

Consequences of density-dependent heterotrophic feeding for a partial autotroph

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ABSTRACT: Population regulation in sessile clonal animals has been poorly studied. The prevailing paradigm is that competition is primarily for space, although this is changing. I use a laboratory flume experiment to show that particle capture by the marine intertidal zoanthid *Palythoa caesia* is negatively related to density (% cover) and positively related to colony size. Using models of colony growth and subsequent population dynamics, which incorporate this density- and size-dependent feeding response, I then show that it is potentially an important component of population regulation. The other important vital rate for regulating population size is fission—as this species is clonal it can reproduce asexually by splitting into 2 or more daughter colonies. Fission rates decrease with density and increase with colony size. When both feeding and fission are density-dependent, model cover is regulated to just under 80%, but when either process is made density-independent, population growth is exponential. Importantly, when no heterotrophic feeding is allowed, and all respiratory requirements must come from the translocation of photosynthetic products from symbiotic zooxanthellae, the model population rapidly becomes extinct, whereas eliminating photosynthesis decreases cover but allows the population to persist. The colony level model shows that individual growth rates of large colonies are increased at low densities, while those of small colonies are decreased at high densities.

KEY WORDS: Clonal organisms · Population regulation · Suspension feeding · Density-dependence · Growth model · Population model

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INTRODUCTION

In sessile marine organisms, competition has traditionally been attributed to the need to obtain space in which to grow (e.g. Connell 1961, Lang 1973, Buss & Jackson 1979, Lang & Chornesky 1990). There has also been increasing attention paid to competition for food in high density aggregations, with evidence that reduced feeding rates at increased density place major restrictions on the growth rates of some individuals (e.g. bryozoans: Buss 1979, Okamura 1992; sponges: Buss & Jackson 1981; mussels: Fréchette et al. 1992). The population level consequences of intraspecific

competition for food in sessile filter feeders has been the subject of some speculation (e.g. Fréchette et al. 1992, Okamura 1992), but has to my knowledge never been explicitly addressed.

Some groups of sessile marine invertebrates also have a means of escaping the full impact of competition for food that is unavailable to most animals, although it may simultaneously intensify competition for space. These species, such as many corals, sponges, giant clams and didemnid ascidians, contain symbiotic zooxanthellae or *Prochloron*, and thus are at least partially autotrophic. It has been well documented that some of the products of photosynthesis are indeed transferred to the animal host, and in some cases can provide the majority of the host's carbon requirements (e.g. Sebens 1977, Muscatine et al. 1981, Olson & Porter 1985, Sorokin 1991, Fabricius & Klumpp 1995).

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For other species, however, photosynthesis only provides a small component of the host's requirements, with heterotrophic feeding still providing the majority (e.g. Porter 1976, Muscatine et al. 1984, Lewis 1992, Fabricius & Klumpp 1995). Thus, for such organisms it is of interest to determine just how important this ability to photosynthesise is in ameliorating the effects of competition for food. Another unique feature of this group of animals is that many frequently reproduce asexually through colony fission, and this ability can also have important consequences for demography (e.g. Highsmith 1982, Ryland et al. 1984, Karlson 1991, Hughes & Tanner 2000).

In this paper, I report the results of a laboratory flume experiment examining the effects of both upstream density and colony size on particle capture rates of the intertidal zoanthid *Palythoa caesia*. Like many sessile marine invertebrates, *P. caesia* is a suspension feeder, and relies on ambient water flow to deliver food items, mostly plankton, to within the capture range of its tentacles. I then go on to combine these results with existing information on colony level population dynamics of *P. caesia* across a range of densities (Tanner 1997, 1999), and with published energetic data for the same species at the same location at which this study was conducted (Sorokin 1991). The energetic data include details on rates of carbon uptake through photosynthesis and heterotrophic feeding and loss through respiration. Using these 3 sets of information, I develop models of both individual colony growth and population dynamics. These models allow me to determine the potential importance of density-dependent feeding rates at both the individual colony and population levels. I also examine what effect changing the rates of photosynthesis, heterotrophy and respiration has on both colony growth and population dynamics using an extensive series of sensitivity analyses to examine the robustness of the models to the assumptions made.

Palythoa caesia is unusual in comparison to most other species in which population regulation has been studied as it is clonal and can therefore reproduce extensively via asexual fission. Subsequent to fission, 2 genetically identical colonies are also able to fuse back into a single colony. In previous studies (Tanner 1997, 1999, 2000) I showed that fission rates decreased as density increased, while fusion rates increased, and that the population studied appeared to be regulated at around 80% cover. The main demographic process responsible for this regulation was the production of small colonies from large individuals through fission, as density-dependent fusion had a minimal effect on population dynamics. Further to these results, I suggested that regulation was probably maintained by a combination of density-dependence in fission and

growth rates, possibly due to a reduction in food availability as density increased. However, unlike the model presented in this paper, the previous models did not explicitly incorporate fission and growth, and thus this hypothesis could not be tested. The model developed here explicitly includes specific vital rates, and its purpose is to determine whether density-dependent feeding and fission do in fact have the potential to regulate population size.

METHODS AND RESULTS

Feeding trials

To determine the consequences of the density (% cover) of surrounding colonies and colony size for feeding in the zoanthid *Palythoa caesia*, colonies were fed hydrated *Artemia* cysts in a laboratory flume. The flume was similar in design to that shown by Vogel & La-Barbera (1978, their Fig. 1). The working section of the flume was 170 cm long, 30 cm wide and filled to a depth of 25 cm. At the upstream end was a 10 cm long collimator made of 10 mm diameter PVC pipe, which filled the entire cross-section of the flume. Water was directed into the return pipe at the downstream end by a face-plate at an angle of 45°, and was moved by a propeller attached to a variable speed motor. The return pipe was constructed of 20 cm diameter PVC pipe. Overall, the entire system held approximately 220 l of water.

