

THE ALLOMETRY OF FEEDING, ENERGETICS, AND BODY SIZE IN THREE SEA ANEMONE SPECIES

KENNETH P. SEBENS

Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138

ABSTRACT

Three sea anemone species (*Anthopleura elegantissima*, *A. xanthogrammica*, and *Metridium senile*) were used to examine allometric and energetic properties of body size in passive suspension feeders. Photographs of expanded anemones in the field showed that projected feeding surface area (tentacle crown) as a function of body size increased at, or less than, the rate expected for a geometric solid (0.45–0.73 power or weight). Energetic cost, measured as weight loss, was found to relate differently to body size for each of the three species (0.77–1.08 power of weight).

Number of prey captured was closely related to the feeding surface area in all three species (0.36–0.7 power of weight). The exponent for prey biomass capture as a function of body weight was greater than that for energetic cost in *A. xanthogrammica*, (1.65 power of weight), but not for the other two species (0.33–0.54 power of weight). Prey size increased with predator size only in *A. xanthogrammica* (up to 10-cm anemone diameter), accounting for the higher increase in biomass capture. Numbers of prey captured by *A. xanthogrammica* continued to follow a surface-area function. Once the largest size classes of prey can be captured, further energy intake is probably directly related to feeding surface.

INTRODUCTION

As animals grow, their various appendages, organs, and physiological processes change at different rates (Thompson, 1917; Kleiber, 1932; Gould, 1966; Alexander, 1971; Schmidt-Nielsen, 1974). Few organisms grow as geometric solids, where all dimensions increase such that outward form remains the same (isometric growth). For example, feeding structures and absorptive surfaces can become convoluted or amplified, thus increasing their surface to volume ratio (Thompson, 1917; Gould, 1966). Energy balance, as intake minus cost, is determined in part by these geometric relationships.

Metabolic cost (as oxygen consumption) usually increases as a 0.60–1.0 power of weight, averaging 0.8 for marine invertebrates (Kleiber, 1932; Zeuthen, 1948a, 1953; Reichle, 1967; Vahl, 1972, 1973; McMahon, 1973; Jones, 1976; Bayne *et al.*, 1976; Newell *et al.* 1977). If energy intake increases as a lesser power of weight (e.g., a surface area function) than does cost, the difference between the two (scope for growth, Warren and Davis, 1967; Vahl 1972, 1973; Kitchell *et al.*, 1977, 1978) rises to some maximum and then decreases (Sebens, 1977a, 1979, in press). Cessation of growth at this maximum point subsequently generates the greatest possible energy for reproduction. If energy intake increases as a greater power of weight than does energetic cost, there is no such obvious optimum individual size. However, allocation of all or most energy to reproduction may still cause individual size to asymptote.

Received 3 April 1981; accepted 1 June 1981.

The relationship between energy intake, metabolic cost, and body size has been investigated in several actively filtering mollusks (Winter, 1969, 1973, 1978; McLusky, 1973; Vahl, 1972, 1973; Jørgenson, 1975; Bayne *et al.*, 1976; Newell *et al.*, 1977; Griffiths and King, 1979; Widdows, 1978; Thompson and Bayne, 1979) and ascidians (Randløv and Riisgard, 1979). Such relationships have not been investigated for any passive suspension feeder (*e.g.* corals, sea anemones, certain polychaetes, echinoderms, or gooseneck barnacles).

The present study quantifies feeding surface, prey intake, and energetic cost for three sea anemone species with different morphologies and habitat distributions: *Anthopleura elegantissima* (Brandt), *Anthopleura xanthogrammica* (Brandt), and *Metridium senile* (L.). The results are used to examine the control of body size as it relates to the species' habitat conditions. Some of the data on weight loss and prey capture in *A. xanthogrammica* have also been used to illustrate a more extensive general model of optimal body size for invertebrates with indeterminate growth (Sebens, in press) and are included here for comparison with the other two species.

MATERIALS AND METHODS

The anemone species

Anthopleura elegantissima is the most common intertidal sea anemone along the west coast of North America. It divides (longitudinal fission) to form clonal aggregations, sometimes with thousands of individuals (<1–6 cm diameter) (Hand, 1955a; Ford, 1964; Francis, 1973a, b, 1976, 1979; Sebens, 1977a, 1980; Jennison, 1979). Its prey include zooplankton, invertebrate larvae, and intertidal invertebrates (Sebens, 1977a). *Anthopleura xanthogrammica* is much larger (to at least 25 cm diameter intertidally), extends several meters into the subtidal in areas with extensive mussel beds, and never reproduces by fission (Hand, 1955a; Dayton, 1973; Sebens, 1977a, in press). It preys on mussels, sea urchins, barnacles, and other intertidal invertebrates (Dayton, 1973; Sebens, in press). Both *Anthopleura* species also harbor symbiotic algae (zooxanthellae and/or zoochlorellae) (Hand, 1955a).

Metridium senile is a primarily subtidal species forming large aggregations of individuals (to at least 18 cm basal diameter, 70 cm height) and sometimes reproducing by pedal laceration, especially in the low intertidal (Hand, 1955b; Hoffman, 1977; Purcell, 1977a; Shick and Hoffman, 1980). *M. senile*'s large crown of numerous small tentacles is held away from the substratum in areas of appreciable current, so that water flows along the upper column, through the aboral side of the fluted oral disc, and across the tentacles (Koehl, 1976, 1977; Robbins and Shick, 1980) (Fig. 1). These anemones prey on zooplankton and invertebrate larvae (Purcell, 1977b; Sebens, 1977a).

Feeding surface area

Projected surface of the tentacle crown and total surface area of all tentacles were measured on a full size range of all three species. Anemones were photographed laterally and vertically in the field, while tentacles were fully expanded (*A. xanthogrammica*, *A. elegantissima* at Tatoosh Island, Washington, and *M. senile* at Harper, Washington). The projected surface of the tentacle crown described by the expanded tentacle tips was calculated as πr^2 .

To calculate total surface area of all tentacles, tentacles of *A. xanthogrammica* and *A. elegantissima* were counted, and five were selected at random and measured

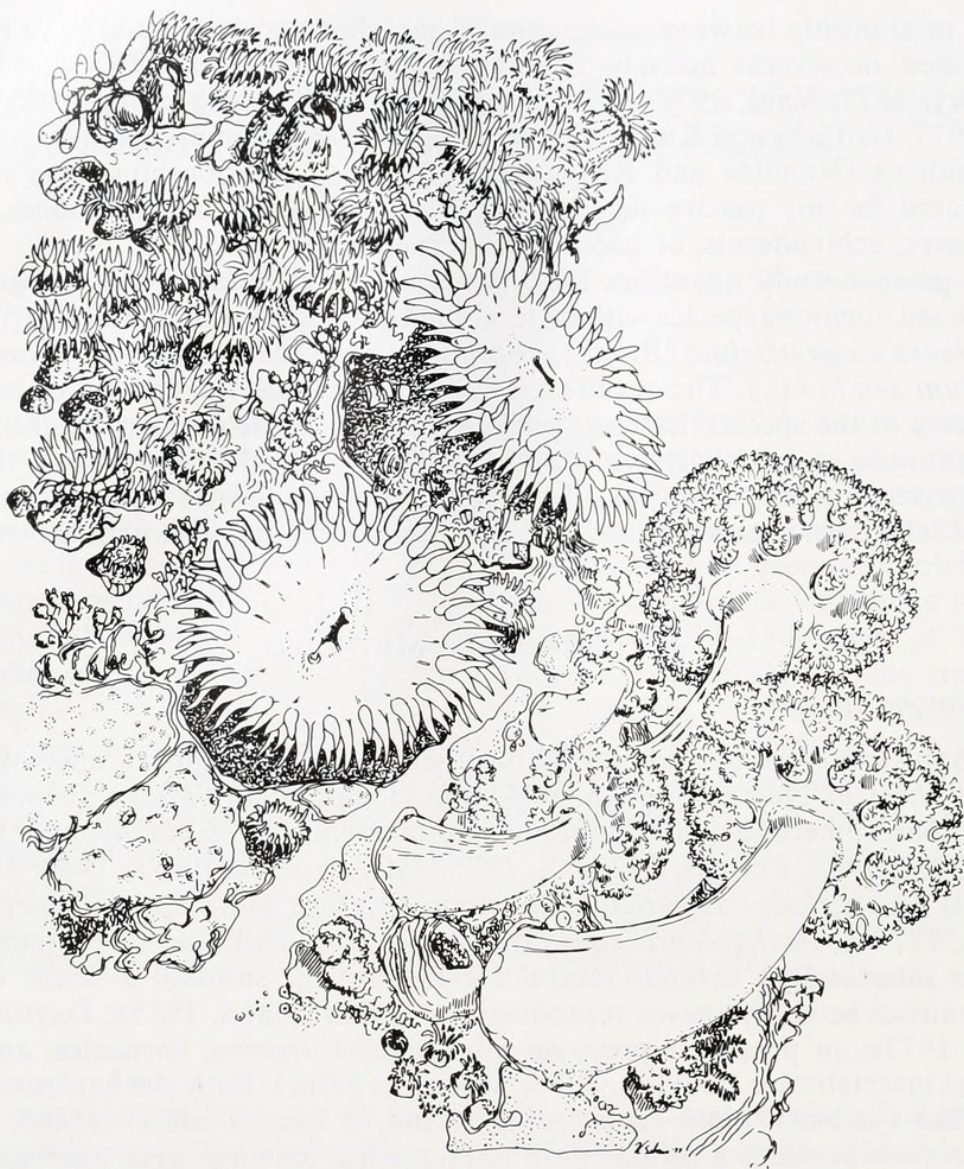


FIGURE 1. Clonal aggregations of *Anthopleura elegantissima* (left) above *A. xanthogrammica* (middle) on a rock surface and *Metridium senile* (right) on a subtidal rock wall (positioned next to the others for comparison).

(tentacle length and width at mid-length). The surface of each tentacle was calculated as that of a cylinder, since much of the taper occurs near the tip in *M. senile* and *A. elegantissima*. A cone could have been used, but the difference between the two methods was less than 5%. Total tentacle surface was calculated as the number of tentacles multiplied by the mean surface area of the five single tentacles.

