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Short-term variability in chitobiase-based planktonic crustacean production rates in a highly eutrophic tropical estuary

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ABSTRACT: Although tropical oceans are generally assumed to have low zooplankton biomass throughout the year, high copepod abundance coupled with fast growth rates can result in a significant amount of crustacean zooplankton production. Here, we use the crustacean moulting enzyme chitobiase to obtain routine estimates of community-level crustacean productivity over a 3-mo period in Guanabara Bay, Rio de Janeiro, Brazil. Chitobiase-based daily production to biomass ratios (*P*/*B*) and production rates were compared to values derived from more traditional global predictive models. We examined the abiotic and biotic factors most strongly influencing copepod biomass, daily *P*/*B*, and production rates. Mean copepod biomass was 24.0 mg C m^{-3} over the sampling period, while daily *P*/*B* ranged between 0.15 and 1.20. Copepod biomass was negatively related to dissolved oxygen and tidal amplitude, characteristic of the highly eutrophic waters from the inner bay. Mean crustacean productivity over our sampling period was 22.0 mg C m^{-3} d^{-1}, varying more over monthly timescales compared to weekly or daily variations. No relationship was found between production rates and biomass, suggesting that biomass, alone, does not explain productivity in Guanabara Bay. Chitobiase-based daily *P*/*B* and crustacean production rates were almost always higher than production estimates from global models. Results from this study highlight the need for accurate estimates of crustacean production rates in order to fully understand trophic relationships given that biomass, alone, did not explain the short-term variability in crustacean production. Ultimately, this study reveals that small, fast-growing copepods can contribute just as much, if not more, energy to higher trophic levels in eutrophic tropical estuaries compared to temperate regions.

KEY WORDS: Chitobiase · Copepods · Guanabara Bay · Secondary production · Crustacean · Zooplankton

INTRODUCTION

Examining energy transfer between trophic levels is critical to our understanding of marine food webs. Estimates of zooplankton production, i.e. the rate of biomass generated per unit time, rather than biomass estimates alone, are crucial when examining trophic dynamics (Longhurst 1984) because they reveal how much energy is being transferred from phytoplankton and heterotrophic microflagellates to zooplankton and, ultimately, the amount of energy available to higher trophic levels. Estimates of production require the measurement of both biomass and individual growth rates (Huntley & Lopez 1992). Compared to measurements of primary production, there is still a lack of consensus as to how zooplankton production

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should be measured. Historically, measurements of zooplankton production have relied on time-consuming incubations of specific size classes or cohorts of copepods (Kimmerer & McKinnon 1987, Peterson et al. 1991, Webber & Roff 1995). Alternatively, global mathematical models (e.g. Huntley & Lopez 1992, Hirst & Lampitt 1998, Hirst & Bunker 2003) have been used to estimate copepod growth rates because they allow for broad-scale temporal and spatial estimates of zooplankton production with relatively little effort compared to the more traditional field methods.

More recently, the chitobiase method has been validated for routinely and rapidly estimating *in situ* community-level crustacean production rates at sea (Sastri & Dower 2006, Sastri & Dower 2009). Chitobiase, a crustacean moulting enzyme, is released into the surrounding water upon moulting (Oosterhuis et al. 2000, Sastri & Roff 2000, Knotz et al. 2006). Measurements of the decay rate of chitobiase activity (CBA) in the water column can then be used to directly estimate crustacean production rates. Significant relationships between body length (and weight) and the rate of production of chitobiase activity have already been established for marine copepods in both temperate (Sastri & Dower 2006) and subtropical regions (Avila et al. 2011). The major benefit of using this enzymatic approach is that it avoids biases associated with underestimating abundance and biomass due to net selectivity, the repeated handling of animals, and the difficulties that arise when identifying and measuring small individuals. Therefore, the chitobiase method takes into account the production of all planktonic crustaceans — including those that are too small (e.g. nauplii) or too large (e.g. krill) to be effectively sampled by traditional plankton nets.

The majority of zooplankton productivity estimates come from mid- to high-latitudes dominated by large-bodied copepods with annual life cycles (see Turner 2004). Compared to temperate regions, studies of zooplankton dynamics in the tropics are sparse and are often limited to records of species abundance and biomass (e.g. Moore & Sander 1976, Youngbluth 1980, Yoshioka et al. 1985, Webber et al. 1996). Given that the copepod assemblage is typically dominated by small (<1 mm) individuals, estimates of abundance and biomass in tropical regions are confounded by the choice of the mesh size used to collect zooplankton, potentially resulting in severe underestimations of the contribution of smaller species (Hopcroft et al. 1998a, Gallienne & Robins 2001, Avila et al. 2012). Although tropical regions have lower overall zooplankton biomass, the high growth rates exhibited by small copepods with multigenerational annual life cycles can still result in high amounts of production (Hopcroft & Roff 1998a). Furthermore, large inputs of nutrients and organic matter from tropical rivers contribute to high phytoplankton and crustacean production rates in estuaries and adjacent coastal regions year round, which may be comparable to the most productive upwelling regions of the world's ocean (Nittrouer et al. 1995).

Some of the most notable studies of the tropics have provided a comprehensive examination of naupliar (Hopcroft & Roff 1998a), copepodite (Hopcroft et al. 1998b), and general copepod production in the coastal waters of the Caribbean (Hopcroft & Roff 1998b, Hopcroft et al. 1998a, 2001). Studies of copepod production in food-limited (e.g. oceanic) tropical ecosystems, on the other hand, are even more rare (Webber & Roff 1995, McKinnon & Duggan 2003). While these studies have led to a clearer understanding of copepod production in tropical regions, the magnitude by which production is underestimated because of the historical reliance on traditional incubation methods or net-based biomass estimates is unknown.

The overall aim of this study was to determine the abiotic and biotic factors most strongly influencing crustacean biomass and chitobiase-based estimates of community-level crustacean productivity over a short timescale in the highly eutrophic Guanabara Bay, Rio de Janeiro, Brazil. Chitobiase-based community-level production rates have recently been estimated for Patos Lagoon estuary in southern Brazil (Avila et al. 2012); however, despite numerous recent studies on population dynamics of zooplankton in Guanabara Bay (e.g. Marazzo & Valentin 2000, 2001, Schwamborn et al. 2004), crustacean production has yet to be studied in the region. Given the dynamic nature of this estuary and the short life cycle of tropical planktonic crustaceans, sampling was conducted across different timescales (monthly, weekly, daily) over a 3-mo period in order to capture how quickly planktonic crustaceans respond to changes in hydrological conditions. In addition, chitobiase-based production rates were compared with previous estimates for tropical regions and with those derived from global mathematical models using biomass estimates from zooplankton nets. Results from this study provide the first routine analysis of community-level crustacean productivity for a eutrophic tropical estuary. Given that small copepods, including nauplii and copepodites, provide a key link between the microbial food web and fish larvae or other planktivores

(Hopcroft et al. 2001, Turner 2004), accurate estimates of production are imperative in terms of understanding trophic relationships in these regions. Ultimately, results from this study will provide insight as to how much energy is potentially available to higher trophic levels in tropical regions.

MATERIALS AND METHODS

Study site

Sampling was conducted over different timescales at a single site (22° 54′ 11″ S, 43° 09′ 29″ W) near the entrance to Guanabara Bay, Rio de Janeiro, Brazil (Fig. 1) from April to June, 2012. Guanabara Bay is a highly eutrophic, tropical coastal estuary characterized by high levels of pollution due to a large input of untreated domestic and industrial waste (Kjerfve et al. 1997). Water is exchanged throughout most of the bay during the tidal cycles, with coastal water being brought in via a central Channel with a depth of 30 m (Kjerfve et al. 1997, Paranhos et al. 1998, Schwamborn et al. 2004); however, the mean depth of the entire bay is 5.7 m (Kjerfve et al. 1997). Although Guanabara Bay is influenced by semidiurnal tidal forcing as well as the 14 d tidal cycle, tidal ranges and currents are small in comparison to those of other coastal bays (Kjerfve et al. 1997).

