

Short-term growth measurements of corals using an accurate buoyant weighing technique *

P. Spencer Davies

Department of Zoology, University of Glasgow, Glasgow G12 8QQ, Scotland, and
Discovery Bay Marine Laboratory, Jamaica

Abstract

An accurate method for determining the growth rates of the skeleton of isolated branch tips (nubbins) of corals over intervals of less than 24 h is described. The skeletal weight of the coral was estimated from its buoyant weight in seawater whose density had been accurately determined. The coral tissues accounted for between 1 and 5% of the total buoyant weight in *Pocillopora verrucosa* and *Acropora humilis* with differing relative tissue biomass. After correcting for tissue buoyant weight, predictions of skeletal weight were accurate to within 1%. The method was used to estimate the growth of sample nubbins of *Porites porites* of similar diameter, in 2 m of water at Discovery Bay, Jamaica. Since growth of these branch tips is apical, growth rate could be expressed without correction for the size. The mean 24 h skeletal growth rate ranged between 40 and 47 mg. Differences could be measured between day-time and night-time growth, the day:night ratio being 3.7. The method also showed that *P. porites* virtually ceases calcification during the 4 to 5 d periods that it becomes enclosed in a mucus tunic. Nubbins of *P. porites* attached to the reef at different locations showed clear differences in growth rate with depth, and between clear and turbid water sites. The growth rate of nubbins was compared with that of branch tips of whole corals by measuring the linear extension after staining with Alizarin Red S. After 3½ mo, the mean linear extension was 4.1 mm in each case, indicating that the growth rate of nubbins is the same as that of branch tips of the whole colony. It is suggested that this buoyant weighing technique will find applications in laboratory experiments with calcification mechanisms and as a bioassay on reefs exposed to environmental stress.

Introduction

Growth rate in corals has invariably been measured in terms of skeletal accretion rates. Laboratory and field experiments

aimed at understanding the calcification mechanism, have mainly followed the technique of Goreau (1959), involving measurement of the rate of incorporation of ⁴⁵Ca into the skeleton. This sensitive technique does nevertheless have serious drawbacks (Barnes and Crossland 1982) and the coral has to be killed in order to measure the growth increment. A recent laboratory adaptation (Dennison and Barnes 1988) of the alkalinity anomaly technique of Smith and Kinsey (1978) appears to offer an alternative methodology for short-term incubations, and has the advantage of being non-destructive.

A large number of determinations of coral growth rates in the field have been made, often as a measure of environmental stress. The methods, including x-radiography, measurements of linear growth either directly or following Alizarin Red S staining of the skeleton, and increases in skeletal weight, have been reviewed by Buddemeier and Kinzie (1976), Gladfelter et al. (1978) and Brown and Howard (1985). Most of these methods have the disadvantage of either requiring long time intervals in order to measure the growth increment or of requiring the coral to be sacrificed. The method of buoyant weighing is simple and non-destructive. It involves weighing the coral underwater and predicting from this weight, the weight of the skeleton. The method was used experimentally by Franzisket (1964), Bak (1973, 1976), Jokiel et al. (1978) and Dodge et al. (1984). Jokiel et al. described the theoretical basis of the technique and gave details of a method for small corals using an analytical beam balance. Adaptations of this method were used by Davies (1984) and Edmunds and Davies (1986) to measure the rate of growth of *Pocillopora eydouxi* and *Porites porites*, respectively, from weekly measurements of the buoyant weight of isolated branch tips or nubbins (Birke-land 1976) living in shallow water.

The purpose of the present study was to increase the accuracy of the method by introducing a correction for the buoyant weight of the tissues of the coral, and to overcome the handling artefacts which limited the precision of the method in short-term growth determinations (Jokiel et al.

* Contribution No. 464 of the Discovery Bay Marine Laboratory

1978). The method now described gives reproducible results for growth over a 24 h period and clearly demonstrates the differences between day-time and night-time calcification rates. The method probably has potential both for environmental monitoring of growth rate and for laboratory experiments on calcification mechanisms.

