Incongruent long-term trends of a marine consumer and primary producers in a habitat affected by nutrient pollution

CHRISTOPHER A. LONG,† RYAN M. CHABOT, MIA N. EL-KHAZEN, JAKE R. KELLEY, CÉLINE MOLLET-SAINT BENOIT, AND KATHERINE L. MANSFIELD

1University of Central Florida, Orlando, Florida 32816 USA
2Inwater Research Group, Inc., Jensen Beach, Florida 34957 USA
3Metropolitan North Georgia Water Planning District, Atlanta Regional Commission, Atlanta, Georgia 30303 USA

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Abstract. Nutrient pollution, defined as excess nitrogen and phosphorus related to human activities, is a widespread anthropogenic impact that decreases water quality and limits light penetration in estuarine habitats. These factors can lead to shifts in primary producer communities, but the association between these changes and marine consumer patterns of abundance and growth is relatively unknown. Understanding these relationships is necessary for herbivorous species of conservation concern like the green turtle (Chelonia mydas). We used generalized additive models to analyze concurrent 18-yr data sets of seagrass cover, drift macroalgae cover, juvenile green turtle abundance, and growth to (1) evaluate long-term trends in primary producer cover and green turtle demographics; and (2) gain insights into their interrelatedness at a study site known to be affected by nutrient pollution throughout the study period. We found that seagrass cover sharply declined during our study period while macroalgae cover was more resilient with trends varying over time. Juvenile green turtle abundance slowly declined throughout the study period with altered intra-annual trends, while growth rates remained relatively stable. The incongruence of these trends suggests that relationships between marine consumers and nutrient pollution are more complex than effects on food availability alone. Our results focus on the green turtle but highlight the need for greater understanding of relationships between marine consumer species and nutrient pollution at both local and regional scales.

Key words: abundance trend analysis; macroalgae; marine primary producers; marine turtle; nutrient pollution; seagrass; water quality.

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† E-mail: clong@knights.ucf.edu

INTRODUCTION

Conservation biology focuses on species, populations, and ecosystems that are negatively impacted by human activities (Soulé 1985). Marine systems in general are often perturbed by a suite of anthropogenic threats (Halpern et al. 2007); however, coastal systems are closest to concentrated human populations, with 29% of the world’s overall population and 46% of the world’s urban population found within 100 km of the coast (Kummu et al. 2016). As a result of these concentrated human populations, coastal ecosystems are threatened by commercial,
recreational, and residential activities (Kennish 2002, Todd et al. 2019).

Estuaries are representative of the diffuse and diverse threats faced by coastal ecosystems; it is likely that nearly all estuaries face anthropogenic impacts in some way (Kennish 2002, Todd et al. 2019). Of particular note is the impact of nutrient pollution and eutrophication. Increased availability of nutrients within an estuary can stimulate the growth of both macroalgae and phytoplankton (Tomasko and Lapointe 1991, Short et al. 1995, Lapointe et al. 2015). Epiphytic macroalgae and microscopic phytoplankton compete for and decrease the available light for benthic species such as seagrasses, leading to decreased growth and survival (Tomasko and Lapointe 1991, Short et al. 1995, McGlathery 2001, Lee et al. 2007). Excess nutrients are also often implicated in harmful microalgal and phytoplankton blooms (Anderson et al. 2008, Heisler et al. 2008; hereafter, we use the acronym HAB(s) to refer to blooms of microscopic taxa, although the term “harmful algal bloom” is also sometimes used to describe macroalgal blooms), which can extend and exacerbate existing impacts of nutrient pollution on primary producers (Phlips et al. 2015, Lapointe et al. 2020).

Despite the widespread occurrence of nutrient pollution and its known potential for affecting primary producers, our understanding of nutrient pollution impacts on consumers is limited. While the direct toxicological effects of some bloom-causing taxa (e.g., brevetoxins produced by the red tide algae *Karenia brevis*, Baden 1989) are relatively well known (e.g., Landsberg 2002, Hallegaard 2003), the indirect impacts of nutrient pollution on large marine consumers are not well studied. Theoretically, changes in food levels could correlate with the abundance of consumers. Additionally, the habitat use and selection of an animal dependent on visual systems for foraging or predator avoidance may be affected independently of food availability. There are few long-term observations of these potential consumer responses to ecosystem changes related to nutrient pollution, but some experimental work documented behavioral changes in fish in response to changes in water clarity (Chiu and Abrahams 2010, Kimbell and Morrell 2015, Chacin and Stallings 2016).

