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# Effects of feeding regime on growth rate in the Mediterranean Sea anemone *Actinia equina* (Linnaeus)

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## Abstract

Polyps of *Actinia equina* are the most common sea anemones in the rocky intertidal zone of the Mediterranean coast of Israel, where they occur in one of the southernmost populations of this species in the northern hemisphere. We examined effects of feeding rate on polyp growth at ambient sea temperature for this population. Under laboratory conditions, polyps were left unfed, or were fed with brine shrimp (*Artemia*) once every 2 weeks, once a week, or twice a week. Of the four experimental treatments, only feeding twice a week resulted in polyp growth; under all other regimes, the sea anemones lost body mass. We conclude that a high rate of feeding is required at sea temperatures in the eastern Mediterranean, where these sea anemones may have high metabolic rates relative to more northern populations.

*Keywords:* Actiniaria; *Actinia equina*; Sea anemone; Growth; Feeding; Mediterranean; Israel; Body size; Metabolic rate; Tissue hydration

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## 1. Introduction

Benthic marine invertebrates often have habitat-dependent body size and indeterminate growth (Sebens, 1977). Indeterminate growth is defined as a capacity for pronounced size changes as environmental and nutritional conditions vary, implying that maximum body

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size is not genetically defined (Sebens, 1987). Among sea anemones, regularly fed juveniles grow rapidly (Chia and Rostron, 1970; Chia and Spaulding, 1972). Regularly fed adults, however, may show no appreciable changes in size for as long as 8 years (Ashworth and Annandale, 1904). Also, since sea anemones may undergo negative growth (shrinkage) during times of stress or starvation (Sebens, 1979), individual size is an indicator of recent habitat conditions. Both body size and mode of reproduction of sea anemones appear to be determined in part by success in catching particulate prey (Sebens and Koehl, 1984).

In many sessile marine organisms, body size has more impact on life history processes than does age, and controls rates of survival and of sexual and asexual reproduction (Hughes, 1984; Jackson and Hughes, 1985). Accurate measurement of body size in sea anemones is difficult, since they may retain variable amounts of water in the coelenteron, which produces errors in wet mass measurements. The body size of sea anemones is not necessarily related to polyp age, but may be closely related to nutritional history (Stephenson, 1928). Morphological parameters such as height of the column, diameter of the oral and pedal discs, number of acrorhagi, number of tentacles, and mass in "crude units of biomass" (Crisp, 1971) may reflect in part the maturity grade or relative age of individuals (Doumenc et al., 1989). The number of acrorhagi and the diameter of the pedal disk and column have been used as indicators of size class and maturity in polyps of the sea anemones *Actinia tenebrosa* (Ayre, 1984; Ottaway, 1979a) and *A. equina* (Quicke et al., 1985; Donoghue et al., 1985). Based on the presence of brooded offspring (Quicke and Brace, 1983) and on the ontogeny of aggressive behavior (Rees, 1984), *A. equina* individuals having a pedal disk diameter of >15 mm have been classed as adults, and age at maturity has been estimated as "a few years" (Dalyell, 1848; M'Bain, 1878). Chintiroglou et al. (1997) found that both wet and dry polyp mass correlated positively with other morphological parameters, and thus could be used as reliable indicators of body size in *A. equina*.

Although sea anemones occur in the rocky intertidal zone of the Mediterranean Sea, little is known about their biology in this region. Information on polyps of the sea anemone *A. equina* in Israel, where they are the most common sea anemones along the Mediterranean coast, is limited and mainly qualitative (Lipkin and Safriel, 1971). Individuals of *A. equina* occur along the Atlantic and Mediterranean coasts of Europe and North Africa (Stephenson, 1935; Schmidt, 1971; Dayton, 1973; Manuel, 1988), but the exact boundaries of the geographical distribution of this species are unknown, as these anemones also may be found in South Africa (Stephenson, 1935). In Israel, polyps of *A. equina* usually occur at the mid-tide level, in shaded positions under ledges or in caves, but sometimes also are found in unshaded rock pools (Chomsky, personal observation).

Members of this species are opportunistic omnivorous suspension feeders (Ormond and Caldwell, 1982). They have relatively short tentacles and are unable to actively search for prey, and thus feed on organisms or organic detritus that fall onto their oral discs (Chintiroglou and Koukouras, 1992). Due to vigorous water movement, organic detritus is abundant in the midlittoral zone where *A. equina* occurs. Macroalgal fragments also are common in the coelenteron contents of *A. equina*, however, it is uncertain whether these anemones have the enzymic machinery to digest algal material (Shick, 1991).

In the present study, we report on effects of feeding regime on the growth rate of polyps of *A. equina* in Israel, and discuss the energetic requirements of individuals in this population, which occur near the southernmost limit of their distribution in the northern hemisphere.