The tentacles of *M. senile* were too small and numerous to count from photographs. Individuals were measured in the field (basal diameter), collected, relaxed in 7.5% MgCl_2 (1:1 in sea water), and frozen. Depending on its size, the tentacle crown was subdivided into 4, 8, 16, or 64 parts, and three samples were chosen for tentacle counts. Tentacle number was calculated as the mean (\pm standard deviation) of the three samples (multiplied by the number of tentacle crown subdivisions) and tentacle surface as the number of tentacles multiplied by the surface area of a single tentacle. Correlations and principal axes were determined on double log-

arithmetic transforms of the data to estimate the relationship as a power function of individual weight (Sokal and Rohlf, 1969).

Ash-free dry weight was calculated for 38 specimens of *A. elegantissima*, 16 of *A. xanthogrammica*, and 36 of *M. senile*, collected March 1976 on Tatoosh Island (*A. xanthogrammica* and *A. elegantissima*) and May 1976 at Harper (*M. senile*), of a full size range for that site and date. Attached-pedal-disc diameter was measured. The anemones were strung in order on monofilament line, and were brought alive to Seattle, where they were frozen at -20°C . They were later cleaned of adhering material, dried to a constant weight (less than 0.2% weight change per day) at 78°C ($T = 28$ days) to give total dry weight. They then were combusted at 500°C for 10 h to give ashed weight and ash-free dry weight. Principal axes were determined from double logarithmic transforms of pedal disc diameter versus ash-free dry weight.

Energetic cost

Anemone oxygen consumption depends on size, activity, state of expansion or contraction, illumination, temperature, and oxygen tension (Brafield and Chapman, 1965; Beattie, 1971; Sassaman and Mangum, 1973, 1974; Shick and Brown, 1977; Shick *et al.*, 1979; Robbins and Shick, 1980). Estimating metabolic cost as a function of body size using oxygen consumption requires numerous trials with anemones of known activity and history. Metabolic cost can also be estimated as weight loss per unit of original weight during starvation (Zeuthen, 1948b), thus averaging cost over a long time period, several activity levels, and periods of expansion or contraction. This method assumes that catabolic costs are approximately equal to, or less than, anabolic costs. Anemones spend much of their time without prey in the coelenteron (this study) and catabolic costs are likely to be applicable most of the time.

For the present study, 13 specimens of each species were marked with a pattern of small dye spots around their bases (Sebens, 1976) so that they could be identified in large aquaria. Three days later, they were weighed in sea water on a torsion balance (reduced weight method, W_r) (Holter and Zeuthen 1948, Zeuthen 1948b, Muscatine 1961), and placed in aquaria at 10°C (approximately 8 h light, $50\text{--}70$ microeinsteins $\cdot \text{m}^{-2} \cdot \text{sec}^{-1}$) with aerated seawater filtered to remove particles greater than $20\text{ }\mu\text{m}$. They were weighed again at 28 and 56 days (with sea water from the same batch used in the first weighing). Excess water was always removed from anemones before weighing by squeezing them gently to cause full contraction. Air bubbles were not allowed to enter the coelenteron or adhere to the surface of the anemones during weighing. Weight loss per individual per 28 days ($N = 26$ estimates) was compared to initial weight. Double logarithmic transforms of the data were used to plot regression lines and to estimate cost (tissue metabolized) as a power function of weight.

Prey capture

Capture rates and the relationship of such rates to individual size depend upon prey size, current or wave velocity, and a host of other factors that make laboratory measurements of limited usefulness. Therefore, prey capture success as a function of individual size was investigated in the field by sampling and by experimental prey release.

One thousand small mussels (3.0 ± 0.5 cm length) collected on Tatoosh Island

(March 1976) were marked with short file grooves across the valve closure, frozen, then distributed haphazardly back into the mussel bed at low tide a few meters above populations of *A. xanthogrammica*. Wave action during the next high tide washed these unattached mussels out of the bed, and many were captured by anemones. At the next low tide, anemones were sampled by probing their coelenterons, removing any contents, and checking mussels for file marks. One hundred anemones (3 cm or greater basal diameter) were examined at each of the two sites, and prey capture per individual anemone in each size class (every 2 cm diameter) was calculated.

Naturally captured prey of *A. xanthogrammica* were sampled by coelenteron probing over the period September 1974 to October 1977 at three population monitoring areas on Tatoosh Island (Sebens, 1977a). All items (>1 mm length) (usually wrapped in a mucous bolus surrounded by mesenterial filaments) were removed, measured, and identified. Several individuals were also examined for the presence of microscopic zooplankters (coelenteron sampled with a large syringe). Few were encountered and their total mass was insignificant compared to that of the macro-invertebrates. The results were plotted as dry weight of mussel tissue (from Fox and Coe, 1943) versus anemone weight for each anemone size class (mussels constituted more than 78% of the diet by weight).

Since *A. elegantissima* normally captures much smaller prey (zooplankton and small intertidal invertebrates), it was fed frozen adult brine shrimp (0.5 cm body length) which were of the appropriate size and were easily identified in coelenteron contents, as they were different from naturally occurring prey. Five pounds of frozen shrimp (purchased at a local aquarium supply store) were thawed in 5-gal buckets of sea water and dumped into the mouth of a surge channel at Shi Shi Beach, Washington (May 1976) in three pulses 5 min apart. Wave action dispersed the shrimp throughout the channel. After 30 min, anemones of a full size range were collected about 5 m landward from the mouth of the channel. The animals were placed in separate vials and fixed with 7% buffered formalin in sea water. Later, they were transferred to petri dishes, slit lengthwise to open the coelenteron, and all mesenterial filaments, coelenteron contents (food bolus), and many of the mesenteries were scraped into the dish. The contents of the petri dish and of the original vial (in case anemones egested prey) were systematically searched under a dissecting microscope. All brine shrimp, shrimp pieces, and naturally occurring prey were counted and measured with an ocular micrometer.

Scraping removed all coelenteron contents, and floating the fixed contents in a petri dish with about 2 mm water depth made prey items easy to identify and measure. This method is probably more accurately quantitative than the suction and filtration method for removing prey from corals (Porter, 1974) or zoanthids (Sebens, 1977b), because all prey and tissue to which prey might adhere were removed.

Prey items included planktonic larvae (barnacle cyprids), copepods, and various intertidal crustaceans, small bivalves, and barnacles. For comparative purposes, prey wet weight per individual anemone was calculated. Prey density was assumed to be close to that of sea water (0.00102 g/mm³, Pickard, 1975) and prey volume was approximated as a cyprid-shaped geometrical solid (two cones with bases attached):

$$\text{Volume (mm}^3\text{)} = \pi L^3/192$$

$$\text{Wet weight (g)} = \text{volume (mm}^3\text{)} \cdot 0.00102 \text{ (g/mm}^3\text{)}$$

where L is prey item length in mm, and $\pi L^3/192$ is the volume of two cones with base diameter half their height. This comparative method of weight estimation considers both size and number of prey items in case prey size changes with predator size.

Metridium senile preys primarily on zooplankton. At Harper 10 lbs of frozen adult brine shrimp were thawed in two 5-gal buckets with lids. Divers using SCUBA gear took the buckets 2–3 m deep and released the shrimp in two pulses approximately 10 min apart 5 m up-current from an area (2–3 m depth) covered with *M. senile* specimens to 40 cm tall. After 20 min, 107 anemones were collected by two divers, basal diameters were measured, and the anemones were placed in individually marked vials or plastic bags. On shore, anemones were fixed in 7% buffered formalin in sea water (also injected into the coelenteron). Coelenteron contents were sampled and quantified as described for *A. elegantissima*.

Large solitary *A. elegantissima* anemones from Southern California (Arroyo Hondo) were examined for prey during May 1975. These anemones reach basal diameters to 16 cm and do not form clonal aggregations (Hand, 1955a; Sebens, 1977a; Francis, 1979).

Statistics

All statistical tests, regression analysis (with coefficient of determination; R^2), Pearson's product-moment correlation (with correlation coefficient, R) and principal axis determinations were calculated as described by Sokal and Rohlf (1969). All power functions were determined from double logarithmic plots of the data and 95% confidence intervals for the slope of the regression or principal axis were calculated. These are also the confidence limits for the exponent in the power function and they are given with each graph of the data.

RESULTS

Feeding surface area

Ash free dry weight to basal diameter correlations (principal axis) were as follows:

$$A. \textit{elegantissima} \quad W_d = 0.0188 D^{3.27} \quad R = 0.96 \quad N = 38$$

$$A. \textit{xanthogrammica} \quad W_d = 0.0346 D^{2.67} \quad R = 0.94 \quad N = 16$$

$$M. \textit{senile} \quad W_d = 0.0073 D^{2.78} \quad R = 0.88 \quad N = 36$$

where W_d is ash-free dry weight (g), D is diameter (cm), N is number of individuals, and R is the correlation coefficient.