The Indian River Lagoon (IRL) is a 156 mile long estuary along the east coast of Florida, USA, which extends from Volusia County in the north into Palm Beach County in the south. The IRL is designated as an Estuary of National Significance by the National Estuary Program and is highly biodiverse, hosting over 4000 species (IRLNEP 2007). The IRL is surrounded by a human population that expanded by 69% from 1990 to 2019 (U.S. Census Bureau 1995, 2019). This increasing human population has contributed to groundwater contamination from septic tanks, continued agricultural run-off, endogenous nutrient pools (e.g., mucky sediments), and atmospheric nitrogen deposition (Lapointe et al. 2015, Phlips et al. 2015, Barile 2018). In turn, these factors contributed to repeated, intense microalgal and phytoplankton blooms in the IRL throughout the past two decades (Phlips et al. 2015, Barile 2018). In particular, two nearly concurrent and long-lasting blooms, one of Pediphycae and pico-cyanobacteria and the other predominantly of *Aureoumbra lagunensis*, occurred from early 2011 to late 2012 (Phlips et al. 2015). Some of the blooms over the past two decades have heavily impacted primary producer communities and some IRL bloom taxa had known toxicological effects (Phlips et al. 2011, Phlips et al. 2015). But the relationship of long-term trends in primary producers with that of higher trophic levels has not been analyzed rigorously.

During these periods of rapid change, the IRL also served as a foraging habitat for juvenile green turtles (*Chelonia mydas*). Juvenile green turtles move to nearshore habitats like the IRL after spending the first few years of their lives in offshore habitats (Carr and Meylan 1980, Bolten 2003, Reich et al. 2007). Once they reach these nearshore habitats as larger juveniles, green turtles worldwide are considered generalist herbivores that exhibit differing foraging preferences among sites, with occasional omnivory as well (Jones and Seminoff 2013). In the IRL, juvenile green turtles predominantly forage on drift macroalgae (>85% of overall diet volume; Holloway-Adkins 2001, Redfoot et al. 2014), indicating the potential for resilience to nutrient pollution. But this resilience is uncertain because drift macroalgae and seagrasses experienced die-offs during the HABs of the 2010s (Phlips et al. 2015), green turtles may be at risk due to HAB-
related toxins (Perrault et al. 2020), and long-term trends of green turtle abundance in the IRL have not been analyzed since the mid-2000s (Ehrhart et al. 2007).

The ocean basin-scale trends for green turtles in the North Atlantic are encouraging (Seminoff et al. 2015), but also demonstrate a mismatch of scales. Green turtle population management units and Distinct Population Segments under the Endangered Species Act are on the scale of tens of thousands of square kilometers (Wallace et al. 2010, Seminoff et al. 2015), while the impacts of nutrient pollution vary at much smaller spatial scales and with land use, human population density, and oceanographic conditions (Howarth 2008, Oelsner and Stets 2019). Therefore, understanding how nutrient pollution may affect green turtle abundance and distributions necessarily includes analysis of site-specific trends in green turtle abundance and growth, and an examination of their correlations with biotic factors such as seagrass cover and food availability that are related to nutrient pollution. In the IRL, a long-term analysis of these trends is needed to assess impacts of sustained nutrient pollution on primary producers and juvenile green turtles that rely on them for food.

Here, we synthesize concurrent 18-yr data sets of IRL seagrass and drift macroalgae benthic coverage, along with juvenile green turtle abundance and growth rates in order to (1) document long-term changes in these four metrics (seagrass coverage, drift macroalgae coverage, and green turtle abundance and growth), and (2) compare any observed trends in order to assess the relationship of green turtle abundance and growth with primary producer communities. In so doing, our goal is not only to conduct the first long-term study of nutrient pollution impacts on marine turtles, but also contribute to a broader understanding of how marine consumer abundance and growth relate to primary producer abundance and nutrient pollution.