Materials and methods

Buoyant-weight equations

The weight of an object in air, its density [D], its buoyant weight and the density of the water are inter-related and can be expressed in a series of equations. These were derived by simple algebraic manipulation from Eq. (1) below, the derivation of which has been explained in more detail by Jokiel et al. (1978).

$$\begin{aligned} \text{Weight of object in air} &= \text{wt in water} + \left(\frac{\text{wt in air}}{D_{\text{object}}} \cdot D_{\text{water}} \right) \\ &\text{or } \frac{\text{wt in water}}{\left(1 - \frac{D_{\text{water}}}{D_{\text{object}}} \right)}. \end{aligned} \quad (1)$$

$$\begin{aligned} \text{Weight of object in water} &= \text{wt in air} - \left(\frac{\text{wt in air}}{D_{\text{object}}} \cdot D_{\text{water}} \right) \\ &\text{or } \text{wt in air} \cdot \left(1 - \frac{D_{\text{water}}}{D_{\text{object}}} \right). \end{aligned} \quad (2)$$

$$\begin{aligned} \text{Density of water} &= \frac{\text{wt in air} - \text{wt in water}}{\frac{\text{wt in air}}{D_{\text{object}}}} \\ &\text{or } D_{\text{object}} \cdot \left(1 - \frac{\text{wt in water}}{\text{wt in air}} \right). \end{aligned} \quad (3)$$

$$\begin{aligned} \text{Density of object} &= \frac{\text{wt in air} \cdot D_{\text{water}}}{\text{wt in air} - \text{wt in water}} \\ &\text{or } \frac{D_{\text{water}}}{\left(1 - \frac{\text{wt in water}}{\text{wt in air}} \right)}. \end{aligned} \quad (4)$$

In order to determine the air weight of the coral skeleton from its weight in seawater, it is therefore necessary to know the density of the skeleton, and the density of the seawater in which it is weighed. Methods for calculating these values are presented below.

Buoyant-weighting method

Buoyant weighings were made using a Precisa 80A or 120A electronic balance, reading to 0.1 mg. The balance was mounted on a 30 × 25 × 20 cm wooden box whose interior formed the weighing chamber. The front of this box was fitted with a transparent sliding acrylic panel which could be lowered to seal the chamber and hence exclude air movements during weighing. The weighing platform was a 5 cm

watchglass suspended by three 0.05 mm diam tungsten wires attached to an 0.5 mm tungsten wire which passed through a hole in the top of the weighing chamber to the attachment point on the underside of the balance. Monofilament nylon was found to be unsatisfactory because the hydrophobic nature of the plastic produces surface tension problems at the air/water boundary.

The watchglass was suspended in a 6 cm deep bath of seawater which occupied most of the floor of the weighing chamber. Optimal weighing conditions were obtained when the apparatus was located in a room with a stable air temperature close to that of the seawater. Before weighing, the corals were placed in the bath for 5 min to achieve temperature equilibration, since it is necessary for the density of the pore water inside the coral to be the same as that of the bath water. It was essential to ensure that any air bubbles adhering to the coral during its brief emersion in air whilst being transferred to the bath, were removed with a fine paintbrush. Care also had to be taken to see that the aerial portion of the suspending wires was not splashed or wetted.

Density of seawater

This is most easily and accurately determined from Eq. (3) by weighing an inert reference object of known air weight and density in the seawater. The reference object used was a solid glass stopper of approximately 10 g air weight. Its density was determined from Eq. (4), by weighing it in air and then in distilled water. The density of distilled water was obtained from Table F5-6 and F11 of the CRC Handbook of Chemistry and Physics (1984).

In practice, the density of the seawater was determined immediately before buoyant-weighting the corals and at intervals during the weighing. This is because the density of the seawater will change if mucus is liberated into it by the corals. In addition, it is necessary to monitor the temperature of the seawater, and if it changes by 0.1°C or more, the new density is obtained by reweighing the reference object.