As they became larger, *Anthopleura xanthogrammica* and *A. elegantissima* produced new tentacles (to 6 cycles) in a hexamorous arrangement. The maximum number was reached rather quickly (*A. xanthogrammica*, 218 ± 42 (SD), $N = 17$; *A. elegantissima*, 119 ± 17 (SD), $N = 18$, Fig. 2). Above that size, tentacle length and width increased so that tentacle surface continued to increase without an increase in tentacle number. For *A. xanthogrammica*, tentacle surface area increased as the 0.87 power of individual weight ($N = 19$, $R = 0.95$) and for *A. elegantissima* as the 0.54 power ($N = 17$, $R = 0.89$) (Fig. 3). The difference appeared to depend on tentacle growth in length and width, which is proportionally greater in *A. xanthogrammica*. For *M. Senile*, however, tentacle number (N_t) increased as the 0.84 power of weight ($N = 19$, $R = 0.99$) (Fig. 2) as did tentacle

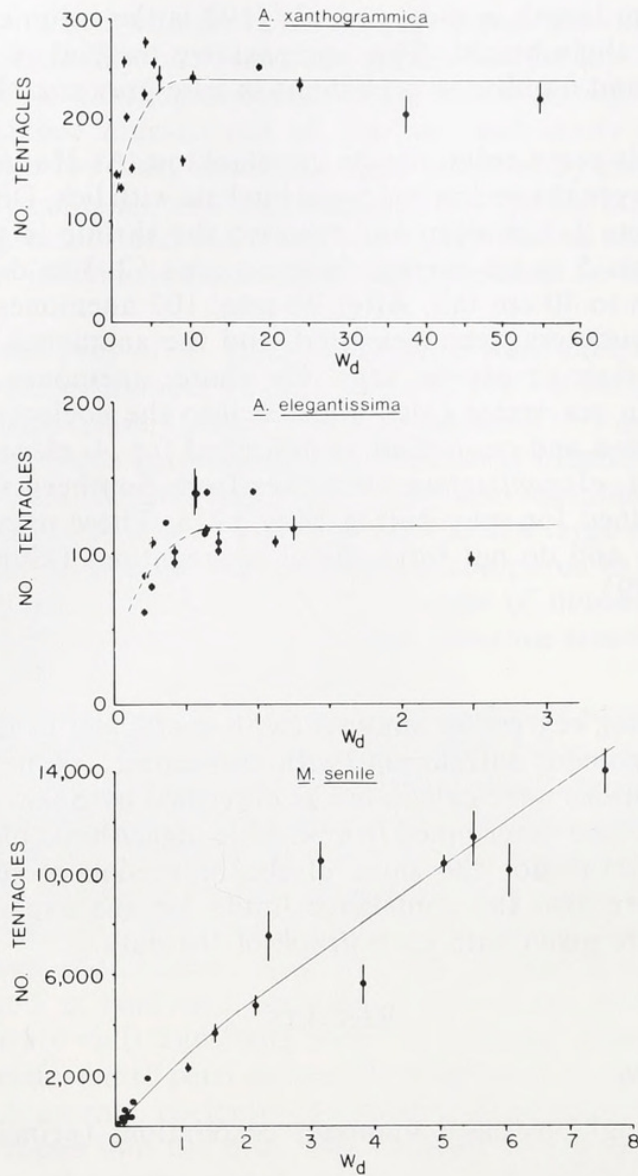


FIGURE 2. Number of tentacles as a function of individual ash-free dry weight (grams). Bars = \pm one standard deviation (SD) for three measurements.

A. *A. xanthogrammica* ($N_t = 218$ tentacles ± 42 (SD), $N = 15$)

B. *A. elegantissima* ($N_t = 119$ tentacles ± 17 (SD), $N = 19$)

C. *M. senile* ($N_t = 2673 W_d^{0.84}$, $R = 0.99$, $N = 19$, $P < 0.001$). The 95% confidence limits for the exponent of W_d are 0.77 and 0.91.

surface (Fig. 3). Tentacle size was similar for *M. senile* of a range of sizes (6.0 ± 1.0 mm tentacle length, 0.8 ± 0.1 mm width).

Projected oral surface of *A. xanthogrammica* increased as the 0.74 power of weight ($N = 17$, $R = 0.98$), of *A. elegantissima* as the 0.43 power of weight ($N = 17$, $R = 0.93$) and of *M. senile* as the 0.72 power of weight ($N = 42$, $R = 0.93$). Although two of the values are close to a geometric surface area (0.67) relationship, that for *A. elegantissima* falls well below it (Fig. 3). Slower increase of *A. elegantissima*'s tentacle length probably accounts for this difference.

Energetic cost

Weight loss as a function of initial weight increased as a higher power of weight than did projected oral surface area in each species. Cost increased as the 1.08

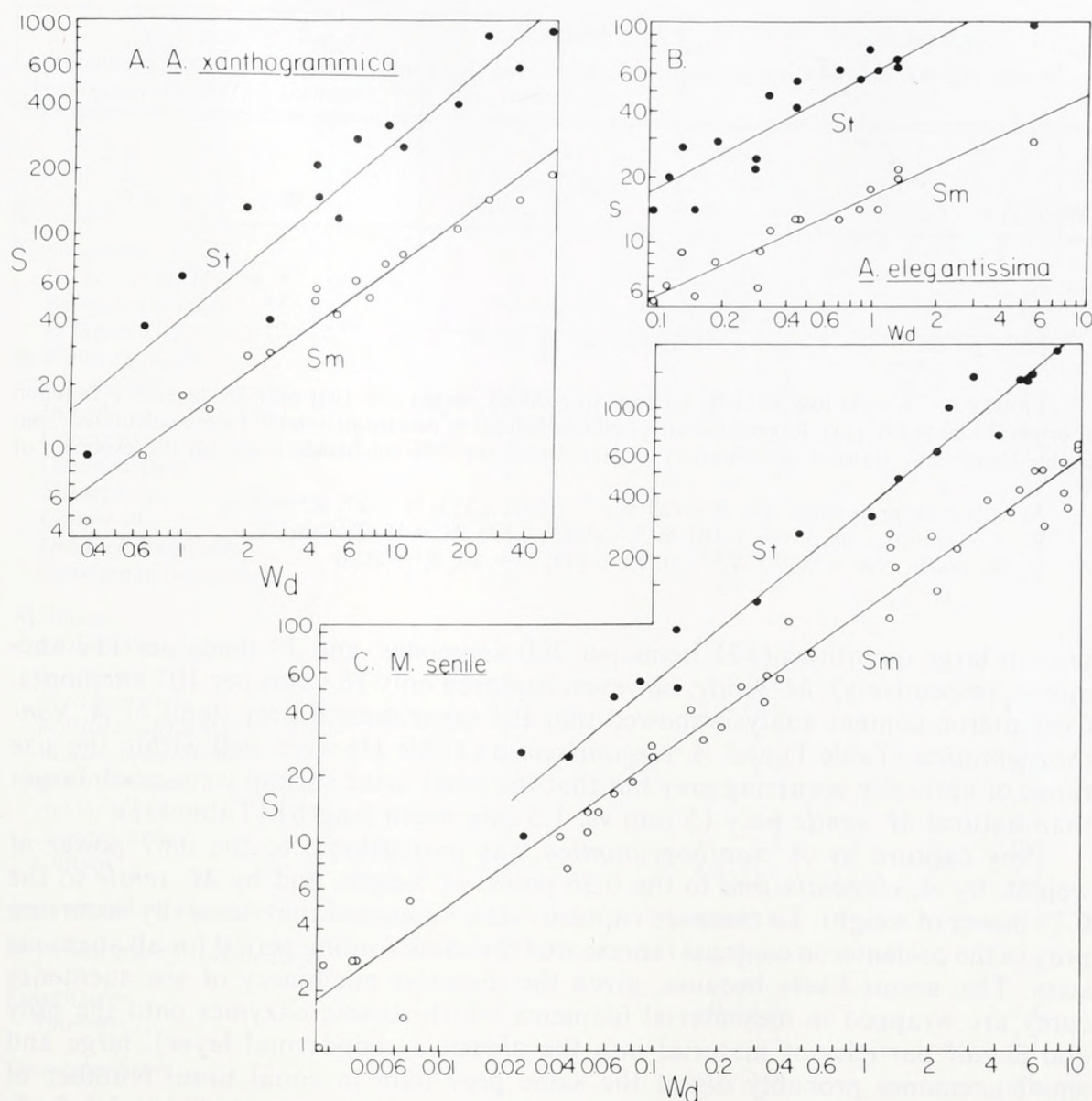


FIGURE 3. Projected oral surface of tentacle crown (S_m) and surface area of tentacles (S_t). Principal axis lines and correlation coefficients (R , all significant at $P < 0.001$) determined from double logarithmic transforms. Numbers in parentheses are 95% confidence limits for the exponent of W_d .

A. *A. xanthogrammica*, $S_m = 13.9 W_d^{0.74}$, (0.67, 0.81), $N = 17$, $R = 0.98$

$S_t = 41 W_d^{0.87}$, (0.73, 1.03), $N = 15$, $R = 0.95$.

B. *A. elegantissima*, $S_m = 15.6 W_d^{0.43}$, (0.35, 0.51), $N = 17$, $R = 0.93$

$S_t = 58 W_d^{0.54}$, (0.42, 0.68), $N = 17$, $R = 0.89$.

C. *M. senile*, $S_m = 119 W_d^{0.72}$, (0.68, 0.76), $N = 42$, $R = 0.98$

$S_t = 353 W_d^{0.84}$, (0.77, 0.91), $N = 19$, $R = 0.99$.

power of weight for *A. xanthogrammica* ($N = 21$, $R^2 = 0.96$), as the 0.77 power of weight for *A. elegantissima* ($N = 19$, $R^2 = 0.92$), and as the 0.80 power of weight for *M. senile* ($N = 24$, $R^2 = 0.90$) (Fig. 4). These results agree well with values reported for other invertebrates and for fish (Kleiber, 1932; Zeuthen, 1948a, 1953; Jones, 1976). The exponent was also very close to that reported for oxygen consumption in *A. elegantissima* (Shick *et al.*, 1979).

Prey capture

A. xanthogrammica and *A. elegantissima* captured experimentally released

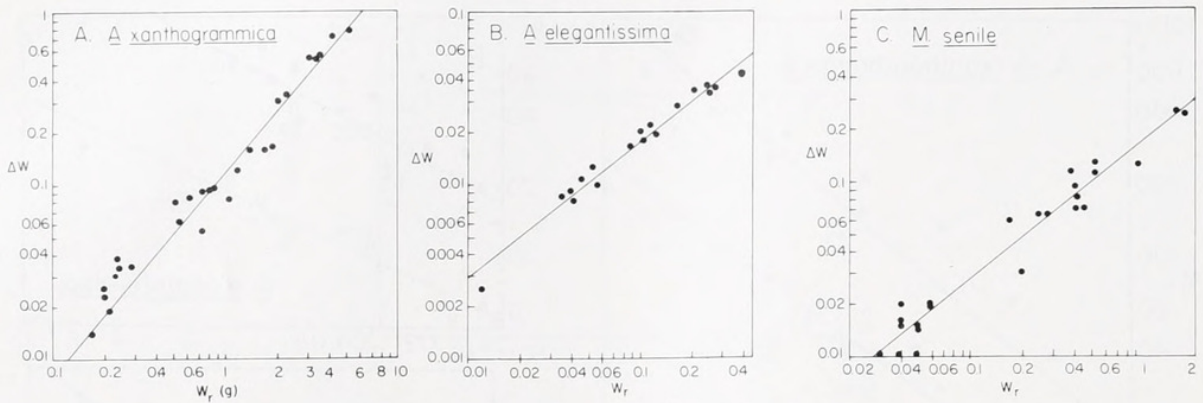


FIGURE 4. Weight loss at 10°C (change in reduced weight ΔW (g)) over 28 days, as a function of original weight (W_r (g)). Regression lines and coefficients of determination (R^2) were calculated from double logarithmic transforms. Numbers in parentheses are 95% confidence limits for the exponent of W_r .