Physicochemical and biological measurements

Water column temperature, salinity, and dissolved oxygen were recorded on each sampling date from just above the seafloor (~20 m) to the surface at approximately 0.5 m intervals with a Seacat SBE 19 CTD with an attached SBE 43 dissolved oxygen sensor (Seabird). Hourly tidal heights were obtained from the National Oceanographic Database provided by the Brazilian Marines. Seawater samples for particulate organic carbon (POC) and chlorophyll *a* (a proxy for phytoplankton biomass) were collected from a single depth near the surface (1 m). For POC, samples were measured on pre-combusted (550°C for 2 h) GF/F filters after filtration of 200 ml of seawater. Filters were analyzed on an elemental analyzer CHN in the Geochemistry Laboratory at the Rio de Janeiro State University.

For chlorophyll *a* analysis, 2 replicates of a variable volume (50–300 ml) of total and <20 µm size-fractionated (filtered through Nitex mesh) seawater was filtered onto 0.7 µm pore size, 47 mm diameter glass fiber filters (GF/F) under low pressure and stored at −20°C until further analysis. Pigments were extracted in 90% acetone and measured with fluorometric techniques on a Varian Cary Eclipse® spectrofluorometer. Chlorophyll was assessed using a modified version of the Neveux & Lantoine (1993) method. Modifications described in Tenório et al. (2005) were as follows: (1) data acquisition was performed by recording the fluorescence emission spectra for each of 31 excitation wavelengths (3 nm increments from 390 to 480 nm). Emission spectra were recorded at 2 nm intervals from 615 to 715 nm, yielding 51 data points for each spectrum. Pigment concentrations were estimated from the resulting 1581 data points, and (2) where the least squares approximation technique was constrained to discard negative solutions.

Zooplankton community composition

Zooplankton samples were collected by replicate (n = 3) vertical hauls from just above the sea floor to the surface at 0.3 m s^{-1} using a 64 µm mesh ring net with an attached flowmeter. Contents of the non-filtering cod end were immediately preserved in 4% borate-buffered formalin. In the laboratory, 3 subsamples of 10 ml were counted using a binocular microscope. Copepod measurements (prosome length) were determined using an inverted microscope equipped with a video camera attached to a computer with image analysis software (Axiovision 4.7). Zooplankton samples were identified according to taxonomic descriptions provided by Boltovskoy (1999). Abundances (ind. m^{-3}) were converted to biomass (mg C m^{-3}) using known length–weight regressions for tropical copepods (Chisholm & Roff 1990a) with a carbon conversion factor of 0.4 (Postel et al. 2000).

Crustacean production rates

Water samples for chitobiase incubations were collected from 2 depths in the water column (1 and 15 m). Chitobiase decay rates were estimated from 200 ml seawater samples screened with a 20 µm mesh in order to remove any crustaceans. Approximately 20 ml of the seawater sample from each treatment was immediately filtered (0.2 µm) in order to remove any bacteria and subsequently used to estimate the native *in situ* chitobiase activity (CBA_{nat}). A crude homogenate of approximately 100 small-sized copepods (freshly ground in 3 ml of seawater; 0.2 µm

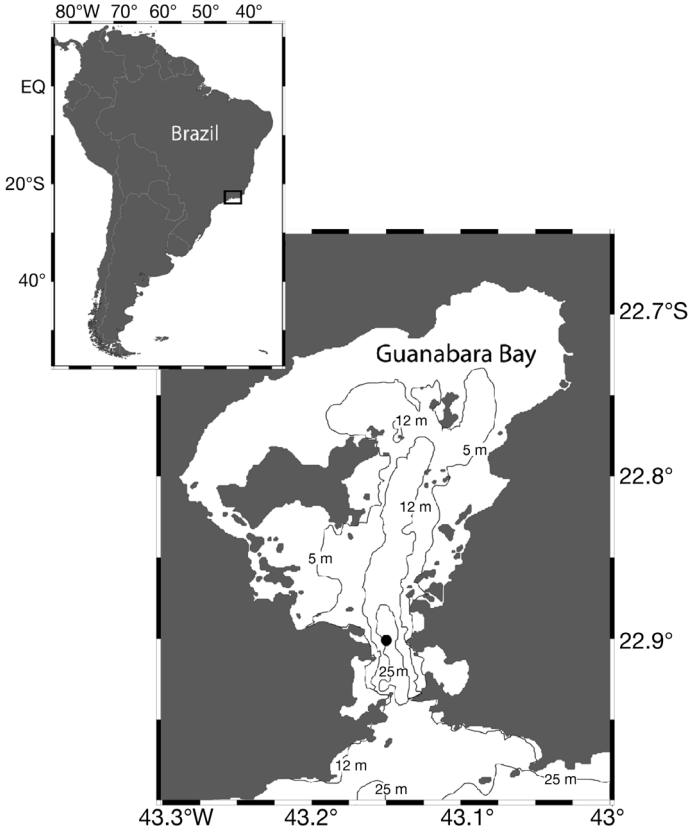

Fig. 1. Location of sampling site (●) in Guanabara Bay, Rio de Janeiro, Brazil

filtered) was used to 'spike' the original treatment samples in order to differentiate the decay of CBA from background fluorescence (see Sastri & Dower 2006). Samples were maintained at ambient seawater temperature over the 24 h incubation period, and subsamples were taken at regular intervals (i.e. at 2, 4, 6, and 24 h), 0.2 µm filtered, and stored in the freezer (–20°C) in glass scintillation vials until assayed.

Measurements of CBA followed Sastri & Dower (2006). Briefly, frozen samples were left to thaw at room temperature for 2 h prior to analysis. Enzyme assays were initiated by adding the substrate 4-methylumbelliferyl-β-D-glucosaminide (0.1 mmol MBF-NAG; Sigma) to seawater samples. Assays were conducted at 25°C and terminated after 60 min with the addition of a 2 M NaOH and 0.4 M EDTA solution. The reaction was buffered to pH 6.0 (optimal for copepods) using a 0.15 M citrate-phosphate buffer. Chitobiase activity (nmol MBF liberated l^{-1} h^{-1}) was estimated by measuring the fluorescence of the liberated MBF using a Turner Designs TD700 fluorometer with a long wavelength bulb (300–400 nm excitation and 410–600 nm emission lenses). Raw fluorescence was converted to nanomoles of MBF using a standard curve of known 4-methylumbelliferone concentrations against fluorescence.

Estimates of the CBA decay rate (h^{-1}) were calculated as the slope (k) of the natural logarithm of CBA versus time (Sastri & Dower 2006). The reciprocal of the negative slope ($1/-k$) was used as a proxy for stage duration (T_{CBA}), which is the time taken for moulting individuals to produce CBA equivalent to that measured *in situ* (CBA_{nat}). T_{CBA} has previously been shown to be strongly correlated to stage duration for the average-sized individual in the community (Sastri & Dower 2006, Suchy et al. 2013) and is not a species-specific estimate of stage duration, per se. The chitobiase method assumes that (1) the crustacean community is in steady state for the duration of the 24 h incubation period, i.e. the size-frequency distribution and the mean moulting rate of the community remain constant, and (2) chitobiase production is balanced by its rate of decay (Sastri & Dower 2006, Sastri & Dower 2009). Given that CBA is related to individual dry weight in copepods, decapod larvae, and mysids by the following relationship: $\log_e(CBA) = 1.55 \log_e(DM) + 5.60$, where DM represents individual dry mass in milligrams (Sastri & Dower 2009), and that the gain in dry weight between stages (ΔB_i) is positively correlated with mass, CBA is related to the growth rate of copepods. Therefore, using literature-based reports of specific body weight for the dominant taxa in Guanabara Bay (Table 1), a modified relationship between CBA and the growth increment [$\log_{10}(\Delta B_i) = 0.634\log_{10}(CBA_i) - 2.039$; Table 1, Fig. 2] was derived for tropical waters. Production rates would be severely overestimated without this modification due to the smaller body size of tropical copepods compared to the larger size of temperate species for which this relationship was originally derived. Similar modifications have also been made in freshwater studies (Sastri et al. 2013). This relationship was then applied to the mean CBA_{nat} in each treatment to calculate the absolute amount of biomass produced (ΔB). Daily crustacean production rates (mg C m^{-3} d^{-1}) were calculated as the biomass production divided by the turnover rate, or $\Delta B/T_{CBA}$. Net-based production rates were calculated using biomass estimates from 64 µm zooplankton nets by applying the Huntley & Lopez (1992), Hirst & Lampitt (1998), and Hirst & Bunker (2003) global mathematical models, which incorporate temperature, body size, chlorophyll *a*, or a combination of these variables into growth rate equations. The ratio of daily crustacean productivity to the developing biomass (daily P/B) was estimated from our values of CBA_{nat} and was used as an equivalent to the daily growth rate (d^{-1}) (Sastri et al. 2012).