Density of skeleton

A sample of coral branch tips was soaked in a 10% solution of commercial bleach (Chlorox) in seawater for 24 h before carefully removing any residual traces of tissue by forcing pumped seawater through the perforate skeleton. The skeleton was held beneath the surface of seawater in a large dish during this process and care was taken not to introduce any air bubbles into the skeleton voids. The cleaned skeleton was then buoyant-weighted before being washed in distilled water, and dried to constant weight at 70°C. Drying at temperatures higher than 70°C can cause the residual organic matrix in the skeleton of corals such as *Pocillopora* spp. to melt. Imperforate corals, including *Pocillopora* spp. can take 3 to 4 wk to reach constant weight under these conditions. Freeze-drying may be a quicker alternative to hot-air drying. The dried skeleton was weighed and its density determined from Eq. (4).

Accuracy of prediction of skeleton weight

The effects of the tissue biomass on estimates of skeletal weight was investigated in the corals *Pocillopora verrucosa* and *Acropora humilis*. The former has an imperforate skeleton and a relatively small tissue biomass, whilst the latter has a perforate skeleton with large tissue biomass.

Corals were collected from a fringing reef adjacent to the Marine Laboratory of King Abdulaziz University, Jeddah in April 1988, and branch tips ($n=10$ for each species) removed. After 5 d recovery in running seawater, their buoyant weights were determined. Cleaned skeletons were then prepared by soaking in Chlorox, followed by rinsing and soaking in seawater. The buoyant weights of the skeleton were then measured and the skeletal densities calculated as before. The difference in buoyant weights of whole coral and skeleton yielded a value for the buoyant weight of the tissues. This was then used to produce a correction factor for the tissue buoyant-weight.

A second group of branch tips ($n=12$ for each species) was then buoyant-weighed. The predicted skeletal weights uncorrected and corrected for the tissue component were then compared with the actual dry weights of skeletons.

Growth determinations

Whole colonies of the branching coral *Porites porites* were collected from water depths of 2 to 3 m at Discovery Bay, Jamaica in August 1987. Branch tips of 3 to 4 cm length from branches of similar diameter were removed and their cut faces were ground flat. They were then cemented to $30 \times 30 \times 3$ mm acrylic tiles with viscous cyanoacrylate glue ("Superglue") to form nubbins (Birkeland 1976, Davies 1984). The corals could be handled thereafter by the tile, so minimising any damage to the tissues. They were then left in running seawater and buoyant-weighed at intervals of approx 24 h. After 3 d, normal growth rates had been resumed and examination with a binocular microscope revealed that damaged tissues had been regenerated.

For growth studies, groups of nubbins were placed in acrylic racks which were secured to concrete breeze blocks at a water depth of 2 m on the reef. At intervals, the racks were returned to the laboratory and the buoyant weights of the nubbin plus tile were measured to the nearest 0.1 mg. At the termination of the growth experiment, the coral nubbin was prised from the tile and any adhering skeletal material was dissolved in dilute HCl. The tile and adhesive were then dried and weighed. To obtain the net buoyant weight of the coral, the buoyant weight of the tile at each weighing was then calculated, using predetermined values for the density of the acrylic material, and subtracted from the total buoyant weight.

Initial experiments indicated that very similar coefficients of variation were obtained when growth rates were (a) uncorrected, (b) corrected for weight, and (c) corrected for surface area. This was not unexpected, since the branch types were of similar diameter and growth is apical. All growth rates were therefore expressed in uncorrected form.

Results

Accuracy of prediction of skeleton weight

The mean density of the skeleton of *Pocillopora verrucosa* was 2.783, that of *Acropora humilis* 2.622. In *P. verrucosa*, the tissue buoyant-weight represented $0.81 \pm 0.17\%$ of the whole buoyant-weight, and in *A. humilis* $5.32 \pm 0.58\%$.

Correcting for the tissue buoyant-weight in the second group of corals, the mean percentage differences between predicted and actual dry skeleton weights were:

	uncorrected	corrected
<i>Pocillopora verrucosa</i>	$+0.58 \pm 0.14\%$	$-0.22 \pm 0.14\%$
<i>Acropora humilis</i>	$+4.72 \pm 0.19\%$	$-0.87 \pm 0.18\%$

It is clear, therefore, that with imperforate corals very little inaccuracy is introduced by using the uncorrected formulae. With perforate corals with tissues penetrating deep below the surface, errors of about 5% may be introduced. However, for most accurate work these errors can be reduced to about 1% by correcting for the buoyant weight of the tissue.