**Methods**

**Long-term marine turtle data collection**

Since 1982, the University of Central Florida Marine Turtle Research Group (UCFMTTRG) has collected abundance data on marine turtles in the IRL at a site just south of Sebastian Inlet, Florida (approximately 27.8312° N, −80.4395° W; Fig. 1). We captured turtles using a 455 m long large-mesh tangle net. During each sampling event, the start and end times of each capture session were recorded along with the number of turtles captured. The net was continuously monitored for entangled turtles by two small vessels. We used capture data from the beginning of 2001 through the end of 2018 in our analyses. This 18-yr period represents a consistent sampling effort in terms of duration of net soak time and number of sampling trips per year and season. This time period also allows us to effectively capture trends in marine turtle captures and growth before, during, and after the algal blooms of the early 2010s. For all of our data sets (turtle, seagrass, and algae), we defined the study day as the number of days since the beginning of 2001 (e.g., 1 January 2001 was study day 1 and 1 January 2002 was study day 366).

Captured turtles were transferred to an anchored vessel where we collected a suite of morphometric measurements, including straight carapace length (SCL), a standard measure of turtle size taken using calipers (Bolten 1999). Each turtle was examined for existing external Inconel flipper tags and scanned for an internal passive integrative transponder (PIT) tag; if these were not present, we applied new tags using standardized procedures (Balazs 1999). These tags allowed us to identify individual turtles captured over time during subsequent sampling events.

**Growth rates**

For recaptured individuals, we calculated a growth rate by calculating the difference between SCL from the two most recent captures and dividing by the number of years in between these captures (as in other marine turtle growth rate studies, e.g., Bjorndal et al. 2017). Some individuals had multiple recaptures and therefore were represented multiple times in this study. We used all recaptured turtles with a midpoint between any two captures occurring between 1 January 2001 and 31 December 2018 (i.e., an included individual may have been first captured before 2001 or last captured after 2018). We also defined a mean study day for growth rate analyses as the midpoint between the two captures converted into a study day as described in the previous section.
Seagrass and algae long-term data collection

We used St. John’s River Water Management District (SJRWMD) fixed transect data from seven seagrass bed study sites near the turtle study site to model long-term trends in seagrass and drift macroalgae (Fig. 1). These data were provided to us by the SJRWMD. For clarity, in the remainder of this study we refer to the large, weedy species of algae that marine turtles forage on as drift macroalgae and microscopic algae that cause HABs in the IRL as phytoplankton or HABs. We selected SJRWMD transect sites that

Fig. 1. Map of study sites. Star indicates the sea turtle capture site, circles indicate seagrass and algae transect sites. Numbers next to seagrass and algae transect sites are their SJRWMD site numbers. Site numbers with asterisks are sites that switched to monthly monitoring in 2010.
fell within the areas used by satellite-tracked juvenile green turtles captured and released at the UCFMTRG study site in 2008 (W. E. Redfoot, unpublished data). Each SJRWMD site was surveyed in summer and winter every year from 2001 to 2018; two sites (sites 42 and 43) switched to monthly surveys from 2010 to 2017.

Briefly, at each site trained SJRWMD staff collected seagrass percent cover and algae percent occupancy along a fixed transect from shore out to the deep edge of the seagrass bed. At 10-m intervals along a transect, a 1-m quadrat with a $10 \times 10$ cm grid was placed and percent cover of seagrass and the number of cells occupied by drift macroalgae (hereafter referred to as percent occupancy) were estimated. The seagrass species documented by SJRWMD were Halodule wrightii, Syringodium filiforme, Thalassia testudinum, Ruppia maritima, Halophila englemanii, Halophila decipiens, and Halophila johnsonii. Drift algae were not identified taxonomically in the SJRWMD data, but typical IRL taxa include rhodophytes (red algae) Gracilaria spp. and Hypnea spp., and in recent years, chlorophytes (green algae) such as Chaetomorpha spp. and Ulva spp. have become more common (Whitehouse and Lapointe 2015). In our analyses, we used the average total percent cover of all seagrass species and the average percent occupancy of drift algae for a given transect on a given day (rather than the plot level data). For a more detailed description of SJRWMD seagrass and algae field methods, see Vinrstein 2000, Morris et al. 2001.