Table 1. Stage-specific individual body weight (µg dry wt. ind.$^{-1}$) for 4 common tropical copepod species as reported in the literature. ΔB_i was calculated as the difference in weight between successive developmental stages. Weights reported for species denoted with an asterisk (*) were calculated from length using the length–weight regressions reported in Ara (2001). [1]Heinle (1966). [2]Ara (2002). [3]Ara (2001). [4]Webber & Roff (1995). N: naupliar stages 1–6; C: copopodite stages 1–6

Stage	Weight (µg ind.$^{-1}$)	ΔB_i (µg ind.$^{-1}$)
Acartia tonsa*[1]		
NI	0.016	
NII	0.011	0.005
NIII	0.019	0.008
NIV	0.03	0.011
NV	0.045	0.014
NVI	0.064	0.019
CI	0.398	0.334
CII	0.642	0.245
CIII	1.235	0.593
CIV	1.969	0.734
CV	3.409	1.440
CVI	6.092	2.689
Temora turbinata*[2]		
CI	0.105	
CII	0.197	0.092
CIII	0.344	0.147
CIV	0.587	0.243
CV	1.204	0.617
CVI	2.144	0.939
Oithona plumifera*[3]		
NI	0.026	
NII	0.053	0.027
NIII	0.067	0.014
NIV	0.111	0.044
NV	0.149	0.038
NVI	0.222	0.073
CI	0.33	0.108
CII	0.53	0.2
CIII	0.96	0.43
CIV	1.380	0.42
CV	1.710	0.33
CVI	1.900	0.19
***Paracalanus* sp.[4]**		
CI	0.22	
CII	0.46	0.24
CIII	0.88	0.42
CIV	1.430	0.55
CV	1.740	0.31
CVI	3.090	1.350

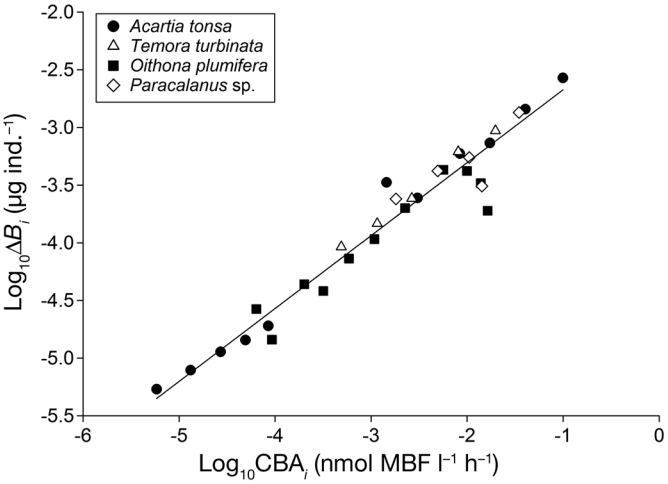

Fig. 2. Relationship between change in body weight between successive developmental stages (ΔB_i) and individual chitobiase activity (CBA_i). CBA was estimated by applying a known relationship between individual CBA and post-moult body weight (Sastri & Dower 2009) to each of the successive weights presented in Table 1. The solid line is a linear regression ($R^2 = 0.95$, $p < 0.0001$)

Statistical analysis

Best subsets regression was used to select the best-fitting model to explain our biomass and daily *P/B* estimates. Abundances of the dominant crustacean taxa and hydrological indicators (salinity, temperature, and tidal amplitude) were used as explanatory variables for biomass, whereas the relative biomass (%) of the dominant copepod taxa, food quantity parameters (total chlorophyll *a* and POC), temperature, and median prosome length were used as explanatory variables for daily *P/B*. Temperature, daily *P/B*, median prosome length, and biomass of the dominant copepod taxa were included as explanatory variables for crustacean productivity. All explanatory variables were transformed when appropriate using logarithmic (abundance and biomass) or arcsine-square root (percentage data) transformations. Models with significant parameters were selected based on the highest adjusted R^2, lowest mean squared error values, and Mallow's C_p criterion. Multiple linear regressions were then performed on the explanatory variables represented in the best model. All analyses were performed using Sigmaplot® Version 12.3 and R Version 3.0.2 (R Development Core Team 2013).

RESULTS

Physicochemical and biological data

Water column temperature at the sampling site in Guanabara Bay followed a typical seasonal pattern showing a gradual decrease from 25°C to <22°C from Day 101 to 170 (April–June) (Fig. 3a). Salinity values showed little variation during the study period, ranging between 31.8 and 33.0 (Fig. 3b). Oxygen was lowest between Days 108 and 123,

ranging between 3 and 5 mg l^{-1} throughout the sampling period (Fig. 3c). Tidal amplitude, the difference between the highest and lowest measured tides on our sampling days, was fairly constant in April (approximately 1 m) but fluctuated after mid-May (Fig. 3d). Slight variations in temperature and salinity were observed during our daily sampling in May (Days 142–145). POC ranged between 1.4 and 12.2 mg l^{-1} (Fig. 4a). Maximum POC concentrations were observed in early May (8.3 and 12.2 mg l^{-1} on Days 130 and 136, respectively). In terms of phytoplankton biomass, the <20 µm size fraction dominated; however, >20 µm cells (diatoms) also contributed to the total chlorophyll concentration in May (Fig. 4b).

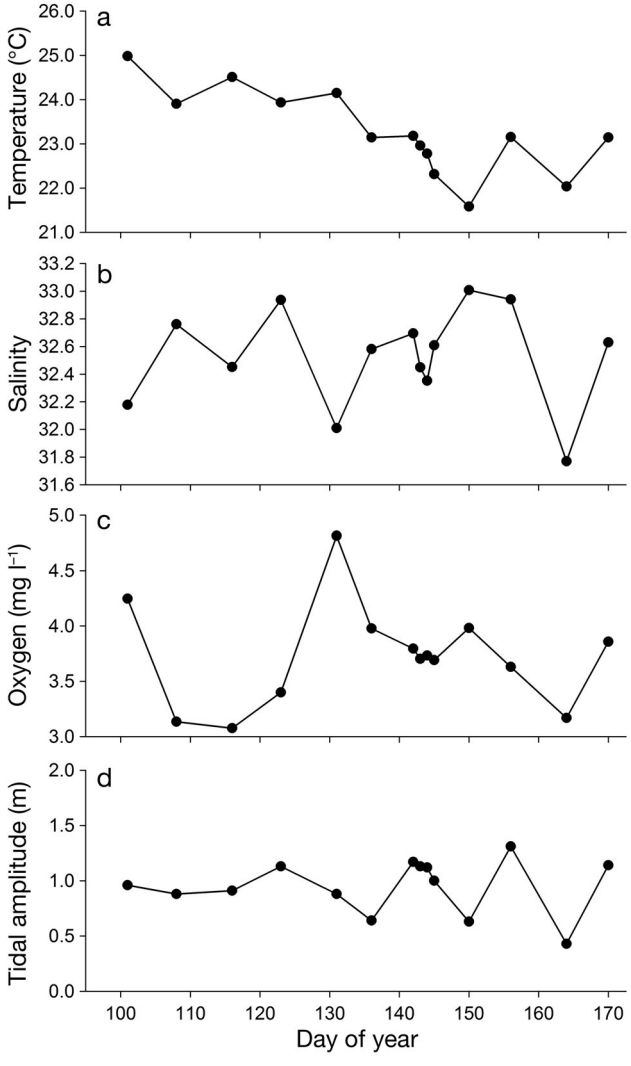

Fig. 3. Mean water column (a) temperature, (b) salinity, (c) oxygen, and (d) tidal amplitude (the maximum difference in tidal height [m] from the lowest to highest measured tide) on sampling days from April to June, 2012