Pattern of growth of *Porites porites* on reef

In order to assess the effects of handling artefacts which can result in suppression of growth (Jokiel et al. 1978), buoyant weighings were made at intervals of 3 wk, 1 wk and each day, and the mean 24 h growth rates were compared.

Weekly growth

The increase in weight of one group ($n=8$) which was left on the reef for 3 wk of continuous growth was compared with that of another group ($n=8$) which was taken to the laboratory and weighed each week for 3 wk (Table 1). Towards the end of the first week, all of the *Porites porites* on the reef started to produce mucus tunics (Lewis 1973) and their rate of calcification was depressed (see below: "Effect of mucus-tunic production on growth rate of *Porites porites*"), resulting in a slightly reduced overall mean rate in Week 1 and a much reduced mean rate in Week 2. Comparison of the mean daily increase of 34.6 mg for the group sampled weekly with the mean daily increase of 33.3 mg for the group measured only at the end of the 21 d period, using a Student's *t*-test ($P > 0.05$), showed that there was no significant difference.

Daily growth

A group of six nubbins was weighed at intervals of 24 h for 3 d during the final 7 d period of uninterrupted growth of the group described in the preceding subsection (Table 2).

The difference in the mean daily growth increment of 44.7 mg for the group which was weighed every 24 h, and the value of 47.1 mg for the group which was left for 7 d uninterrupted growth is not significant (Student's *t*-test).

Under the conditions of these experiments, in which the corals were removed from the reef for a maximum of 30 min for laboratory weighing, it was therefore possible to obtain measurements of growth at intervals of 24 h which were not significantly affected by handling artefacts.

Table 1. *Porites porites*. Mean total and daily growth increments of two groups of nubbins living at 2 m water depth at Discovery Bay, Jamaica in August and September 1987. First group ($n=8$) was left for 3 wk continuous growth, whilst second group ($n=8$) was returned to the laboratory for weighing at intervals of one week, for 3 wk

Group	Total growth (mg \pm SD)	Daily mean increment (mg \pm SD)
Group 1 (3 wk continuous)		
26 Aug.–16 Sep.	733.3 \pm 249.2	33.3 \pm 11.3
Group 2		
Week 1		
26 Aug.–2 Sep.	280.3 \pm 117.5	41.82 \pm 17.1
Week 2		
2 Sep.–9 Sep.	105.7 \pm 60.8	15.1 \pm 8.6
Week 3		
9 Sep.–16 Sep.	329.7 \pm 79.2	47.1 \pm 11.3
21 d total	728.2 \pm 209.5	34.6 \pm 9.9

Table 2. *Porites porites*. Mean total and daily growth increments of two groups of nubbins living at 2 m water depth at Discovery Bay, Jamaica in September 1987. First group ($n=8$) had 1 wk of uninterrupted growth, whilst second group ($n=6$) was returned to the laboratory for weighing at daily intervals for 3 d

Group	Mean increase in wt (mg \pm SD)	Daily mean increment (mg \pm SD)
Group 1		
7 d continuous (9–16 Sep.)	329.7 \pm 79.2	47.1 \pm 11.3
Group 2		
Day 1 (10 Sep.)	46.6 \pm 3.8	
Day 2 (11 Sep.)	39.1 \pm 4.3	
Day 3 (12 Sep.)	48.5 \pm 5.1	
3 d total	134.1 \pm 11.1	44.7 \pm 3.0

Table 3. *Porites porites*. Mean 24 h growth of nubbins ($n=8$) in 3 m of water at Discovery Bay, Jamaica in September 1987. From 2–7 September some nubbins developed mucus tunics and their reduced growth rate is shown separately