- A. *A. xanthogrammica*, $\Delta W = 0.123 W_r^{1.08}$, (0.99, 1.17), $N = 27$, $R^2 = 0.96$
 B. *A. elegantissima*, $\Delta W = 0.105 W_r^{0.77}$, (0.69, 0.84), $N = 19$, $R^2 = 0.92$
 C. *M. senile*, $\Delta W = 0.170 W_r^{0.80}$, (0.72, 0.87), $N = 24$, $R^2 = 0.90$

prey in large quantities (171 items per 200 anemones, and 29 items per 112 anemones, respectively). *M. senile*, however, captured only 16 items per 107 anemones. Coelenteron-content analysis showed that the experimental prey items of *A. xanthogrammica* (Table I) and *A. elegantissima* (Table II) were well within the size range of naturally occurring prey but that the adult brine shrimp were much larger than natural *M. senile* prey (5 mm vs. 1.5 mm mean length) (Table III).

Prey capture by *A. xanthogrammica* was proportional to the 0.67 power of weight, by *A. elegantissima* to the 0.36 power of weight, and by *M. senile* to the 0.71 power of weight. To compare capture rates, I assumed that naturally occurring prey in the coelenteron contents represented the same feeding period for all anemone sizes. This seems likely because, given the digestive machinery of sea anemones (prey are wrapped in mesenterial filaments which secrete enzymes onto the prey and engulf particles of material into the digestive endodermal layer), large and small anemones probably digest the same prey item in equal time. Number of naturally occurring prey captured by *A. xanthogrammica* (prey · individual⁻¹ · feeding period⁻¹) was proportional to the 0.73 power of weight (Fig. 5). For *A. elegantissima* it was proportional to the 0.18 power and for *M. senile* it was proportional to the 0.59 power. However, natural prey capture in this species increased with size over the first six size classes (as the 1.19 power of weight; $R^2 = 0.94$) and decreased significantly over the last five size classes (as the -1.65 power of weight, $R^2 = 0.96$). Large and small individuals were intermingled but probably not so crowded as to interfere with each other's prey capture. Collections were made during moderate current velocity (<10 cm/sec), and large individuals may do better in higher velocities. The large number of prey in coelenterons (538 prey in 107 anemones) indicated that this was a real phenomenon on that particular day. In addition, Bucklin and Hedgecock (in press) have shown that there is a third *Metridium* species on the Washington Coast. It may be that the smallest individuals in this study are of the clonal species (*M. senile*) while the majority belong to the large, typically subtidal, nonclonal species (as yet undescribed).

Natural prey in coelenteron contents, transformed to relative prey weight per individual (grams/individual) indicates the effect of changing prey size on intake rate. Natural prey weight was proportional to anemone weight to the 1.65 power

TABLE I

Anthopleura elegantissima prey items (>50 μm length) from coelenteron samples, Shi Shi Beach, Washington, 1976 (112 anemones, 113 prey items).

Prey items	No. items	Prey length (mm)	% of items
Crustaceans:			
Barnacle cyprids	2	0.6–0.8	1.8
<i>Balanus glandula</i>	4	2.0–4.0	3.5
<i>B. cariosus</i>	1	6.0	0.9
Barnacle molts	4	2.0–2.5	3.5
Amphipods	4	0.6–4.0	3.5
Isopods	7	1.0–3.0	6.3
Copepods	3	2.5–4.0	2.7
Decapod zoea	1	2.0	0.9
<i>Pugettia</i> sp.	2	4.0	1.8
<i>Cancer</i> sp.	1	5.0	0.9
Decapod fragments	6	2.0–9.0	5.3
Crustacean fragments	8	0.8–1.8	7.1
Molluscs:			
<i>Littorina scutulata</i>	3	4.0–6.0	2.6
<i>L. sitkana</i>	6	1.0–6.0	5.2
<i>Mytilus edulis</i>	13	2.0–11.0	11.6
<i>Mytilus californianus</i>	1	1.5	0.9
<i>Adula californiensis</i>	1	2.0	0.9
Other bivalves	3	1.8–3.0	2.4
<i>Acmaea scutum</i>	1	5.0	0.9
<i>Acmaea pelta</i>	1	2.5	0.9
Chitons	6	4.0–11.0	5.3
Hydroid colony fragments:	8	2.0–12.0	7.1
Bryozoan colony fragments:	9	2.0–10.0	7.9
Polychaetes:	5	3.0–14.0	4.4
<i>Spirorbis</i> sp.	3	2.5	2.7
Platyhelminthes:	1	3.0	0.9
Echinoid spine:			
<i>Strongylocentrotus purpuratus</i>	2	5.0–6.0	1.8
Foraminifera:	2	0.5–1.5	1.8
Eggs:	3	1.0	2.7
Insect fragments:	1	6.0	0.9
Mite:	1	2.0	0.9
Plant Material:	60	1.0–16.0	not included
(algae, <i>Zostera</i> , terrestrial plant fragments, probably undigested)			

for *A. xanthogrammica*, to the 0.33 power for *A. elegantissima*, and to the 0.54 power for *M. senile* (Fig. 6). Prey capture by *M. senile* by weight increased over the first seven size classes, then decreased. It was proportional to the 1.16 power for the first seven size classes and to the -2.56 power for the last four size classes.

TABLE II

Anthopleura xanthogrammica prey items (>1 mm length) from coelenteron samples, Tatoosh Island, Washington, 1974–1975 (481 anemones, 177 prey).

Prey items	No. items	Prey length (cm)	% of items
Mussels:			
(<i>Mytilus californianus</i>) with some <i>M. edulis</i>)	122	0.8–10.0	68.9
Barnacles:			
(<i>Balanus cariosus</i> , <i>B. glandula</i>)	24	0.8–3.0	13.6
Barnacle molts:	18	0.8–1.4	10.1
Decapods:			
<i>Petrolisthes</i> sp.	4	1.0–3.0	2.3
Gastropods:			
<i>Acmaea</i> spp.	2	1.4–2.0	1.1
<i>Amphissa columbiana</i>	1	1.0	0.6
<i>Ceratostoma foliatum</i>	2	4.4–5.5	1.1
<i>Tegula funebris</i>	1	2.5	0.6
Colonial ascidians	2	4.0–6.0	1.1
Echinoids:			
<i>Strongylocentrotus purpuratus</i>	1	3.0	0.6

Prey sizes remained essentially the same for all sizes of *M. senile* (1.5 ± 0.3 mm SD, N = 538) and *A. elegantissima* (4.4 ± 3.2 mm SD, N = 17) but increased for *A. xanthogrammica* ($R = 0.44$, $P < 0.01$, N = 122). Comparing only the largest

TABLE III

Metridium senile prey items (>50 μ m length) from coelenteron samples, Harper, Washington, 1976 (107 anemones, 538 prey).

Prey items	No. items	Prey length (mm)	% of items
Crustaceans:			
Barnacle cyprids (<i>Balanus cariosus</i> , <i>B. glandula</i> , <i>Cthamalus dalli</i>)	380	1.0–1.8	75.2
Barnacle nauplii:	6	0.6–1.2	0.9
Copepods	71	0.6–1.2	11.1
Decapod zoea larvae	25	1.6–2.6	3.9
Eggs:	28	0.2–1.2	4.4
Bryozoan colony fragments:	8	2.0–3.0	1.3
Gastropod veligers:	6	1.4–1.8	0.9
Bivalve veligers:	8	1.0–1.4	1.3
Polychaetes:	3	3.0–6.0	0.5
Asteroid bipinnaria:	3	1.0–1.2	0.5

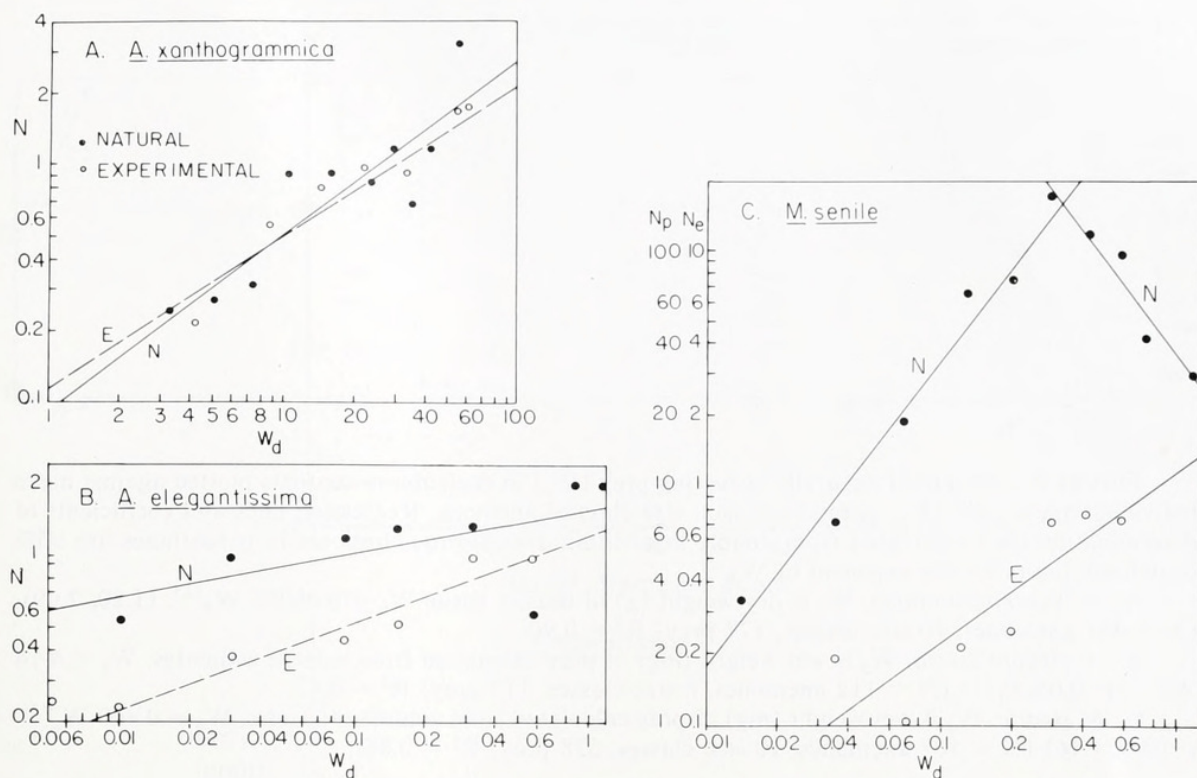


FIGURE 5. Numbers of experimental and natural prey captured in the field. Regression lines and coefficients of determination (R^2) calculated from double logarithmic transforms. Numbers in parentheses are 95% confidence limits for the exponent of W_d .