**Statistical analyses**

We used generalized additive models (GAMs) to assess trends in green turtle abundance and hierarchical GAMs (HGAMs) to assess trends in green turtle growth rates, seagrass cover, and drift macroalgal cover. These models use non-parametric smoothing functions (referred to as “smooths” or “smoothers” hereafter) within a similar framework to that of generalized linear models: They fit the data by allowing for the incorporation of categorical, continuous, and/or hierarchical model factors, but allow for the use of smoothers in addition to linear or otherwise predetermined forms (Wood 2017, Pedersen et al. 2019). Smoothers balance minimizing residual error and overfitting through the use of penalty matrices that differ among smoother types. We used thin plate (Wood 2003) and cyclic cubic splines (Wood 2017), both of which penalize changes in the derivative(s) of a function. Cyclic cubic splines are also constrained so that the values and first derivative match at the ends of the function, making them useful for modeling seasonal variation (Wood 2017, Pedersen et al. 2019). Finally, we used tensor product smoothers, which are analogous to interaction terms in a mixed effect model (Wood 2017, Pedersen et al. 2019). The flexibility of this modeling framework allowed us to evaluate not only trends over time but the nature and timing of these trends. We constructed these models in R version 4.0.2 using the package mgcv (Wood 2011, Wood et al. 2016). See Data S1 for the R code for all analyses.

For green turtle abundance, we used a quasipoisson GAM to model the number of green turtle captures in a capture session. Quasipoisson distributions are similar to negative binomial distributions in that they can be used for overdispersed count data, but quasipoisson variance is a linear function of the mean and higher values of the dependent variable are weighted more heavily in fitting (Ver Hoef and Boveng 2007). Our model of green turtle abundance included the default thin plate smooths of study day (number of days since the beginning of 2001) and effort (length of net used/soak time), a cubic cyclic smooth of month to account for seasonal variation, and a tensor product smooth of study day and month to model non-additive effects of these two variables.

We used an HGAM structure to analyze green turtle growth rates with a thin plate smooth of the mean study day between the two captures, a thin plate smooth of the mean SCL of the turtle between the two captures, a tensor product smooth of those two factors, and a random effect of turtle ID number to account for multiple recaptures of some individuals. This model structure is analogous to a random intercept generalized linear mixed model (GLMM; Pedersen et al. 2019). Because of the large number of individuals relative to the size of the data set, we used the bam function in the package mgcv (instead of gam) for model construction as it more efficiently conducts the analysis over a high number of random effect levels (Pedersen et al. 2019). In addition, we used an HGAM with a thin plate smooth of mean study day and a random effect
of turtle ID number to examine changes in mean SCL over time in order to be sure that there was not a systematic change in the size structure of the growth rate data set.

Untransformed proportion data (e.g., percent cover and percent occupancy) are difficult to analyze because they do not fit the assumptions of most regression techniques (Warton and Hui 2011, Chen et al. 2017). For both seagrass percent cover and drift macroalgal percent occupancy, we used the logit transformation approach suggested by Warton and Hui (2011). The logit transformation cannot be used on values of 0; to alleviate this issue, we added a small constant value of 0.001 to all seagrass and drift macroalgae values, again as suggested by Warton and Hui (2011). After data transformation, for both seagrass and drift macroalgae data we used an HGAM structure including a thin plate smooth of study day, a cubic cyclic smooth of month, a tensor product smooth of those two variables, and a random effect for each site. This model structure is analogous to a random intercept GLMM (Pedersen et al. 2019).

We created figures using the package ggplot2 (Wickham 2016). We did not define a seasonal variable in the models, as we felt this created artificial bins of months. However, they do simplify the visualization of the data. For data visualization purposes only, we defined the seasons as follows: Winter includes the months December, January, and February; spring includes the months March, April, and May; summer includes the months June, July, and August; and fall includes the months September, October, and November. Monthly figures are presented in Appendix S1: Figs. S6–S8.

Given the relative unreliability of Akaike’s information criterion for evaluating the fit of hierarchical GAM models, especially among different model structures (Pedersen et al. 2019), we evaluated our models by incrementally increasing the wiggliness (i.e., increasing \(k\), the maximum number of knots) for the smoothing function for study day. As we did so, we evaluated the change in restricted maximum-likelihood and root-mean-squared residuals, with the goal of minimizing both (i.e., additional increases in \(k\) increased error). In the case that there were minimal differences in these metrics among potential models, we used the smallest \(k\) to avoid overfitting. We maximized \(k\) for month variables \((k = 12)\) and site-level random factors \((k = 7)\) when they were included in a model formulation. For mean SCL in the growth rate models, increasing \(k\) did not appreciably impact model results; therefore, we left it at the minimum \((k = 3)\). See Data S1 for model code related to this process.