Group	Mean 24 h growth (mg) on September:										
	2	3	4	5	6	7	8	9	20	22	12
Whole group	26.7	17.75	9.2	8.7	9.9	10.9	32.4	35.6	42.7	35.5	44.7
Mucus tunics only (n)	5.4 (1)	14.2 (6)	4.5 (6)	2.6 (6)	1.6 (5)	2.3 (5)					

Effect of mucus-tunic production on growth rate of *Porites porites*

A group of nubbins ($n=8$) was placed on the reef on 1 September 1987 and removed to the laboratory at dawn each day for weighing, until 12 September 1987. During the first week, all except two nubbins developed mucus tunics. The daily growth increments are presented as means for the whole group and means for those having mucus tunics at the time of weighing in Table 3 and Fig. 1.

The average duration of the mucus tunics was about 5 d. During this time the rate of calcification declined and had virtually stopped by the fourth day.

Day and night growth rates of *Porites porites*

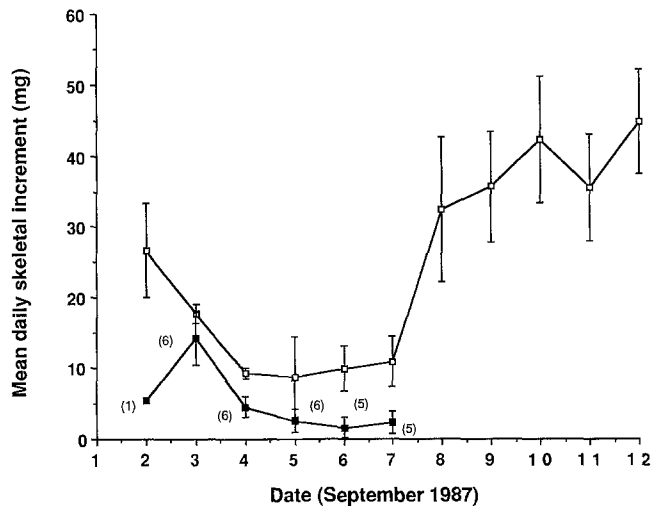
In order to compare day and night growth rates, a group of nubbins ($n=6$) was placed on the reef just before dusk at 18.00 hrs in August 1987 and their growth measured 24 h later. They were then returned to the reef and their weights were determined after dawn at 6.00 hrs the following day and again at 18.00 hrs. The mean values were: 22–23 August, 24 h growth, 40.81 \pm 7.1 mg; 23–24 August, 12 h night-time growth, 8.7 \pm 0.25 mg; 24 August, 12 h day-time growth, 32.5 \pm 5.3 mg. The ratio of day-time to night-time growth was therefore 3.7.

Comparison of growth rates of nubbins and whole colony of *Porites porites*

In order to test whether the growth rates recorded for the nubbins were comparable with those of intact colonies, growth was compared over a 3½ mo period using measurements of the linear extension of branch tips. A whole colony of *Porites porites* with approximately 25 branch tips, and a group of nubbins were incubated for 10 h in large desiccator jars containing 10 mg l⁻¹ Alizarin Red S (Lamberts 1978) in seawater. The seawater was aerated with a diffuser stone and the jars were kept in the shade. The stained nubbins and colony were placed on the reef on 4 September 1987 and retrieved again on 23 December 1987. The tips of the colony were then removed and tissues of both nubbins and tips were removed by soaking for 24 h in a Chlorox solution. The tips were then bisected vertically with a diamond saw and the distance from apex to Alizarin band was measured to the

Table 4. *Porites porites*. Growth rates ($\text{mg} \pm \text{SD}$) during day time and night time of nubbins ($n=8$) measured in laboratory with artificial lighting regime in September 1987

	1–2 September		2–3 September		3–4 September	
	Night	Day	Night	Day	Night	Day
	4.9 ± 2.6	23.2 ± 7.7	5.2 ± 3.3	24.6 ± 6.9	6.5 ± 1.9	27.0 ± 5.4
Total	28.1		29.8		33.5	
Ratio day:night	4.7		4.7		4.2	

**Fig. 1.** *Porites porites*. Daily skeletal growth of group ($n=8$) of nubbins in 2 m of water at Discovery Bay, Jamaica (□), showing depression of growth when coral tissues are covered by mucus tunic. Growth of those nubbins displaying visible mucus tunic (■) and number involved, is also shown. Values are means \pm SD

nearest 0.07 mm under a binocular microscope using a pre-calibrated eyepiece graticule.

