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Temporal variation in food utilisation by three species of temperate demosponge

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ABSTRACT: Temperate marine ecosystems exhibit a marked seasonal variation in environmental conditions that strongly affects the bioenergetics and population dynamics of benthic organisms. As benthic suspension feeders, sponges are subjected to seasonal changes in the supply of their food in the water column. In this study, we examined the temporal variation in the concentration of the picoplanktonic food particles present in the water column and their retention by 3 common demosponges (*Crella incrustans*, *Haliclona venustina* and *Strongylacidon* sp.) from the south coast of Wellington, New Zealand. We sampled 3 times each year over a 2 yr period to examine temporal variation in particle retention efficiency and in the number of particles retained by each species relative to the abundance of particles in the water column. Our results showed that the picoplanktonic species composition and abundance in the water column changed seasonally and between years, as did sponge retention efficiencies and amounts of the available picoplanktonic organisms retained. Averaged across a year, the consumption of non-photosynthetic bacteria is likely to provide the study species with between 20 and 40 times more carbon than the consumption of *Synechococcus* and *Prochlorococcus* (marine cyanobacteria). Although the concentration of food particles in the water column positively correlated with the amount of particles retained across all species, we found that retention efficiency did not change with particle concentration. This suggests that retention efficiency is independent of ambient particle concentration, and sponges are unable to increase their particle capture efficiency when food concentrations are lower (e.g. during winter months) and are therefore likely to be susceptible to low levels of food availability.

KEY WORDS: Sponges · Picoplankton · Seasonal · Retention · Carbon · Temperate

INTRODUCTION

In the marine environment, changes in the abundance of phytoplankton have significant implications for ecosystem functioning and are a biological trigger of seasonal variation in benthic processes (Bavestrello et al. 2006). An example of such seasonal patterns are phytoplankton blooms, which are the rapid production and accumulation of phytoplankton biomass in response to increased sunlight, water column stability, changing physical forces such as tides, winds or rainfall and river runoff (Cloern 1996). These blooms, or changes in phytoplankton biomass, affect the biochemical composition and reactivity of suspended particulate matter and the synthesis of organic matter that is required for the reproduction and growth of heterotrophs including bacteria, zooplankton and benthic organisms (Cloern 1996).

Seasonality in the supply of potential food may be an important factor that influences the life strategies of benthic organisms (Orejas et al. 2000, Bavestrello et al. 2006). Temperate marine ecosystems exhibit a marked seasonal variation in environmental conditions that strongly affects the bioenergetics of benthic organisms (Coma & Ribes 2003). Temperature and food availability are important environmental

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factors affecting the bioenergetics of benthic invertebrates (Coma et al. 2000); however, competition for space, food abundance (spatial and temporal changes in food quality, quantity and availability), water movement, larval supply and predation are also likely to be important factors explaining seasonal patterns of growth, reproduction and abundance of benthic suspension feeders (Boero et al. 1986, Smaal et al. 1986, Grémare et al. 1997, Coma et al. 2000). Studies of seasonal patterns in the activity and secondary production of benthic suspension feeders have been primarily conducted in temperate seas, and from these studies an annual trend has emerged. The most characteristic aspects of these temporal patterns are winter dormancy and summer activity of organisms (Coma et al. 2000), with settlement and recruitment occurring during spring (Duckworth & Battershill 2001). Some of the most important suspension-feeding groups that exhibit such seasonal variation include hydroids (Gili et al. 1998), ascidians (Ribes et al. 1998), bivalves (Ahn et al. 2003, Cloern & Jassby 2008) and sponges (Turon et al. 1998, Duckworth & Battershill 2001). In addition, several studies have also demonstrated marked seasonal variation in the feeding activity of other abundant benthic suspension feeders including holothurians, polychaetes and bryozoans (Barnes & Clarke 1995).

Sponges are sessile suspension-feeding metazoans whose entire body is specialised to effectively and rapidly remove food particles from the water column (Riisgård et al. 1993). Sponges acquire their food by filtering suspended particulate matter (planktonic particles) and dissolved organic matter from the water column, thereby linking the pelagic and benthic environments. Sponges are often among the most conspicuous components of freshwater and marine benthic communities and have been previously shown to feed on pico- and ultra-plankton (organisms <5 µm including heterotrophic bacteria and photosynthetic prokaryotes; e.g. Reiswig 1971, Pile 1997, Lesser 2006, Yahel et al. 2006, Hanson et al. 2009), as well as virus-like particles (Marie et al. 1999, Hadas et al. 2006, Patten et al. 2006). There is also evidence that sponges are able to capture larger cells (up to 70 µm), such as eukaryotic phytoplankton (e.g. diatoms, coccolithophores, dinoflagellates; Reiswig 1971, Frost 1981, Yahel et al. 1998, Ribes et al. 1999a). In this study, we focused on the consumption of picoplankton by sponges, where the term 'picoplankton' refers to the different microorganisms whose cells are <2 µm in size. The technical improvement of microbiological techniques, such as flow cytometry, has allowed the separation and enumeration of the different populations (components) of the picoplankton, particularly heterotrophic bacteria, picoeukaryotes and cyanobacteria (Cucci et al. 1985, Lesser et al. 1992). Marine cyanobacteria of the genera *Synechococcus* and *Prochlorococcus* comprise the prokaryotic component of the photosynthetic picoplankton (Heldal et al. 2003). These microscopic cells contribute around half of the carbon fixed in marine systems and hence are of particular ecological significance with regard to global carbon cycling (Partensky et al. 1999); they are therefore immensely important in the world's oceans.

In temperate shallow waters, planktonic production is more readily available to benthic organisms because of their proximity to the photic layer, and because of tidally-induced or wind-driven vertical mixing (Gili et al. 1998). The feeding activity of benthic suspension feeders is highly influenced by the species composition and the intensity of phytoplankton blooms (Beukema & Cadée 1991). In temperate waters, these blooms are a well known phenomenon in spring and autumn (Cadée 1986), and picoplankton abundance and biomass have been found to display strong seasonal signals in temperate coastal ecosystems (Morán 2007), and to account for a substantial fraction of planktonic biomass in the early stages of the spring bloom (Calvo-Díaz et al. 2004).

