

Diet and growth of juvenile queen conch *Lobatus gigas* (Gastropoda: Strombidae) in native, mixed and invasive seagrass habitats

Erik Maitz Boman^{1,2,*}, Tadzio Bervoets³, Martin de Graaf⁴, Jana Dewenter⁵,
Anna Maitz⁶, Melanie P. Meijer Zu Schlochtern³, Johan Stapel⁶, Aad C. Smaal^{1,2},
Leopold A. J. Nagelkerke²

¹Wageningen Marine Research, Wageningen University & Research, 4401 NT Yerseke, The Netherlands

²Aquaculture and Fisheries group (AFI), Wageningen University & Research, 6708 WD Wageningen, The Netherlands

³Nature Foundation St Maarten, Wellsburg St, Cole Bay, St Maarten

⁴Department of Primary Industries, New South Wales Government (NSW), 2700 Narrandera, Riverina, NSW, Australia

⁵Vrije Universiteit Brussel, 1050 Brussels, Belgium

⁶Caribbean Netherlands Science Institute (CNSI), L. E. Saddlerweg Oranjestad, St Eustatius, Caribbean Netherlands

ABSTRACT: Juvenile queen conch are primarily associated with native seagrass such as *Thalassia testudinum* in large parts of their range in the Caribbean and the southern Gulf of Mexico. Here, a number of non-native seagrass species have been introduced including *Halophila stipulacea*, which is natural to the Red Sea and the Indo-Pacific. In the Caribbean, *H. stipulacea* often creates dense continuous mats with little or no sediment exposed, compared to native seagrass, which grows much less dense. We examined the diet and growth of juvenile conch in both native, mixed, and invasive seagrass beds using stable isotope analysis and an *in situ* growth enclosure experiment. Organic material in the sediment (i.e. benthic diatoms and particulate organic matter) was found to be the most important source of carbon and nitrogen for juvenile queen conch in all 3 habitats investigated, and there was a significantly higher probability of positive growth in the native seagrass compared to the invasive seagrass. Due to the importance of the organic material in the sediment as a source of nutrition for juvenile conch, limited access to the sediment in the invasive seagrass can potentially cause inadequate nutritional conditions to sustain high growth rates. Thus, it is likely that there is a negative effect on juvenile queen conch growth currently inhabiting invasive seagrass beds, compared to native seagrass beds, when other potential sources of nutrition are not available.

KEY WORDS: *Halophila stipulacea* · Invasive species · Stable isotope · Mollusca · Caribbean

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1. INTRODUCTION

Lobatus gigas, commonly called queen conch (Gastropoda: Strombidae), is an economically and culturally important marine gastropod (Brownell & Stevely 1981, Appeldoorn 1994) found throughout the Wider Caribbean Region and the southern Gulf of Mexico. The species is heavily exploited throughout large parts of its natural range (Stoner 1997), which has led

to a decrease in population densities, a truncation of size classes (Stoner et al. 2012b) across much of the species' distribution range (Acosta 2006), and even towards overfishing (Stoner et al. 2019). Due to concerns for the continued over-exploitation of the species (Stoner et al. 2012b), measures have been taken such as the listing of the species to Appendix II of the Convention on International Trade in Endangered Species of Fauna and Flora (CITES) in 1992.

Adult conch can be found in a wide range of environmental conditions (Stoner et al. 1994) such as in sand and algal or coral rubble (Acosta 2001, Stoner & Davis 2010). Juvenile conch, on the other hand, appear to have more specific habitat requirements (Stoner et al. 1994), and in large parts of their distribution range (e.g. The Bahamas) juvenile conch are associated primarily with native seagrass such as *Thalassia testudinum* (Stoner 2003), which provides both nutrition and protection from predators (Ray & Stoner 1995, Stoner 2003, Stoner & Davis 2010). The primary diet of juvenile conch consists of native seagrass detritus, and red and green macroalgae, primarily *Laurencia* spp. and *Batophora oerstedii* (Randall 1964, Stoner & Sandt 1991, Stoner & Waite 1991, Serviere-Zaragoza et al. 2009). The production of red and green algae, which can be highly variable, has been shown to directly affect the growth of juvenile conch (Stoner et al. 1994, 1995, Stoner 2003). Organic material in the sediment (benthic diatoms and particulate organic matter [POM]) and cyanobacteria have also been suggested to be sources of nutrition to juvenile conch (Stoner & Waite 1991, Stoner et al. 1995, Serviere-Zaragoza et al. 2009).

Different species of seagrass vary in leaf width, leaf structure, canopy height, and leaf lifespan (Trautman & Borowitzka 1999, Horinouchi et al. 2009). As a result, individual seagrass species host unique epiphytic communities, which form different food sources and provide shelter to a variable degree, depending on their morphological characteristics (Trautman & Borowitzka 1999, Horinouchi et al. 2009). Consequently, seagrass composition determines the associated species assemblages (Bologna & Heck 1999, Willette & Ambrose 2012, Olinger et al. 2017). Alterations to the composition of seagrass beds, such as through the introduction of invasive species, can thus cause changes in the associated biota and change the level of shelter and the quality and quantity of food sources (Willette & Ambrose 2012).

In the Caribbean, a number of such non-native species have been introduced (Kairo et al. 2003) including the seagrass *Halophila stipulacea* (Williams 2007), which is natural to the Red Sea and the Indo-Pacific. *H. stipulacea* has, since its first observation in 2002 on Grenada (Ruiz & Ballantine 2004), spread rapidly and can now be found around at least 19 islands throughout the eastern Caribbean and the northern parts of South America (Vera et al. 2014, Willette et al. 2014). *H. stipulacea* can displace native seagrass species such as *Syringodium filiforme*, *Halodule wrightii*, and *Halophila decipiens* (Willette & Ambrose 2012). It is able to spread at a high rate, with an

observed expansion from 316 to 773 ha in Dominica during a 5 yr period (Steiner & Willette 2013). Knowledge of the impact of *H. stipulacea* on the local fauna is limited, although reductions in the relative number of small and juvenile fishes have been reported (Willette & Ambrose 2012, Olinger et al. 2017). The effects of *H. stipulacea* on the habitat quality for juvenile queen conch are not clear. It can be expected that the presence and abundance of certain food items may change due to changed seagrass composition, which could translate to diet shifts and eventually to altered growth rates (Stoner et al. 1994, 1995, Stoner 2003). Direct examination of stomach contents to determine diets is problematic and only provides an estimate of recently ingested items and limited information on the degree of assimilation of dietary items (Garcia et al. 2007, Pasquaud et al. 2008). These limitations have promoted the use of stable isotope analysis and isotopic mixing models, which have the major advantage that they can provide information on the direct assimilation of dietary items by the consumer (Fry 2006, Bond & Diamond 2011, Parnell et al. 2013). Interpretation of stable isotope ratios is generally based on the assumption that with each trophic level there is a constant enrichment in the heavier isotopes due to the discrimination towards lighter isotopes during metabolism and excretion (DeNiro & Epstein 1981, Peterson & Fry 1987). Enrichment of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ differs between habitats and taxa, with mollusks, in general, having a low $\delta^{15}\text{N}$ enrichment of approximately 1–1.5‰ between diet and consumer (Vanderklift & Ponsard 2003). Gastropods have also been found to have $\delta^{15}\text{N}$ isotopic values reflecting the exposure of sites to anthropogenic impact (Vermeulen et al. 2011), with higher $\delta^{15}\text{N}$ isotopic values at sites with higher $\delta^{15}\text{N}$ baseline (Vermeulen et al. 2011). This provides the opportunity to use stable isotope analysis not only for diet investigation but also for assessing nitrogen pollution (Bannon & Roman 2008).