Colonies of *Palythoa caesia* were collected from the reef crest at Heron Island at the southern end of Australia's Great Barrier Reef, and held in flow-through aquaria for a minimum of 48 h prior to use in any experiment. Only colonies which appeared healthy and fed actively at the end of this period were retained for use. Each 45 min feeding trial involved placing a randomly selected colony (the focal colony) in the centre of the flume at the downstream end of the working section, and a variable number of colonies within 30 cm upstream of it. A total of 2 g hydrated *Artemia* cysts (microwaved for 1 min prior to hydration to prevent hatching) were added to the flume and allowed to circulate for 2 to 3 min to allow time for mixing to occur. To determine cyst concentrations, two 50 ml water samples were then taken from near the bottom of the flume using a syringe, prior to the addition of the *P. caesia*. As this species is a nocturnal feeder, all colonies were kept in the dark and experiments were conducted at night with the aid of a red light, which did not appear to disturb them. At the end of each trial a photograph was taken of the layout of the colonies. The focal colony was then removed, gently washed in seawater to remove any cysts adhering to the colony surface and placed in a bowl of seawater to regurgitate

any ingested cysts. The remaining colonies were then removed from the flume, and free-stream flow speed was measured by determining the time required for a plume of dye to travel 50 cm. Egested cysts were counted 36 h after removing the focal colony from the flume, to obtain colony feeding rates. At this time, the number of polyps in each focal colony was also counted. Preliminary studies indicated that cysts were not egested for at least 6 h, and that dissected colonies retained no cysts after 36 h.

To ensure an approximately constant concentration of *Artemia* cysts throughout the study, the flume was emptied and rinsed between trials and refilled with unfiltered seawater pumped from the nearby reef slope. A total of 116 trials were conducted in October 1998, with focal colony sizes ranging from 4.5 to 47 cm², and upstream densities from 0 to 99% cover. Water temperatures at this time ranged between 25 and 27°C.

To determine the size of each focal colony, the photographs were traced and digitised, giving a measure of the colony's planar area (PA). The outlines of all upstream colonies were also digitised to determine upstream density (as % cover of an area 20 cm wide, 30 cm long). Percent cover was used as a biologically relevant measure of density, as it integrates number of colonies and colony size in a natural way. Ingestion rates were originally analysed using generalised additive models (GAM, a form of non-linear regression) with a Poisson distribution (for count data, Hastie &

Table 1. Factors determining colony feeding rates in *Palythoa caesia*. ANOVA table for best fit GAM. $p < 0.01$ in all cases

	df	Deviance	% variance accounted for
Total	109	3515	
Density	4	1233	35
Size	4	529	15
Concentration	4	154	4.4
Flow speed	4	146	4.1

Tibshirani 1990), with focal colony size, upstream density, concentration of *Artemia* (average concentration from the two 50 ml water samples) and flow speed as predictors. The GAM was fit by using a forwards-backwards stepwise method in S-plus (Insightful Corp., Seattle, WA), where the variable accounting for the greatest amount of variance was added to the model first, and the next best added at each step, checking that all variables were still necessary after each addition. Each variable in the GAM was fit using a cubic spline smooth with 4 df.

Looking firstly at the effect of each predictor variable on ingestion rates in isolation, we see that neighbours had a substantial influence (Fig. 1a). Ingestion rates decreased by ~70% from 0 to 20% upstream cover, with only slight decreases thereafter. As expected, increases in colony size lead to increases in whole colony ingestion rates, although this occurred mainly for the larger colonies (Fig. 1b). Results for particle concentration and flow speed were much more erratic, with no obvious consistent trends (Fig. 1c,d).

Taking all 4 variables into account simultaneously, while all contributed significantly to the model fit, upstream density and colony size accounted for half of the variance in feeding rate, whereas particle concentration and flow speed only accounted for just over 4% each (Table 1). As previously, when colony density (% cover) increased, feeding rate decreased monotonically (Fig. 2a), while feeding increased with colony size (Fig. 2b). Particle concentration varied little (2 to 4 cysts ml⁻¹) and had a very minimal effect (Fig. 2c, although there was a mean decrease at high concentrations, the error bands encompass the case of no concentration effect). Flow speed also had little effect on ingestion over the narrow range (10 to 14 cm⁻¹) examined, although there was a slight decrease at high flow (Fig. 2d). The GAM indicated that each variable entered into the model in an approximately linear fashion, so a generalised linear model (GLM, with Poisson distribution)

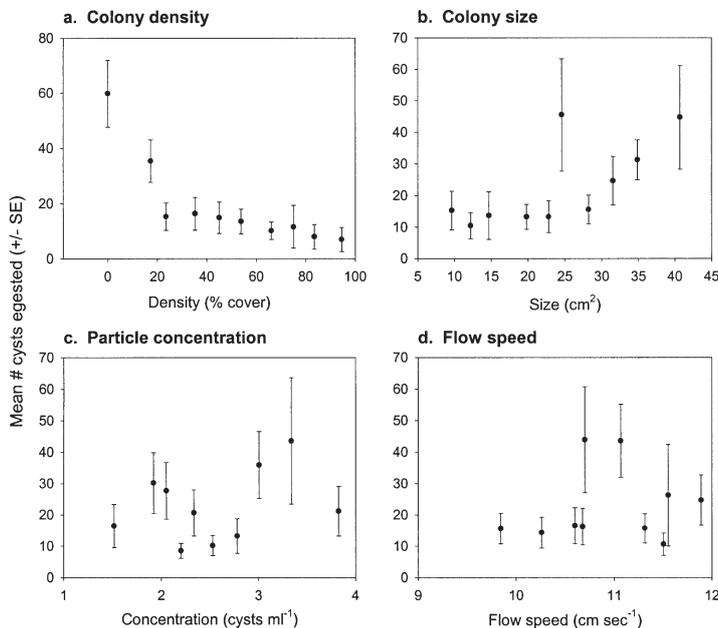


Fig. 1. *Palythoa caesia*. Relationship between colony ingestion rates and density, size, particle concentration and flow speed, for each variable taken independently. Means \pm SE are plotted for 10 approximately equal-sized groups of colonies