Some sponge species can change their feeding strategies in response to temporal differences in food availability (Duckworth & Battershill 2001). However, whether this is a general response of sponges is not known (Lesser 2006). We investigated the temporal variation in the concentration of 3 types of food particles in a temperate coastal ecosystem, and the retention efficiency of 3 encrusting sponge species for these different food types. We also investigated whether the number of particles retained and retention efficiency changes with food availability. This study addressed 4 main questions: (1) Does the abundance of specific picoplankton types change seasonally and inter-annually? (2) Is there any temporal variation in the retention efficiencies of the different types of picoplankton by sponges? (3) Is there any temporal variation in retention efficiency of picoplanktonic particles by sponges, and is retention efficiency correlated with ambient picoplankton concentration? (4) Does the amount of carbon acquired by sponges from different picoplankton sources show temporal variation, and is the amount of carbon acquired correlated with picoplankton concentration? To measure changes in the retention efficiency and the abundance of picoplankton retained for several

sponge species, a factorial ANOVA was used to test the effect of picoplankton type and time of year on the retention efficiency and picoplankton abundance. Also, correlation analyses were used to examine whether there were any relationships between the total number of cells retained by sponges and the concentration of cells present in the ambient water; and between retention efficiency and the ambient cell concentrations. Water samples were analysed over time to test the hypothesis that there are temporal changes in the amount and types of picoplankton available to sponges, which might result in temporal changes in the amount of picoplankton retained by sponges and in their retention efficiency.

MATERIALS AND METHODS

Study site and species description

This study was conducted on the south coast of Wellington, New Zealand, within the Taputeranga Marine Reserve (The Sirens, 41° 20′ 58.5″ S, 174° 45′ 50.8″ E and Mermaids Kitchen, 41° 21′ 60″ S, 174° 45′ 47.5″ E). The south coast of Wellington is a high-energy environment, with its tidal and oceanic flows strongly influenced by Cook Strait weather (Carter 2008); water temperatures range between 11°C in winter and 16°C in summer (Berman & Bell 2010). This area supports a high diversity and abundance of encrusting and massive sponges commonly found on the sides of channels, crevices, boulders, rock walls and overhangs (Berman et al. 2008). Three encrusting demosponges were studied: *Haliclona venustina* (Bergquist), *Strongylacidon* sp., and *Crella incrustans* (Carter, 1885). These species were chosen because they are very common in the study area, and their well defined exhalant oscula facilitate *in situ* sampling of exhalant water. *H. venustina* is often found on vertical rock walls, on the sides of channels and boulders; it is yellow and has large well-defined oscula (~4–5 mm diameter) and finger-like outgrowths from a basal mass. *C. incrustans* is a very conspicuous encrusting species found on boulders, rock walls and crevices; it has a bright orange-red colour and a smooth surface with raised and well-defined oscula (~4–5 mm diameter). *Strongylacidon* sp. is commonly found on boulders and rocky walls; it has well-defined oscula (~3–4 mm diameter) and has a smooth surface with a blue-grey colour. Most specimens measured ranged in size from 10 to 30 cm^2 (area of the substratum covered), which are typical sizes for these species at this site.

In situ sampling

Sampling occurred in winter (June to August, 2008, 2009), spring (September to November, 2008, 2009) and autumn (March to April, 2009, 2010). Due to poor weather conditions that limited dive time in the study area, 3 sponge specimens of each species were used for this study at each time interval. Methodological problems were encountered with some samples during collection and during the flow cytometry analyses; hence, no summer data (December to February) were available. During the 3 seasons, several days were sampled, but on 1 dive the 3 specimens of 1 species were sampled. Seawater samples for flow cytometry analysis were collected *in situ* by SCUBA. Fluorescein dye was released at the base of each specimen to visually confirm that sponges were actively pumping prior to sampling. Paired inhalant and exhalant (from a single osculum) water samples were taken from each specimen using 5 ml sterile plastic syringes with blunt-ended needles. Specimens were haphazardly chosen. The inhalant water of each specimen was sampled by slowly drawing water at a distance of ~3 cm from the sponge ostia, and the exhalant water was sampled from inside the oscular aperture taking care not to touch the sponge. There are some drawbacks of the use of the syringe method as discussed by Yahel et al. (2005); however, this method has been successfully applied in other studies looking at the diet composition of temperate sponges (Pile et al. 1996, Perea-Blázquez et al. 2010, Topçu et al. 2010). To overcome the problems identified by Yahel et al. (2005), care was taken to draw the water slowly over a period of a couple of minutes to ensure the exhalant water leaving the sponge was sampled, rather than being sucked from the sponge. After collection, water samples were transferred into sterile 1.5 ml cryovials (each sample was down-sized to1.5 ml from the original 5 ml sampled) with freshly prepared glutaraldehyde (0.1% final concentration). Samples were then taken to the laboratory (which is 100 m from the sampling site), frozen in liquid nitrogen and stored at −80°C following the protocol described by Marie et al. (1999) for natural seawater samples, until the flow cytometric analysis could be performed.

Flow cytometry analyses

Samples were thawed to room temperature, then stained in the dark with the DNA-specific dye Hoechst 33342 (0.2 µg ml^{-1} final concentration) for bacterial identification. It is noteworthy that the

sponge species studied here were found to feed mainly on picoplankton, and only in a few ambient samples were we able to detect the fluorescence emission of a small percentage of larger cells (~5 µm in size), that could possibly be pico- or nano-eukaryotic algae. Because of their low percentage (~0.4–0.7 %) and presence only in a few samples, these cells were not included in the subsequent analysis.

Seawater samples were analysed for quantification of non-photosynthetic bacteria ('Bac') and cyanobacterial cells (*Prochlorococcus* spp.: 'Prochlo', and *Synechococcus* spp.: 'Synecho') using a BD LSR II Special Order Research Product cytometer equipped with 5 lasers. All samples were processed within 2 wk of collection to prevent pigment breakdown. The non-photosynthetic microbes detected with Hoechst stain were considered as bacterioplankton. The use of the term heterotrophic bacteria is common in the literature to describe these DNA-containing particles; however, we assigned the operative term 'Bac' for these bacterioplankton since we do not know whether they are heterotrophic, chemosynthetic or chemoheterotrophic. Forward scattered light was collected using a photodiode and side scattered light was collected using a photomultiplier tube with a 488 nm band-pass filter (488/10); due to the small size of the micro-organisms, the cytometer was set to trigger off side scattered light. Identification of all organisms of interest was initially based on the DNA gate (see Perea-Blázquez et al. 2010 for a detailed description of the flow cytometric method).