The purpose of this study is 2-fold. First, it examines the diet of juvenile conch in a variety of native, invasive, and mixed native/invasive seagrass beds using stable isotope analysis. Isotopic values of conch are expected to vary in accordance with their diet but also in accordance with factors such as the baseline $\delta^{15}\text{N}$ at the different sites, which may include different levels of anthropogenic disturbance. In addition, the contribution of *H. stipulacea* detritus to the diet of juvenile conch is explored.

Secondly, this study examines juvenile queen conch growth in an *in situ* enclosure experiment comparing growth rates of juveniles in native, invasive and mixed native/invasive seagrass beds.

Growth is expected to be better in habitats which provide better and more abundant access to food sources of the proper nutritional quality. Both the dietary study and the growth experiment will be used to discuss the potential consequences of the *H. stipulacea* invasion on the development of queen conch populations.

2. MATERIALS AND METHODS

2.1. Study area

The study was performed in seagrass beds at 3 geographic locations in the eastern Caribbean (St Barthélemy, St Eustatius, and St Maarten; Fig. 1). Samples for dietary analysis were collected at all 3 locations, from sites with sandy bottoms, located at 1–20 m depth, 20–900 m from shore, with 20–95% seagrass cover, and with <1% macroalgae cover. Seagrass species composition differed between sites (St Barthélemy: native, St Eustatius: invasive, and St Maarten: mixed native/invasive) (Table 1). Only native seagrass species were found at the native site, while both native and invasive seagrass species were found at the mixed and invasive site. However, only

a very small proportion (<1% of total cover) of native seagrass (i.e. *Syringodium filiforme*) were found at the invasive site, while the proportion of native and invasive seagrass species at the mixed site were roughly equal (Table 1). The growth experiment was conducted at 2 sites in Simpson Bay, St Maarten (Fig. 1), which differed in seagrass composition (i.e. native vs. invasive), while all other relevant environmental variables were similar. Both sites had sandy substrates, were located at 4–5 m depth, were 250–270 m from shore, had 40–95% seagrass cover, and <1% macroalgae cover. Variations in water temperature, light availability and nutrient concentrations were considered negligible in view of the proximity (~500 m) of both locations towards each other (Table 2).

2.2. Diet analysis

2.2.1. Sample collection, preparation, and stable isotope analysis

Juvenile conch, which could be identified by the absence of a developed lip (Stoner et al. 2012a, Boman et al. 2018), ranging from 106–215 mm shell length, were collected by hand for dietary analysis from each of the 3 collection sites. A mantle tissue sample of approximately 0.5×0.5 cm \times thickness of mantle (ca. 0.5 cm) was taken from each collected conch before returning it live to the collection site. In addition, at each site, between 1 and 24 food items, previously indicated to be a source of conch nutrition (Randall 1964, Stoner & Sandt 1991, Stoner & Waite 1991, Serviere-Zaragoza et al. 2009), were collected by hand in close proximity to the conch (Table 2). The upper 3 cm of the surface sediment was also collected, using a 4 cm diameter core sampler (as sediment was expected to contain diatoms as potential food source), as well as seagrass detritus, and seagrass epiphytes, whenever present. Seagrass detritus was defined as dead leaves (no traces of green) that started to break down but were still visually recognizable to belong to a certain species. Leaves with heavy epiphytic growth were collected, and the epiphytes on the

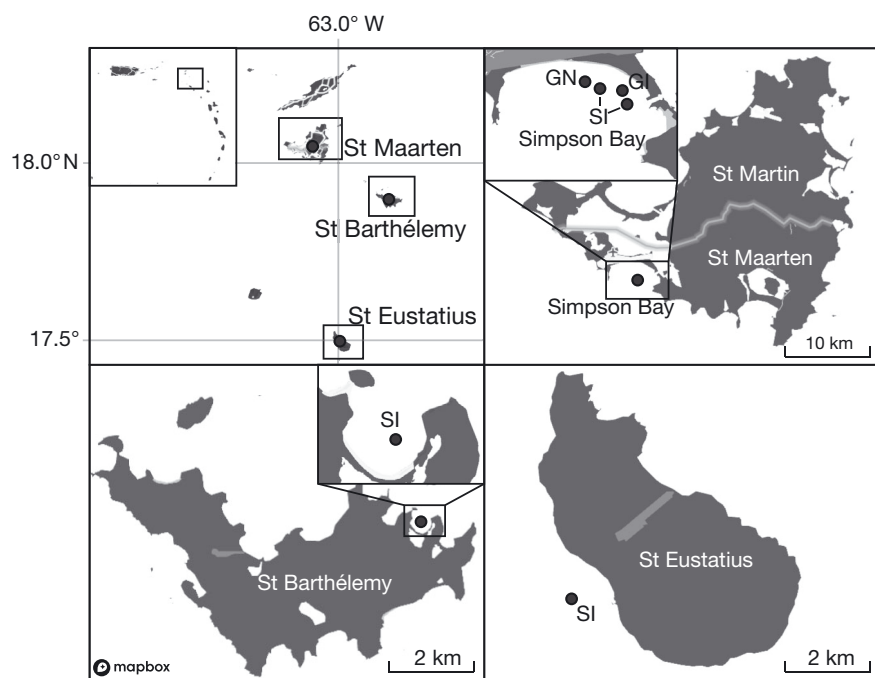


Fig. 1. Locations of the growth experiments and stable isotope analysis collection areas in St Barthélemy (native site), St Eustatius (invasive site) and St Maarten (mixed native/invasive site) in the eastern Caribbean. SI: stable isotope sampling location; GN: growth experiment in native seagrass (*Thalassia testudinum* and *Syringodium filiforme*); GI: growth experiment in invasive seagrass (*Halophila stipulacea*)

Table 1. Stable isotope collection site (STB: St Barthelemy; STM: St Maarten; STE: St Eustatius) conditions (seagrass habitat, substrate, conch shell length [SL], depth, distance to shore, total area of seagrass and macroalgae covering the substrate, and relative cover of each individual seagrass species). *H.s.*: *Halophila stipulacea*; *T.t.*: *Thalassia testudinum*; *S.f.*: *Syringodium filiforme*; *H.w.*: *Halodule wrightii*

Site	Seagrass	Substrate habitat	Conch SL (mm)	Depth (m)	Distance shore (m)	—Total cover (%)—		—Relative cover total (%)—			
						Seagrass	Macro algae	<i>H.s.</i>	<i>T.t.</i>	<i>S.f.</i>	<i>H.w.</i>
STB	Native	Sand	106–206	1–3	20–200	30–60	<1	0	35	35	30
STM	Mixed	Sand	112–160	4–6	200–300	20–>95	<1	35	35	30	0
STM	Mixed	Sand	115–203	4–6	200–300	20–>95	<1	30	35	35	0
STE	Invasive	Sand	106–215	14–20	400–900	20–>95	<1	99	0	1	0

Table 2. Growth experiment site conditions (seagrass habitat, substrate, conch shell length [SL], depth, distance to shore, total area of seagrass and macroalgae covering the substrate [total cover (%)], and seagrass shoot density [shoot m⁻²]) of the 6 enclosures (E) at St Maarten. Seagrass are *Halophila stipulacea* (*H.s.*), *Thalassia testudinum* (*T.t.*), and *Syringodium filiforme* (*S.f.*)

E (no.)	Seagrass habitat	Substrate	Conch SL (mm)	Depth (m)	Distance shore (m)	—Total cover (%)—		—Shoot m ⁻² —		
						Seagrass	Macro algae	<i>H.s.</i>	<i>T.t.</i>	<i>S.f.</i>
1	Native	Sand	120–136	5	270	45	<1	0	842	640
2	Native	Sand	120–139	5	270	45	<1	0	821	608
3	Native	Sand	120–136	5	270	40	<1	0	741	618
4	Invasive	Sand	120–138	4	250	>95	<1	3493	0	0
5	Invasive	Sand	121–139	4	250	>95	<1	3701	0	0
6	Invasive	Sand	120–135	4	250	>95	<1	3482	0	0

leaves were later carefully scraped off with a scalpel in the lab. Sampling in St Eustatius was done between 10 August and 11 October 2017, both before and after hurricane Irma (6 September 2017), which had no perceivable impact at this location. Sampling in St Maarten took place between 29 and 31 of August 2017, and sampling in St Barthélemy was done between 9 and 11 January 2018.