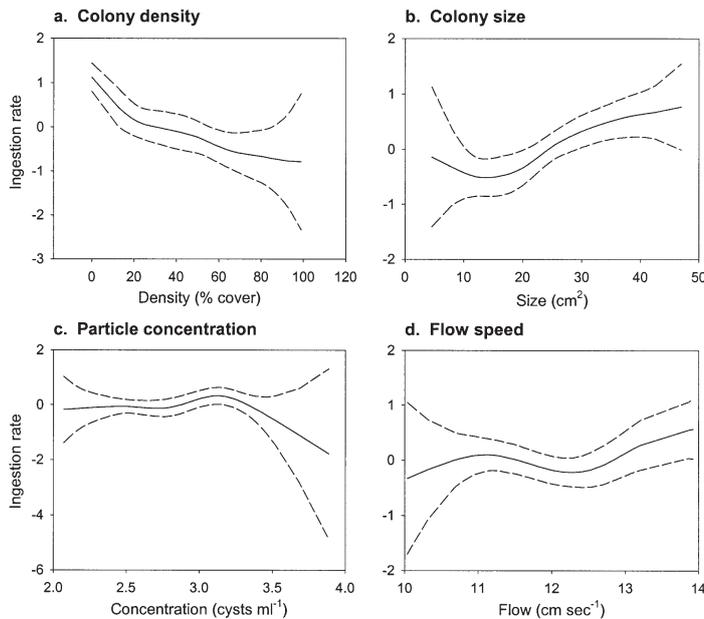


Fig. 2. Simultaneous influence on particle ingestion rates of *Palythoa caesia* of (a) population density (% cover), (b) colony size, (c) Particle concentration and (d) flow speed. (—) represents the GAM fit, (---) $\pm 2 \times$ SE. As all 4 variables are involved in determining feeding rates, plotting the actual data obscures any relationship, and is therefore not included. Each panel represents the contribution of the associated variable to ingestion, log-transformed (to account for the Poisson distribution) and centred to a mean of zero

was fit to obtain an equation for modelling particle ingestion (and later colony growth) as a function of upstream density and colony size. Flow rate and food concentration were not included in this model as they only varied over a relatively small range, and are not examined in the growth models developed later. The resulting GLM accounted for 44.3% of the variance in feeding ($p \ll 0.001$), and gave the equation (symbols defined in Table 2):

$$F_e = \exp(2.86 - 0.0266 \times d + 0.0423 \times PA) \quad (1)$$

To determine the relationship between colony size measured as projected area from the photographs, and the number of polyps in a colony, linear regression was used. This resulted in the equation:

$$p = 15.1 + 3.26 \times PA \\ (F = 217, p \ll 0.001, r^2 = 0.67) \quad (2)$$

Colony growth model

To determine the potential effects of density-dependence in heterotrophic feeding

rates on colony growth, a model directly incorporating information from the above experiment was developed. This model was used to examine the sensitivity of colony growth to the different physiological parameters used, and to feed into a subsequent model of population dynamics. Size- and density-dependent growth rates of individual colonies were calculated based on experimental ingestion rates, and data published by Sorokin (1991) on rates of heterotrophic carbon uptake, photosynthesis and respiration, as well as the biomass of individual polyps of *Palythoa caesia*. The colonies used by Sorokin (1991) were from the same reef as those used in the flume experiment presented here, although their exact collection location is unknown. The model tracks net carbon gain as the balance of heterotrophic feeding and photosynthesis versus respiration, and converts this to relative growth. Food uptake depends on colony density as found in the feeding experiment, while all 3 physiological rates also depend on colony size.

While Sorokin (1991) gives data on a per gram wet weight basis, photosynthesis was scaled to colony surface area as only the outer layer of the colony is exposed to light, and heterotrophic uptake was scaled to projected area to fit with the experimental data on feeding rates obtained above. Respiration was scaled to colony volume as a surrogate for biomass, although the use of surface area only produced slight quantitative changes to the

Table 2. Symbols used

Symbol	Definition
d	Density (% cover)
F_{dd}	Density-dependent ingestion rate ($\mu\text{g C g dry wt}^{-1} \text{d}^{-1}$)
F_{di}	Density-independent ingestion rate
F_e	Ingestion rate from flume experiment (Eq. 1, cysts 45 min^{-1})
F_r	Ingestion rate of a colony with radius 2.25 cm (from Eq. 1)
FS	Ingestion rate from Sorokin (1991) 250 $\mu\text{g C g dry wt}^{-1} \text{d}^{-1}$
P	Size-dependent photosynthetic rate ($\mu\text{g C cm}^{-2} \text{d}^{-1}$)
PA	Colony planar (projected) area (cm^2)
p	Number of polyps in colony (Eq. 2)
p_g	Number of polyps g dry wt^{-1} (from Sorokin 1991)
p_r	Number of polyps in a colony with radius 2.25 cm
PS	Photosynthetic rate from Sorokin (1991) 190 $\mu\text{g C g dry wt}^{-1} \text{d}^{-1}$
r	Colony radius (cm)
R	Size-dependent respiration rate ($\mu\text{g C cm}^{-2} \text{d}^{-1}$)
RGR	Relative daily growth rate
RS	Respiration rate from Sorokin (1991) 160 $\mu\text{g C g dry wt}^{-1} \text{d}^{-1}$
SA	Surface area (cm^2)
SA_e	Surface area of model colony
SA_r	Surface area of colony with radius 2.25 cm
V	Colony volume (cm^3)
V_e	Volume of model colony
V_r	Volume of colony with radius 2.25 cm

results (data not shown). To perform these conversions, it was assumed that colonies were shaped as a hemi-ellipsoid, with a circular cross-section in the horizontal plane, and a height of half the basal radius. Thus for a colony of radius r , the projected (or planar) area (PA), surface area (SA) and volume (V) are:

$$PA = \pi r^2 \quad (3)$$

$$SA = \pi r^2 + \frac{\pi r^2}{4\sqrt{3}} \log \frac{2+\sqrt{3}}{2-\sqrt{3}} \quad (4)$$

$$V = \frac{\pi r^3}{3} \quad (5)$$

There was only slight qualitative variation in the model output if different shapes, ranging from a flat sheet to a hemisphere, were used (data not shown).