**RESULTS**

**Long-term marine turtle capture data**

We conducted 419 turtle capture sessions from January 2001 to December 2018 with a total of 1289.9 h of net soak time. Only one capture session used a net length different from the standard (0.455 km), when on 7 July 2009 we used 0.220 km of net. Overall, our mean capture effort was 1.40 (SE 0.02) net kilometer hours per capture session. Over the 18-yr study period, we captured 2535 green turtles (mean per capture session: 6.05 captures, SE 0.31).

**Recaptured turtles for growth rate analysis**

Of the 2535 captured turtles, 202 had been previously captured and tagged (7.96%). These recaptured turtles consisted of 164 unique individuals (maximum eight recaptures, mean number of recaptures 1.23, SE 0.059); 21 individuals were recaptured more than once over the study period. The average interval between successive captures was 2.89 yr (range 0.76–7.61 yr, SE 0.12 yr), the average mean SCL of turtles used in growth rate analyses was 46.6 cm (SE 0.52, range 32.6–71.15 cm), and the average growth rate was 3.74 cm/yr (range 0.43–8.38 cm/yr, SE 0.09 cm/yr).

**Seagrass and drift macroalgae coverage**

We used SJRWMD data from a total of 382 seagrass and drift macroalgae surveys conducted across 170 sampling days at seven sites. Of these sites, two switched to monthly surveys in 2010 and totaled 101 and 102 surveys across the study period, respectively. The other five sites were monitored once per summer and once per winter, except for winter 2011 at site 35, for an average of 35.8 surveys across the study period.

Mean percent cover of seagrass for the entire study period ranged from 5.8% for site 40 to 24.6% for site 44 (mean 12.4%, SD 7.3%). The two
sites that had monthly surveys in the latter portion of the study period averaged 7.1% and 8.7% percent cover, respectively. Mean percent occupancy of drift macroalgae for the entire study period ranged from 6.3% for site 42 to 13.2% for site 40 (mean 9.3%, SD 2.5%).

**Long-term trends**

Juvenile green turtle abundance declined over the 18-yr study period. This decline occurred in two interrelated ways. First, the intra-annual variation decreased over time. Winter month captures (December, January, February) declined the most over the study period, with much smaller reductions in spring (March, April, May) and summer (June, July, August) turtle captures (Fig. 2). These changes resulted in reduced intra-annual variation in turtle abundance and, because winter captures were typically highest but declined the most, contributed to a long-term decline.

![Fig. 2. Green turtle abundance (a–d), seagrass percent cover (e–h), and algae percent occupancy (i–l) over the 18-yr study period (2001–2018). Points are actual data, blue solid lines are the predictions of the applicable GAM or HGAM, and blue dashed lines represent 95% confidence intervals (CIs). Rug plots along the x-axis and the right side of each figure represent the distribution of the sampled data; the green turtle captures y-axis rug is jittered to better visualize the distribution of these count data. Predictions and CIs were smoothed using the default loess smooth in geom_smooth in ggplot2 to avoid jagged steps from month to month. A portion of the turtle abundance data were also used by Ehrhart et al. (2007).](image)
decline in turtle abundance. After accounting for this change in intra-annual variation over time, there was also a slow but sustained long-term decline in the number of turtles captured (Appendix S1: Fig. S1a). Overall, after accounting for capture effort, monthly variations, and the change in monthly variation over the study period, mean model-predicted green turtle captures dropped from 7.89 captures per session in 2001 (SE 1.09) to 5.00 captures per session in 2018 (SE 0.32). We present the individual smooths and model coefficients for the turtle abundance model in Appendix S1: Fig. S1, Table S1. Juvenile green turtle growth rates declined slowly until the latter half of 2011 and then slowly increased after that (Fig. 3), although it should be noted that the confidence intervals are wide throughout the study period and even at the growth rate minimum, the confidence intervals still contain the maxima at the beginning and end of the study period. This long-term trend and the random effect to account for individual differences were the two statistically significant factors in our GAM. Turtle size, the non-additive change in the relationship between size and growth rates over time, and the interval between captures did not have statistically significant effects; we present the individual smooths and model coefficients for the growth rate model in Appendix S1: Fig. S2, Table S2. Mean SCL changed over time across the growth rate data set (Appendix S1: Fig. S3 and Table S3), but not.