A. *Anthopleura xanthogrammica*, number of prey captured per individual (N_e experimental (E), N_p natural (N)) versus mean dry weight of each anemone size class (W_d grams).

$$N_e = 0.11 W_d^{0.67}, (0.47, 0.88), (N = 200 \text{ anemones, 7 size classes, 171 prey}), R^2 = 0.93$$

$$N_p = 0.0095 W_d^{0.73}, (0.40, 1.06), (N = 481 \text{ anemones, 10 size classes, 177 prey}), R^2 = 0.77$$

B. *Anthopleura elegantissima*, number of prey captured per individual versus mean dry weight of each size class.

$$N_e = 1.24 W_d^{0.36}, (-0.06, 0.42), (N = 112 \text{ anemones, 8 size classes, 29 prey}), R^2 = 0.95$$

$$N_p = 1.57 W_d^{0.18}, (0.24, 0.48), (N = 112 \text{ anemones, 8 size classes, 113 prey}), R^2 = 0.35$$

C. *Metridium senile*, number of prey captured per individual versus mean dry weight of each size class.

$$N_e = 1.17 W_d^{0.70}, (0.23, 1.19), (N = 107 \text{ anemones, 7 size classes, 16 prey}), R^2 = 0.74$$

$$N_p = 9.97 W_d^{0.59}, (0.07, 1.11), (N = 107 \text{ anemones, 10 size classes, 538 prey}), R^2 = 0.46$$

For the first six size classes, $N_p = 61.688 W_d^{1.19}, (0.79, 1.59), R^2 = 0.94$

For the last five size classes, $N_p = 0.0094 W_d^{-1.65}, (-2.23, -1.06), R^2 = 0.96$

five prey for each size class of *A. xanthogrammica* up to 10 cm diameter (prey length (cm) = $0.97 \text{ anemone diameter} - 2.3$, $R^2 = 0.85$, $N = 30$) shows that maximum prey size increases with *A. xanthogrammica* diameter up to about 10 cm basal diameter (Fig. 7). Through this range, the largest prey taken are approximately equal in length to basal diameter of the anemone.

Figure 8 shows prey size distributions for all three species and for large solitary *A. elegantissima* (≥ 6 cm diameter). The large solitary *A. elegantissima* preys on items (mostly mussels) larger than do the small clonal individuals. Mussels constitute the major part of *A. xanthogrammica*'s diet (Table I) and the size distribution of mussels captured is quite comparable to the size distribution of mussels

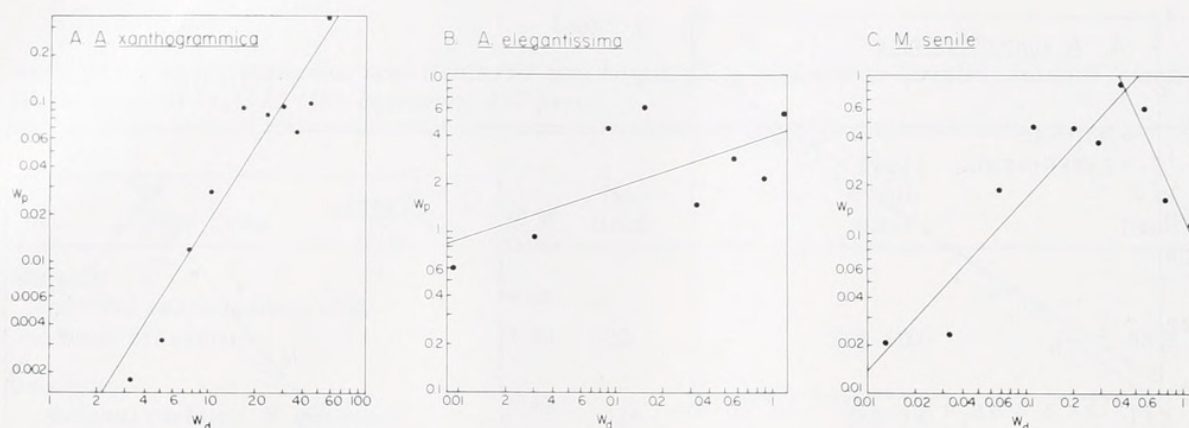


FIGURE 6. Weight of naturally occurring prey (W_p) in coelenteron contents plotted against mean individual dry weight (W_d , grams) for each size class of anemone. Regression lines and coefficients of determination (R^2) calculated from double logarithmic transforms. Numbers in parentheses are 95% confidence limits for the exponent of W_d .

A. *A. xanthogrammica*, W_p is dry weight (g) of mussel tissue $W_p = 0.00032 W_d^{1.65}$, (1.20, 2.09), ($N = 481$ anemones, 10 size classes, 177 prey) $R^2 = 0.90$

B. *A. elegantissima*, W_p is wet weight (mg) of prey calculated from volume estimates, $W_p = 4.14 W_d^{0.33}$, (-0.05, 0.71) ($N = 112$ anemones, 8 size classes, 113 prey) $R^2 = 0.42$

C. *M. senile*, W_p is wet weight (mg) of prey calculated from volume estimates, $W_p = 0.469 W_d^{0.54}$, (-0.09, 1.16) ($N = 107$ anemones, 10 size classes, 538 prey) $R^2 = 0.86$

For the first seven size classes, $W_p = 2.66 W_d^{1.16}$, (0.66, 1.66), $R^2 = 0.88$

For the last four size classes, $W_p = 0.109 W_d^{-2.56}$, (-4.30, -0.84), $R^2 = 0.95$

in beds adjacent to the anemones on Tatoosh Island (mussel sizes from T. Suchanek, unpublished data).

DISCUSSION

Sea anemones capture prey by three somewhat distinct methods. First, prey suspended in the water column, usually zooplankton, are intercepted by one or more tentacles and the tentacles transfer prey to the mouth (Sebens, 1976; Purcell, 1977a). Second, sessile prey dislodged by wave action or by foraging predators are washed into the tentacle crown (Dayton, 1973; Sebens and Paine, 1978). Third, motile prey blunder into the anemone's tentacles. Sea urchins (Dayton, 1973; Dayton *et al.*, 1974; Sebens, 1976), crabs (Sebens and Laakso, 1977), and fishes (Sebens and Laakso, 1977; Hamner and Dunn, 1980) are captured in this third manner. Turbid or turbulent water conditions may facilitate this type of capture. When large prey are captured, the entire oral disc closes around the prey, and the marginal sphincter muscle contracts trapping the prey while it is being engulfed by the mouth.

Metridium senile feeds only by the first method. Its fluted oral disc and extensible column allow it to position the tentacle crown near or far from the substratum, adjusting the current velocity experienced (Koehl, 1976, 1977). Robbins and Shick (1980) showed that *M. senile* capture more prey as current velocity increases but that there is an upper level of velocity where large individuals collapse and probably cannot feed.

Anthopleura elegantissima feeds by at least the first two methods, since both zooplankton and sessile invertebrate prey occur in coelenteron contents. Single tentacles capture zooplankton and transfer them to the mouth. Oral disc closure is used for larger prey.