Sorokin (1991) gives rates for photosynthesis of $190 \mu\text{g C g dry colony wt}^{-1} \text{d}^{-1}$, respiration of $160 \mu\text{g C g dry colony wt}^{-1} \text{d}^{-1}$, and total heterotrophic feeding of $250 \mu\text{g C g dry colony wt}^{-1} \text{d}^{-1}$. These measurements were all made on colonies of 3 to 6 cm diameter. To convert photosynthesis (P) to a surface-area-dependent rate, and respiration (R) to a volume-dependent rate, the following equations were used (assuming the above size-independent rates applied to a reference colony of 2.25 cm radius—the midpoint of the size range used to obtain them; symbols defined in Table 2):

$$P = \frac{SA_e}{SA_r} \times \frac{P_r}{p_g} \times PS \quad (6)$$

$$R = \frac{V_e}{V_r} \times \frac{P_r}{p_g} \times RS \quad (7)$$

The number of polyps g dry wt^{-1} (p_g) was calculated from the number of polyps in 1 g of wet tissue (Eq. 6), and the ratio between dry and wet weights of 0.45:1 given by Sorokin (1991).

Size- and density-dependent food consumption in terms of carbon uptake were obtained by combining Eq. (1) from experimental work on density-dependent feeding rates, with Sorokin's (1991) data on feeding, assuming that in both experiments colonies of the same size had the same food intake when neighbours were absent. This resulted in the Equation (symbols defined in Table 2):

$$F_{dd} = \frac{F_e}{F_r} \times \frac{P_r}{p_g} \times FS \quad (8)$$

To determine the consequences of making feeding density-dependent, we also need a density-independent version of Eq. (8):

$$F_{di} = \frac{\exp(2.01 + 0.043 \times PA)}{\exp(2.01 + 0.043 \times 15.9)} \times \frac{P_r}{p_g} \times FS \quad (9)$$

This feeding rate is derived from data on colonies at all densities by using GLM to obtain an expression for ingestion as a function of colony size only (the density independent equivalent of Eq. 1). Data from all colonies and not just those at zero upstream density were used, as the latter would only allow a comparison between colony growth rates in a population of closely spaced individuals and a population where colonies were sufficiently spaced for there to be no feeding interactions. Combining the equations for feeding, photosynthesis and respiration, and assuming for the moment that all excess carbon is used for growth (effectively giving maximum potential growth), we obtain a relative daily growth rate (RGR):

$$RGR = \frac{F + P - R}{610 \times p} \quad (10)$$

where 610 is the biomass of a single polyp in $\mu\text{g C}$ (Sorokin 1991). Ingestion rate F is either F_{dd} or F_{di} , depending on the situation being modelled. As responses of *Palythoa caesia* in the laboratory are being extrapolated to a field situation, and it is assumed that feeding rates in the flume experiment are the same as feeding rates in Sorokin's (1991) study, a comprehensive series of sensitivity analyses are conducted to determine the likely consequences of any errors in the model.

The density-dependent model of colony growth indicates that the highest relative growth rates are achieved by small colonies at low densities (Fig. 3a). At low density, as colony size increases, growth first decreases, and then increases slightly for the largest colonies. Conversely, at high densities, small colonies fare poorly, intermediate-sized individuals do the best, and the largest colonies actually shrink (as observed in the field; Tanner 1997). At all sizes, colony growth rates decrease as density increases. Replacing the den-

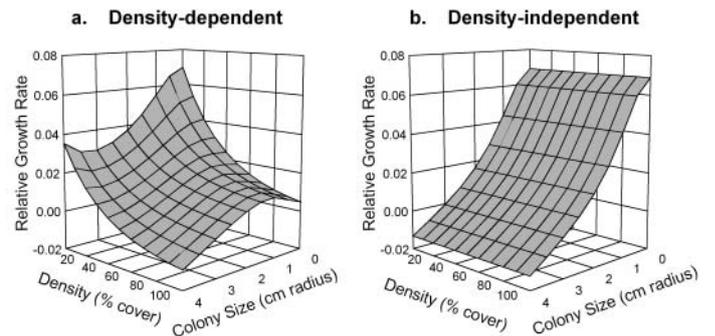


Fig. 3. Comparison of relative colony growth rates for *Palythoa caesia* derived from the model under the assumptions of (a) density-dependent and (b) density-independent feeding

sity-dependent feeding equation (Eq. 8) by the density-independent equation (Eq. 9) shows that increasing density affects *Palythoa caesia* by decreasing the growth of small colonies, but increasing that of large colonies (compare Fig. 3b to 3a).

Increasing the base level of food consumption (by increasing *FS* in Eq. 8), results in an exaggeration of the density effects, while decreasing it reduces the importance of density (Fig. 4). At the same time, the extent of the size effects changes in the opposite direction, i.e. when heterotrophic feeding is reduced there is a larger size effect on colony growth. As would be expected, not only does a reduction in feeding change the shape of the growth curve, but it also consistently moves it down, and results in a greater size range of colonies shrinking. Increasing photosynthesis in a similar way results in the peak in growth of intermediate colonies at high densities and the trough at low densities, becoming more pronounced, while reducing photosynthesis smooths both of these features out (Fig. 5). Changes in the rate of photosynthesis do not influence the effect of density on colony growth, as photosynthesis is not density-dependent. Finally, with high respiration rates, density and colony size both have substantial effects on growth, which decrease as respiration rate decreases (Fig. 6).

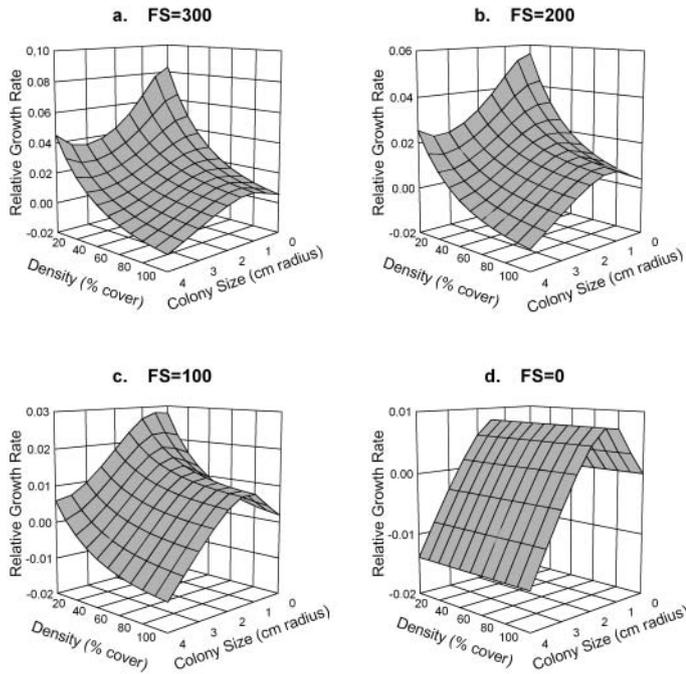


Fig. 4. Influence of altering heterotrophic feeding rates while maintaining size- and density-dependence on modelled colony growth of *Palythoa caesia*. *FS* is the ingestion rate of a solitary 16 cm² colony in $\mu\text{g C g}^{-1} \text{d}^{-1}$ (final term in Eq. 8). Fig. 3a gives the case when *FS* = 250. Note change in scale on the vertical axis