Crustacean abundance and copepod biomass

Median copepod prosome length was around 200 µm across all sampling dates; however, the range of values representing the 25th and 75th percentiles was quite variable (Fig. 5a). Crustacean abundance ranged between 26 365 and 273 080 ind. m^{-3} (mean: 113 467 ind. m^{-3}) with the highest abundance occurring on Day 108 (mid-April; Table 2). Nauplii contributed substantially to overall crustacean abundance on most of the sampling dates. Although *Acartia* and *Oithona* were the dominant copepod genera throughout our study, *Paracalanus*, *Temora*, and *Oncaea* were also abundant in most of the zooplankton samples. In contrast to abundance, peak copepod biomass occurred on Day 156 (early June), when biomass was 62.0 mg C m^{-3} (Fig. 5b), whereas mean biomass across all sampling dates was 24.0 mg C m^{-3}. Nauplii and copepodites contributed to a large proportion of

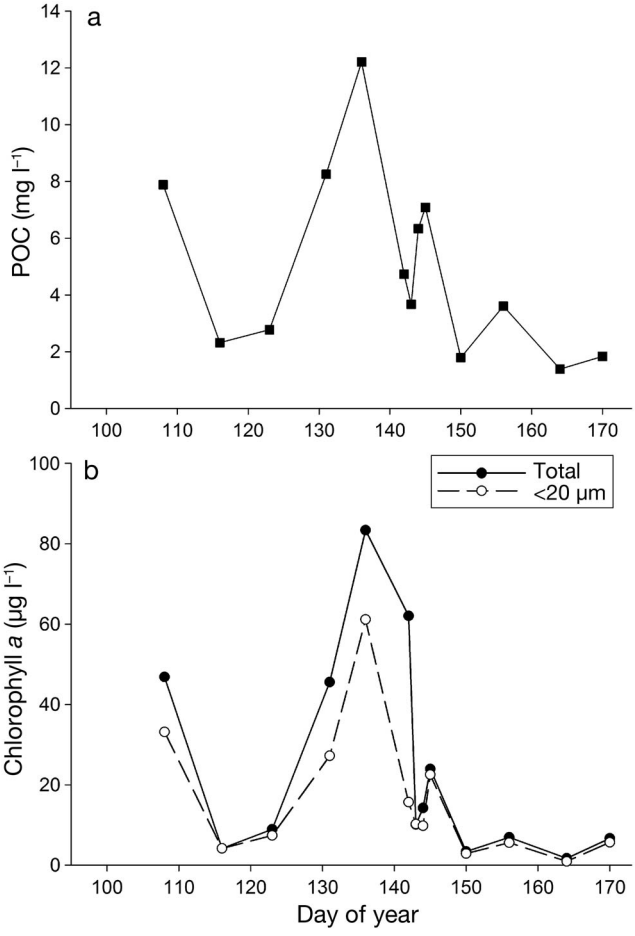

Fig. 4. (a) Particulate organic carbon (POC) and (b) total and <20 µm chlorophyll *a* on sampling days from April to June, 2012

the biomass throughout the study, representing up to 47.4 and 65.0% of the total biomass of the dominant copepods, respectively (Table 3). Crustacean abundance showed little variation during our daily sampling in May; however, biomass in the 64 µm mesh net decreased substantially on Day 143 before increasing again on Days 144 and 145 (Fig. 5b).

Chitobiase-based production rates

Mean CBA_{nat} was higher in April (14.38 nmol l^{-1} h^{-1}) than in May and June (Table 4). In addition, the mean T_{CBA} was longer in April (approximately 1.3 d) than in May and June (<0.5 d). Overall, planktonic crustacean production rates ranged between 9.95 and 29.33 mg C m^{-3} d^{-1} and were slightly higher in April (Days 94–116) than in May/June (Days 123–170) (Table 5). Crustacean production rates varied more on a weekly timescale compared to the daily timescale examined in May.

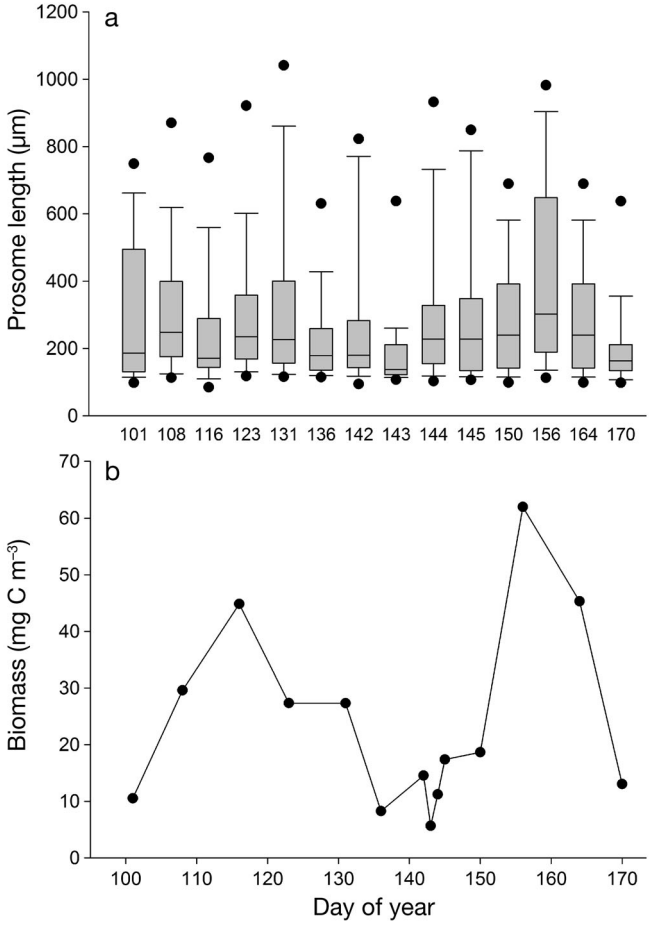

Fig. 5. (a) Prosome lengths (n = 50) for copepods measured on each sampling date. Boxes represent the 25th and 75th percentiles; the solid line in the box is the median. The upper and lower whiskers represent the greatest and least values (excluding outliers), respectively. The 5th and 95th percentiles of the outliers are indicated by dots. (b) Net-based copepod biomass on sampling days from April to June, 2012

Daily *P*/*B* was highest at the end of May (Days 144, 145, and 150) and in mid-June (Day 164), ranging between 1.05 and 1.20 (Table 5). During April and early May, chitobiase estimates of daily *P*/*B* were mostly lower than daily growth rates predicted by the mathematical models (Table 5). Daily *P*/*B* values were higher than growth rates predicted by the models for the rest of the sampling period, with the exception of Days 131 and 136 (mid-May) as predicted by the Hirst & Bunker (2003) model. Chitobiase-based crustacean production rates were substantially higher than production rates estimated from the mathematical models on the majority of our sampling dates with a few exceptions (Table 5). For example, chitobiase-based productivity on 25 April (Day 116) was lower than the production rates estimated by all of the models. In addition, the Huntley & Lopez (1992) model predicated higher production rates on 10 May (Day 131), 4 June (150), and 12 June (164), and Hirst & Bunker (2003) production rates were higher than chitobiase rates on 10 May (Table 5).