The samples were stored in plastic bags in a cooler at ca. 4°C, while transported to the laboratory, where they were dried overnight at 60–70°C and subsequently homogenized using a mortar and pestle. All sediment samples were treated with phosphoric acid to remove excess calcium carbonate, leaving the organic material in the sediment, most likely consisting of benthic diatoms and POM, which are common in marine sediment (MacIntyre et al. 1996, Mann 1999, Jones et al. 2014). All other categories of food items were tested for inorganic content and were also treated with phosphoric acid if necessary. Between 0.5 and 60 mg of powdered sample were analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, using a Flash 2000 elemental analyzer coupled to an isotope ratio monitoring mass spectrometer (EA-irMS) via an Isolink IV (Thermo Scientific), at the stable isotope laboratory at the Royal Netherlands Institute for Sea Research (NIOZ) at Texel, the Netherlands. As the C:N ratio of the conch

mantle tissue was <3.8, with the majority of the samples (81%) having a value <3.5, there was no need for a lipid correction (Post et al. 2007).

2.2.2. Statistical analysis of the diet data

A Kruskal-Wallis rank sum test was used to analyze differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among the detritus from seagrass species at each site separately, as well as for the 3 cyanobacteria mats found in St Eustatius. In case of significant overall differences, pairwise comparisons were applied and presented, using the `kruskalmc` function from the package `pgirmess` (Giraudoux 2018) in the R environment v.3.5.0. (R Core Team 2018).

The stable isotope mixing model package (`simmr`), using a Bayesian statistical framework (Parnell 2016) was used to estimate proportional contributions of potential food sources to the diet of juvenile conch. `simmr` was implemented with 100 000 iterations (discarding the first 10 000). The estimated proportions of food sources in the diet mixture of juvenile conch were subsequently determined using a Markov Chain Monte Carlo function to repeatedly estimate the proportions of the various sources in the mixture and determine the values which best fit the mixture data

(Parnell 2016). The median (50 % quantile), lower (25 %) and upper (75 %) quartiles, and 95 % credibility interval (2.5 and 97.5 % quantiles) of the contribution of each of the food sources were determined.

2.3. Growth experiment

2.3.1. Conch collection and experimental set-up

Growth experiments were performed at 2 sites in Simpson Bay, St Maarten (i.e. Simpson Bay Airport and Simpson Bay Bridge) (Fig. 1). In total 60 juvenile conch of shell lengths between 120 and 139 mm were collected by hand on 5 and 6 July 2017 and distributed over 3 enclosures at each site. Enclosures (4.5 × 4.5 m) consisted of ridged plastic netting approximately 30 cm high, held in place with steel bars driven into the sand. Ten conch were placed in each enclosure, with 3 enclosures located in the invasive seagrass *Halophila stipulacea* and 3 in a mix of native seagrass (*Thalassia testudinum* and *Syringodium filiforme*) (Table 2). Each conch was fitted with a small metal tag and a unique number to be able to recognize each individual. Initial shell length of each individual was measured as well as a final shell measurement at the end of the experimental period. No conch went missing or was found dead inside the enclosures during the length of the experiment. Conch density (0.5 conch m⁻²) in the enclosures was thus kept constant throughout the experiment. Seagrass shoot density and macroalgae cover was counted before the experiment within 3 quadrates (25 × 25 cm) randomly placed inside each enclosure (Table 3). Mean seagrass shoot densities at the native seagrass beds ranged between 608 and 640 shoots m⁻² for *T. testudinum* and between 741 and 842 shoots m⁻²

for *S. filiforme*, while seagrass shoot density of invasive *H. stipulacea* ranged between 3482 and 3701 shoots m⁻². Macroalgae in the enclosures consisted entirely of calcified macroalgae species (i.e. *Dictyota* sp., *Caulerpa* spp., *Udotea* spp., *Halimeda* spp., *Pennicillia* spp.). The intent was to run the growth experiment for a total of 16 wk, but due to a direct hit of a major hurricane (Irma), the growth experiment already ended after 47 d, because all macrophyte cover, much of the substrate, all conch, and all enclosure structures were removed by the hurricane. Also, a count of seagrass shoots after the experiment and grain size estimation of the substrate was not possible due to these circumstances. Yet, it was possible to collect data on conch growth based on 47 d (6.5 wk) of observation.

2.3.2. Statistical analysis of the growth experiment

Growth rates (shell length growth in mm d⁻¹) were calculated for each individual for the entire experimental period (6.5 wk) and subsequently assigned to growth rate bins of 0.05 mm d⁻¹, ranging from -0.10 to 0.15 mm d⁻¹. The probability of a positive growth rate was modelled as a binomial generalized linear model (GLM) with a logit function, with habitat (categorical covariate with 2 levels: native and invasive) as a fixed covariate. A binomial model with enclosure as random intercept was also fitted, but the simpler model without the random effect had a lower Akaike's information criterion (AIC) value and was thus chosen as the final model. Statistical analysis was conducted using the packages car (Fox & Weisberg 2011), lme4 (Bates et al. 2015), and rmisc (Hope 2013), in the R software environment v.3.4.4. (R Core Team 2018).

Table 3. Items and number of items collected and analysed at the 3 collection sites for dietary analysis

	St Barthélemy	St Eustatius	St Maarten
Conch	24	25	23
Cyanobacteria (Red)	0	14	0
Cyanobacteria (Brown A)	0	5	0
Cyanobacteria (Brown B)	0	7	0
Sediment	14	16	10
<i>Halophila stipulacea</i> detritus	0	24	22
<i>Halophila stipulacea</i> epiphytes	0	1	0
<i>Syringodium filiforme</i> detritus	7	3	17
<i>Halodule wrightii</i> detritus	6	0	0
<i>Thalassia testudinum</i> detritus	18	0	15
<i>Thalassia testudinum</i> epiphytes	5	0	0

3. RESULTS

3.1. Diet

3.1.1. Stable isotope profiles

Juvenile conch. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values varied between and within sampling sites (Figs. 2 & 3), but in the different habitats juvenile conch had a similar position in the iso-space plot in relation to the potential food sources (Fig. 2). Juvenile conch in St Eustatius did, however, have more depleted