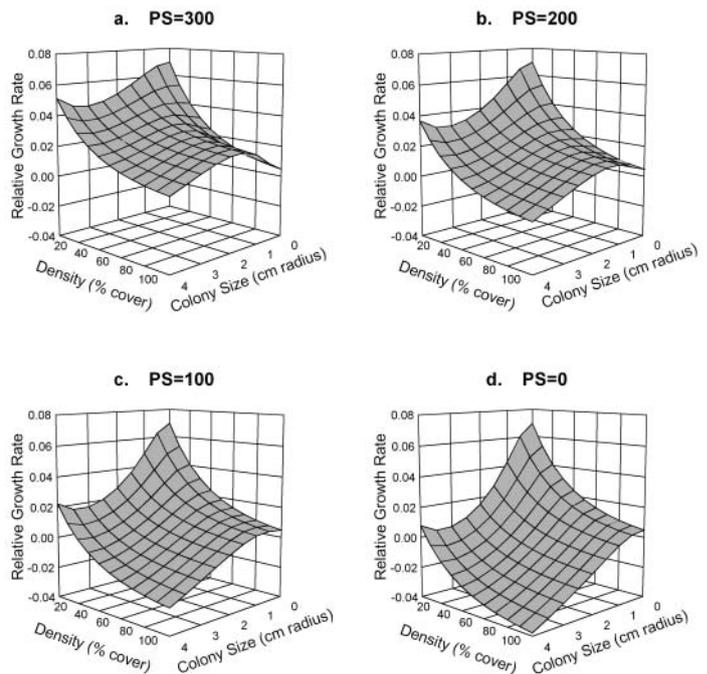


Fig. 5. Influence of altering the rate of photosynthesis on modelled *Palythoa caesia* colony growth. *PS* is the base photosynthetic rate of a solitary 16 cm² colony in $\mu\text{g C g}^{-1} \text{d}^{-1}$ (final term in Eq. 6). Fig. 3a gives the case when *PS* = 190

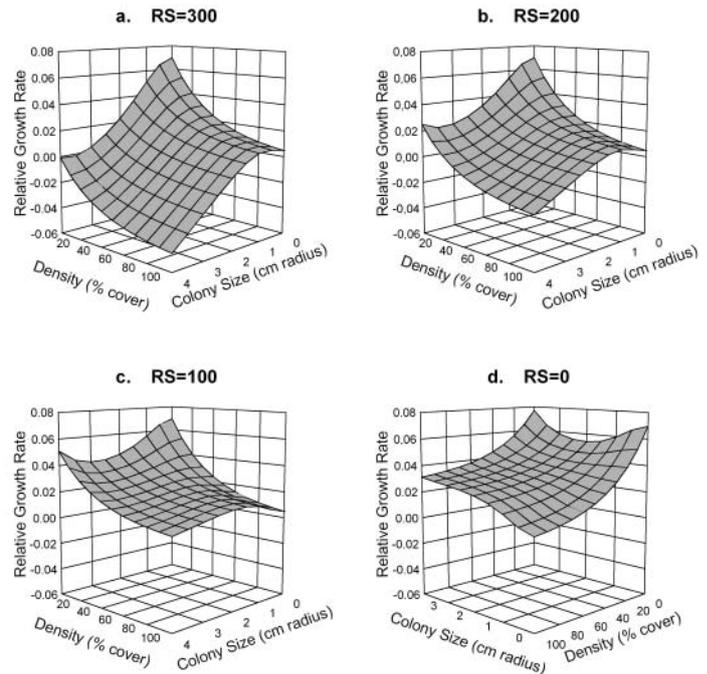


Fig. 6. Influence of altering respiration rate on modelled colony growth of *Palythoa caesia*. *RS* is the respiration rate in $\mu\text{g C g}^{-1} \text{d}^{-1}$ for a solitary 16 cm² colony (final term in Eq. 7). Fig. 2a gives the case when *RS* = 160. Note the change in orientation of the axes in (d)

Population dynamics model

The influence of density-dependence in colony feeding rates on population regulation was examined by combining the above equations into a simulation model of population dynamics. This model was also used to determine how sensitive population dynamics are to changes in feeding, photosynthesis and respiration rates (thus, also changes or errors in the model assumptions). The model kept track of the number of colonies in each of 1200 size classes in a 1 m² area, with colonies undergoing growth, mortality, fission and fusion as a function of size and density. Maximum observed size of nearly 2000 colonies in the field was 12 399 mm². Based on this, model sizes ranged from <10 to ≥12 000 mm² (in 10 mm increments). Each simulation commenced with 10 colonies in size class 1, which were first exposed to size- and density-dependent mortality (probabilities given in Fig. 2 of Tanner 1997), with the survivors growing in size over 1 mo (28 d) according to Eq. (10) for *RGR* (multiplied by 28). After growth, colonies also underwent fission and fusion according to the probabilities given in Tanner (1997; Figs. 3 & 4). All simulations were carried out for 2000 iterations (167 yr), although unless exponential growth occurred, equilibrium was always attained within the first 500. Except for simulations explicitly looking at the effects of larval recruitment, all population growth is by asexual fission, and hence involves an increase in the number of colonies, but not the number of genets (i.e. genetically distinct individuals). Previous models (Tanner 1999) indicated that recruitment was not important for population dynamics once an area was colonised. Indeed, mean recruitment was only 0.45 colonies m⁻² yr⁻¹, with almost complete mortality after 8 mo (Tanner 1997, 1999).