Data analysis

The efficiency of the sponges in retaining picoplanktonic particles (retention efficiency) was calculated from the difference in concentrations found in ambient (inhalant) and exhalant water samples as: RE = 1 – (C_{exh}/C_{amb}) where RE is retention efficiency, C_{exh} is the concentration of cells in the exhalant water, and C_{amb} is the concentration of cells in the ambient water. The number of cells retained per second was calculated by multiplying retention efficiency (no units), volume flow rate (ml s^{-1}, see below) and ambient concentration of cells (cells ml^{-1}), as described by Trussell et al. (2006). To calculate carbon captured by sponges, we assumed that cells filtered per second are retained as food, that the number of cells retained per unit volume was constant within a season, and that the average pumping rate used was constant within a season (although it may vary on consistent daily cycles). The amount of carbon consumed from each cell type was calculated by multiplying the number of cells retained per second by the mean quantity of carbon contained in each cell according to its type, by using carbon conversions from the literature as follows: non-photosynthetic bacteria, 20 fg C $cell^{-1}$(Ducklow et al. 1993); *Prochlorococcus* sp., 61 fg C $cell^{-1}$ (Bertilsson et al. 2003); *Synechococcus* spp., 178 fg C $cell^{-1}$ (Charpy & Blanchot 1998). These conversions were used because they were calculated for cells with mean diameters that correspond to the cell diameters found during our study, which were visually confirmed using confocal microscopy. To calculate the carbon consumed per aquiferous unit, per unit time (s) for each species, we assumed the following mean daily pumping rates: 14.2 l d^{-1} for *Haliclona venustina*, 28.8 l d^{-2} for *Crella incrustans* and 21.6 l d^{-1} for *Strongylacidon* sp. For the purposes of our calculations, the pumping rates used here were taken from data obtained from encrusting sponges with similar size and morphology from the study area (see Perea-Blázquez et al. 2012). The aquiferous 'unit' considered is the biomass associated with a single osculum in an encrusting species. Calculations were performed for each specimen.

To examine changes in the concentration of picoplankton in the water column over time, a factorial ANOVA was conducted where each sponge species was analysed separately, and the factorial model included the terms 'concentration of cells', 'type of picoplankton', 'time of year' and all interactions among these terms. The same analysis was performed to examine whether the retention efficiency of picoplankton varied with time of year. The ANOVA for retention efficiency was conducted on arcsine-square root transformed data to meet assumptions of normality and equal variance. Likewise, to examine changes in the amount of picoplankton retained per aquiferous unit per second by the study species over time, a factorial ANOVA was conducted and data were log-transformed to meet the assumptions of parametric analysis when necessary. To determine whether the amount of carbon acquired by the sponges changed over time, a factorial ANOVA was conducted and data were log-transformed to meet the assumptions when necessary. The assumption of homogeneity of variance was examined using Bartlett's test ($p < 0.05$ in all cases). We used correlation analyses to examine whether there were relationships between the number of cells retained and the concentration of cells present in the ambient water, and between retention efficiency and the concentration of cells in the ambient water. To determine the significance of the correlations, a Pearson's product-moment correlation method

Table 1. Factorial analysis of variance showing the effect of type of picoplankton and time of year on the concentration of cells present in the ambient water. Significance at the 5% level

Source of variation	df	Ambient cells	
		F	p
Picoplankton	2,144	851.802	0.001
Time of year	5,144	40.807	0.001
Picoplankton × Time of year	10,114	21.997	0.001

was used, and the critical value of 0.05 was adjusted in multiple correlations using a sequential Bonferroni (Quinn & Keough 2002). The relationship between number of cells retained and ambient concentration of cells was used to test whether the retention efficiency changed significantly with the concentration of particles in the ambient water, since retention efficiency is related to the slope of the regression of cells retained versus ambient concentration of cells. This correlation was compared against the slope equalling 1, where a slope of 1 indicates that retention efficiency does not change with particle concentration. All statistical analyses were performed by R ver. 2.10 (R Development Core Team). All means are presented with standard errors (SE).

RESULTS

Changes in picoplankton concentration over time

The factorial ANOVA showed that ambient concentrations of different picoplankton groups in the study area (as determined from ambient samples collected next to the study species) varied significantly over time (Table 1). Our results indicated that Bac were the most abundant cell type in the water column throughout the 2 yr period ($2.6 \times 10^6 \pm 1.6 \times 10^6$ cells ml^{-1}), followed by Synecho ($9.8 \times 10^3 \pm 3.7 \times 10^3$ cells ml^{-1}) and then Prochlo ($9.6 \times 10^3 \pm 4.0 \times 10^3$ cells ml^{-1}). With respect to the time of year, Bac were most abundant in spring of the second year ($4.8 \times 10^6 \pm 1.5 \times 10^6$ cells ml^{-1}), and the lowest concentration was observed in the autumn of the first year ($2.8 \times 10^5 \pm 1.0 \times 10^5$ cells ml^{-1}). Synecho were found in their highest numbers during winter of the second year ($1.5 \times 10^4 \pm 5.3 \times 10^3$ cells ml^{-1}), and the lowest concentration was observed in spring of the first year (3000 ± 550 cells ml^{-1}). Prochlo showed their highest numbers in winter of the first year ($1.7 \times 10^4 \pm 3.5 \times 10^3$ cells ml^{-1}) and the lowest concentration was found in spring of the first year (130 ± 83 cells ml^{-1}) (Fig. 1).