## 2. Materials and methods

Polyps of *Actinia equina* were collected during low tide in August 2000 at three sites along the coast of the Mediterranean Sea, Israel (32°28′ N; 30°53′ E): Achziv, Neve-Yam, and Bat-Yam. Individuals were removed from the rocks using a small metal spatula, and transported to temperature- and light-controlled rooms at Bar-Ilan University. They were acclimated to laboratory conditions for 1 week, in aquaria supplied with aerated filtered seawater, in order to remove residual particulate food and to provide a baseline unfed level for feeding experiments. During acclimation, individuals that did not survive (mainly juveniles) were removed from the aquaria. The remaining 84 polyps ranged in size from 1.3 to 86.5 g wet mass ($\bar{X} \pm$ S.D. = 19.2 ± 13.9 g) and 13–73-mm pedal disk diameter (38.3 ± 12.4 mm). Seawater was transported from the Mediterranean Sea and circulated in a closed system through a biological filter during experiments. Temperature was maintained at 23 °C (= annual mean seawater temperature at Haifa, Israel, during 1992–1999 at 1-km distance from the shore line, 0.5-m depth). The light regime was a 12:12-h light/dark cycle, controlled by an automatic timer. Light intensity was 200 μmol quanta $m^{-2}$ $s^{-1}$ at the water surface, similar to the light intensity during daytime in typical sea anemone habitats that were measured during collection (Chomsky, personal observation).

Polyps from the three collection sites were distributed randomly into four aquaria, for a total of 21 polyps per aquarium. All polyps in each aquarium were subjected to one of four treatments: (1) unfed (0 × ), (2) fed once every 2 weeks (0.5 × ), (3) fed once each week (1 × ), or (4) fed twice each week (2 × , modified after Muscatine, 1961; Tsuchida and Potts, 1994). During each feeding period, the anemones were fed to repletion: they were provided with as many *Artemia* brine shrimps as their oral discs could hold. Larger anemones thus received more food than smaller ones, but the amount of food was proportional to body size. The anemones engulfed the *Artemia* shrimps quickly and completely. On the following day, boluses egested by each anemone were removed from the aquaria. All aquaria were cleaned weekly. In preliminary trials, other foods were tried (frozen fish and mollusks), but these often were incompletely consumed, or were dropped by the anemones.

Individual anemones were allowed to attach to small labeled glass Petri dishes (10-cm diameter × 1.5-cm height) at 15 cm below the water surface. The positions of the dishes in the aquaria were rotated each week, and anemones were weighed every 1–2 weeks for 80 days (about 12 weeks).

The mass of each Petri dish was measured before the experiment, and each dish was removed and gently dried along with its anemone for each wet mass determination. To assess whether wet mass was an accurate indicator of body size, we examined the relationship between three size parameters: pedal disk diameter, and wet and dry body mass. During August 2000, 20 additional polyps of *A. equina,* spanning a size range of 1.9–45.4 g wet mass ($\bar{X}$= 16.6 g), were collected from the above three field sites for dry mass determinations. Each was measured for pedal disk diameter to the nearest 0.5 mm using calipers. If the disk was markedly elliptical, size was calculated as the mean of the minimum and maximum diameters (after Brace and Quicke, 1986). The wet mass of each polyp was determined on a pre-weighed, labeled foil dish using a Sartorius electronic scale, accurate to 0.01 g. Then polyps were dried in an oven at 100 °C for 96 h, and the dry mass of each was measured.

The computer program SPSS version 11.0 (Norusis, 1999) was used for all statistical analyses. A Bonferroni correction was applied to all multiple comparisons.

## 3. Results

Polyp dry mass depended on wet mass (Fig. 1), and both wet and dry mass increased exponentially with the diameter of the pedal disk (Fig. 2).