In the initial phases of the original simulation, population growth was very high, with density reaching 77% cover within 18 yr (Fig. 7a). After this time, cover oscillated slightly between about 76 and 78%, due to time lags associated with the 1 mo iteration period in the model (i.e. model colonies do not respond to gradual changes in density, but to the accumulated change over 1 mo). Decreasing this period resulted in a smoothing of these oscillations, while increasing it exaggerated them, until they became unstable and caused extinction with a 1 yr iteration period (data not shown). While I only present simulations showing % cover, similar patterns always appeared for the number of colonies. If observed colony growth rates over a 1 yr period are used (derived from Tanner 1997), initial population growth is slower, and the oscillations are longer, but equilibrium population size is still ~80% (Fig. 7b).

Of course, feeding and photosynthesis are unlikely to be constant, and will depend on the vagaries of food supply and cloud cover (among other variables). Respiration is less likely to fluctuate, although may still vary somewhat with environmental conditions. Adding independent random variation to either feeding or photosynthesis (multiplying them by δ , a uniformly distributed random variable between 0.5 and 1.5, i.e. $\delta \sim U[0.5, 1.5]$), gave similar results (Fig. 7c), with random variation in photosynthesis causing greater fluctuations than in feeding. Further increasing the size of the random fluctuations by making $\delta \sim U[0, 2]$ resulted in substantially slower initial growth, with many episodes of near extinction for random feeding but not photosynthesis, and wider fluctuations in the 'equilibrium' phase for both processes. When both feeding and photosynthesis were multiplied by $\delta \sim U[0, 2]$ extinction invariably occurred (Figs. 7d & 8a). In most cases, the addition of random variation slightly increased the mean cover over the last 1000 iterations, except when photosynthesis fluctuated over the greater range, when mean cover decreased (Fig. 8a).

Eliminating density-dependence in food consumption by using Eq. (9) in the model in place of Eq. (8) (but retaining density-dependence in mortality, fission and fusion), resulted in exponential growth (Fig. 8b), indicating that at least in the model density-dependence in feeding is necessary to regulate population size. Similarly, making fission rates, but not feeding, density-independent also resulted in exponential growth. In

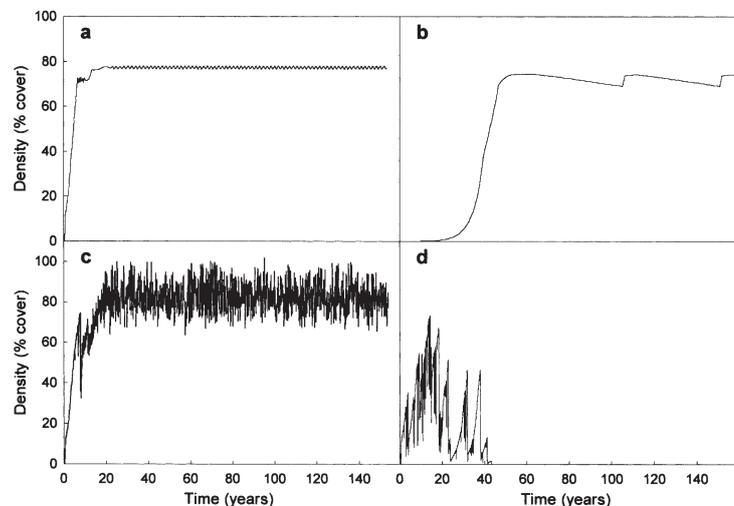


Fig. 7. *Palythoa caesia* population trajectories for models incorporating density-dependent feeding: (a) original model with growth dependent on feeding; (b) model with observed colony growth rates from Tanner (1997); (c) typical example showing the influence of stochastic variation in feeding and photosynthesis (obtained by multiplying *FS* and *PS* by independent uniformly distributed random variables $\delta \sim U[0.5, 1.5]$); (d) typical example showing the influence of multiplying *FS* and *PS* by independent uniformly distributed random variables $\delta \sim U[0, 2]$

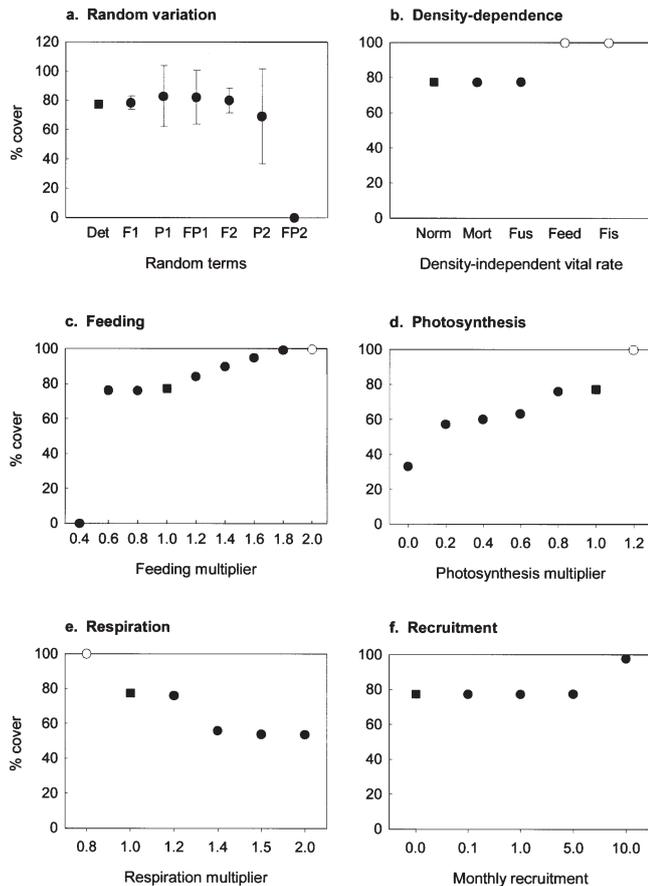


Fig. 8. *Palythoa caesia* sensitivity of the population model to changes in major model parameters. (■) Values for the original unmodified model with colony growth as in Fig. 2a, (●) responses to changes in the parameter investigated, (○) exponential growth to infinity for that parameter value (indicating that under the model assumptions, that value is not biologically realistic). Plotted values are means of the final 500 iterations and error bars in (a) indicate the range of values observed. Values on the x-axis for photosynthesis, respiration and feeding are multipliers for *PS*, *RS* and *FS* respectively. For the addition of random variation (a), Det indicates the base deterministic model, F1, P1 and FP1 indicate that *FS*, *PS* and both *FS* and *PS* are multiplied by $\delta \sim U[0.5, 1.5]$, while F2, P2 and FP2 indicate that $\delta \sim U[0, 2]$. (b) Density-independent vital rates are mortality (Mort), fusion (Fus), feeding (Feed) and fission (Fis), with Norm being the model with all rates density-dependent

contrast, density-dependence in mortality and fusion had little influence on population dynamics, and making these processes density-independent did not change cover appreciably.