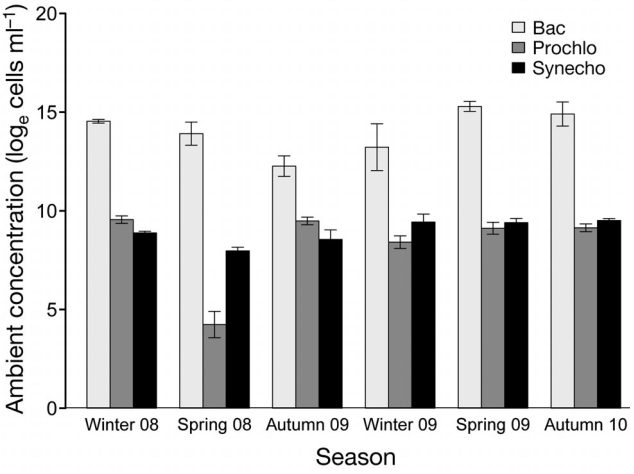

Fig. 1. Ambient concentration of picoplankton (mean ± SE, n = 3) showing differences in the number of cells present in the water column over time. The number of cells was plotted on a log-scale in order to visually compare the concentrations of each type of picoplankton (Bac: non-photosynthetic bacteria; Prochlo: *Prochlorococcus*; Synecho: *Synechococcus*)

Temporal variation in the retention efficiency of picoplankton by sponges

The diet composition of *Crella incrustans*, *Haliclona venustina* and *Strongylacidon* sp. included Bac, Prochlo and Synecho. Retention efficiencies varied significantly among picoplanktonic organisms

Table 2. Factorial analysis of variance showing the interaction between type of picoplankton and time of year, on the retention efficiency of each of the study species. Significance at the 5% level

Source of variation	df	*Crella incrustans*		*Haliclona venustina*		*Strongylacidon* sp.	
		F	p	*F*	p	*F*	p
Picoplankton	2,36	446.81	0.001	664.05	0.001	363.14	0.001
Time of year	5,36	12.506	0.001	15.037	0.001	47.647	0.001
Picoplankton × Time of year	10,36	27.024	0.001	20.706	0.001	28.472	0.001

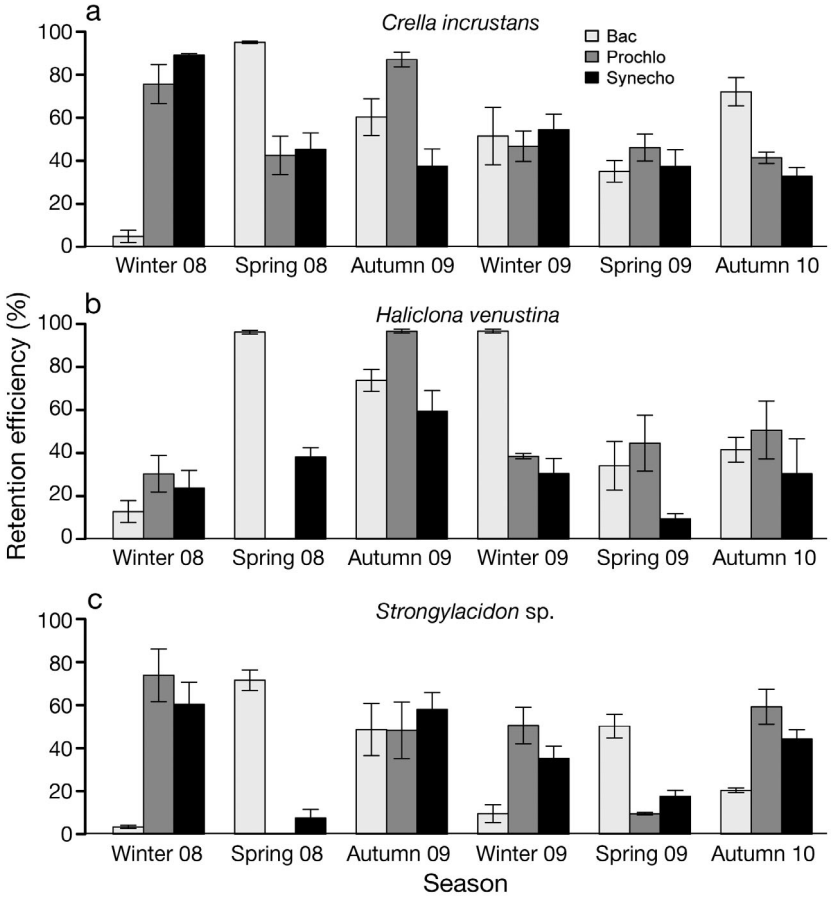

Fig. 2. *Crella incrustans, Haliclona venustina* and *Strongylacidon* sp. Retention efficiency (mean ± SE, n = 3) across sampling times during the 2 yr period for (a) *C. incrustans*, (b) *H. venustina* and (c) *Strongylacidon* sp. Retention efficiency is expressed as the percentage removal of non-photosynthetic bacteria (Bac), *Prochlorococcus* (Prochlo) and *Synechococcus* (Synecho) cells by the 3 study species

and with sampling periods for the 3 study species (Table 2). *C. incrustans* retained Bac with the highest efficiency during spring 2008 (95.1 ± 0.5%) and autumn 2010 (72.1 ± 6.5%). It showed a low retention efficiency during winter 2008 (4.9 ± 2.8%); the retention of Prochlo was higher during autumn of 2009 (87.1 ± 3.4%), and Synecho were retained with a higher efficiency during winter 2008 (89 ± 0.7%; Fig. 2a). *H. venustina* mainly retained Prochlo during autumn 2009 (96.6 ± 0.9%) and Bac during spring 2008 and winter 2009 (96.2 ± 0.8 and 96.6 ± 0.9%, respectively), with a lower retention efficiency in winter 2008 (12.7 ± 5%), whereas Synecho was retained with no more than 59% efficiency over the sampling period. Very low numbers of Prochlo cells (<1%) were retained by this species during spring 2008, but more were retained in spring 2009 (43.2 ± 7.2%; Fig. 2b). *Strongylacidon* sp. mainly retained Prochlo during winter 2008 (73.8 ± 12.2%) and Bac during spring 2008 (71.6 ± 4.7%). Contrastingly, this species had a very low retention efficiency of Bac during winter 2008 (3.3 ± 0.7%), and virtually no Prochlo cells were retained by this species during spring 2008, but more were retained in spring 2009 with a low efficiency (9.5 ± 0.6%); Synecho cells were retained with a higher efficiency than the other particle types during autumn 2009 (58.1 ± 7.8%) and a very low retention was measured during spring 2008 (7.5 ± 4%; Fig 2c).