Best subset regression analysis was used to determine which explanatory variables best explained variations in net-based copepod biomass and chitobiase-based daily *P*/*B* (Table 6). Positive, significant relationships were found between copepod biomass and *Oithona* abundance, whereas negative, significant relationships were found between biomass and *Acartia* abundance, dissolved oxygen, and tidal amplitude (Adj R^2 = 0.586). The significant variables best predicting chitobiase-based estimates of daily *P*/*B* included temperature (negative), median prosome length (positive), and the relative biomass of *Paracalanus* nauplii (positive) (Adj R^2 = 0.864) (Table 6). A significant, positive relationship was found between crustacean productivity and nauplii biomass, whereas a significant negative relationship was found between productivity and copepodite biomass (Table 6). No relationship was found between net-based biomass and crustacean productivity (Fig. 6).

DISCUSSION

Despite the fact that tropical regions are generally viewed as having low zooplankton biomass and thus low productivity throughout the year compared to temperate regions (Webber & Roff 1995), the eutrophic

Table 2. Abundance (ind. m^{-3}) and relative abundance (in brackets) of the dominant crustacean taxa from April to June, 2012

10 Apr	17 Apr	25 Apr	2 May	10 May	15 May	21 May	22 May	23 May	24 May	29 May	4 Jun	12 Jun	18 Jun
Acartia													
3190	21328	710	2906	1800	4129	4487	1842	2418	2495	13848	0	1009	5978
(0.12)	(0.08)	(0.01)	(0.06)	(0.02)	(0.05)	(0.04)	(0.02)	(0.03)	(0.02)	(0.19)	(0)	(0.08)	(0.04)
Oithona													
1328	18980	1396	2377	5208	3042	3522	775	3585	8445	6535	3292	3372	11525
(0.05)	(0.07)	(0.01)	(0.05)	(0.06)	(0.04)	(0.03)	(0.01)	(0.04)	(0.08)	(0.09)	(0.02)	(0.02)	(0.08)
Oncaea													
8773	10968	30232	7347	2006	4439	686	836	1372	1622	8118	0	14503	1898
(0.33)	(0.04)	(0.28)	(0.14)	(0.02)	(0.05)	(0.01)	(0.01)	(0.02)	(0.02)	(0.11)	(0)	(0.1)	(0.01)
Paracalanus													
7521	0	2329	12223	3376	705	1767	2348	1964	1190	16345	0	2382	2004
(0.29)	(0)	(0.02)	(0.24)	(0.04)	(0.01)	(0.02)	(0.03)	(0.02)	(0.01)	(0.23)	(0)	(0.02)	(0.01)
Temora													
998	7600	12092	6327	3197	2401	3106	1512	1388	78	1302	21655	2841	9631
(0.04)	(0.03)	(0.11)	(0.12)	(0.04)	(0.03)	(0.03)	(0.02)	(0.02)	(0)	(0.02)	(0.12)	(0.02)	(0.07)
Nauplii													
795	198588	882	7160	32931	56648	75500	66765	65596	78677	13569	110490	90100	85025
(0.03)	(0.73)	(0.01)	(0.14)	(0.4)	(0.69)	(0.74)	(0.78)	(0.77)	(0.75)	(0.19)	(0.61)	(0.63)	(0.59)
Copepodites													
2958	12416	53697	12081	33604	9877	12248	11066	8565	11370	12016	43253	18858	27913
(0.11)	(0.05)	(0.49)	(0.24)	(0.41)	(0.12)	(0.12)	(0.13)	(0.1)	(0.11)	(0.17)	(0.24)	(0.13)	(0.19)
Other crustaceans													
802	3201	8032	427	0	991	404	161	0	833	185	3341	0	0
(0.03)	(0.01)	(0.07)	(0.01)	(0)	(0.01)	(0)	(0)	(0)	(0.01)	(0)	(0.02)	(0)	(0)
Total													
26365	273080	109371	50848	82123	82232	101721	85304	84888	104711	71918	182030	143065	143974

Table 3. Relative biomass (%) of the dominant copepod taxa from April to June, 2012

	10 Apr	17 Apr	25 Apr	2 May	10 May	15 May	21 May	22 May	23 May	24 May	29 May	4 Jun	12 Jun	18 Jun
Acartia	13.64	19.53	0.75	6.92	3.48	11.33	13.15	5.28	8.56	7.04	22.50	0.00	20.86	6.98
Oithona	4.83	15.82	1.18	4.62	7.80	8.11	8.17	2.21	10.62	18.71	10.64	3.16	4.78	14.77
Oncaea	31.87	9.14	25.61	14.27	3.00	11.83	1.59	2.39	4.06	3.59	13.22	0.00	20.55	2.43
Paracalanus	32.16	6.96	2.47	29.11	6.53	1.93	5.18	6.73	6.96	3.36	26.56	0.00	4.51	2.34
Temora	4.27	0.00	12.83	15.07	6.19	6.59	9.10	4.33	4.92	0.22	2.12	28.53	5.38	11.24
Nauplii	0.58	37.17	0.15	1.24	7.96	33.12	26.93	47.37	34.55	35.01	5.44	11.34	8.18	29.67
Copepodites	12.65	11.37	56.99	28.77	65.03	27.09	35.88	31.70	30.33	32.08	19.52	56.98	35.74	32.57

Table 4. Mean monthly chitobiase-based estimates of native chitobiase (CBA_{nat}), and chitobiase turnover rate or stage duration (T_{CBA}). Range of values is also presented

	CBA_{nat} (nmol l^{-1} h^{-1})		T_{CBA} (d)	
	Mean	Range	Mean	Range
Apr	14.38	12.19–16.77	1.27	0.75–2.23
May	3.93	1.33–12.82	0.42	0.28–0.71
Jun	3.53	2.04–4.86	0.37	0.31–0.42

nature of Guanabara Bay supports high crustacean abundance, biomass, and production. Our values for mean crustacean abundance (113 467 ind. m^{-3}) and mean biomass (24.0 mg C m^{-3}) were higher than those observed in Kingston Harbour, Jamaica (92 500 ind. m^{-3} and 22.1 mg C m^{-3} for mean abundance and biomass, respectively) (Hopcroft et al. 1998a). In addition, mean biomass in Guanabara Bay was higher relative to that observed in Patos Lagoon estuary in southern Brazil (13.64 mg C m^{-3}) (Avila et

Table 5. Comparison of chitobiase-based daily production to biomass ratios (*P/B*) and crustacean production rates (mg C m^{-3} d^{-1}) with growth rates (d^{-1}) and production rates derived from the global predictive models of Huntley & Lopez (1992), Hirst & Lampitt (1998), and Hirst & Bunker (2003). Model values were produced using net-based biomass estimates

Sampling date	Day of year	Daily *P/B* or growth rate				Crustacean productivity			
		Chitobiase	Huntley & Lopez (1992)	Hirst & Lampitt (1998)	Hirst & Bunker (2003)	Chitobiase	Huntley & Lopez (1992)	Hirst & Lampitt (1998)	Hirst & Bunker (2003)
10 Apr	101	0.46	0.71	0.39	1.07	28.00	7.49	4.07	11.28
17 Apr	108	0.39	0.63	0.47	0.46	29.33	18.71	13.99	13.64
25 Apr	116	0.15	0.68	0.39	0.54	9.95	30.33	17.51	24.22
02 May	123	0.46	0.63	0.35	0.98	29.06	17.33	9.62	26.67
10 May	131	0.67	0.65	0.33	1.19	12.23	17.74	9.05	32.62
15 May	136	0.72	0.58	0.47	1.41	23.73	4.80	3.88	11.65
21 May	142	0.79	0.58	0.41	0.59	23.36	8.47	5.92	8.54
22 May	143	0.96	0.57	0.56	0.88	22.82	3.21	3.13	4.95
23 May	144	1.08	0.56	0.35	0.74	17.52	6.25	3.94	8.33
24 May	145	1.05	0.53	0.36	0.33	22.08	9.20	6.20	5.78
29 May	150	1.20	0.49	0.34	0.43	17.54	9.11	6.39	8.06
04 Jun	156	0.88	0.58	0.28	0.20	24.69	36.06	17.06	12.46
12 Jun	164	1.09	0.51	0.26	0.34	20.99	23.28	11.93	15.48
18 Jun	170	0.79	0.58	0.53	0.62	26.64	7.57	6.91	8.03

al. 2012). Furthermore, although nauplii dominated our samples numerically, copepodite stages contributed to the bulk of biomass on most sampling dates.