Fig. 3. Green turtle growth rates over the 18-yr study period (2001–2018). Points are actual data; the blue solid line is the predictions of the applicable HGAM. Blue dashed lines represent 95% confidence intervals (CIs), which are particularly wide due to the individual-turtle random effect structure of the model. Rug plots along the x-axis and the right side represent the distribution of the sampled data.
in a consistent manner; mean SCL fluctuated but remained essentially the same throughout the study period except for approximately the first and last years when it was slightly higher.

Seagrass declines occurred throughout the study period, but declines were steeper and percent cover dropped to nearly zero following the intense algal blooms which began in early 2011 (Fig. 2). Seagrass percent cover was typically higher in summer months than winter, with relatively small changes in the seasonality of seagrass cover over the study period (Fig. 2, Appendix S1: Fig. S4b). Site-level variation was also important and of a similar magnitude to seasonal differences (Appendix S1: Fig. S4d). After accounting for seasonal and site-level variation, mean model-predicted seagrass percent cover dropped from 36.8% (SE 4.9%) in 2001 to 1.8% (SE 0.2%) in 2018.

Drift macroalgal percent occupancy rose slightly over the early portions of the study period and peaked around 2008 before declining during the 2011–2012 HABs and remaining low but recovering very slowly through the end of the study period. However, it should be noted that the macroalgal model did a relatively poorer job of fitting the observed data after 2012; this is perhaps due to the changing nature of the distribution of the data, which shifted from a relatively Gaussian distribution before the HABs to a right-skewed distribution afterward. As with seagrasses, monthly variation in macroalgal percent occupancy was an important factor but showed relatively small changes over time (Fig. 2, Appendix S1: Fig. S5b). Site-level variation was an important factor but lower than these same effects for seagrass (Appendix S1: Fig. S5d). After accounting for seasonal and site-level variation, mean model-predicted macroalgal percent occupancy rose from 8.2% (SE 0.6%) in 2001 to a peak of 9.6% (SE 0.6%) in 2008, then declined to a low of 0.4% (SE 0.05%) in 2012 and remained below 2% for the remainder of the study period. We present seagrass and drift macroalgal model component smooths and coefficients in Appendix S1: Figs. S4, S5, Table S1.

**DISCUSSION**

Our study provides the first simultaneous and long-term assessment of juvenile marine turtle abundance, juvenile marine turtle growth, and seagrass and drift macroalgal cover. Overall, although each long-term trend analysis has different features, green turtle abundance, green turtle growth, and seagrass cover each declined from 2001 through 2010. In contrast, drift macroalgal cover changed very little and may have even slightly increased over the same time period. During the severe HABs of 2011–2012, seagrass and drift macroalgal cover both dropped to nearly zero, but drift macroalgae began to recover slowly through the end of 2018 while seagrass cover remained very low relative to pre-HAB cover. Juvenile green turtle abundance continued to steadily and slowly decline through 2018, while growth rates returned to their previous levels.

These trends point to differences in the sensitivity of taxa to sustained nutrient pollution and resulting low water clarity in the IRL. Most seagrasses require high light levels for growth and survival (Dennison et al. 1993, Lee et al. 2007), and previous work in the IRL has shown correlations between nutrient inputs, freshwater influx, and light limitation of seagrass growth (Lapointe et al. 2020). Our results showing long-term and precipitous seagrass cover declines indicate the impacts of decreased light levels and nutrient pollution on seagrass cover in the IRL. In contrast, drift macroalgae are less sensitive to low-light levels and high nutrient conditions stimulate their growth (Markager and Sand-Jensen 1992, Dennison et al. 1993, Lapointe et al. 2015); to a degree, our data also indicate a tolerance of the impacts of nutrient pollution, with drift macroalgal cover stable while seagrass declined from 2001 to 2010. For both seagrass and drift macroalgae, our results show a similar precipitous drop-off during the HABs of 2011–2012 as that found in the northern IRL by Phlips et al. 2015, indicating that both are susceptible to die-offs under extreme conditions.