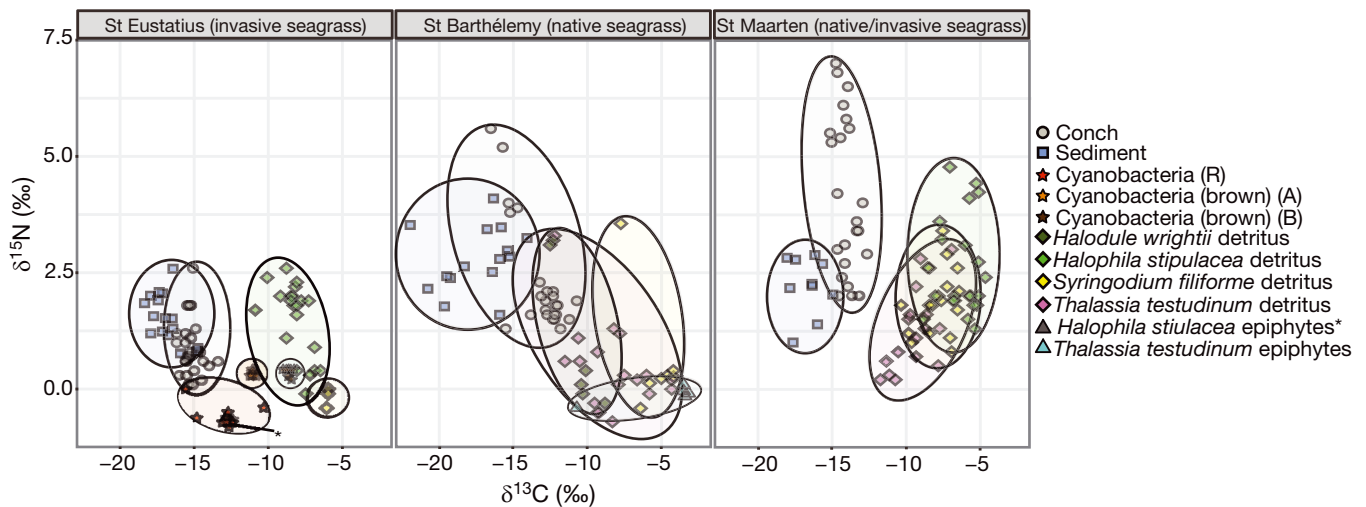


Fig. 2. Iso-space plot of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the conch and the potential food sources from the 3 sampling sites: St Eustatius (invasive seagrass), St Barthélemy (native seagrass) and St Maarten (mixed native/invasive seagrass). Ellipses indicate the spread of values of each potential food source. The line with asterisk indicates the position of the single sample of *H. stipulacea* epiphytes

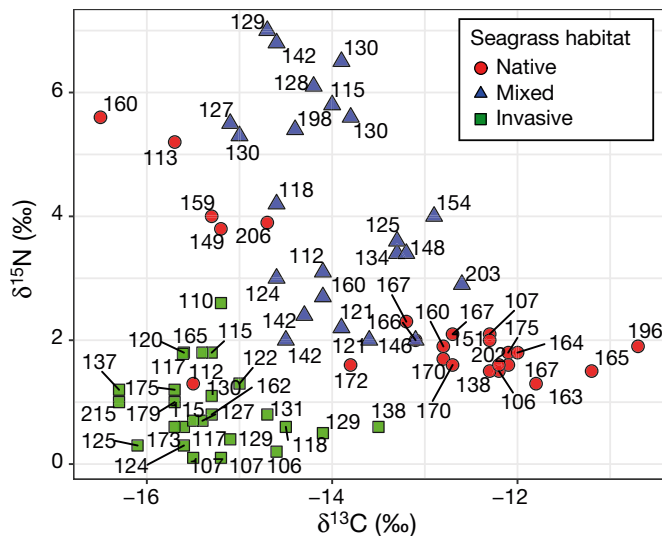


Fig. 3. Juvenile queen conch *Lobatus gigas* values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from the 3 seagrass habitats (invasive [St Eustatius], native [St Barthélemy], and mixed [St Maarten]) with corresponding shell length (mm) indicated next to each point

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than the conch in St Maarten and in St Barthélemy (Fig. 3). Organic matter in the sediment was the only sampled food source which consistently had values of $\delta^{15}\text{N}$ which were similar or more depleted than the conch and with $\delta^{13}\text{C}$ values consistently more depleted than the conch at each site (Fig. 2).

Seagrass detritus. The $\delta^{13}\text{C}$ detrital values from the native and invasive seagrass species were in general

more enriched compared to conch with only a few values of *Thalassia testudinum* and *Halodule wrightii* in St Barthélemy (native), which overlapped with conch at that site (Fig. 2). The $\delta^{15}\text{N}$ values of the detritus of invasive seagrass in St Eustatius largely overlapped with conch, while there was less overlap with the seagrass detritus and conch in St Maarten (mixed native/invasive) and St Barthélemy (native), with conch having more enriched $\delta^{15}\text{N}$ values than seagrass detritus. The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of the detritus from the different seagrass species were mostly overlapping, although with some significant differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ among the different species. $\delta^{15}\text{N}$ values of *Halophila stipulacea* detritus were consistently more enriched compared to the detritus of native seagrass species, i.e. of *Syringodium filiforme* detritus in St Eustatius ($p < 0.01$, $df = 1$) and St Maarten ($p < 0.05$, $df = 1$), as well as of *T. testudinum* in St Maarten ($p < 0.01$, $df = 1$) (Fig. 2). *H. stipulacea* detritus also differed in $\delta^{13}\text{C}$ from the other species and showed more depleted $\delta^{13}\text{C}$ values compared to the detritus of *S. filiforme* in St Eustatius ($p < 0.01$, $df = 1$). In St Maarten the difference was reversed with $\delta^{13}\text{C}$ values of *H. stipulacea* detritus being more enriched compared to *S. filiforme* ($p < 0.01$, $df = 1$) and *T. testudinum* ($p < 0.01$, $df = 1$). *S. filiforme* detritus also had more enriched $\delta^{13}\text{C}$ values compared to *H. wrightii* ($p < 0.01$, $df = 1$) and *T. testudinum* ($p < 0.01$, $df = 1$) detritus in St Barthélemy.

Sediment. Organic matter from sediment samples was in general more depleted in $\delta^{13}\text{C}$ than the other food sources (Fig. 2). All other food sources were

between 1.77 and 8.77‰, 1.56 and 10.91‰, and 3.21 and 10.29‰ more enriched in $\delta^{13}\text{C}$ compared to organic matter from sediment from St Eustatius, St Barthélemy, and St Maarten, respectively (Fig. 3).

Cyanobacteria. Three cyanobacteria mats (1 red, likely *Blennothrix* spp., and 2 brown, likely *Oscillatoria* spp.) found in St Eustatius were significantly ($p < 0.01$, $df = 2$) different from each other (Fig. 2) in $\delta^{13}\text{C}$. With cyanobacteria red (CyR) being more depleted than cyanobacteria brown A (CyB A) ($p < 0.01$, $df = 1$) and B (CyB B) ($p < 0.01$, $df = 1$). CyB B was also more depleted than CyB A ($p < 0.01$, $df = 1$). For $\delta^{15}\text{N}$, CyR was significantly more depleted than CyB A ($p < 0.01$, $df = 1$) and CyB B ($p < 0.01$, $df = 1$) in $\delta^{15}\text{N}$.

3.1.2. Diet composition

Conch had similar diets in all 3 habitats, with organic matter from the sediment being the primary dietary source, as apparent from the stable isotope mixing model (Fig. 4). Median proportions of sediment organic matter ranged from 58.4 % at St Barthélemy (95 % credibility interval: 45.6–66.8 %) to 68.5 % (CI: 63.5–73.2 %) at St Maarten, and 69.5 % (CI: 61.9–77.7 %) at St Eustatius (Fig. 4). Seagrass detritus and seagrass epiphytes had a relatively small predicted contribution to the juvenile conch diet, irrespective of seagrass species (Fig. 4). Cyanobacteria

mats were only found in St Eustatius and had a median contribution to the juvenile queen conch diet of 3.6 % (CI: 0.6–9.6 %), 5.6 % (CI: 0.7–16.2 %), and 15.1 % (CI: 2.7–28.0 %), respectively (Fig. 4).

3.2. Growth

Nineteen juvenile conch in the native seagrass habitat showed positive growth rates ($>0 \text{ mm d}^{-1}$), with a maximum individual growth rate of 0.17 mm d^{-1} , while only 5 juvenile conch in the invasive seagrass habitat had positive growth rates, with a maximum of 0.03 mm d^{-1} (Fig. 5). The predicted probability of positive growth rate in juvenile conch in the native seagrass bed was 0.63 (CI: 0.45–0.79), which was significantly higher than in the invasive seagrass bed, with a probability of 0.17 (CI: 0.07–0.35) (Fig. 6).