In order to compare our production rates with previous studies, we converted our chitobiase-based productivity estimates into energy density using a conversion factor of 25 kJ g^{-1} C (Chisholm & Roff 1990b). Across the entire sampling period, mean crustacean productivity in the present study was 550 J m^{-3} d^{-1}, which is almost double the mean copepod community productivity of 307 J m^{-3} d^{-1} estimated for Kingston Harbour by Hopcroft et al. (1998a) using incubation methods. It should be noted that we were unable to determine the contribution of chitobiase by moulting benthic crustaceans, which may have resulted in slight overestimations in planktonic crustacean production due to the shallow nature of Guanabara Bay. That said, the relative abundance of other crustaceans was from 0 to 3% on all but one sampling date, and thus their influence on our chitobiase estimates was likely negligible. In contrast to our results, in more oligotrophic tropical regions where food may become limiting to copepod growth (i.e. oceanic or shelf regions), production is lower than the values reported in our study (Webber & Roff 1995, McKinnon & Duggan 2003). Therefore, the high production rates observed in

Table 6. Results of multiple linear regressions and the significance of the model variables chosen by the best subsets regression best describing copepod biomass (mg C m^{-3}), chitobiase-based daily *P/B*, and crustacean productivity (mg C m^{-3} d^{-1}). Significant values are indicated in **bold**. Asinsqrt is the arcsine-square root transformation

	Coefficient	SE	p-value
Log_{10}copepod biomass (N = 14, R^2 = 0.777, Adj R^2 = 0.586)			
Constant	−1.988	1.899	0.33
Log_{10}*Acartia* abundance	−0.263	0.07	**0.007**
Log_{10}*Oithona* abundance	0.638	0.222	**0.024**
Log_{10}*Paracalanus* abundance	0.105	0.057	0.11
Dissolved oxygen	−0.404	0.14	**0.023**
Tidal amplitude	−0.728	0.273	**0.032**
Temperature	0.162	0.07	0.053
Daily *P/B* (N = 14, R^2 = 0.927, Adj R^2= 0.864)			
Constant	4.376	1.338	**0.014**
Temperature	−0.227	0.044	**0.001**
Median Prosome Length	0.003	0.001	**0.048**
Asinsqrt % *Paracalanus* biomass	0.996	0.356	**0.027**
Asinsqrt % *Temora* biomass	0.191	0.308	0.556
Asinsqrt % nauplii biomass	0.988	0.316	**0.017**
Asinsqrt % copepodite biomass	0.563	0.308	0.119
Log_{10}crustacean productivity (N = 14, R^2 = 0.614, Adj R^2 = 0.372)			
Constant	1.423	0.179	**<0.001**
Daily *P/B*	−0.375	0.174	0.064
Median size	0.002	0.001	0.074
Log_{10}*Temora* biomass	0.063	0.044	0.196
Log_{10}nauplii biomass	0.224	0.083	**0.027**
Log_{10}copepodite biomass	−0.431	0.138	**0.014**

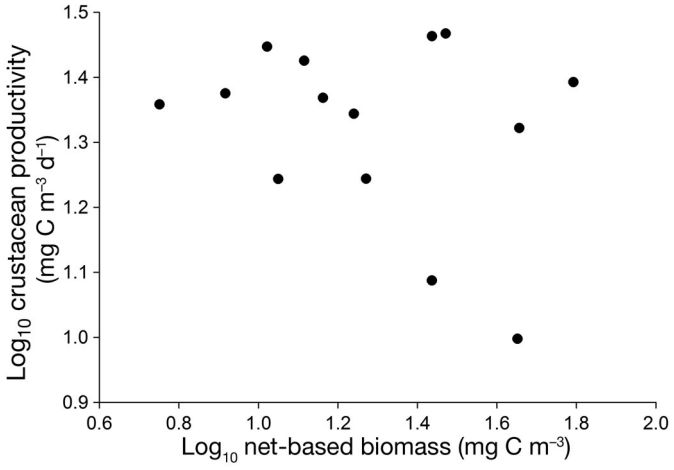

Fig. 6. Relationship between crustacean productivity (mg C m^{-3} d^{-1}) and net-based copepod biomass (mg C m^{-3}) from April to June, 2012

Guanabara Bay can be attributed to a combination of high copepod abundance, fast growth rates, and higher food concentrations as a consequence of the high eutrophication in the bay. As a result, production values in Guanabara Bay and other eutrophic tropical estuaries may be even higher than those observed in temperate water bodies, which was also observed by Hopcroft et al. (1998a).

Copepod biomass in Guanabara Bay was negatively related to both tidal amplitude and dissolved oxygen, which indicates biomass was strongly influenced by the water from the inner region of the bay. Although low oxygen concentrations (<1 mg l^{-1}) are known to correlate with low abundances of copepods (Roman et al. 1993), the oxygen concentrations in our study were never below 3 mg l^{-1}. Thus, it is more likely that the negative relationship between copepod biomass and dissolved oxygen resulted from the movement of low oxygenated water from the inner bay to our sampling station during neap tides. Furthermore, most of our samples were collected close to the lowest tide of the day and were thus more influenced by inner bay waters than by the colder coastal waters that enter the bay during high tides. Our results indicated that the entrance of coastal waters, driven by tidal changes, determined variations in copepod biomass. Thus, by sampling on different timescales (weekly, daily), we found large variations in copepod biomass on a weekly basis compared to the variations on a daily basis.

In addition to abiotic factors, copepod biomass was also related to the composition of the dominant taxa, including *Oithona*, *Paracalanus*, and *Acartia*. Horizontal advection due to tidal currents is known to influence the abundance of both cladocerans (Marazzo & Valentin 2000) and copepods (Gomes et al. 2004) in the region. Certain copepod species (e.g. *Acartia tonsa* and *Paracalanus parvus*) have been shown to exhibit diel vertical migration in order to avoid advection in and out of Guanabara Bay (Gomes et al. 2004). Therefore, the short-term variations in biomass observed during this study were likely influenced by shifts in copepod community composition due, in part, to the horizontal advection of species that do not undergo diel migration.

Chitobiase estimates of daily *P/B*, the equivalent to daily growth rate (d^{-1}), were within the range of 0.1 to 1.2 d^{-1} that was reported by Hopcroft et al. (1998b) for copepodites in the nearshore waters of Jamaica and only slightly higher than the copepodite growth rate reported by McKinnon & Duggan (2003) in the subtropical waters off Australia's North West Cape. Daily *P/B* was highest in late May, when copepod biomass was low and dominated by nauplii, copepodites, and *Paracalanus*. Results from our regression analysis show that daily *P/B* was most strongly influenced by median prosome length and the relative biomass of *Paracalanus* and nauplii. Body size has previously been shown to explain nearly half of observed variations in the growth rates of copepodites in tropical waters (Hopcroft et al. 1998b). Furthermore, reported growth rates for naupliar and copepodite stages of *Paracalanus* are higher than those reported for other calanoids and cyclopoid species in the tropics (Hopcroft & Roff 1998b, Hopcroft et al. 1998a). It is important to note that daily *P/B* estimated from the chitobiase method represents the mean daily growth rate for all moulting individuals in the water column. Therefore, relationships between growth rate and body size may not be as clear as when growth rates are calculated for specific development stages or species.