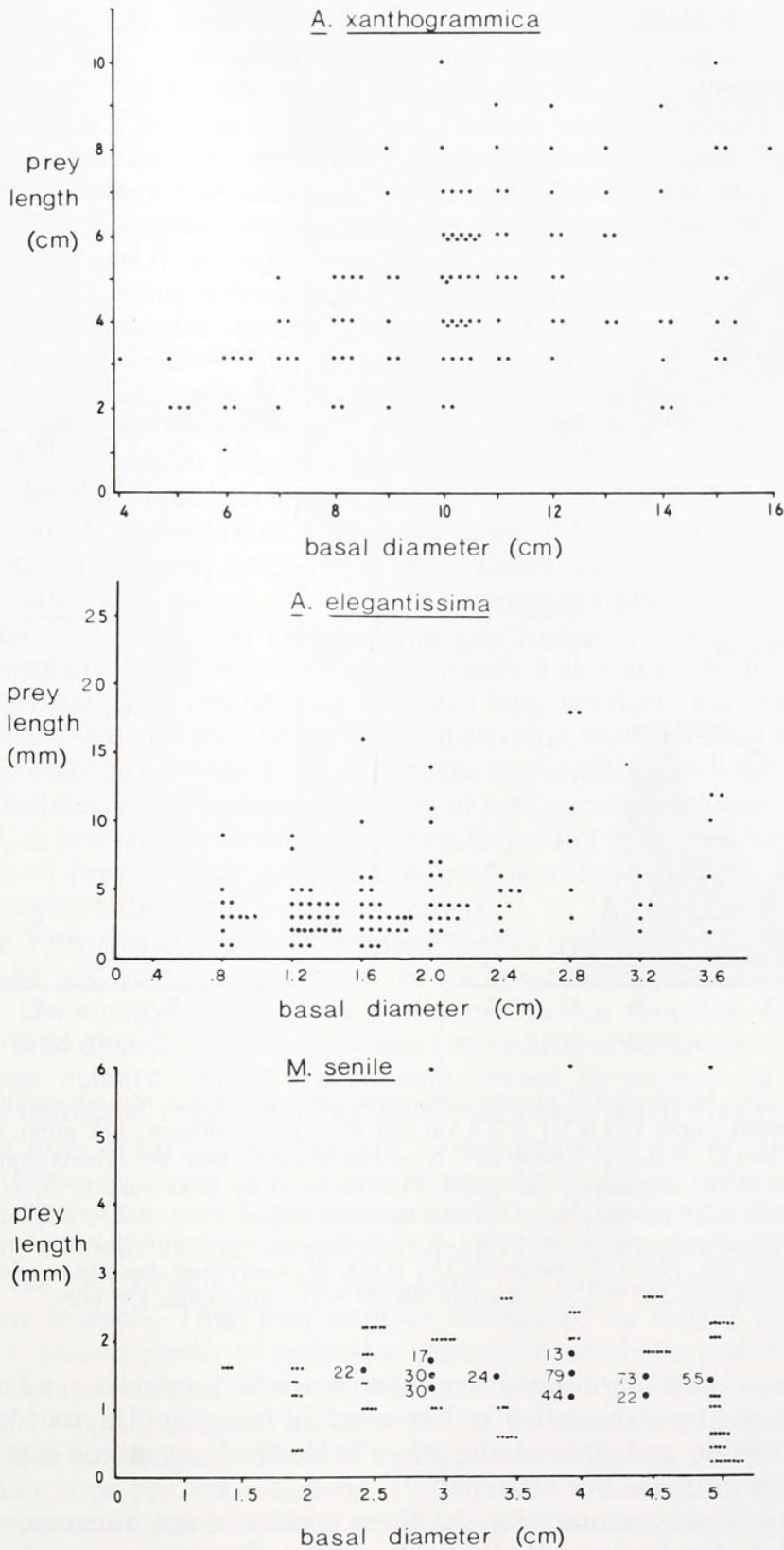


FIGURE 7. Lengths of naturally occurring prey items in anemone coelenteron contents; by basal diameter (D).

A. *A. xanthogrammica*, $R = 0.44$, $P < 0.01$, $N = 481$ anemones, 122 prey items).

B. *A. elegantissima*, $R = 0.09$, $P > 0.05$ ($N = 112$ anemones, 113 prey).

C. *M. senile*, $R = 0.08$, $P > 0.05$ ($N = 107$ anemones, 538 prey). Large numbered dots represent that number of overlapping points.

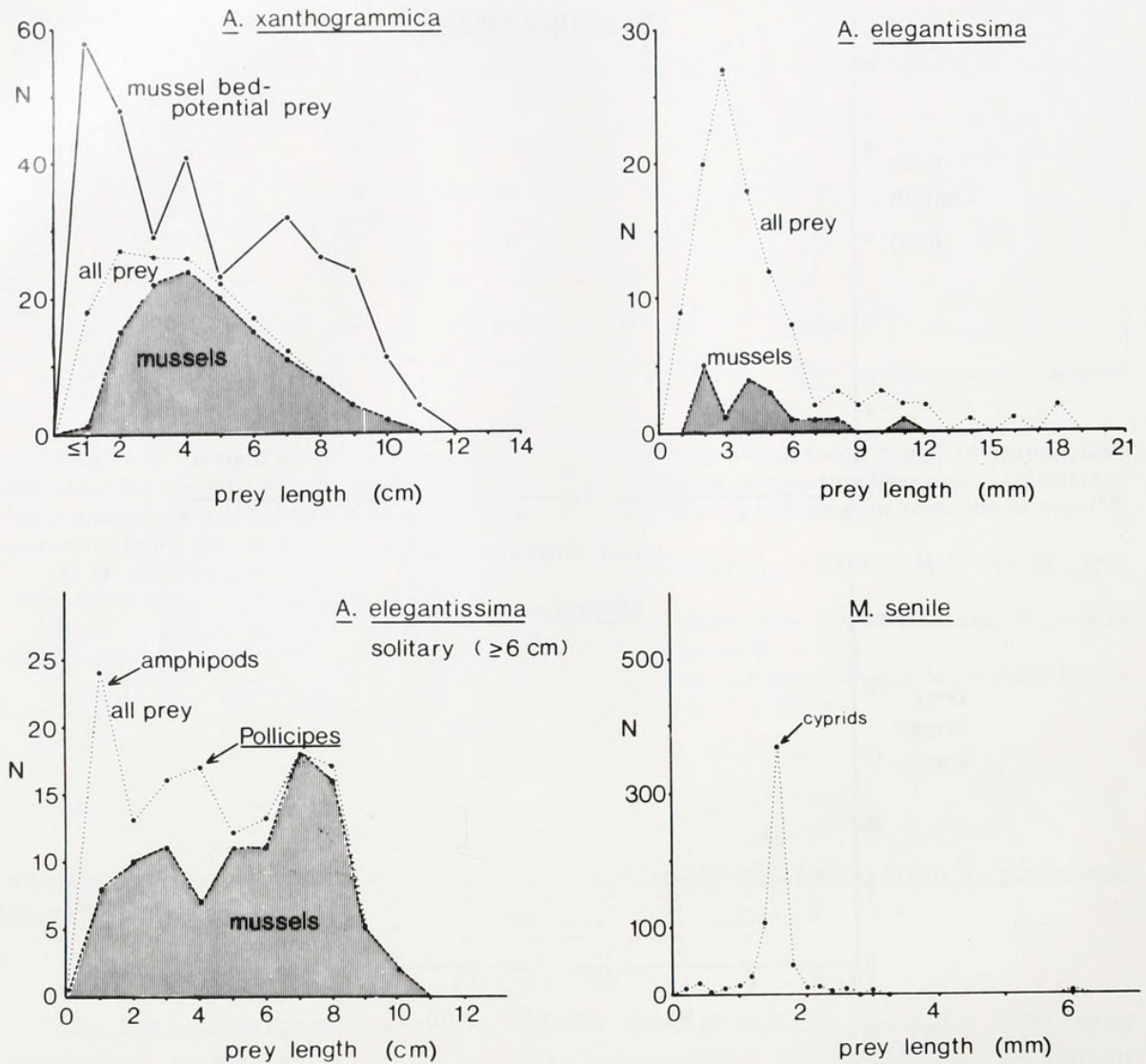


FIGURE 8. Size distribution of prey in coelenteron content samples. Mussels captured by *A. xanthogrammica* (mean length (\bar{L}) = 5.1 ± 2.2 cm SD, $N = 481$ anemones, 122 prey), mussels in the adjacent mussel bed ($\bar{L} = 4.6 \pm 2.9$ cm SD, $N = 316$ mussels), total prey items captured ($\bar{L} = 4.3 \pm 2.3$ cm SD, $N = 481$ anemones, 177 prey), prey captured by large solitary *A. elegantissima* in California ($\bar{L} = 4.6 \pm 2.6$ cm SD, $N = 330$ anemones, 136 prey, $\bar{L} = 5.4 \pm 2.5$ cm SD for mussel prey only, $N = 99$ prey), prey captured by clonal *A. elegantissima* (macroinvertebrates and zooplankters ($\bar{L} = 4.5 \pm 3.4$ mm SD, $N = 112$ anemones, 113 prey), *M. senile* prey (mostly zooplankters such as barnacle cyprids, copepods) $\bar{L} = 1.5 \pm 0.4$ mm SD, $N = 107$ anemones, 538 prey).

Anthopleura xanthogrammica captures mussels, barnacles, and other invertebrates dislodged by wave action and by asteroid foraging (Dayton, 1973) as well as crabs, gastropods, and other motile prey (Table I). Zooplankton capture by adult *A. xanthogrammica* was not observed.

Probability of prey contact for the three species of sea anemones depends on the projected surface area of the tentacle crown. The tentacles may act as filter elements to intercept zooplankton carried by currents (*M. senile*, *A. elegantissima*) (Rubenstein and Koehl, 1977) or as a target for intertidal prey dislodged by wave action and by predator activity (*A. xanthogrammica*, *A. elegantissima*) (Dayton, 1973; Sebens, 1977, in press). Anemone growth is close to isometric in *A. xan-*

thogrammica and in *M. senile*; their feeding surface areas increase as the 0.74 and 0.72 power of weight, respectively. In *A. elegantissima*, feeding surface increases more slowly, as the 0.43 power of weight. None of the three anemones amplifies its projected surface area as it grows. *M. senile*, however, adds tentacles with increasing size, such that tentacle number is a 0.84 power of weight. This allometric increase cannot change the volume of water passing the oral disc, but may be needed for efficient capture and retention of prey items. However, *M. senile* is unable to capture and hold large invertebrates such as mussels.

Capture of prey items increased as a lesser power of weight than did energetic cost for all three anemone species. This contrasts with some studies of actively pumping suspension feeders (McLusky, 1973; Bayne *et al.*, 1976; Newell *et al.*, 1977; Randløv and Riisgard, 1979; Griffiths and King, 1979) but agrees with others (Vahl, 1972, 1973; Bayne *et al.*, 1977). If feeding surfaces are not amplified allometrically during growth, passive suspension feeders have no way to compensate for their decreasing surface-to-volume ratio.

Benthic marine invertebrates often have habitat-dependent body size and indeterminate growth (Paine, 1965, 1969, 1976; Ebert, 1968; Kohn, 1971; Bertness, 1977; Sebens, 1977a, in press). Maximum size appears to depend on the energetic characteristics of a particular habitat (*e.g.* physiological stress and food availability). Transplanted individuals eventually reach a size near the mean for adults in that habitat and fluctuate around that size (*e.g.* seastars, Paine, 1976). Such patterns indicate that size may be set by the difference between local energy intake and cost. The body size at which this difference is maximized will decrease as prey availability declines, energetic cost increases, or both occur simultaneously (Sebens, 1977a, 1979, in press). It is difficult, however, to predict this optimum size directly without data on prey capture, assimilation, and metabolic cost for individuals of all sizes throughout the year (Sebens, in press).

Optimum body size of the three anemone species should be where the difference between intake and cost is at a maximum (Sebens, 1977a, 1979, in press). This difference is the energy available for gonad production summed over the entire season. It is thus directly related to fitness (reproductive success).