4. DISCUSSION

The similarities between habitats in the positioning of the stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of each potential food source and the juvenile conch (Fig. 2), as well as the predicted dietary contributions of the mixing model, indicate comparable feeding patterns for juvenile conch in native, invasive and a mix of native and invasive seagrass, irrespective of sam-

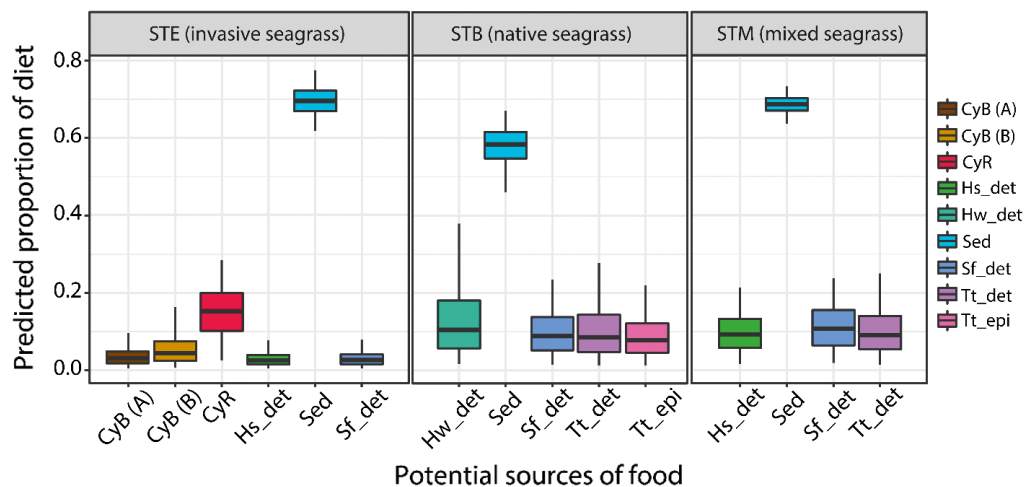


Fig. 4. Median (horizontal line within the box), first and second quartile (boundaries of the box), and 95 % credibility interval (whiskers of the box) of predicted proportion of food source contribution to the diets of juvenile (shell length = 100 – 205 mm) queen conch *Lobatus gigas* at St Eustatius (STE) (majority invasive [$>99\%$] seagrass), St Barthélemy (STB) (native seagrass), and St Maarten (STM) (mixed native/invasive seagrass) estimated by Stable Isotope Models in R ('simmr'). CyB (A): cyanobacteria (brown) species A; CyB (B): cyanobacteria (brown) species B; CyR: cyanobacteria (red); Hs_det: *Halophila stipulacea* detritus (invasive seagrass); Sed: sediment; Sf_det: *Syringodium filiforme* detritus (native seagrass); Hw_det: *Halodule wrightii* detritus (native seagrass); Tt_det: *Thalassia testudinum* detritus (native seagrass); Tt_epi: *T. testudinum* epiphytes (native seagrass). Missing values indicated that the potential food source was not found in the particular site

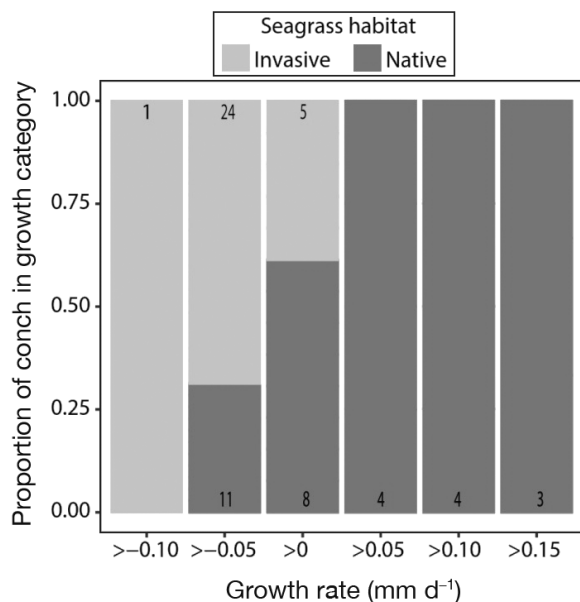


Fig. 5. Proportion of juvenile conch of each habitat (native and invasive) in each of the growth rate increment category. Numbers at top (invasive) and the bottom (native) show the number (n) of conch in each growth increment category

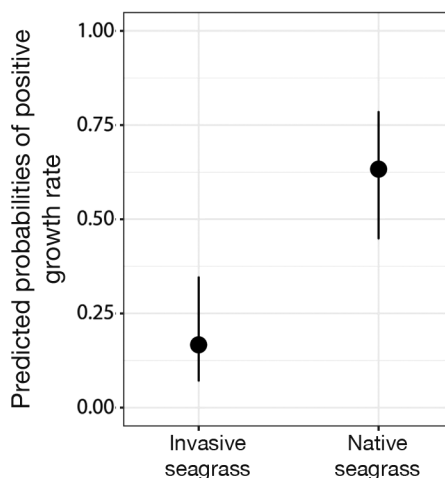


Fig. 6. Predicted probabilities of positive growth rate in the invasive (*Halophila stipulacea*) and the native (*Thalassia testudinum* and *Syringodium filiforme*) seagrass with 95% confidence interval

pling site. In all habitats the most important source of nutrition appears to be sediment organic matter (benthic diatoms and POM), despite differences between the habitats in variables such as depth, distance to shore, and anthropogenic nutrient input (Figs. 2 & 4).

The importance of the organic material in the sediment for juvenile queen conch was already suggested by Stoner & Waite (1991), who found large

amounts of sediment in the stomach of juvenile conch. Similar findings have also been reported for *Laevistrombus canarium*, another Strombidae species, of which juveniles feed up to 40% on surface sediment (Husna et al. 2017). Stoner & Waite (1991) further showed that macroalgae (particularly *Laurencia* spp. and *Batophora oerstedii*) were the most likely food source of juvenile conch in the shell length range of 120–140 mm, found in native seagrass (*Thalassia testudinum* and *Syringodium filiforme*) beds in the Bahamas. However, the general importance of macroalgae to the diet of juvenile conch in our study area could not be confirmed as these macroalgae species were not found at any of the survey sites in this study. Several studies have also indicated that seagrass detritus is an important food source for juvenile queen conch, in particular detritus of *T. testudinum* (Stoner 1989b, Stoner & Waite 1991). While this study indicated that detritus is likely a food source for juvenile conch (Figs. 2 & 4), the importance of this source in our study area appears to be less than previously attributed by Stoner & Waite (1991).

