PJ, Rosemond, AD (2014) Consistent nutrient storage and supply mediated by diverse fish

- communities in coral reef ecosystems. *Glob Chang Biol* [doi:10.1111/gcb.12566]
- Bishop JKB, Davis RE, Sherman JT (2002) Robotic observations of dust storm enhancement of carbon biomass in the North Pacific. *Science* 298:817–821
- Bouletreau S, Cucherousset J, Villeger S, Masson R, Santoul F (2011) Colossal aggregations of giant alien freshwater fish as a potential biogeochemical hotspot. *PLoS One* 6:e25732
- Capps KA, Flecker AS (2013) Invasive fishes generate biogeochemical hotspots in a nutrient limited system. *PLoS One* 8:e54093
- Cherubin LM, Nemeth RS, Idrisi N (2011) Flow and transport characteristics at an *Epinephelus guttatus* (red hind grouper) spawning aggregation site in St. Thomas (US Virgin Islands). *Ecol Modell* 222:3132–3148
- Domeier ML, Colin PL (1997) Tropical reef fish spawning aggregations: defined and reviewed. *Bull Mar Sci* 60:698–726
- Eyre BD, Glud RN, Patten N (2008) Mass coral spawning: A natural large-scale nutrient addition experiment. *Limnol Oceanogr* 53:997–1013
- Frank DA, Inouye RS, Huntly N, Minshall GW, Anderson JE (1994) The biogeochemistry of a North-temperate grassland with native ungulates- nitrogen dynamics in Yellowstone National Park. *Biogeochemistry* 26:163–188
- Glud RN, Eyre BD, Patten N (2008) Biogeochemical responses to mass coral spawning at the Great Barrier Reef: effects on respiration and primary production. *Limnol Oceanogr* 53:1014–1024
- Guest J (2008) How reefs respond to mass coral spawning. *Science* 320:621–623
- Heppell SA, Semmens BX, Archer SK, Pattengill-Semmens CV, Bush PG, McCoy CM, Heppell SS, Johnson BC (2012) Documenting recovery of a spawning aggregation through size frequency analysis from underwater laser calipers measurements. *Biol Conserv* 155(119):127
- King K, Balogh J, Hughes K, Harmel R (2007) Nutrient load generated by storm event runoff from a golf course watershed. *J Environ Qual* 36:1021–1030
- Layman CA, Allgeier JE, Yeager LA, Stoner EW (2013) Thresholds of ecosystem response to nutrient enrichment from fish aggregations. *Ecology* 94:530–536
- Layman CA, Allgeier JE, Rosemond AD, Dahlgren CP, Yeager LA (2011) Marine fisheries declines viewed upside down: human impacts on consumer-driven nutrient recycling. *Ecol App* 21:343–349
- Leichter JJ, Stewart HL, Miller SL (2003) Episodic nutrient transport to Florida coral reefs. *Limnol Oceanogr* 48:1394–1407
- Lesser MP, Slattery M, Leichter JJ (2009) Ecology of mesophotic coral reefs. *J Exp Mar Bio Ecol* 375:1–8
- McClain ME, Boyer EW, Dent CL, Gergel SE, Grimm NB, Groffman PM, Hart SC, Harvey JW, Johnston CA, Mayorga E, McDowell WH, Pinay G (2003) Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. *Ecosystems* 6:301–312
- McIntyre PB, Flecker AS, Vanni MJ, Hood JM, Taylor BW, Thomas SA (2008) Fish distributions and nutrient cycling in streams: Can fish create biogeochemical hotspots? *Ecology* 89:2335–2346
- Meyer JL, Schultz ET, Helfman GS (1983) Fish schools - an asset to corals. *Science* 220:1047–1049
- Peterson BJ, Valentine JF, Heck KL Jr (2013) The snapper-grunt pump: Habitat modification and facilitation of the associated benthic plant communities by reef-resident fish. *J Exp Mar Bio Ecol* 441:50–54
- Post DM, Taylor JP, Kitchell JF, Olson MH, Schindler DE, Herwig BR (1998) The role of migratory waterfowl as nutrient vectors in a managed wetland. *Conserv Biol* 12:910–920
- Powell GVN, Kenworthy JW, Fourqurean JW (1989) Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. *Bull Mar Sci* 44:324–340
- Ruhl HA, Ellena JA, Wilson RC, Helly J (2011) Seabird aggregation around free-drifting icebergs in the northwest Weddell and Scotia Seas. *Deep Sea Res Part 2 Top Stud Oceanogr* 58:1497–1504
- Sadovy de Mitcheson Y, Cornish A, Domeier M, Colin PL, Russell M, Lindeman KC (2008) A global baseline for spawning aggregations of reef fishes. *Conserv Biol* 22:1233–1244
- Sadovy Y (1997) The case of the disappearing grouper: *Epinephelus striatus* the Nassau grouper, in the Caribbean and Western Atlantic. *Proceedings of the Forty-Fifth Annual Gulf and Caribbean Fisheries Institute* 45:5–22
- Sadovy Y, Eklund A-M (1999) Synopsis of biological data on the Nassau grouper, *Epinephelus striatus* (Bloch, 1792), and the Jewfish, *E. itajara* (Lichtenstein, 1822) NOAA Technical Report NMFS 146 Food and Agriculture Organization (FAO) fisheries synopsis 157, FAO, Rome
- Sadovy Y, Domeier M (2005) Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. *Coral Reefs* 24:254–262
- Schreck CB, Moyle PB (eds) (1990) *Methods for fish biology*. American Fisheries Society, Bethesda, ML
- Smith CL (1972) A spawning aggregation of Nassau grouper, *Epinephelus striatus* (Bloch). *Trans Am Fish Soc* 101:257–261
- Whaylen L, Pattengill-Semmens CV, Semmens BX, Bush PG, Boardman MR (2004) Observations of a Nassau grouper, *Epinephelus striatus*, spawning aggregation site in Little Cayman, Cayman Islands, including multi-species spawning information. *Environ Biol Fishes* 70:305–313
- Whaylen L, Bush P, Johnson B, Luke KE, McCoy C, Heppell S, Semmens B, Boardman M (2006) Aggregation dynamics and lessons learned from five years of monitoring at a Nassau grouper (*Epinephelus striatus*) spawning aggregation in Little Cayman, Cayman Islands, BWI. *Proceedings of the 59th Annual Gulf and Caribbean Fisheries Institute*. Fort Pierce Florida, Gulf and Caribbean Fisheries Institute
- Yang LH, Bastow JL, Spence KO, Wright AN (2008) What can we learn from resource pulses? *Ecology* 89:621–634