The energy balance can be further complicated by changes in prey size as predator size increases. Predators could potentially drop small prey from their diet or add larger prey as they grow. Neither *A. elegantissima* nor *M. senile* changed prey size as they got larger, but *A. xanthogrammica* did so quite dramatically. Large specimens of *A. xanthogrammica* in the study area ate mainly mussels (*Mytilus californianus* and *M. edulis*) although other intertidal invertebrates also occurred in the diet (Table I). As they grow, *A. xanthogrammica* are able to capture larger mussels. Thus prey capture (measured as weight per unit time) increases as a greater power of body size than does metabolic cost. Once all prey size categories can be captured, prey intake increases as does feeding surface area, since capture depends solely on the chance that a dislodged prey item is intercepted.

Anthopleura elegantissima divides by longitudinal fission, individuals dividing less often than once per year (Sebens, 1977a, 1980). Formation of these clonal aggregations creates the potential for growth to continue indefinitely. If the entire clone is considered energetically, adding new individuals by fission increases clone feeding surface and metabolic cost linearly, as functions of biomass. There is no optimum size for the aggregate, although there may be one for individual units within the clone (Fig. 10) (Sebens, 1979). Clone formation is common among sea anemones (Stephenson, 1929; Chia, 1976; Minasian, 1976; Minasian and Mariscal,

1979; Smith and Lenhoff, 1976; Johnson and Shick, 1977; Sebens, 1977a, 1979, 1980), and probably increases feeding-surface-to-biomass ratios, helping to capture relatively small prey efficiently (Sebens, 1979).

Anthopleura xanthogrammica never reproduces asexually, nor does subtidal *Metridium* (possibly a new species; Bucklin and Hedgecock, in press) although small specimens of *M. senile* in the low intertidal produce pedal lacerates frequently (Hand, 1955b; Purcell, 1977a; Hoffman, 1977; Bucklin and Hedgecock, in press). Division of *A. xanthogrammica* individuals would usually produce individuals too small to use the large mussels that make up much of their diet. Large subtidal *M. senile* anemones are crowded in dense conspecific assemblages where individual height may be important to bring the tentacle crown into currents carrying zooplankton. Thus, where vertical relief is competitively important, or where large size is necessary to capture large prey, fission may be energetically disadvantageous despite its allometric benefits.

ACKNOWLEDGMENTS

I thank the following persons for their important contributions to the formulation and realization of this research: R. T. Paine, L. Muscatine, G. H. Orians, A. J. Kohn, T. H. Suchanek, M. A. R. Koehl, S. A. Wainwright, and L. Francis for continued encouragement, assistance and discussion; R. T. Paine, T. H. Suchanek, and E. Shaffer for volunteered assistance in the field, laboratory, and SCUBA diving parts of the project; and D. Denninger, V. Gallucci, A. J. Kohn, G. H. Orians, R. T. Paine, P. Petraitis, B. L. Thorne, and P. Lobel for reading and commenting on the manuscript. P. K. Dayton, T. Schoener, P. Calow, and J. M. Shick provided helpful comments and discussion.

I also thank A. O. D. Willows, Director, Friday Harbor Laboratories, for the use of laboratory equipment and facilities; the U. S. Coast Guard for the use of facilities at Cape Flattery Light Station, Tatoosh Island, Wa.; the personnel of the light station for generous assistance; and especially Officer in Charge BM-1 G. Swaney and D. Swaney for uncommon hospitality and interest.

This research fulfilled part of the requirements for the PhD degree, Department of Zoology, University of Washington, Seattle, and was supported by a National Science Foundation Dissertation Improvement Award to the author and by National Science Foundation Grant No. OCE 74 02307 to R. T. Paine. Some computer and laboratory facilities were provided by Harvard University, Museum of Comparative Zoology.

LITERATURE CITED

- ALEXANDER, R. M. 1971. *Size and shape*. Edward Arnold Publishing Co., London. 59 pp.
- BAYNE, B. L., R. J. THOMPSON, AND J. WIDDOWS. 1976. Physiology I. Pp. 121-265 in B. Bayne, Ed., *Marine mussels*, International Biological Programme Vol. 10, Cambridge University Press, Cambridge, Massachusetts.
- BAYNE, B. L., J. WIDDOWS, AND R. I. E. NEWELL. 1977. Physiological measurements on estuarine bivalve molluscs in the field. Pp. 57-68 in B. F. Keegan, P. O. Ceidigh, and P. J. S. Boaden, Eds., *Biology of benthic organisms*. Proc. of the 12th European Symposium on Marine Biology, Pergamon, Oxford.
- BEATTIE, C. W. 1971. Respiratory adjustments of an estuarine coelenterate to abnormal levels of environmental phosphate and oxygen. *Comp. Biochem. Physiol.* **40B**: 907-916.
- BERTNESS, M. D. 1977. Behavioral and ecological aspects of shore-level size gradients in *Thais lamellosa* and *Thais emarginata*. *Ecology* **58**: 86-97.
- BRAFIELD, A. E., AND G. CHAPMAN. 1965. The oxygen consumption of *Pennatula rubra* Ellis and some other anthozoans. *Z. Vergl. Physiol.* **50**: 363-370.

- BUCKLIN, A., AND D. HEDGECOCK. In press. Biochemical genetic evidence for a third species of *Metridium* (Coelenterata, Actiniaria). *Mar. Biol.*
- CHIA, F. S. 1976. Sea anemone reproduction: patterns and adaptive radiations. Pp. 261-270 in G. O. Mackie, Ed., *Coelenterate ecology and behavior*. Plenum Press, New York.
- DAYTON, P. K. 1973. Two cases of resource partitioning in an intertidal community: making the right prediction for the wrong reason. *Am. Nat.* **107**: 662-670.
- DAYTON, P. K., G. A. ROBILIARD, R. T. PAINE, AND L. B. DAYTON. 1974. Biological accommodation in the benthic community at McMurdo Sound, Antarctica. *Ecol. Monogr.* **44**: 105-128.
- EBERT, T. A. 1968. Growth rates of the sea urchin *Strongylocentrotus purpuratus* related to food availability and spine abrasion. *Ecology* **49**: 1075-1093.
- FORD, C. E. 1964. Reproduction in the aggregating sea anemone *Anthopleura elegantissima*. *Pac. Sci.* **18**: 138-145.
- FOX, D. L., AND W. R. COE. 1943. Biology of the California sea mussel, *Mytilus Californianus*. *J. Exp. Zool.* **93**: 205-249.
- FRANCIS, L. 1973a. Clone specific segregation in the sea anemone *Anthopleura elegantissima*. *Biol. Bull.* **144**: 64-72.
- FRANCIS, L. 1973b. Intraspecific aggression and its effect on the distribution of *Anthopleura elegantissima* and some related anemones. *Biol. Bull.* **144**: 73-92.
- FRANCIS, L. 1976. Social organization within clones of the sea anemone *Anthopleura elegantissima*. *Biol. Bull.* **150**: 361-376.
- FRANCIS, L. 1979. Contrast between solitary and clonal lifestyles in the sea anemone *Anthopleura elegantissima*. *Am. Zool.* **19**: 669-681.
- GOULD, S. J. 1966. Allometry and size in ontogeny and phylogeny. *Biol. Rev.* **41**: 587-640.
- GRIFFITHS, C. L., AND J. A. KING. 1979. Some relationships between size, food availability and energy balance in the ribbed mussel *Aulacomya ater*. *Mar. Biol.* **51**: 141-149.
- HAMNER, W. M., AND D. F. DUNN. 1980. Tropical corallimorpharia (Coelenterata: Anthozoa): feeding by envelopment. *Micronesica* **16**: 37-42.
- HAND, C. 1955a. The sea anemones of central California. II, The endomyarian and mesomyarian anemones. *Wassmann J. Biol.* **13**: 37-99.
- HAND, C. 1955b. The sea anemones of central California. III. The acontiarian anemones. *Wassmann J. Biol.* **13**: 189-251.
- HOFFMANN, R. 1977. Genetics and asexual reproduction of the sea anemone *Metridium senile*. *Biol. Bull.* **151**: 478-488.
- HOLTER, H., AND E. ZEUTHEN. 1948. Metabolism and reduced weight in starving *Chaos chaos* (L.). *C. R. Lab. Carlsberg Ser. Chim.* **26**: 277-296.
- JENNISON, B. L. 1979. Gametogenesis and reproductive cycles in the sea anemone *Anthopleura elegantissima* (Brandt, 1835). *Can. J. Zool.* **57**: 403-411.
- JOHNSON, L. L. AND J. M. SHICK. 1977. Effects of fluctuating temperature and immersion on asexual reproduction in the intertidal sea anemone *Haliplanella luciae* (Verrill) in laboratory culture. *J. Exp. Mar. Biol. Ecol.* **28**: 141-149.
- JONES, R. 1976. Growth of fishes. Pp. 251-279. in D. H. Cushing and J. J. Walsh, Eds. *The ecology of the seas*. Blackwell Scientific Publications, Oxford.
- JØRGENSEN, C. G. 1975. Comparative physiology of suspension feeding. *Ann. Rev. Physiol.* **37**: 57-79.
- KITCHELL, J. F., D. J. STEWART, AND D. WEININGER. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and Walleye (*Stizostedion vitreum vitreum*). *J. Fish. Res. Board Can.* **34**: 1922-1935.
- KITCHELL, J. F., W. H. NEAL, A. E. DIZON, AND J. J. MAGNUSON. 1978. Bioenergetic spectra of skipjack and yellowfin tunas. Pp. 357-369. in G. Sharp and A. Dizon, Eds., *The physiological ecology of tunas*. Academic Press, New York.
- KLEIBER, M. 1932. Body size and metabolism. *Hilgardia* **6**: 315-353.
- KOEHL, M. A. R. 1976. Mechanical design in sea anemones. Pp. 23-31 in G. O. Mackie, Ed., *Coelenterate ecology and behavior*. Plenum Press, New York.
- KOEHL, M. A. R. 1977. Effects of sea anemones on the flow forces they encounter. *J. Exp. Biol.* **69**: 87-106.
- KOHN, A. J. 1971. Diversity, utilization of resources, and adaptive radiation in shallow-water marine invertebrates of tropical oceanic islands. *Limnol. Oceanogr.* **16**: 332-348.
- MCLUSKY, D. S. 1973. The effect of temperature on the oxygen consumption and filtration rates of *Chlamys (Aequipecten) opercularis* (L.) (Bivalvia). *Ophelia* **10**: 141-154.
- MCMAHON, T. 1973. Size and shape in biology. *Science* **179**: 1201-1204.
- MINASIAN, L. L. 1976. Characteristics of asexual reproduction in the sea anemone *Haliplanella luciae* (Verrill), reared in the laboratory. Pp. 289-298. in G. O. Mackie, Ed., *Coelenterate ecology and behavior*. Plenum Press, New York.