Temporal variation in filtration of cell types by each species

The number of cells filtered by the 3 study species varied significantly for the different types of picoplankton and with sampling periods (Table 3). The 3 species showed a higher consumption of Bac than the 2 types of cyanobacteria over the 2 yr period. *Crella incrustans* filtered a higher number of Bac per second during spring of both years ($5.5 \times 10^5 \pm 1.1 \times 10^5$ cells s^{-1}, spring 2008; $4.7 \times 10^5 \pm 9.8 \times 10^4$ cells s^{-1}, spring 2009) and the lowest consumption was found during winter and autumn of the first year ($3.1 \times 10^4 \pm 1.9 \times$

Table 3. Factorial analysis of variance showing the interaction between type of picoplankton and time of year, on the number of cells filtered per aquiferous unit per second by each of the study species. Significance at the 5% level

Source of variation	df	*Crella incrustans*		*Haliclona venustina*		*Strongylacidon* sp.	
		F	p	*F*	p	*F*	p
Picoplankton	2,36	276.67	0.001	583.33	0.001	252.68	0.001
Time of year	5,36	7.748	0.001	13.22	0.001	33.18	0.001
Picoplankton × Time of year	10,36	16.731	0.001	18.21	0.001	19.81	0.001

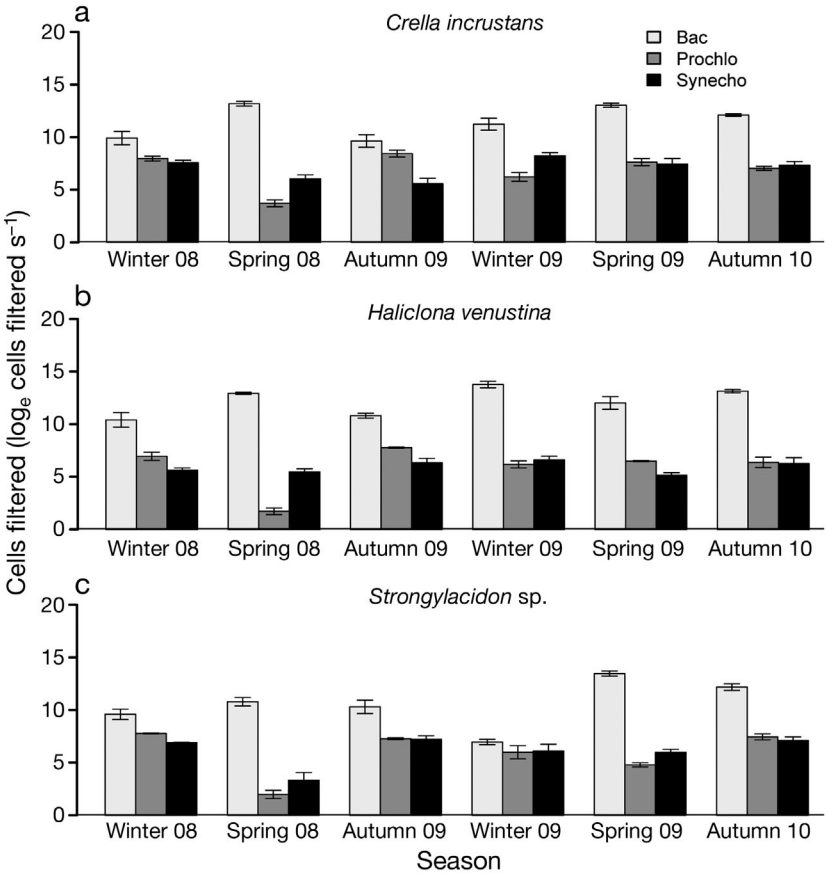

Fig. 3. *Crella incrustans, Haliclona venustina* and *Strongylacidon* sp. Number (mean ± SE, n = 3) of cells filtered of each type of picoplankton (Bac: non-photosynthetic bacteria, Prochlo: *Prochlorococcus*, Synecho: *Synechococcus*) by the 3 sponge species over time: (a) *C. incrustans*, (b) *H. venustina* and (c) *Strongylacidon* sp. The number of cells filtered was plotted on a log-scale in order to visually compare the number of cells of each type of picoplankton

10^4 cells s^{-1}, winter 2008; $2.1 \times 10^4 \pm 9.3 \times 10^3$ cells s^{-1}, autumn 2009). The most Prochlo cells were consumed by this species during autumn 2009 ($5.1 \times 10^3 \pm 1.4 \times 10^3$ cells s^{-1}), and the least during spring 2008 (46 ± 16 cells s^{-1}). The most Synecho were consumed by this species in winter 2009 ($4.2 \times 10^3 \pm 1.4 \times 10^3$ cells s^{-1}) and the least in autumn 2009 (350 × ± 180 cells s^{-1}; Fig. 3a). *Haliclona venustina* consumed the most Bac in winter 2009 ($1.0 \times 10^6 \pm 3.1 \times 10^5$ cells ml^{-1}) and the least in winter 2008 ($4.9 \times 10^4 \pm 2.4 \times 10^4$ cells s^{-1}). The most Prochlo were consumed by this species in autumn 2009 (2400 ± 140 cells s^{-1}) and the least in spring 2008 (6.2 ± 2.1 cells s^{-1}), and the most Synecho were consumed in winter 2009 (820 ± 250 cells s^{-1}) and the least in spring 2009 (180 ± 40 cells s^{-1}; Fig. 3b). Finally, *Strongylacidon* sp. removed the most Bac in spring 2009 ($7.4 \times 10^5 \pm 1.5 \times 10^5$ cells s^{-1}) and the least in winter 2009 (1100 ± 310 cells s^{-1}), whereas the most Prochlo cells were consumed during winter 2008 (2400 ± 79 cells s^{-1}) and the least during spring 2008 ($8.4 \times 10^3 \pm 3.3 \times 10^3$ cells s^{-1}). The most Synecho were consumed by this species in autumn 2009 (1500 ± 480 cells s^{-1}) and the least in spring 2008 (44 ± 26 cells s^{-1}; Fig. 3c).