Worth noting is that daily *P/B* was negatively related to temperature. In general, we would expect that growth rates would increase with temperature (Landry 1975). However, the range in temperature during our study was minimal (21.6–25.0°C) reflecting the seasonal transition into autumnal temperatures. Thus, daily *P/B* was higher during May and June, when lower seasonal temperatures were observed. In addition, no relationships were found between daily *P/B* and either chlorophyll *a* or POC concentrations in Guanabara Bay. The lack of relationship between food and growth rates may be a result of the fact that the small copepods dominating the bay are less affected by periods of low food concentrations (Hopcroft et al. 1998b). Furthermore, these smaller individuals likely exploit food by directly feeding on

the 2–20 µm phytoplankton cells that comprise the bulk of the phytoplankton community at the entrance to Guanabara Bay, or indirectly via the microbial foodweb (Guenther et al. 2012). Large inputs of organic material originating from continental and sewage wastes enter the bay via rivers (Guenther & Valentin 2008, Guenther et al. 2008), fueling the microbial foodweb and supporting high bacterial production (Guenther & Valentin 2008). Heterotrophic nano- and microflagellates, in turn, feed on bacteria (Azam et al. 1983), thus providing an additional food source for small copepods (including nauplii and smaller copepodites) throughout Guanabara Bay (Guenther et al. 2012).

Chitobiase-based crustacean production rates in our study were consistently higher (i.e. 2 to 5 times) than productivity estimates from global predictive models. Recent production rates calculated for Patos Lagoon using the chitobiase method were also consistently higher than those generated by the Huntley & Lopez (1992) and Hirst & Bunker (2003) mathematical models (Avila et al. 2012). Studies that have used the chitobiase method in coastal temperate waters on the west coast of Canada have shown that both the Huntley & Lopez (1992) and Hirst & Lampitt (1998) models underestimate production when crustacean growth rates are higher than 0.25 d^{-1} (Suchy et al. 2016, this volume). Our productivity values derived from the mathematical models only considered copepod productivity, because these were the only organisms for which we had measurements. As a result, the inclusion of other crustaceans in these calculations may have resulted in higher estimates stemming from the models. In addition, the use of smaller mesh sizes (<100 µm) may result in a higher abundance and biomass of small-bodied zooplankton compared to larger individuals (see Turner 2004 for review), which can contribute to an underestimate in abundance, biomass, and production estimates (Gallienne & Robins 2001). Our results also showed that production rates derived from the Huntley & Lopez (1992) model were similar to chitobiase productivity in June when both copepod biomass and daily *P*/*B* estimates were high. In terms of overestimation, production rates from all 3 models were much higher than chitobiase productivity estimates on 25 April (Day 116), when biomass was high despite the low daily *P*/*B* (0.15). Furthermore, production estimated by the Hirst & Bunker (2003) model, which takes chlorophyll *a* into account, was higher than chitobiase production rates when the concentration of chlorophyll *a* increased around Day 131; however, caution should be used when applying this model in eutrophic tropical regions where copepods are also feeding on the microbial foodweb. In addition, the lack of correlation between production rates estimated from global models likely results from the temporal variability in the specific parameters (e.g. either temperature, body size, chlorophyll *a*, or a combination of these factors) used to calculate growth rates. Altogether, given the high growth rates of copepods in tropical regions, it is likely that the use of these models will continue to underestimate production until new models are derived using a larger number of growth rate measurements from tropical copepods.

Crustacean productivity showed more variation on monthly timescales compared to weekly or daily timescales sampled over the course of our study. Overall, productivity was higher in April compared to May or June. CBA_{nat} was also highest in April, suggesting that more individuals were moulting during this month than in May and June. In addition, the longest mean stage duration (T_{CBA}), which represents the time taken for all moulting individuals to produce a quantity of biomass equivalent to CBA_{nat} (Sastri et al. 2013), occurred in April, when the average individual was spending more time in a given stage (either due to their larger size or because development rates were slower). Although accurate estimates of biomass have been suggested to be more important than accurate measurements of growth rate in terms of estimating production (Huntley & Lopez 1992), the lack of a relationship between copepod biomass and crustacean productivity in our study suggests that biomass, alone, cannot explain the observed variability in production in Guanabara Bay. Instead, our productivity rates were influenced by a combination of interacting factors including the biomass of different copepod taxa, daily *P*/*B*, and the median size (prosome length) of copepods on each sampling day. We observed that low crustacean productivity could occur even when copepod biomass was high and vice versa. For example, crustacean productivity increased on the last sampling date (18 June, Day 170), yet there was a substantial decrease in copepod biomass coinciding with a decrease in the median prosome length of the copepod community. In contrast, the lowest productivity observed during our study occurred on 25 April (Day 116), when copepod biomass was high and growth rates were low. Therefore, while abiotic factors (e.g. oxygen, tidal amplitude) and species composition affect the biomass estimates, variability in size and growth rates also influences productivity in Guanabara Bay.

Despite the lack of a consistent method for estimating crustacean zooplankton productivity as of

yet, the fact that our production rates were comparable with previous estimates for tropical regions suggests that the chitobiase method is a reliable tool for estimating *in situ* productivity without the need for repeatedly handling or incubating animals. Furthermore, this method estimates production rates for all moulting crustaceans in the water column, including nauplii and smaller copepodites that are often missed in net collections. Results from this study highlight the importance of incorporating routine estimates of crustacean productivity (at least on a monthly timescale) in estuarine waters, particularly in tropical regions where some of the world's largest estuaries are located (Blaber 2002). By examining the spatial and temporal variability in crustacean productivity in dynamic estuaries like Guanabara Bay, we can better understand the impacts that this variability may have throughout the foodweb in other eutrophic regions.

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LITERATURE CITED

Ara K (2001) Length–weight relationships and chemical content of the planktonic copepods in the Cananéia Lagoon estuarine system, São Paulo, Brazil. Plankton Biol Ecol 48:121–127

Ara K (2002) Temporal variability and production of *Temora turbinata* (Copepoda: Calanoida) in the Cananéia Lagoon estuarine system, São Paulo, Brazil. Sci Mar 66: 399–406

Avila TR, Machado AAS, Bianchini A (2011) Chitobiase of planktonic crustaceans from South Atlantic coast (southern Brazil): characterization and influence of abiotic parameters on enzyme activity. J Exp Mar Biol Ecol 407: 323–329

Avila TR, Machado AAS, Bianchini A (2012) Estimation of zooplankton secondary production in estuarine waters: comparison between the enzymatic (chitobiase) method and mathematical models. J Exp Mar Biol Ecol 416/417: 144–152

Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad F (1983) The ecological role of water-column microbes in the sea. Mar Ecol Prog Ser 10:257–263

Blaber SJM (2002) 'Fish in hot water': the challenges facing fish and fisheries research in tropical estuaries. J Fish Biol 61:1–20

Boltovskoy D (1999) South Atlantic zooplankton. Backhuys, Leiden

Chisholm LA, Roff JC (1990a) Size–weight relationships and biomass of tropical neritic copepods off Kingston, Jamaica. Mar Biol 106:71–77

Chisholm LA, Roff JC (1990b) Abundances, growth rates, and production of tropical neritic copepods off Kingston, Jamaica. Mar Biol 106:79–89

Gallienne CP, Robins DB (2001) Is *Oithona* the most important copepod in the world's oceans? J Plankton Res 23: 1421–1432

Gomes CL, Marazzo A, Valentin JL (2004) The vertical migration behavior of two calanoid copepods, *Acartia tonsa* Dana, 1849 and *Paracalanus parvus* (Claus, 1863) in a stratified tropical bay in Brazil. Crustaceana 77: 941–954

Guenther M, Valentin JL (2008) Bacterial and phytoplankton production in two coastal systems influenced by distinct eutrophication processes. Oecol Bras 12:172–178