In the IRL, juvenile green turtle diet is composed mostly of drift macroalgae with a small portion of seagrass (Holloway-Adkins 2001, Redfoot et al., 2014, Long unpublished data). Juvenile green turtles are typically considered generalist herbivores, as their diet varies among sites, but in some locations they may be omnivorous (Jones and Seminoff 2013). Therefore, the availability of any one type of food (e.g., seagrass...
or drift macroalgae) may not be a strong determinant of juvenile green turtle abundance or growth. In our analysis of growth rates and primary producer cover, this hypothesis is partially supported. Growth rates slowly declined through mid-2011 and then slowly returned to previous levels through the end of the study period, but seagrass cover declined sharply throughout the study period and macroalgal cover showed more variable trends but a large drop out the study period and macroalgal cover showed more variable trends but a large drop during the HABs of 2011–2012. One possible explanation for the more moderate trends in green turtle growth rates could be their ability to forage on multiple taxonomic groups, which would serve to moderate the impact of a change in relative abundances of primary producers on growth. Additionally, given our relatively low recapture rate (7.96%), it is likely that individuals do not exhibit strong residency in or fidelity to the IRL. Drift macroalgal and seagrass cover varied among sites in our study (Appendix S1: Figs. S3d, S4d) and it is certainly possible that green turtles moved among these patches and others to choose the patches where food availability was highest. This could be an explanation why we saw growth rates return to previous levels after the 2011–2012 HABs even though the modeled averages of macroalgal and seagrass cover remained low. Some transects showed much higher macroalgal cover than the modeled average (Fig. 2) and it is possible that the turtles preferentially foraged at sites such as these. Finally, trends in green turtle growth rates from our IRL study site are likely an integration of trends in foraging resources among nearby IRL seagrass and macroalgal beds that we studied here and other sites that we did not have data for (e.g., nearshore sabellariid worm-rock reefs, Kubis et al. 2009).

In contrast, the abundance of individuals is more likely to depend on more than just the availability of food alone, and one hypothesis explaining our results is that these other factors may be contributing to the long-term declines in juvenile green turtle abundance in the IRL. The primary driver of seagrass declines in the IRL is reduced water clarity and light availability required for growth (Fletcher and Fletcher 1995, Steward and Green 2007, Lapointe et al. 2020). For marine turtles, these changes in water clarity may also have costs; marine turtles as a group are primarily visual foragers (Constantino and Salmon 2003, Southwood et al. 2008) and reduced visibility could make it harder for them to find food. This may especially be true for juveniles that may be new to the habitat, and approximately 92% of green turtles we captured from 2001 to 2018 had not been captured previously.

Perhaps equally important as the actual impact of water clarity and nutrients on green turtle habitats may be its perceived impact. The influence of animal perceptions of food availability or predation risk can heavily influence their habitat use (Laundré et al. 2010, Gallagher et al. 2017). For example, low visibility conditions may make it more difficult for juvenile green turtles to avoid large predators like sharks. The number of large sharks in the IRL is low (Snelson and Williams 1981, Curtis et al. 2011, Roskar et al. 2021), but marine turtles may have evolved to avoid low visibility areas because of perceived association with low food levels or perceived higher potential for predation; however, our understanding of the habitat cues that marine turtles use is very limited. The importance of factors other than food availability is further supported by the relatively low congruence between juvenile green turtle growth rates and abundance we found in this study, especially after 2012 when drift macroalgal availability and turtle growth rates slowly increased but turtle abundance continued to decline. Understanding whether juvenile green turtle habitat selection and use are more influenced by primary factors like food availability or perceived risks of high search costs and high predation is worthy of future study.

An increase in local green turtle abundance is hypothesized as the cause of decreasing seagrass abundance at some locations, especially in light of recent declines of top predators that regulate turtle herbivory (Christianen et al. 2014, Heinhaus et al. 2014). However, our data do not show evidence supporting this hypothesis. The turtles in the IRL do not forage as extensively on seagrasses as they do elsewhere (<10% of diet volume; Holloway-Adkins 2001, Redfoot et al. 2014, Jones and Seminoff 2013; Long, unpublished data), and therefore, it is unlikely that either turtle abundance or seagrass cover are directly related to one another.