Although the organic material in the sediment was found to be the most important food source for juvenile conch, this study also shows that the organic material in the sediment was not the sole source of carbon and nitrogen for juvenile conch in any of the habitats. In addition, there were differences in food items between the sites, depending on their availability, confirming previous suggestions that juvenile conch are partly opportunistic in their feeding pattern (Robertson 1961, Randall 1964, Stoner & Waite 1991). Different food items have also been found in the stomach of juvenile conch, giving further support to the suggestion of a mixed diet (Stoner & Waite 1991, Stoner & Sandt 1992). In St Eustatius (invasive site) a mix of sediment and a species of red cyanobacteria (likely *Blennothrix* spp. or *Oscillatoria* spp.) were identified as a food source for juvenile conch. At this site 3 distinct cyanobacteria mats were found, but the 2 brown cyanobacteria mats seem to have contributed little to the diet of conch (Fig. 4). This indicates a possible preference for conch for specific species of cyanobacteria as a source of nutrition. Both the detritus of native seagrass (*S. filiforme*) and invasive seagrass (*Halophila stipulacea*) were unlikely food sources for conch in St Eustatius, given the large separation between $\delta^{13}\text{C}$ of conch and the seagrass detritus (>7.3 and >2.4 ‰, respectively) (Figs. 2 & 4). In contrast, for at least part of the conch in St Barthélemy (native site) and St Maarten (mixed site), a contribution to the diet from seagrass detritus was

likely (Figs. 2 & 4). The proportional contribution of detritus to the diet of conch from the native and the invasive species remains uncertain, due to the overlap in the isotopic signatures of the detritus of the different seagrass species (Figs. 2 & 4). Even though there were significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between the detritus of the different seagrass species in St Eustatius, St Barthélemy, and St Maarten, this was not reflected in any distinct difference in the contribution of the seagrass species' detritus to the diet of juvenile conch (Fig. 4). *H. stipulacea* has so far been found in depths from <1 to 30 m in the Caribbean (Willette et al. 2014, Scheibling et al. 2018) and was found in abundance at the sampling site in St Eustatius (invasive, 14–20 m depth) and St Maarten (mixed, 4–6 m depth) (Table 1), and its detritus was abundant at both sites (St Eustatius and St Maarten). However, it was unlikely to contribute to the diet of conch in St Eustatius, and its contribution to the diet of conch in St Maarten appears to be limited (Figs. 2 & 4). This raises the question whether there is a difference in nutritional value of detritus from different species of seagrass for juvenile conch and if detritus of *H. stipulacea* can be utilized by conch as a source of nutrition to any extent.

In comparison to St Eustatius, more enriched $\delta^{15}\text{N}$ values were found in conch from the collection sites at St Barthélemy and St Maarten (Fig. 1). Higher $\delta^{15}\text{N}$ values may be caused by the restricted water flow and by higher anthropogenic nutrient pollution (Tett et al. 2003), which is the case for both sampling sites at St Barthélemy and St Maarten. Both sites were close to outlets from enclosed water bodies as well as hotels with ca. 120 and 650 hotel rooms in St Barthélemy and St Maarten, respectively. The site in St Eustatius was located further from shore (Table 1), and anthropogenic sources of nitrogen were considerably fewer (hotel rooms ca. 40) (Fig. 1) (E. M. Boman pers. obs). Therefore, the more enriched values of $\delta^{15}\text{N}$ of conch in St Maarten and in St Barthélemy are likely to be at least partly a consequence of a higher $\delta^{15}\text{N}$ baseline caused by more available anthropogenic nitrogen. This was particularly evident in St Maarten, where all the conch with a $\delta^{15}\text{N}$ isotope signature $>5\text{‰}$ were collected close to a large source of anthropogenic nitrogen (outlet from Simpson Bay lagoon) (Lips & van Slooten 2009) (Fig. 3). Previous studies have also found $\delta^{15}\text{N}$ in gastropods to reflect the exposure of sites to anthropogenic nitrogen, with a higher $\delta^{15}\text{N}$ baseline at impacted compared to pristine sites (Vermeulen et al. 2011).

Our growth experiment showed that there was a higher probability of positive growth rates in the

native seagrass compared to the invasive seagrass (0.63 vs. 0.17). Even if conch in the invasive seagrass did grow, none had growth rates comparable to previously recorded high summer growth rates at nursery sites in native habitats in the Wider Caribbean Region (0.06–0.54 mm d⁻¹) (Randall 1964, Weil & Laughlin 1984, Iversen et al. 1987, Stoner 1989a,b, Stoner & Sandt 1992). In contrast, 11 of the 30 conch in the native seagrass did show such high growth rates, suggesting that the native seagrass habitat had a higher potential for higher growth of juvenile conch. The observed negative growth rates are not unique and have been linked to low food abundance, habitat quality, and shell erosion (Stoner 1989b, Stoner & Sandt 1991). Due to the relatively short duration of the experiment (47 d) the negative growth rates were unlikely to be due to shell erosion and more likely due to poor habitat quality and low food abundance (Stoner 1989b, Stoner & Sandt 1991). Even though the growth experiment had a shorter duration than desired, the results suggest higher growth rates of juvenile conch in native compared to invasive seagrass beds, at least under conditions in which other sources of non-seagrass related food items are not available (i.e. cyanobacteria, macroalgae, such as *Laurencia* spp. and *Batophora oerstedii*) (Stoner & Sandt 1991).

A possible reason for the poorer growth performance of juvenile queen conch in invasive seagrass compared to native seagrass is reduced quality of, access to, and/or availability of food sources in invasive seagrass meadows. This could be related to the vegetation density and growth strategy of *H. stipulacea*. In the Caribbean, *H. stipulacea* often creates dense continuous mats with little or no sediment exposed, especially under high nutrient conditions (van Tussenbroek et al. 2016) and with a dense maze of rhizomes often on top of the sediment surface. Native *T. testudinum* usually grows to seagrass shoot densities between 300 and 1200 shoots m⁻² (Linton & Fisher 2004), while shoot densities of *H. stipulacea* can often be between 3 and 5 times higher (ca. 3500–5500 shoots m⁻²) (Becking et al. 2014). Such dense *H. stipulacea* beds are found throughout the species' range in the Caribbean at depths ranging from 1 to 30 m (Willette et al. 2014, Scheibling et al. 2018), and seagrass shoot densities of *H. stipulacea* were also high in the experimental enclosures in this study, while total seagrass shoot densities in the enclosures at the native seagrass bed were approximately 2 to 3 times lower (Table 3). In dense seagrass beds of *H. stipulacea* the area of exposed sediment will be lower compared to most beds of *T. testudinum* *S. filiforme*, and other na-

tive seagrass species. Due to the importance of the organic material in the sediment as a source of nutrition for juvenile conch, a restricted access to the sediment, when other sources of nutrition are not readily available (e.g. macroalgae, high epiphytic growth, *T. testudinum* detritus, cyanobacteria), could affect growth negatively as observed in this study. This is corroborated by Stoner & Sandt (1991), who showed that juvenile conch transplanted to sites of high accumulation of detritus and native seagrass biomass, similar to the conditions of the invasive seagrass beds in this study, also showed lower growth compared to sites with low and medium native seagrass biomass. This suggests that high biomass seagrass beds, both native and invasive, can create unfavorable conditions to support high juvenile conch growth rates. Restricted benthic foraging driven by *H. stipulacea* and other habitat-forming invasive species (e.g. the macroalgae *Caulerpa taxifolia*) have also been observed in fish (e.g. *Mullus surmuletus*) in the Caribbean and elsewhere (Longepierre et al. 2005, Olinger et al. 2017). Furthermore, the dense canopy structure of *H. stipulacea* reduces the amount of light reaching the sediment surface, which may negatively affect benthic diatom production (Hill 1996, Yang & Flower 2012), thereby reducing the abundance of potential food sources for queen conch in the sediment (i.e. benthic diatoms) (Stoner & Waite 1991). In addition, *H. stipulacea* appears to respond favorably to high nutrient conditions (van Tussenbroek et al. 2016), whereas *T. testudinum* responds negatively (Tomasko et al. 1996). High nutrient conditions may thus exacerbate the possible negative effects of high-density *H. stipulacea* to growth rates of juvenile queen conch, while simultaneously negatively affecting areal coverage of native seagrasses (i.e. *T. testudinum*).