Correlations of ambient picoplankton concentration with abundance of particles filtered and retention efficiency

Correlation analyses were conducted to determine whether sponges retained different amounts of picoplankton in relation to their concentration in the water column. First, we conducted analyses for the individual species. The analysis for *Crella incrustans* showed no correlation between the number of Bac and Synecho in the ambient water and the number of these cells retained, but a significant correlation was found between the abundance of cells and removal of Prochlo ($r^2 = 0.98$; $p < 0.001$). For *Haliclona venustina*, a significant correlation was found between the abundance and removal of Prochlo ($r^2 = 0.98$; $p < 0.001$), but no correlation was found between the abundance and removal of Bac and Synecho. For *Strongylacidon* sp., a significant correlation was found between the abundance and retention of Prochlo ($r^2 = 0.93$; $p < 0.01$), but no correlation was found between the number of Bac and Synecho (Fig. 4). Despite these particle-specific patterns, we did find strong positive relationships between overall ambient concentrations (across all 3 particle types) and cells retained for each sponge species: *C. incrustans* ($r^2 = 0.88$; $p < 0.001$), *H. venustina* ($r^2 = 0.95$; $p < 0.001$) and *Strongylacidon* sp. ($r^2 = 0.89$; $p < 0.001$; Fig. 5). Finally, when we examined the overall relationship between ambient picoplankton concentrations and cells retained across all the 3 picoplankton types and species, we found a significant positive relationship ($r^2 = 0.95$, $p < 0.001$; Fig. 6). These results show that sponges generally retain more picoplankton when more cells are available in the ambient water. However, there were no significant relationships between the number of cells in the ambient

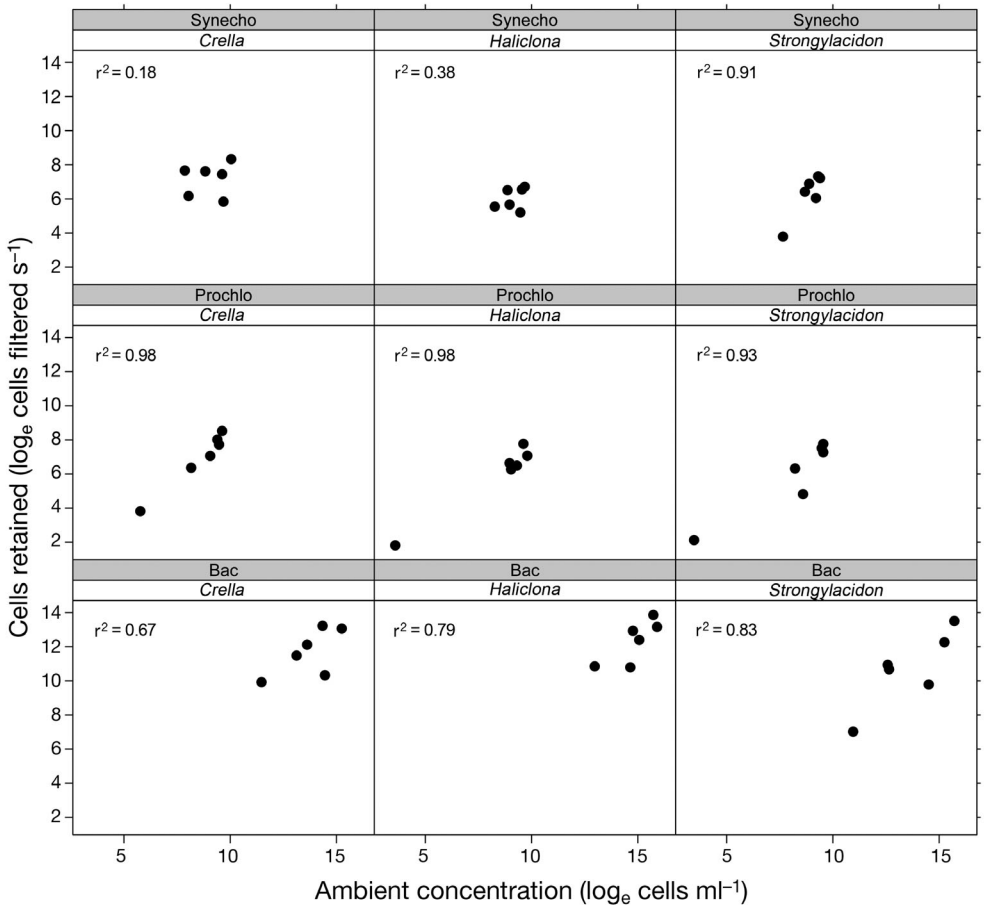

Fig. 4. *Crella incrustans, Haliclona venustina* and *Strongylacidon* sp. Relationships between the number of cells present in the ambient water (horizontal axis) and the number of cells filtered (vertical axis); all data were log-transformed. Data used for the correlation analysis include the 3 types of picoplankton — non-photosynthetic bacteria (Bac), *Prochlorococcus* (Prochlo), *Synechococcus* (Synecho) — present in the ambient water and the number of cells filtered by each sponge species (*C. incrustans*, *H. venustina*, *Strongylacidon* sp.), at each of the sampling points over the 2 yr period

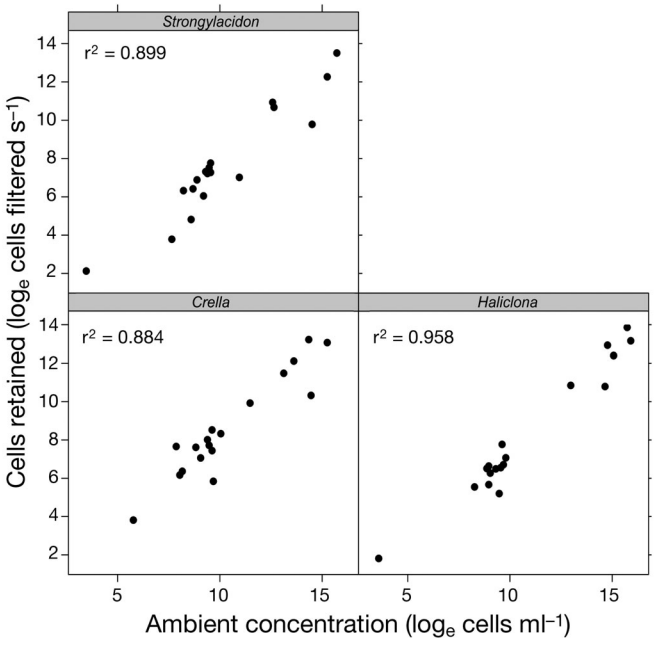

Fig. 5. *Crella incrustans, Haliclona venustina* and *Strongylacidon* sp. Number of cells retained (vertical axis) versus the number of cells present in the ambient water (horizontal axis); all data were log-transformed

water and the retention efficiency for either the individual species relationships or the overall relationship, as both the slopes of the individual species relationships and the overall relationship were not significantly different from 1.