The values obtained were: linear extension mean \pm SD for nubbins = 4.1 ± 1.0 ($n=7$), and for colony branch tips = 4.1 ± 1.1 ($n=8$). It is clear that the rate of growth of the branch tips, when cemented to acrylic tiles as nubbins, does not differ from that when on the whole colony. Extrapolation gives an annual linear growth rate of 13.3 mm which compares well with the range of published values for *Porites porites* of 6 to 21 mm per annum cited by Huston (1985).

Pattern of growth of *Porites porites* in laboratory

It was of interest to determine whether the pattern of day and night growth recorded for nubbins on the reef could be reproduced in the laboratory, using an artificial lighting regime. Coral nubbins ($n=8$) were placed in a shallow acrylic water bath through which seawater was circulated. The bath was supported beneath a bank of fluorescent lights in an aluminium foil-lined light hood. The nubbins were kept in darkness in the hood from 18.30 to 6.00 hrs. The lights were then switched on at an irradiance of $50 \mu\text{E m}^{-2} \text{s}^{-1}$.

The voltage to the fluorescent lights was gradually increased over the succeeding hour to produce a maximum irradiance of $300 \mu\text{E m}^{-2} \text{s}^{-1}$, which was maintained until 17.00 hrs when it was gradually reduced again. The nubbins were removed to the adjacent balance for buoyant weighing at 6.15 and 18.45 hrs. The weight increases ($\text{mg} \pm \text{SD}$) recorded are shown in Table 4.

The 24 h rates of calcification are comparable to those recorded for corals on the reef on 2 September (Table 3). However, whilst all *Porites porites* on the reef developed mucus tunics, only one of those in the laboratory experiment (not included in the data of Table 4) did so. From these preliminary results, it appears that with a suitable lighting regime, the buoyant-weighing method could be used in future for laboratory experiments on calcification mechanisms.

Discussion

The first major studies on weight increases of corals were published by Bak (1973, 1976), who worked with whole colonies, measured *in situ* with a specially devised weighing apparatus. His underwater weights were converted to weights of dry skeleton using a conversion factor. Subsequently Jokiel et al. (1978) described the theoretical basis of the relationship between buoyant weight and dry skeleton weight. In the course of the present study to develop a high-resolution procedure for laboratory and field use, several sources of potential error were identified. The first of these is the assumption that since coral tissue has a density which is similar to that of seawater, it does not contribute significantly to the buoyant weight of the coral when weighted underwater. It was found that in *Pocillopora verrucosa*, an imperforate coral with a relatively low tissue biomass, the tissue contributes only 1% of the buoyant weight. However, in *Acropora humilis*, where the tissue penetrates deep into the skeleton, about 5% of the buoyant weight is attributable to tissue. For highly accurate work, it is possible to correct for the tissue buoyant weight and to reduce the error to about 1% or less.

The second source of error arose from the previously made assumption that the skeleton is composed entirely of aragonite with a density of 2.93 (Jokiel et al. 1978). Direct determinations of the skeletal density have yielded the following values: *Pocillopora eydouxi* 2.783 (Davies 1984),

Table 5. Daily increases in weight of coral nubbins, determined by buoyant-weighing method

Coral	Growth (mg d ⁻¹)	Depth	Habitat	Source
<i>Pocillopora eydouxi</i>	26.2	5 m	Fore reef, Guam	Davies (1984)
<i>Pocillopora damicornis</i>	40.7	2 m	Fringing reef, turbid water, Oahu, Hawaii	Davies (unpublished data)
<i>Montipora verrucosa</i>	27.6			
<i>Porites lutea</i>	51.6			
<i>Porites porites</i>	27.8	10 m	Fore reef, Jamaica	Edmunds and Davies (1986)
	12.5	10 m	Back reef, turbid water, Jamaica	Edmunds (1986)
	47.1	2 m	Back reef, clear water, Jamaica	Present study

P. verrucosa 2.785. *Acropora humilis* 2.622 (present study), and *Porites porites* 2.822 (Edmunds and Davies 1986). These deviations from the density of pure aragonite may be due to the presence of residual organic matrix material within the skeleton.