Although we postulate that the dense growth pattern of *H. stipulacea* is the cause of the observed lower growth of juvenile conch in invasive seagrass, there were potential differences in environmental characteristics (i.e. nutrient level, sediment grain size) between the enclosure sites which could have influenced growth. Higher nutrient availability possibly occurred in the invasive seagrass compared to the native seagrass site, due to differences in distance to a large source of anthropogenic nitrogen (i.e. Simpson Bay lagoon). The invasive seagrass site was located closer to the outlet of Simpson Bay lagoon (350 m) than the enclosures at the native seagrass site (850 m). Higher nutrient availability, e.g. from anthropogenic sources, may change the composition of the benthic diatom community (Licursi et al. 2016), which could have affected growth. However, the re-

sults from the stable isotope analysis showed a similar diet across all investigated seagrass habitats with sediment as the most important source. This was not influenced by differences in habitat characteristics, suggesting that conch can utilize various diatom communities as a source of nutrition, making differences in diatom community less likely to influence conch growth. Benthic diatom abundance, species composition and nutritional quality in relation to environmental parameters such as water quality and grain size were beyond the scope of this study, and their possible effects on queen conch growth remains therefore uncertain.

Although *H. stipulacea* is more sensitive to strong currents and wave action than native seagrasses (den Hartog 1970, Steiner & Willette 2013, Scheibling et al. 2018) and therefore also more vulnerable in shallow waters, the expansion of *H. stipulacea* in the Wider Caribbean Region will continue and likely at the expense of native seagrass beds (Willette & Ambrose 2012), especially in deeper waters and sheltered areas. In areas where native seagrass species will be replaced by *H. stipulacea*, it is to be expected that the growth of juvenile queen conch will deteriorate, due to the growth pattern of *H. stipulacea*, which potentially limits access to and/or reduces the abundance of important food sources (i.e. benthic diatoms and POM). Furthermore, the stable isotope analysis and the mixing model showed that conch found in areas with only invasive seagrass (St Eustatius) did not derive nutrition from the detritus of *H. stipulacea* to any considerable extent, indicating that *H. stipulacea* detritus cannot be considered a replacement of native food sources such as *T. testudinum* detritus.

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LITERATURE CITED

Acosta CA (2001) Assessment of the functional effects of a harvest refuge on spiny lobster and queen conch populations at Glover's Reef Belize. *Gulf Caribb Fish Inst* 52:212–221

- Acosta CA (2006) Impending trade suspensions of Caribbean queen conch under CITES: a case study on fishery impacts and potential for stock recovery. *Fisheries* (Bethesda, MD) 31:601–605
- Appeldoorn RS (1994) Spatial variability in the morphology of queen conch and its implications for management regulations. In: Appeldoorn RS, Rodriguez B (eds) *Queen conch biology, fisheries and mariculture*. Fundacion Cientifica Los Roques, Caracas, p 145–157
- Bannon RO, Roman CT (2008) Using stable isotopes to monitor anthropogenic nitrogen inputs to estuaries. *Ecol Appl* 18:22–30
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67: 1–48
- Becking LE, van Brussel T, Christianen MJA, Debroet AO (2014) Proximate response of fish, conch, and sea turtles to the presence of the invasive seagrass *Halophila stipulacea* in Bonaire. IMARES. Report number C118/14 www.library.wur.nl/WebQuery/wurpubs/456875 (accessed 1 June 2018)
- Bologna PAX, Heck KL Jr (1999) Relative importance of trophic and structural characteristics. *J Exp Mar Biol Ecol* 242:21–39
- Boman EM, de Graaf M, Nagelkerke LAJ, Stoner AW and others (2018) Variability in size at maturity and reproductive season of queen conch *Lobatus gigas* (Gastropoda: Strombidae) in the wider Caribbean Region. *Fish Res* 201:18–25
- Bond AL, Diamond AW (2011) Recent Bayesian stable-isotope mixing models are highly sensitive to variation in discrimination factors. *Ecol Appl* 21:1017–1023
- Brownell WN, Stevely JM (1981) The biology, fisheries, and management of the queen conch *Strombus gigas*. *Mar Fish Rev* 71:1–12
- den Hartog C (1970) *The seagrasses of the world*. North Holland Publishing, Amsterdam
- DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosmochim Acta* 45:341–351
- Fox J, Weisberg S (2011) *An [R] companion to applied regression*, 2nd edn. Sage, Thousand Oaks, CA. <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>
- Fry B (2006) *Stable isotope ecology*. Springer, New York, NY
- Garcia AM, Hoeninghaus DJ, Vieira JP, Winemiller KO (2007) Isotopic variation of fishes in freshwater and estuarine zones of a large subtropical coastal lagoon. *Estuar Coast Shelf Sci* 73:399–408
- Giraudeau P (2018) pgirmess: spatial analysis and data mining for field ecologists. R package version 1.6.9. <https://CRAN.R-project.org/package=pgirmess>
- Hill WR (1996) Effects of light. In: Stevenson RJ, Bothwell ML, Lowe RL (eds) *Algal ecology: freshwater benthic ecosystems*. Academic Press, San Diego, CA
- Hope RM (2013) Rmisc: Ryan miscellaneous. R package version 1.5. <https://CRAN.R-project.org/package=Rmisc>
- Horinouchi M, Mizuno N, Jo Y, Fujita M, Sano M, Suzuki Y (2009) Seagrass habitat complexity does not always decrease foraging efficiencies of piscivorous fishes. *Mar Ecol Prog Ser* 377:43–49
- Husna WNWH, Mazlan AG, Cob ZC (2017) Ontogenetic changes in feeding and food preferences of the dog conch *Laevistrombus canarium* Linnaeus 1758 (Mollusca: Gastropoda) from Merambong shoal, Malaysia. *Chin J Oceanology Limnol* 35:1230–1238
- Iversen ES, Rutherford ES, Bannerot SP, Jory DE (1987) Biological data on Berry Islands (Bahamas) queen conchs, *Strombus gigas*, with mariculture and fisheries management implications. *Fish Bull* 85:229–310
- Jones JJ, Duerdoth CP, Collins AL, Naden PS, Sear DA (2014) Interactions between diatoms and sediment. *Hydrol Processes* 28:1226–1237
- Kairo M, Ali B, Cheesman O, Haysom K, Murphy S (2003) *Invasive species threats in the Caribbean Region*. Report to the nature conservancy. CAB International, Curepe
- Licursi M, Gómez N, Sabater S (2016) Effects of nutrient enrichment on epipelagic diatom assemblages in a nutrient-rich lowland stream, Pampa Region, Argentina. *Hydrobiologia* 766:135–150
- Linton D, Fisher T (2004) Caribbean coastal marine productivity program: 1993–2003. Caribbean coastal marine productivity program (CARICOMP), Kingston
- Lips S, van Slooten L (2009) Water quality in the Simpson Bay Lagoon. A research towards the degree of land-based sewage pollution in the Dutch side of the Simpson Bay Lagoon. BSc dissertation, Van Hall Larenstein University of Applied Sciences, Velp
- Longepierre S, Robert A, Levi F, Francour P (2005) How an invasive alga species (*Caulerpa taxifolia*) induces changes in foraging strategies of the benthivorous fish *Mullus surmuletus* in coastal Mediterranean ecosystems. *Biodivers Conserv* 14:365–376
- MacIntyre HL, Geider RJ, Miller DC (1996) Microphytobenthos: the ecological role of the 'secret garden' of unvegetated, shallow-water marine habitats. I. Distribution, abundance and primary production. *Estuaries* 19: 186–201
- Mann DG (1999) The species concept in diatoms. *Phycologia* 38:437–495
- Olinger LK, Heidmann SL, Durdall AN, Howe C and others (2017) Altered juvenile fish communities associated with invasive *Halophila stipulacea* seagrass habitats in the U.S. Virgin Islands. *PLOS ONE* 12:e0188386
- Parnell A (2016). Stable isotope mixing models in R with simmr. <https://cran.r-project.org/web/packages/simmr/simmr.pdf> (accessed 15 May 2018)
- Parnell AC, Phillips DL, Bearhop S, Semmen BX and others (2013) Bayesian stable isotope mixing models *Andrew. Environmetrics* 24:387–399
- Pasquaudo S, Elie P, Jeantet C, Billy I, Martinez P, Girardin M (2008) A preliminary investigation of the fish food web in the Gironde estuary, France, using dietary and stable isotope analyses. *Estuar Coast Shelf Sci* 78:267–279
- Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Annu Rev Ecol Syst* 18:293–320
- Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montaña CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152:179–189
- R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.r-project.org
- Randall JE (1964) Contribution to the biology of the queen conch *Strombus gigas*. *Bull Mar Sci* 14:246–295
- Ray M, Stoner AW (1995) Growth, survivorship and habitat choice in a newly settled seagrass gastropod, *Strombus gigas*. *Mar Ecol Prog Ser* 123:83–94
- Robertson R (1961) The feeding of *Strombus gigas* and related herbivorous marine gastropods: with a review and field observations. *Mar Fish Rev* 343:1–9