Amount of carbon consumed by the sponges

The amount of carbon acquired by the 3 sponge species differed significantly with picoplankton type and sampling period (Table 4). Bac constituted the most important carbon source for all 3 sponge species throughout the study period. Based on the data for the number of cells filtered, and considering the 2 yr sampling period and season in terms of picoplanktonic biomass, the largest amount of carbon retained by *Crella incrustans* in winter originated from Bac (0.11 ± 0.06 mg d^{-1}), while 0.05 ± 0.02 and 0.01 ± 0.005 mg d^{-1} were supplied by Synecho and Prochlo, respectively. During spring and autumn, most of the carbon was also supplied by Bac (0.89 ± 0.17 and 0.18 ± 0.09 mg d^{-1}, respectively). For *Haliclona venustina*, most of the carbon retained in winter and spring ori-

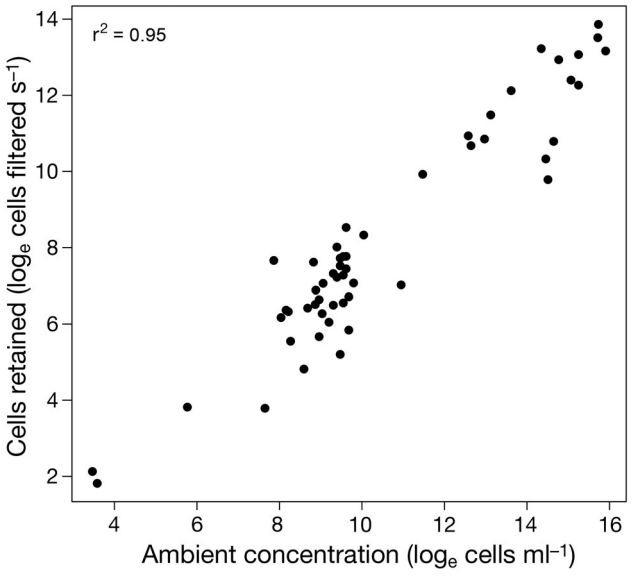

Fig. 6. Overall number of cells retained (vertical axis) versus the number of cells present in the ambient water (horizontal axis); all data were log-transformed. Data used for the correlation analysis include the 3 types of picoplankton (non-photosynthetic bacteria, *Prochlorococcus*, *Synechococcus*) present in the ambient water and the number of cells filtered by each sponge species (*Crella incrustans*, *Haliclona venustina*, *Strongylacidon* sp.), at each of the sampling points over the 2 yr period

ginated from Bac (0.95 ± 0.64 and 0.57 ± 0.20 mg d^{-1}, respectively); in autumn, most of the carbon (0.50 ± 0.27 mg d^{-1}) was also supplied by Bac with only 0.01 ± 0.005 and 0.008 ± 0.003 mg d^{-1} supplied by Synecho and Prochlo, respectively. For *Strongylacidon* sp., Bac supplied 0.02 ± 0.01 mg C d^{-1} in winter, with 0.01 ± 0.003 and 0.008 ± 0.003 mg C d^{-1} supplied by Synecho and Prochlo, respectively. In spring and autumn most of the carbon was also supplied by Bac (0.69 ± 0.41 and 0.22 ± 0.11 mg d^{-1}, respectively).

DISCUSSION

Localised low levels of primary production may result in food limitation to suspension feeders (Helson et al. 2007) unless the organisms can reduce metabolic costs. Furthermore, since benthic organisms graze on different components of the phytoplankton, changes in productivity can affect the production and transport of particulate food to the benthos (Graf et al. 1982). A growing number of studies assessing the role of picoplankton as important primary producers have found that they are important contributors to carbon fluxes in coastal ecosystems (e.g. Morán 2007), and that they follow seasonal cycles in temperate coastal waters (e.g. Zubkov et al. 2000, Calvo-Díaz et al. 2004). Moreover, these organisms constitute a significant food resource for larger benthic suspension-feeding organisms such as bivalves, ascidians and sponges (Langdon & Newell 1990, Gili & Coma 1998, Ribes et al. 2005, Yahel et al. 2005). Since sponges are very abundant and represent one of the most important components of the suspension-feeding community in the rocky temperate reef studied, it is important to determine the temporal variation in the removal of picoplanktonic food particles from the water column, as their feeding activities have the potential to strongly influence other organisms.

Our results showed that the concentration of each type of picoplankton varied over the sampling period. Similarly, retention efficiency and removal of particles (the number of cells removed or retained by the 3 study species) varied among picoplanktonic organisms and with sampling periods. The results from the correlation analysis showed significant positive correlations between the abundance and removal of *Prochlorococcus* for the different sponge species. However, we did not find a significant change in retention efficiency when particles were more abundant for any of the species or picoplankton types. The amount of carbon acquired by the 3 sponge species varied significantly for each type of picoplankton and between sampling periods, and non-photosynthetic bacteria constituted the most important carbon source for all 3 species across all sampling periods.

In an earlier study, we quantified the assemblage level carbon flux for the entire sponge assemblage

Table 4. Factorial analysis of variance showing the interaction between type of picoplankton and time of year, on the amount of carbon acquired per aquiferous unit per second by each of the study species. Significance at the 5% level

Source of variation	df	*Crella incrustans*		*Haliclona venustina*		*Strongylacidon* sp.	
		F	p	*F*	p	*F*	p
Picoplankton	2,48	100.85	0.001	11.706	0.001	139.732	0.001
Time of year	2,48	26.67	0.001	0.316	0.57	1.699	0.199
Picoplankton × Time of year	4,48	54.36	0.001	3.304	0.05	1.863	0.16

in the same location as the present study (Perea-Blázquez et al. 2012). We estimated that depending on sponge abundance (ranging from 0.5 to 5% area occupied), the amount of carbon that sponges consumed as a proportion of the total carbon available was 0.2–12.1% for Bac, 0.4–21.3% for Prochlo and 0.3–15.8% for Synecho. However, this assemblage level estimate was based on a single sampling event (summer), and given the seasonal variation reported in the present study, these fluxes are likely to change seasonally.