- MINASIAN, L. L., AND R. N. MARISCAL. 1979. Characteristics and regulation of fission activity in clonal cultures of the cosmopolitan sea anemone, *Haliplanella luciae* (Verrill). *Biol. Bull.* **157**: 478-493.
- MUSCATINE, L. 1961. Symbiosis in marine and freshwater coelenterates. Pp. 255-268 in H. M. Lenhoff and W. F. Loomis, Eds., *The biology of Hydra*. University of Miami Press, Coral Gables, Florida.
- NEWELL, R. C., L. G. JOHNSON, AND L. H. KOFOED. 1977. Adjustment of the components of energy balance in response to temperature change in *Ostrea edulis*. *Oecologia* **30**: 97-110.
- PAINE, R. T. 1965. Natural history, limiting factors and energetics of the opisthobranch *Navanax inermis*. *Ecology* **46**: 603-619.
- PAINE, R. T. 1976. Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology* **57**: 858-873.
- PICKARD, G. L. 1975. *Descriptive physical oceanography*. Pergamon Press, Oxford. 233 pp.
- PORTER, J. W. 1974. Zooplankton feeding by the Caribbean reef-building coral *Montastrea cavernosa*. Pp. 111-125 in *Proceedings of the second international coral reef symposium*. Great Barrier Reef Committee, Brisbane, Australia.
- PURCELL, J. E. 1977a. The diet of large and small individuals of the sea anemone *Metridium senile*. *Bull. S. Cal. Acad. Sci.* **76**: 168-172.
- PURCELL, J. E. 1977b. Aggressive function and induced development of catch tentacles in the sea anemone *Metridium senile* (Coelenterata, Actiniaria). *Biol. Bull.* **153**: 355-368.
- RANDLØV, A., AND H. U. RIISGARD. 1979. Efficiency of particle retention and filtration rate in four species of ascidians. *Mar. Ecol. Prog. Ser.* **1**: 55-59.
- REICHLE, D. E. 1967. Relation of body size to food intake, oxygen consumption, and trace element metabolism in forest floor arthropods. *Ecology* **49**: 538-541.
- ROBBINS, R. E., AND J. M. SHICK. 1980. Expansion-contraction behavior in the sea anemone *Metridium senile*: environmental cues and energetic consequences. Pp. 101-116 in D. C. Smith and Y. Tiffon, Eds., *Nutrition in the lower metazoa*. Pergamon Press, New York.
- RUBENSTEIN, D. I., AND M. A. R. KOEHL. 1977. The mechanisms of filter-feeding: some theoretical considerations. *Am. Nat.* **111**: 981-994.
- SASSAMAN, C., AND C. P. MANGUM. 1973. Relationship between aerobic and anaerobic metabolism in estuarine anemones. *Comp. Biochem. and Physiol.* **44A**: 1313-1319.
- SASSAMAN, C., AND C. P. MANGUM. 1974. Gas exchange in a cerianthid. *Exp. Zool.* **188**: 297-306.
- SCHMIDT-NIELSON, K. 1974. Scaling in biology: the consequences of size. *Exp. Zool.* **194**: 287-308.
- SEBENS, K. P. 1976. The ecology of Caribbean sea anemones in Panama: utilization of space on a coral reef. Pp. 67-78 in G. O. Mackie, Ed., *Coelenterate ecology and behavior*. Plenum Press, New York.
- SEBENS, K. P. 1977a. Habitat suitability, reproductive ecology, and the plasticity of body size in two sea anemone populations (*Anthopleura elegantissima* and *A. xanthogrammica*). Ph.D. thesis, University of Washington, Seattle. 258 pp.
- SEBENS, K. P., 1977b. Autotrophic and heterotrophic nutrition of coral reef zoanthids. Pp. 397-406 in *Proceedings of the third international coral reef symposium*, I. Committee on Coral Reefs, Miami.
- SEBENS, K. P. 1979. The energetics of asexual reproduction and colony formation in benthic marine invertebrates. *Am. Zool.* **19**: 683-697.
- SEBENS, K. P. 1980. The control of asexual reproduction and indeterminate body size in the sea anemone, *Anthopleura elegantissima* (Brandt). *Biol. Bull.* **158**: 370-382.
- SEBENS, K. P. In press. The limits to indeterminate growth: an optimal size model applied to passive suspension feeders. *Ecology*.
- SEBENS, K. P., AND G. LAAKSO. 1977. The genus *Tealia* (Anthozoa Actiniaria) in the waters of the San Juan Archipelago and the Olympic Peninsula. *Wasmann J. Biol.* **35**: 152-168.
- SEBENS, K. P., AND R. T. PAINE, 1978. The biogeography of anthozoans along the west coast of South America. Pp. 219-237 in *Proceedings of the International Symposium on Marine Biogeography and Ecology of the Southern Hemisphere*. Vol. I. *New Zealand Dept. of Scientific and Industrial Research Inf. Series* 137.
- SHICK, J. M., AND W. I. BROWN. 1977. Zooxanthellae-produced O₂ promotes sea anemone expansion and eliminates oxygen debt under environmental hypoxia. *Exp. Biol.* **201**: 149-155.
- SHICK, J. M., W. I. BROWN, E. G. DOLLIVER, AND S. R. KAYAR. 1979. Oxygen uptake in sea anemones: effects of expansion, contraction and exposure to air and the limitations of diffusion. *Physiol. Zool.* **52**: 50-61.
- SHICK, J. M., AND R. J. HOFFMAN. 1980. Effects of the trophic and physical environments on asexual reproduction and body size in the sea anemone *Metridium senile*. Pp. 211-216 in P. Tardent

- and R. Tardent, Eds., *Developmental and cellular biology of coelenterates*, Elsevier, North-Holland Biomedical Press.
- SMITH, N., III, AND H. M. LENHOFF. 1976. Regulation of frequency of pedal laceration in a sea anemone. Pp. 117-126 in G. O. Mackie, Ed., *Coelenterate ecology and behavior*, Plenum Press, New York.
- SOKAL, R. R. AND J. F. ROHLF. 1969. *Biometry: The principles and practice of statistics in biological research*. W. H. Freeman and Co., San Francisco. 776 pp.
- STEPHENSON, T. A. 1929. On methods of reproduction as specific characters. *J. Mar. Biol. Assoc. U. K.* **16**: 131-172.
- THOMPSON, D. W. 1917. *On growth and form*. Cambridge University Press, London.
- THOMPSON, R. J. AND B. L. BAYNE. 1979. Some relationships between growth, metabolism and food in the mussel *Mytilus edulis*. *Mar. Biol.* **27**: 317-326.
- VADAS, R. L. 1977. Preferential feeding: an optimization strategy in sea urchins. *Ecol. Monogr.* **47**: 337-371.
- VAHL, O. 1972. Particle retention and relation between water transport and oxygen uptake in *Chlamys opercularis* (L.) (Bivalvia). *Ophelia* **10**: 67-74.
- VAHL, O. 1973. Pumping and oxygen consumption rates of *Mytilus edulis* L. of different sizes. *Ophelia* **12**: 45-52.
- WARREN, C. E., AND G. E. DAVIS. 1967. Laboratory studies on the feeding, bioenergetics and growth of fish. Pp. 175-214 in S. D. Gerking, Ed., *The biological basis of fresh water fish production*, Blackwell Scientific Publications, Oxford.
- WIDDOWS, J. V. 1978. Combined effects of body size, food concentration and season on the physiology of *Mytilus edulis*. *J. Mar. Biol. Assoc. U. K.* **58**: 109-124.
- WINTER, J. E. 1969. Über den Einfluß der Nahrungskonzentration und anderer Faktoren auf Filtrierleistung und Nahrungsausnutzung der Muscheln *Artica islandica* und *Modiolus modiolus*. *Mar. Biol.* **4**: 87-135.
- WINTER, J. E. 1973. The filtration rate of *Mytilus edulis* and its dependence of algal concentration, measured by a continuous automatic recording apparatus. *Mar. Biol.* **22**: 317-328.
- WINTER, J. E. 1978. A review of the knowledge of suspension-feeding in lamellibranchiate bivalves, with special reference to artificial aquaculture systems. *Aquaculture* **13**: 1-33.
- ZEUTHEN, E. 1948a. Body size and metabolic rate in the animal kingdom with special regard to the marine microfauna. *C. R. Lab. Carlsberg Ser. Chim.* **26**: 17-161.
- ZEUTHEN, E. 1948b. Reduced weight and volume during starvation of amoeba *Chaos chaos* (L.) *C. R. Lab. Carlsberg Ser. Chim.* **26**: 267-276.
- ZEUTHEN, E. 1953. Oxygen uptake as related to body size in organisms. *Q. Rev. Biol.* **28**: 1-12.



Sebens, Kenneth P. 1981. "THE ALLOMETRY OF FEEDING, ENERGETICS, AND BODY SIZE IN THREE SEA ANEMONE SPECIES." *The Biological bulletin* 161, 152–171. <https://doi.org/10.2307/1541115>.

View This Item Online: <https://www.biodiversitylibrary.org/item/17156>

DOI: <https://doi.org/10.2307/1541115>

Permalink: <https://www.biodiversitylibrary.org/partpdf/37352>

Holding Institution

MBLWHOI Library

Sponsored by

MBLWHOI Library

Copyright & Reuse

Copyright Status: In copyright. Digitized with the permission of the rights holder.

Rights Holder: University of Chicago

License: <http://creativecommons.org/licenses/by-nc-sa/3.0/>

Rights: <https://biodiversitylibrary.org/permissions>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.