- Ruiz H, Ballantine DL (2004) Occurrence of the seagrass *Halophila stipulacea* in the tropical West Atlantic. *Bull Mar Sci* 75:131–135
- ✦ Scheibling RE, Patriquina DG, Filbee-Dexter K (2018) Distribution and abundance of the invasive seagrass *Halophila stipulacea* and associated benthic macrofauna in Carriacou, Grenadines, Eastern Caribbean. *Aquat Bot* 144:1–8
- Serviere-Zaragoza E, Mazariegos-Villareal A, Aldana-Aranda D (2009) Preliminary observations of natural feed of queen conch *Strombus gigas*. *Proc Gulf Caribb Fish Inst* 61:514–517
- Steiner SCC, Willette DA (2013) The invasive seagrass *Halophila stipulacea* (Hydrocharitaceae, Angiospermae) and its impact on the benthic landscape of Dominica, Lesser Antilles. ITME Research Reports 32. www.itme.org/reports.htm (accessed 1 June 2018)
- ✦ Stoner AW (1989a) Winter mass migration of juvenile queen conch *Strombus gigas* and their influence on the benthic environment. *Mar Ecol Prog Ser* 56:99–104
- ✦ Stoner AW (1989b) Density-dependent growth and grazing effects of the juvenile queen conch *Strombus gigas* L. in a tropical seagrass meadow. *J Exp Mar Biol Ecol* 130:119–133
- Stoner AW (1997) Shell middens as indicators of the long-term distributional pattern in *Strombus gigas*, a heavily exploited marine gastropod. *Bull Mar Sci* 61:559–570
- ✦ Stoner AW (2003) What constitutes essential nursery habitat for a marine species? A case study of habitat form and function for queen conch. *Mar Ecol Prog Ser* 257:275–289
- Stoner AW, Davis M (2010) Queen conch stock assessment historical fishing rounds Andros Island, Bahamas. Community Conch Report for the Nature Conservancy Northern Caribbean Office Nassau, Bahamas. www.communityconch.org/our-research/get-the-report/ (accessed 1 June 2018)
- Stoner AW, Sandt VJ (1991) Experimental analysis of habitat quality for juvenile queen conch in seagrass meadows. *Fish Bull* 89:693–700
- Stoner AW, Sandt VJ (1992) Population structure, seasonal movements and feeding of queen conch, *Strombus gigas*, in deepwater habitats of the Bahamas. *Bull Mar Sci* 51:287–300
- ✦ Stoner AW, Waite JM (1991) Trophic biology of *Strombus gigas* in nursery habitats: diets and food sources in seagrass meadows. *J Molluscan Stud* 57:451–460
- Stoner AW, Hanisak MD, Smith NP, Armstrong RA (1994) Large-scale distribution of queen conch nursery habitats: implications for stock enhancement. In: Appeldoorn RS, Rodriguez B (eds) Queen conch biology, fisheries and mariculture. Fundacion Cientifica Los Roques, Caracas
- Stoner AW, Lin J, Hanisak MD (1995) Relationships between seagrass bed characteristics and juvenile queen conch (*Strombus gigas* Linne) abundance in the Bahamas. *J Shellfish Res* 14:315–323
- ✦ Stoner AW, Mueller KW, Brown-Peterson NJ, Davis MH, Booker CJ (2012a) Maturation and age in queen conch (*Strombus gigas*): urgent need for changes in harvest criteria. *Fish Res* 131–133:76–84
- ✦ Stoner AW, Davis MH, Booker CJ (2012b) Abundance and population structure of queen conch inside and outside a marine protected area: Repeat surveys show significant declines. *Mar Ecol Prog Ser* 460:101–114
- ✦ Stoner AW, Davis M, Kough AS (2019) Relationships between fishing pressure and stock structure in queen conch (*Lobatus gigas*) populations: synthesis of long-term surveys and evidence for overfishing in The Bahamas. *Rev Fish Sci Aquacult* 27:51–71
- ✦ Tett P, Gilpin L, Svendsen H, Erlandsson CP and others (2003) Eutrophication and some European waters of restricted exchange. *Cont Shelf Res* 23:1635–1671
- ✦ Tomasko DA, Dawes CJ, Hall MO (1996) The effects of anthropogenic nutrient enrichment on turtle grass (*Thalassia testudinum*) in Sarasota Bay, Florida. *Estuaries* 19:448–456
- ✦ Trautman DA, Borowitzka MA (1999) Distribution of the epiphytic organisms on *Posidonia australis* and *P. sinuosa*, two seagrasses with differing leaf morphology. *Mar Ecol Prog Ser* 179:215–229
- ✦ van Tussenbroek BI, van Katwijk MM, Bouma TJ, van der Heide T, Govers LL, Leuven RSEW (2016) Non-native seagrass *Halophila stipulacea* forms dense mats under eutrophic conditions in the Caribbean. *J Sea Res* 115:1–5
- ✦ Vanderklift MA, Ponsard S (2003) Sources of variation in consumer-diet $\delta^{15}\text{N}$ enrichment: a meta-analysis. *Oecologia* 136:169–182
- ✦ Vera B, Collado-Vides L, Moreno C, van Tussenbroek BI (2014) *Halophila stipulacea* (Hydrocharitaceae): a recent introduction to the continental waters of Venezuela. *Caribb J Sci* 48:66–70
- ✦ Vermeulen S, Sturaro N, Gobert S, Bouqueneau JM, Lepoint G (2011) Potential early indicators of anthropogenically derived nutrients: a multiscale stable isotope analysis. *Mar Ecol Prog Ser* 422:9–22
- Weil E, Laughlin RA (1984) Biology, population dynamics and reproduction of the queen conch, *Strombus gigas* Linne, in the Archipelago de Los Roques National Park. *J Shellfish Res* 4:45–62
- ✦ Willette DA, Ambrose RF (2012) Effects of the invasive seagrass *Halophila stipulacea* on the native seagrass, *Syringodium filiforme*, and associated fish and epibiota communities in the Eastern Caribbean. *Aquat Bot* 103:74–82
- ✦ Willette DA, Chalifour J, Debrot AOD, Engel MS and others (2014) Continued expansion of the trans-Atlantic invasive marine angiosperm *Halophila stipulacea* in the eastern Caribbean. *Aquat Bot* 112:98–102
- ✦ Williams SL (2007) Introduced species in seagrass ecosystems: status and concerns. *J Exp Mar Biol Ecol* 350:89–110
- ✦ Yang H, Flower RJ (2012) Effects of light and substrate on the benthic diatoms in an oligotrophic lake: a comparison between natural and artificial substrates. *J Phycol* 48:1166–1177