Temporal variation of picoplankton in the water column

The amount of picoplankton present in the water column varied significantly over the 2 yr study period. Our results showed that, on average, Bac and Synecho were more abundant throughout the second year, and Prochlo was more abundant in the first year. With respect to inter-annual differences, Bac showed a stronger seasonal trend than did the other components of the picoplankton between years and seasons. However, the amount of Prochlo and Synecho varied between springs of both years. Events such as La Niña or El Niño have different impacts on New Zealand's climate. The last La Niña event was in 2007/08, so it is possible that the resultant water temperature and wind patterns may have had an effect on the abundance of picoplankton in the study area during the study period. At a coastal station in the temperate northern Baltic Sea, Andersson et al. (1994) found that the succession of cyanobacteria and heterotrophic bacteria was influenced by seasonal variation in daylight and temperature, as well as in nutrient concentrations. The low abundance of Prochlo in spring could also be related to downwelling or upwelling conditions at that time of the year, or to the influence of coastal currents as has been reported for other locations (Calvo-Díaz et al. 2004).

Do sponges consume picoplanktonic particles in relation to their abundance in the water column?

In terms of the average number of cells consumed of each type of picoplankton for all species, Bac was the most important group followed by Prochlo and Synecho. The removal (and assumed consumption) of food particles by the sponge species also varied over time. For the 3 species, Bac represented 79 to 93% of the total cells consumed in winter, spring and autumn, whereas Prochlo and Synecho represented only 0.5 to 14% of the cells retained at the same time over the 2 yr period. It is interesting that the numbers of cells removed by the 3 sponge species across the sampling periods were consistent with temporal fluctuations in resource (food) abundance. A Pearson product-moment correlation coefficient analysis with a sequential Bonferroni adjustment was used to determine whether these changes in the number of cells removed were the result of the density declines or increases of the different picoplankton groups available in the water column. A positive correlation was found in the number of *Prochlorococcus* retained by the 3 species and their abundance in the water column, indicating a significant relationship (i.e. more consumed when more of that particular type of picoplankton was available in the water column). However, when the correlation analysis considered an overall average removal and abundance of picoplankton over the study period (including all 3 food types and the 3 times of year/seasons), there was a significant correlation between the number of cells removed by *Crella incrustans*, *Haliclona venustina* and *Strongylacidon* sp. and the abundance of cells in the ambient water (*C. incrustans* $r^2 = 0.938$, $p < 0.001$; *H. venustina* $r^2 = 0.958$, $p < 0.001$; *Strongylacidon* sp. $r^2 = 0.902$, $p < 0.001$).

In this study, we tested the hypothesis that the removal of picoplankton by sponges depends on their concentration or availability in the water surrounding the sponges. Coma et al. (2001) showed for the first time that sessile suspension feeders consumed a broad spectrum of planktonic organisms appropriate to each filtering mechanism relative to their abundance in the water column. In the sponge species studied here, such a positive relationship between particle concentration and number of particles retained was observed for *Prochlorococcus*, suggesting that the sponges exploited the second most abundant food type (Prochlo) in the ambient water and consumed it at rate dependent on its availability (i.e. they consume more when more food is available). However, we also found that the 3 types of picoplankton were retained with different efficiencies by the sponge species over the 2 yr period, but retention efficiency (rather than amount consumed) was unaffected by ambient food concentration. On an annual basis, the 3 species had high retention rates of Prochlo during autumn and winter, but high retention of Bac during spring. *Crella incrustans* showed a higher retention efficiency of Prochlo throughout the study period compared to the other sponge species. In contrast, *Haliclona venustina*

showed a higher retention for Bac, while *Strongylacidon* sp. had a higher retention efficiency of Synecho throughout the study period. Our results demonstrated that the study species removed both heterotrophic and cyanobacterial cells, but with varying efficiencies. These differences in uptake or retention of picoplankton types may be explained by capture mechanisms and particle digestibility (Topçu et al. 2010), variation in choanocyte numbers and physiological mechanisms of feeding (Leys & Eerkes-Medrano 2006), and complexity of aquiferous systems (Weisz et al. 2008). Yahel et al. (2006) examined the mechanisms involved in the selective retention of particles in hexactinellid glass sponges and concluded that the selective retention observed involved individual processing, recognition, sorting and transporting of each particle through the sponge's syncytial tissue. However, the exact mechanism by which sponges might be able to select food particles remains uncertain.

Can sponges select food particles that maximize their nutritional intake?

The results from our study indicate that the study species feed more efficiently on smaller cells (non-photosynthetic bacteria) than on bigger cells (*Prochlorococcus* and *Synechococcus*), and that the higher concentration in the water column of Bac meant that they contributed the most to sponge diets in terms of carbon intake. This was corroborated by calculations of overall carbon consumed by the study species at different time points (winter, spring, summer) over the 2 yr period. The amounts of the different picoplanktonic organisms retained by the sponge species varied between species and over time, although the main source of carbon for the 3 sponge species was Bac. These results are in agreement with previous studies where Bac have been found to be among the primary carbon sources for sponges (Ribes et al. 1999b, Trussell et al. 2006, Yahel et al. 2007, Perea-Blázquez et al. 2012). This is important because the heterotrophic component of the picoplankton has been found to account for a substantial fraction of the planktonic biomass (Calvo-Díaz et al. 2004). Since sponges are able to effectively exploit food resources in the water column, they provide coupling between primary production and the benthos.

Generally, sponges grow and reproduce during spring and summer (Garrabou & Zabala 2001, Coma & Ribes 2003, Bell 2008). The observed differences among months appear to be consistent with the demands of seasonal cycles in growth and reproduction, suggesting that endogenous metabolic demands are an important factor determining the feeding behaviour of temperate sponges (Barthel 1986, Ribes et al. 2003). The relatively constant consumption of food particles by sponges throughout the year, together with a lack of any temporal trend in cell concentrations and energy (carbon) intake, suggests that the dynamics of the sponge species studied here do not show a consistent pattern. However, it remains to be elucidated whether temperate sponges exhibit different growth and reproduction rates as a result of differences in food quality and quantity over annual cycles in the study area. However, Lesser (2006) found increasing picoplankton consumption with depth for tropical sponges, which resulted in an increase in sponge sizes and rates of growth showing how changes in food concentration can influence sponge ecology.

To conclude, our results indicate that there is a wide range of food concentrations on the rocky reefs where the study species live, and that the retention rates of sponges vary temporally. This emphasises the importance of understanding temporal variations in productivity, and suggests that such variations are likely to have important implications for suspension feeders, such as sponges. The sponge species we analysed appear to exhibit different feeding behaviours at varying food concentrations, as well as different retention rates across sampling periods. However, we also found that retention efficiency is independent of ambient particle concentration, although sponges appear to exploit the most abundant food particles in the water column, but at rates independent of their abundance in the water column.

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