Slightly reducing the overall rate of feeding (by multiplying *F* by a constant) had very little effect on population density (Fig. 8c). However, substantial reductions in food uptake (by about $1/2$) resulted in population extinction, indicating that *Palythoa caesia* does not have the potential to be fully autotrophic

under these conditions. Conversely, increasing feeding rates resulted in higher cover. Increasing the feeding rate by a factor of 2 or more resulted in cover exceeding 100%, which is impossible for this species, suggesting that if feeding does actually occur naturally at this rate, not all the resources consumed are directed towards colony growth.

Similar modifications to the rate of photosynthesis produce much more erratic behaviour (Fig. 8d). Increasing *P* by a factor of 1.2 or more results in exponential population growth, while slight reductions have little effect on cover. Further decreases result in a slow decline in cover. Finally, changes in the rate of respiration produce opposite results to changes in photosynthesis (Fig. 8e). Slight reductions in respiration produce exponential growth, whereas increases slowly reduce cover.

All of the above simulations were run without recruitment, so population growth was solely due to asexual fission. Adding a low level of external recruitment to the system did not change the model behaviour substantially (Fig. 8f). In all cases recruits were added to the first size class at the beginning of each iteration. Cover did not change at all until recruitment reached a level of 10 colonies m^{-2} , when it increased. Given the very low rate of observed recruitment ($0.04 \text{ m}^{-2} \text{ mo}^{-1}$, Tanner 1999), it is obvious that recruitment does not play an important role in the colony level dynamics of established aggregations, although it would have important consequences for the genetic structure of the population.

DISCUSSION

The models developed here support the prediction that density-dependent feeding rates, and therefore growth, play an important role in regulating the population size of *Palythoa caesia*. This adds further support to the suggestion that density-dependent food consumption, and not just competition for space, has a potentially important role in regulating the dynamics of sessile organisms (e.g. Fr chet te et al. 1992, Okamura 1992). The other important process appears to be fission, which probably decreases as density increases as a result of direct spatial competition. Thus, population regulation appears to be a result of competition for both food and space, rather than for one resource alone. Density-dependence in fission rates may also occur if the slower growth rates at high densities result in the distribution of colonies within a size class being skewed towards smaller colonies, combined with the previously documented decrease in fission rates as colony size decreases (Tanner 1997).

While the link between feeding and growth has not been explicitly established for *Palythoa caesia*, it has

been for several other sessile marine species, and it can reasonably be assumed. Okamura (1992) demonstrated that changing flow rates changed both food capture and growth in the same way for bryozoans, while Fréchette et al. (1992) showed directly that decreased food availability through addition of upstream competitors could cause mussels to decrease in body size. For soft corals, Fabricius et al. (1995) also showed that flow had the same effects on feeding as it did on growth. Thus, while feeding rate is unlikely to be the only determinant of growth for *P. caesia*, it seems logical to expect it to play an important role.

Of particular note is how similar the population trajectory for the model developed here is to that demonstrated by earlier models (Tanner 1999, 2000), which showed similar logistic type growth to an equilibrium (either deterministic or stochastic) cover of approximately 80%. While these models are unfortunately not completely independent, as the mortality, fission and fusion rates used here were derived from the same experiment as the transition rates between size classes used in the previous models, colony growth rates were derived entirely independently. As colony growth was one of the most important determinants of the model populations behaviour, as indicated by the influence of eliminating density-dependence in growth compared to other vital rates (Fig. 8b), the similarity between the different models increases confidence in their predictions. The explicit incorporation of fission into the model also strengthens the evidence for its importance.

The decrease in particle capture as upstream density increases is in accordance with most other studies of feeding in sessile suspension feeders (e.g. Okamura 1992, Anthony 1997, Sebens et al. 1997). These negative effects can arise either through food depletion (e.g. Fréchette et al. 1992), or a decrease in particle flux due to a decrease in flow speeds (Sebens et al. 1997). The reverse may also occur, with the presence of neighbours increasing particle capture by slowing water flow and reducing shear stress (e.g. Okamura 1985, 1988, McFadden 1986). Thus, it is possible that reduced ingestion rates in *Palythoa caesia* are due to either food depletion by upstream colonies, or changes in the flow regime.

One of the assumptions made by Sorokin (1991) was that *Palythoa caesia* has 12 h night⁻¹ available for feeding. However, as most colonies are intertidal, including those studied here, they will have less time. As feeding is impossible at low tide, heterotrophic consumption will probably be less than assumed, resulting in a shift in growth rates towards those predicted for reduced feeding (see Fig. 4). Other assumptions of the model are that laboratory derived rates of feeding, photosynthesis and respiration are similar to what occurs in the

field. These rates may err on the high side as conditions are favourable in terms of food and light availability, but colonies may also have been stressed in the laboratory and not fully active. I have also assumed that feeding rates of isolated colonies are directly comparable between this study and that of Sorokin (1991). As the latter used radioactively labelled cultures of live *Artemia*, *Brachionus* and *Aplisia*, apparently in still water, this may not be the case. However, sensitivity analysis indicates that substantial differences in feeding under these different sets of conditions would need to occur before major changes in model output would result (Figs. 4 & 8c).