A factor that we were not able to include in our analyses was water temperature, a
potentially key factor for ectotherms like marine turtles. As ectotherms, temperature plays an important role in many, and perhaps all, aspects of marine turtle biology, ecology, and physiology (Hamann et al. 2013). In our data set, there was a pronounced seasonal trend in juvenile green turtle abundance, with higher capture rates in winter and spring months pointing to the potential impact of temperature on juvenile green turtle habitat use. However, it is notable that at other locations juvenile green turtle abundance showed the opposite trend, with abundance decreasing in shallow water habitats in colder temperatures (Shaver 1994, Lamont et al. 2015, Madrak et al. 2016, Williard et al. 2017) or showing no seasonal shift (Hazel et al. 2009). If water temperatures have changed over time, and especially the relative temperatures of the IRL and nearby offshore waters hosting other juvenile green turtle habitats like sabellariid worm-rock reefs (Kubis et al. 2009), it would be an important factor to consider. However, there were no available resources for water temperature over the entire length of our study period, and our ability to make inferences about temperature impacts is therefore limited.

Overall, our analysis of four long-term data sets shows a complex ecological system with varying trends in which it is difficult to assess causality. For seagrasses and drift macroalgae, these trends were opposed to one another until 2011, when both precipitously declined during phytoplankton HABs. For juvenile green turtles, the picture is more varied. On one hand, the relatively small changes in growth rates over time and the ability of juvenile green turtles to rely on drift macroalgae (Holloway-Adkins 2001, Red-foot et al. 2014; Long, unpublished data) as a food resource point to a potential for resilience to habitat changes caused by nutrient pollution. On the other hand, the slow but steady decrease in juvenile green turtle abundance suggests that habitat quality may be on the decline.

This decreasing trend is made more concerning because it appears relatively independent of the increasing green turtle abundance trend at nesting beaches in the North Atlantic (Seminoff et al. 2015) and represents a reversal from previous trends at this same study site (Ehrhart et al. 2007). Juvenile sea turtle aggregations, including the IRL, are typically mixed stocks from multiple nesting beaches (e.g., Bass and Witzell 2000, Bagley 2003, Piovano et al. 2019, Stewart et al. 2019), and it is therefore possible that changes at an important juvenile habitat like the IRL could eventually impact demographic trends over a geographically widespread area. However, it is also possible that changing habitat conditions at one location would have relatively little impact at broader scales. Without studying other areas and the relationships between primary producers, nutrient pollution, and turtle abundance, it is difficult to determine whether the effects of nutrient pollution would impact demographic parameters (e.g., nest numbers or time to maturity) at the population scale. Further study of these factors at other locations would greatly enhance our ability to assess the threat of nutrient pollution to green turtle populations in the North Atlantic.

Conservation mechanisms in place in the United States (e.g., the Endangered Species Act of 1973) and elsewhere primarily regulate direct harm or killing of individuals of that species, or otherwise regulate the impact of government-controlled action on designated Critical Habitat. However, nutrient pollution in the IRL is linked primarily to endogenous nutrient pools (Philips et al. 2015), septic tanks, and local wastewater facilities (Lapointe et al. 2015, 2017, 2020, Barile 2018). Further understanding regarding the interrelatedness of nutrient pollution and decreased juvenile green turtle abundance in the IRL is especially important because it would not typically be directly regulated under the Endangered Species Act.

More broadly, our study adds to the knowledge regarding marine herbivore abundance and growth and provides an example of how these may be related to the widespread threat of nutrient pollution. But it is likely that these relationships are taxon-specific and location-specific. For example, manatees and dolphins in the IRL during this same study period experienced unusual mortality events and have build-ups of HAB-related toxins in their tissues (Capper et al. 2013, Fire et al. 2015, Lapointe and Herren 2015), which are potentially related to increased consumption of macroalgae that differs from their normal diet (Lapointe and Herren 2015). Species that depend more directly on sensitive seagrasses or rely on visual cues are likely to be more influenced, as are those that face other restrictions on
habitat use (e.g., seasonal thermal refuges, salinity). Expanding our understanding of these processes at local and regional levels will aid conservation efforts of many species whose habitats are affected by nutrient pollution.

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