Other sources of error, due to accreting or boring organisms (Bak 1976) or to handling of the corals (Jokiel et al. 1978) were largely overcome by using branch tips which were free of these organisms, and by handling the coral nubbins by the acrylic tiles to which they were cemented.

In order for the buoyant weighing of nubbins to provide a useful predictor of growth of the whole colony, it is necessary to determine whether their growth is affected by their isolation from the parent colony and cementing to the acrylic tile. Over the 3½ mo period of study, the linear extension of the branch tips of nubbins and whole colony in *Porites porites* were almost identical. The observation by Kinzie and Sarmiento (1986) that the rate of linear extension in *Pocillopora damicornis* is independent of colony size appears to agree with this.

The mean daily skeletal increments determined from buoyant weighings of nubbins of the few species that have been studied, all yield values in the range 12.5 to 51.6 mg d⁻¹ (Table 5) and give an indication of differences correlated with environmental change. Thus, in *Porites porites*, the growth rate is 47.1 mg d⁻¹ at a water depth of 3 m, falling to 27.8 mg d⁻¹ 10 m on the fore reef at Discovery Bay, correlated with the attenuation of light with depth. At a depth of 10 m in a turbid back-reef environment at Discovery Bay, the growth rate fell even further to 12.5 mg d⁻¹.

The buoyant-weighing method gave clear resolution of differences in rate of skeletal accretion between day and night. In *Porites porites*, the mean night-time rate on the reef was 8.7 mg compared with 32.5 mg during the day, giving a ratio of 3.7. This ratio is close to the light:dark ratio obtained by Pearse and Muscatine (1971) for incorporation rates of ⁴⁵Ca into isolated branch tips of *Acropora cervicornis* following short-term incubations, and values for diurnal differences in ¹⁴C incorporation into *A. acuminata* (Barnes and Crossland 1978).

An unexpected discovery during the course of this investigation is that skeletal growth virtually stops during the 4 to 5 d periods in which *Porites porites* becomes covered by

mucus tunics. Mucus tunic production by *P. porites* was described by Lewis (1973) and Edmunds (1986), although no satisfactory functional explanation has yet been proposed. Although the tentacles are withdrawn into the corallites whilst the coral is covered by the mucus tunic, the zooxanthellae of the coenosteum are still exposed to light for photosynthesis. The fact that skeletal growth rate falls below that of the normal night-time rate suggests that calcification may be limited by depletion of Ca⁺⁺ ions from the seawater trapped beneath the tunic.

The methods available for determining the growth rate of corals have been reviewed by Brown and Howard (1985) and by Buddemeier and Kinzie (1976). Most techniques suffer from the disadvantage of requiring a long period of time (6 mo to 1 yr) in order to complete a single growth measurement and or require the sacrifice of the coral. The method of buoyant weighing of nubbins has the advantage that it is simple, inexpensive, and can measure differences in day-time and night-time growth rates. On a routine basis it could be used as a tool for the assessment of environmental impact on coral reefs, yielding comparative values for growth rate over intervals of only 1 to 3 d. Measurements of the growth of nubbins have only been made to date with branching corals, where the main growth zone is apical. Modifications of the technique for use with massive corals are currently being investigated.

Acknowledgements. The author is grateful to the Trustees of the Nuffield Foundation for a grant in support of this work. Thanks are due to Dr. J. Woodley and R. Gates for assistance at Discovery Bay Marine Laboratory and to Mr. A. Al Sofyani for assistance with the Red Sea corals.