Probably the most tenuous assumption is that feeding is always density-dependent, which would require smooth linear flow over the substrate. In reality, there are times when wave action causes turbulent flow, and therefore mixing of the food depleted boundary layer with water above it, reducing the potential for food depletion to occur. Small-scale turbulence induced by neighbouring colonies in particular has been shown to be important in modifying food availability to benthic suspension feeders (Fréchette et al. 1989, Monismith et al. 1990, O'Riordan et al. 1993, Eckman & Okamura 1998). Okamura (1992) showed that growth and feeding responses of bryozoans at different densities in smooth and turbulent flow were very similar. Thus, even in turbulent flow, *Palythoa caesia* may experience some density-dependence in feeding rates. As turbulence increases to levels that reduce this density-dependence, it is likely that particle capture is going to decrease anyway due to interference by water motion (e.g. Sebens & Johnson 1991, Fabricius et al. 1995, Anthony 1997, Sebens et al. 1998), again moving the field situation towards the examples of reduced food intake shown in Figs. 4 & 8c. Further support for the importance of density-dependent feeding is provided by field studies of mussel growth which show animals on the edge of patches grow faster, ostensibly due to higher food supply (Okamura 1986, Newell 1990). Thus, a large proportion of food intake may occur under conditions where feeding will be density-dependent.

Under favourable conditions when growth rates are predicted to be high, and possibly at other times, some of the resources which the model allocates to growth will be diverted to reproduction. There is little information available on how resources are allocated between growth and reproduction in any colonial cnidarians. For scleractinian corals, Edmunds & Davies (1989) suggest that less than 50% of photosynthetically fixed carbon goes to somatic growth, and Szmant (1991) determined that reproduction required carbon equivalent to between 15 and 45% of respiratory demand. If this later range applies to *Palythoa caesia*,

then approximately the equivalent of 12 to 38% of photosynthesis will be required for reproduction during the period in which oogenesis occurs. This would only result in slight reductions in colony and population growth rates (e.g. Fig. 4c shows the situation for a 47% decrease in photosynthesis, which would be the same if 47% was diverted to reproduction), and appears to be well within the ability of most colonies to sustain. In another study on scleractinian corals, Falkowski et al. (1984) reported that between 6 and 50% of translocated carbon was released as mucous, larvae and dissolved organic matter (DOM). *P. caesia* appears to release much less mucous than most corals (pers. obs.) but its rate of release of DOM is unknown.

At lower levels of heterotrophic feeding, growth may be constrained by a lack of resources other than carbon, particularly nitrogen. While it has been demonstrated that 97 to 99% of carbon and about 96% of nitrogen is translocated to the scleractinian coral host by zooxanthellae (Falkowski et al. 1984), the C:N ratio of this translocated material is considerably higher than in coral tissue, meaning that this may only represent a small fraction of the host's nitrogen requirements. Falkowski et al. (1984) found that translocated products had C:N ratios between 10 and 30:1, while coral tissue was around 6.5:1. As a consequence, when other sources of nitrogen are not available, photosynthetic carbon is probably used mainly as an energy source, and not for growth. As a likely result of nitrogen limitation, Edmunds & Davies (1989) found that some 67% of photosynthetic carbon was excess energy for a small-polyped species of scleractinian coral.

There is currently some debate about the relative roles of colony volume and surface area in determining respiration rates. Helmuth et al. (1997b) show that the mass flux can vary greatly according to colony shape. Mass flux can be an important determinant of respiration rates (e.g. Dennison & Barnes 1988, Shick 1990), although this will depend on whether the kinetic rate of respiration exceeds what can be supported by the flux of materials across the colony surface (Sanford & Crawford 2000). Given the simple and fairly flat shape of *Palythoa caesia*, there is little difference between model results for kinetically controlled respiration (i.e. respiration scales with biomass or volume) and mass flux controlled respiration (scaled to surface area) (data not shown). Therefore the method chosen to estimate respiration in the model should not be problematic.

The ratios between the different metabolic rates used in the above models are similar to those for scleractinian corals, but substantially different to those for octocorals (soft corals) (Sorokin 1991, Fabricius & Klumpp 1995). Thus, the general conclusions potentially extend to at least some scleractinians, but proba-

bly not to octocorals. Octocorals tend to have much slower metabolic rates, with photosynthesis making up a greater component of their energy intake — about double their respiratory requirements. Most symbiotic octocorals only obtain about 20 to 30% of their respiratory requirements from heterotrophic sources, although obviously asymbiotic species must obtain their entire requirements externally.

Despite the significant contributions made by photosynthesis to *Palythoa caesia*'s respiratory requirements, density-dependence in heterotrophic food capture still proved to be highly important in the model, suggesting this could severely limit both colony and population growth. If some photosynthetic carbon is wasted due to lack of nitrogen from other sources, or carbon is used for other purposes such as reproduction, these results are still likely to hold (see Fig. 8b). Due to the 3-dimensionally complex nature of many hard coral species, food depletion may be less of a problem for them than for *P. caesia*, which has a much less complex shape. However, it has been documented that particle capture rates can be density-dependent even in these more complex forms, and that food depletion can occur even within a colony (Helmuth et al. 1997a). Octocorals are unlikely to be regulated by density-dependent feeding as they rely on heterotrophic food consumption to a much lesser extent than do either *P. caesia* or hard corals (e.g. Sorokin 1991, Fabricius & Klumpp 1995, Fabricius et al. 1995), and they tend to have more open morphologies which may reduce interference in feeding.

The hypothesis that density-dependent growth and fission, linked at least in part to density-dependent food consumption, regulate the population size of *Palythoa caesia* is supported by the model developed here. Importantly, while a large number of assumptions were made about colony shape, how metabolic rates scaled with size and how laboratory results translate to more natural field situations, the final model developed produced realistic behaviour which was very similar to that seen in previous models (Tanner 1999, 2000). Sensitivity analyses (Fig. 8) showed that minor (and in some cases major) departures from many of these assumptions produced only slight changes in population dynamics. In particular, assumptions about colony shape were unimportant (data not shown). Evidence that competition for food in suspension feeding marine invertebrates is potentially important to individual colonies is becoming increasingly common (e.g. Buss 1979, Fréchette et al. 1992, Okamura 1992, Anthony 1997, Sebens et al. 1997). By linking colony growth and feeding with population dynamics, this study has shown that such competition might be one of the primary mechanisms of population regulation.

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