Guenther M, Paranhos R, Rezende CE, Gonzalez-Rodriguez E, Valentin JL (2008) Dynamics of bacterial carbon metabolism at the entrance of a tropical eutrophic bay influenced by tidal oscillation. Aquat Microb Ecol 50: 123–133

Guenther M, Lima I, Mugrabe G, Tenenbaum DR, Gonzalez-Rodriguez E, Valentin JL (2012) Small time scale plankton structure variations at the entrance of a tropical eutrophic bay (Guanabara Bay, Brazil). Braz J Oceanogr 60:405–414

Heinle DR (1966) Production of a calanoid copepod, *Acartia tonsa*, in the Patuxent River Estuary. Chesap Sci 7:59–74

Hirst AG, Bunker AJ (2003) Growth of marine planktonic copepods: global rates and patterns in relation to chlorophyll *a*, temperature, and body weight. Limnol Oceanogr 48:1988–2010

Hirst AG, Lampitt RS (1998) Towards a global model of *in situ* weight-specific growth in marine planktonic copepods. Mar Biol 132:247–257

Hopcroft RR, Roff JC (1998a) Zooplankton growth rates: the influence of size in nauplii of tropical marine copepods. Mar Biol 132:87–96

Hopcroft RR, Roff JC (1998b) Zooplankton growth rates: the influence of female size and resources on egg production of tropical marine copepods. Mar Biol 132:79–86

Hopcroft RR, Roff JC, Lombard D (1998a) Production of tropical copepods in Kingston Harbour, Jamaica: the importance of small species. Mar Biol 130:593–604

Hopcroft RR, Roff JC, Webber MK, Witt JDS (1998b) Zooplankton growth rates: the influence of size and resources in tropical marine copepodites. Mar Biol 132:67–77

Hopcroft RR, Roff JC, Chavez FP (2001) Size paradigms in copepod communities: a re-examination. Hydrobiologia 453:133–141

Huntley ME, Lopez MDG (1992) Temperature-dependent production of marine copepods: a global synthesis. Am Nat 140:201–242

Kimmerer WJ, McKinnon AD (1987) Growth, mortality, and secondary production of the copepod *Acartia tranteri* in Westernport Bay, Australia. Limnol Oceanogr 32:14–28

Kjerfve B, Ribeiro CHA, Dias GTM, Filippo AM, Quaresma VS (1997) Oceanographic characteristics of an impacted

coastal bay: Baía de Guanabara, Rio de Janeiro, Brazil. Cont Shelf Res 17:1609–1643

Knotz S, Boersma M, Saborowski R (2006) Microassays for a set of enzymes in individual small marine copepods. Comp Biochem Physiol A Mol Integr Physiol 145:406–411

Landry MR (1975) The relationship between temperature and the development of life stages of the marine copepod *Acartia clausi* Giesbr. Limnol Oceanogr 20:854–857

Longhurst A (1984) Importance of measuring rates and fluxes in marine ecosystems. In: Fasham MJR (ed) Flows of energy in marine ecosystems. Plenum Press, London, p 3–22

Marazzo A, Valentin JL (2000) Daily variation of marine cladoceran densities in a tropical bay—Brazil. Hydrobiologia 428:205–208

Marazzo A, Valentin JL (2001) Diel changes in embryonic maturation in two species of marine cladocerans in Guanabara Bay, Rio de Janeiro, Brazil. Rev Bras Zool 18: 353–356

McKinnon AD, Duggan S (2003) Summer copepod production in subtropical waters adjacent to Australia's North West Cape. Mar Biol 143:897–907

Moore E, Sander F (1976) Quantitative and qualitative aspects of the zooplankton and breeding patterns of copepods at two Caribbean coral reef stations. Estuar Coast Mar Sci 4:589–607

Neveux J, Lantoine F (1993) Spectrofluorometric assay of chlorophylls and phaeopigments using the least squares approximation technique. Deep-Sea Res I 40:1747–1765

Nittrouer CA, Brunskill GJ, Figueiredo AG (1995) Importance of tropical coastal environments. Geo-Mar Lett 15: 121–126

Oosterhuis SS, Baars MA, Klein Breteler WCM (2000) Release of the enzyme chitobiase by the copepod *Temora longicornis*: characteristics and potential tool for estimating crustacean biomass production in the sea. Mar Ecol Prog Ser 196:195–206

Paranhos R, Pereira AP, Mayr LM (1998) Diel variability of water quality in a tropical polluted bay. Environ Monit Assess 50:131–141

Peterson WT, Tiselius P, Kiørboe T (1991) Copepod egg production, moulting and growth rates, and secondary production, in the Skagerrak in August 1988. J Plankton Res 13:131–154

Postel L, Fock H, Hagen W (2000) Biomass and abundance. In: Harris RP, Weibe PH, Lenz J, Skjoldal HR, Huntley M (eds) ICES zooplankton methodology manual. Academic Press, San Diego, CA, p 83–192

R Development Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.r-project.org

Roman MR, Gauzens AL, Rhinehart WK, White JR (1993) Effects of low oxygen waters on Chesapeake Bay zooplankton. Limnol Oceanogr 38:1603–1614

Sastri AR, Dower JF (2006) Field validation of an instantaneous estimate of *in situ* development and growth for marine copepod communities. Can J Fish Aquat Sci 63: 2639–2647

Sastri A, Dower JF (2009) Interannual variability in chitobiase-based production rates of the crustacean zooplankton community in the Strait of Georgia, British Columbia, Canada. Mar Ecol Prog Ser 388:147–157

Sastri AR, Roff JC (2000) Rate of chitobiase degradation as a measure of development rate in planktonic Crustacea. Can J Fish Aquat Sci 57:1965–1968

Sastri A, Nelson RJ, Varela DE, Young KV, Wrohan I, Williams WJ (2012) Variation of chitobiase-based estimates of crustacean zooplankton production rates in high latitude waters. J Exp Mar Biol Ecol 415/415:54–61

Sastri AR, Juneau P, Beisner BE (2013) Evaluation of chitobiase-based estimates of biomass and production rates for developing freshwater crustacean zooplankton communities. J Plankton Res 35:407–420

Schwamborn R, Bonecker SLC, Galvão IB, Silva TA, Neumann-Leitão S (2004) Mesozooplankton grazing under conditions of extreme eutrophication in Guanabara Bay, Brazil. J Plankton Res 26:983–992

Suchy KD, Dower JF, Sastri AR, Neil MC (2013) Influence of diet on chitobiase-based production rates for the harpacticoid copepod *Tigriopus californicus*. J Plankton Res 35: 657–667

Suchy KD, Dower JF, Varela DE, Lagunas MG (2016) Interannual variability in the relationship between *in situ* primary productivity and somatic crustacean productivity in a temperate fjord. Mar Ecol Prog Ser 545:91–108

Tenório MMB, Le Borgne R, Rodier M, Neveux J (2005) The impact of terrigeneous inputs on the Bay of Ouinné (New Caledonia) phytoplankton communities: a spectrofluorometric and microscopic approach. Estuar Coast Shelf Sci 64:531–545

Turner JT (2004) The importance of small planktonic copepods and their roles in pelagic marine food webs. Zool Stud 43:255–266

Webber MK, Roff JC (1995) Annual biomass and production of the oceanic copepod community off Discovery Bay, Jamaica. Mar Biol 123:481–495

Webber MK, Roff JC, Chisholm LA, Clarke C (1996) Zooplankton distribution and community structure in an area of the south coast shelf of Jamaica. Bull Mar Sci 59: 259–270

Yoshioka PM, Owen GP, Pesante D (1985) Spatial and temporal variations in Caribbean zooplankton near Puerto Rice. J Plankton Res 7:733–751

Youngbluth MJ (1980) Daily, seasonal, and annual fluctuations among zooplankton populations in an unpolluted tropical embayment. Estuar Coast Mar Sci 10:265–287

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