Literature cited

- Bak, R. P. M. (1973). Coral weight increment *in situ*. A new method to determine coral growth. *Mar. Biol.* 20: 45–49
- Bak, R. P. M. (1976). The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. *Neth. J. Sea Res.* 10: 285–337
- Barnes, D. J., Crossland, C. J. (1978). Diurnal productivity and apparent ¹⁴C calcification in the staghorn coral *Acropora acuminata*. *Comp. Biochem. Physiol.* 59A: 133–138
- Barnes, D. J., Crossland, C. J. (1982). Variability in the calcification rate of *Acropora acuminata* measured with radio-isotopes. *Coral Reefs* 1: 53–57

- Birkeland, C. (1976). An experimental method of studying corals during early stages of growth. *Micronesica* 12: 319–322
- Buddemeier, R. W., Kinzie, R. A. (1976). Coral growth. *Oceanogr. mar. Biol. A. Rev.* 14: 183–225
- Brown, B. E., Howard, L. S. (1985). Assessing the effects of “stress” on reef corals. *Adv. mar. Biol.* 22: 1–63
- CRC Handbook of Chemistry and Physics (1984). CRC Press, Boca Raton, Florida
- Davies, P. S. (1984). The role of zooxanthellae in the nutritional energy requirements of *Pocillopora eydouxi*. *Coral Reefs* 2: 181–186
- Dennison, W. C., Barnes, D. J. (1988). Effect of water motion on coral photosynthesis and calcification. *J. exp. mar. Biol. Ecol.* 115: 67–77
- Dodge, R. E., Wyers, S. C., Frith, H. R., Knap, A. H., Smith, S. R., Cook, C. V., Sleeter, R. B. (1984). Coral calcification rates by the buoyant weight technique: effects of alizarin staining. *J. exp. mar. Biol. Ecol.* 75: 217–232
- Edmunds, P. J. (1986). Energy budgets for the Caribbean reef coral *Porites porites* (Pallas). Ph.D. thesis, University of Glasgow
- Edmunds, P. J., Davies, P. S. (1986). An energy budget for *Porites porites* (Scleractinia). *Mar. Biol.* 92: 339–347
- Franzisket, L. (1964). Die Stoffwechselintensität der Riffkorallen und ihre ökologische, phylogenetische und soziologische Bedeutung. *Z. vergl. Physiol.* 49: 91–113
- Gladfelter, E. H., Monahan, R. K., Gladfelter, W. B. (1978). Growth rates of five reef-building corals in the Northeastern Caribbean. *Bull. mar. Sci.* 28: 728–734
- Goreau, T. F. (1959). The physiology of skeleton formation in corals. I. A method for measuring the rate of calcium deposition by corals under different conditions. *Biol. Bull. mar. biol. Lab., Woods Hole* 166: 59–75
- Huston, M. (1985). Variation in coral growth rates with depth at Discovery Bay, Jamaica. *Coral Reefs* 4: 19–26
- Jokiel, R. L., Maragos, J. E., Franzisket, L. (1978). Coral growth: buoyant weight technique. *Monogr. oceanogr. Methodol. (UNESCO)* 5: 529–542
- Kinzie, R. A., III, Sarmiento, T. (1986). Linear extension rate is independent of colony size in the coral *Pocillopora damicornis*. *Coral Reefs* 4: 177–182
- Lamberts, A. E. (1978). Coral growth: alizarin method. *Monogr. oceanogr. Methodol. (UNESCO)* 5: 523–528
- Lewis, J. B. (1973). The formation of mucus envelopes by hermatypic corals of the genus *Porites*. *Caribb. J. Sci.* 13: 207–209
- Pearse, V. B., Muscatine, L. (1971). Role of symbiotic algae (zooxanthellae) in coral calcification. *Biol. Bull. mar. biol. Lab., Woods Hole* 141: 350–363
- Smith, S. V., Kinsey, D. W. (1978). Calcification and organic carbon metabolism as indicated by carbon dioxide. *Monogr. oceanogr. Methodol. (UNESCO)* 5: 469–484

Date of final manuscript acceptance: January 16, 1989.

Communicated by J. Mauchline, Oban