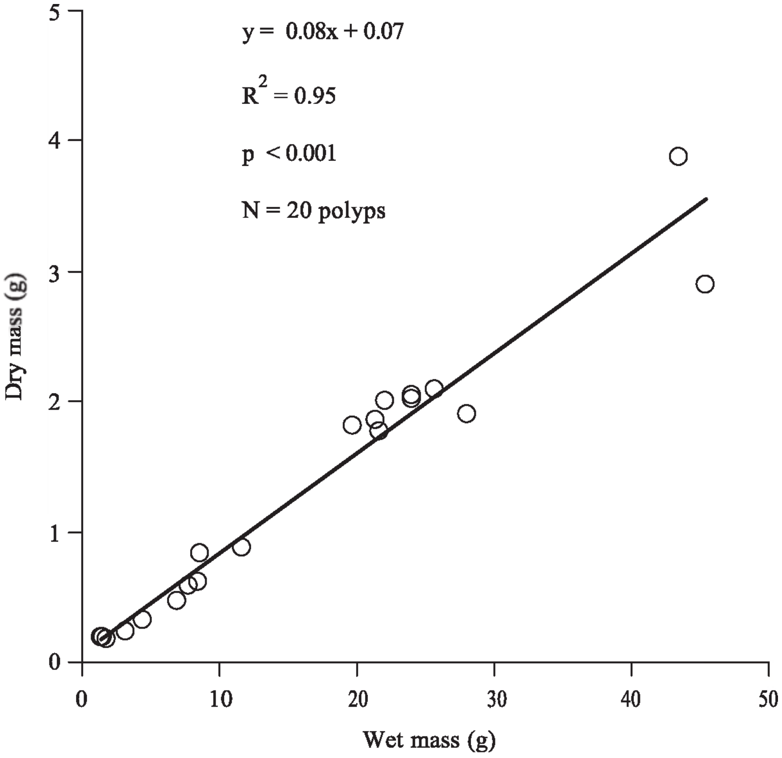

Fig. 1. Variation in dry mass with wet mass in polyps of the sea anemone *A. equina* from the Mediterranean coast of Israel.

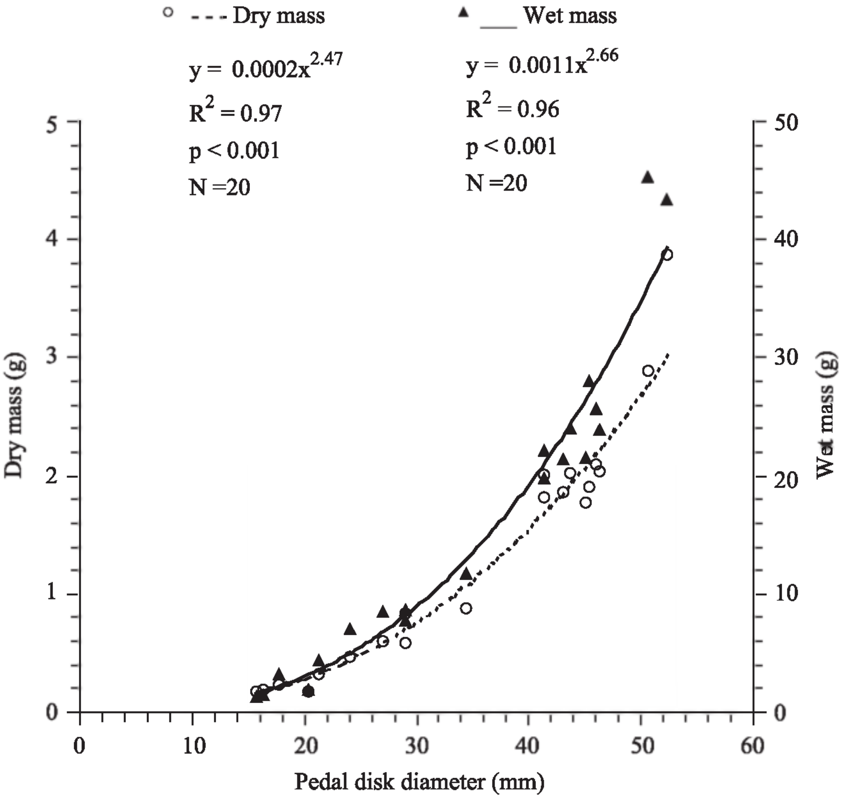

Fig. 2. Variation in dry and wet mass with pedal disk diameter in polyps of the sea anemone *A. equina* from the Mediterranean coast of Israel.

Individuals did not vary among the four feeding treatments in their initial wet mass or pedal disk diameter (ANOVA, $F = 0.267$ and $p = 0.849$ for mass, $F = 0.625$ and $p = 0.601$ for diameter).

During the feeding experiment, only anemones in the 2 × feeding group increased in body mass and diameter, whereas individuals in the other three groups shrank (Fig. 3). Anemones fed 2 × per week increased in mass by about 50%, and in mean diameter by approximately 25%. In contrast, anemones that were unfed, or fed only 0.5–1 × per week, lost about 30–50% of their body mass, and 15–30% of their diameter (Fig. 3).

After 80 days, there was a significant effect of feeding regime on percent change in both polyp mass and diameter (ANOVA, $F = 31.073$ and $p < 0.001$ for mass, $F = 13.534$ and $p < 0.001$ for diameter). The polyps fed 2 × per week differed significantly in both mass and diameter from the other three experimental groups. There was no significant difference in percent change of either mass or diameter between polyps in the 0 × , 0.5 × and 1 × feeding treatments.

Growth rate also varied significantly with initial polyp size in the 0.5 × and 2 × feeding treatments (Fig. 4), but not in the 1 × and 0 × treatments. In the 0.5 × feeding

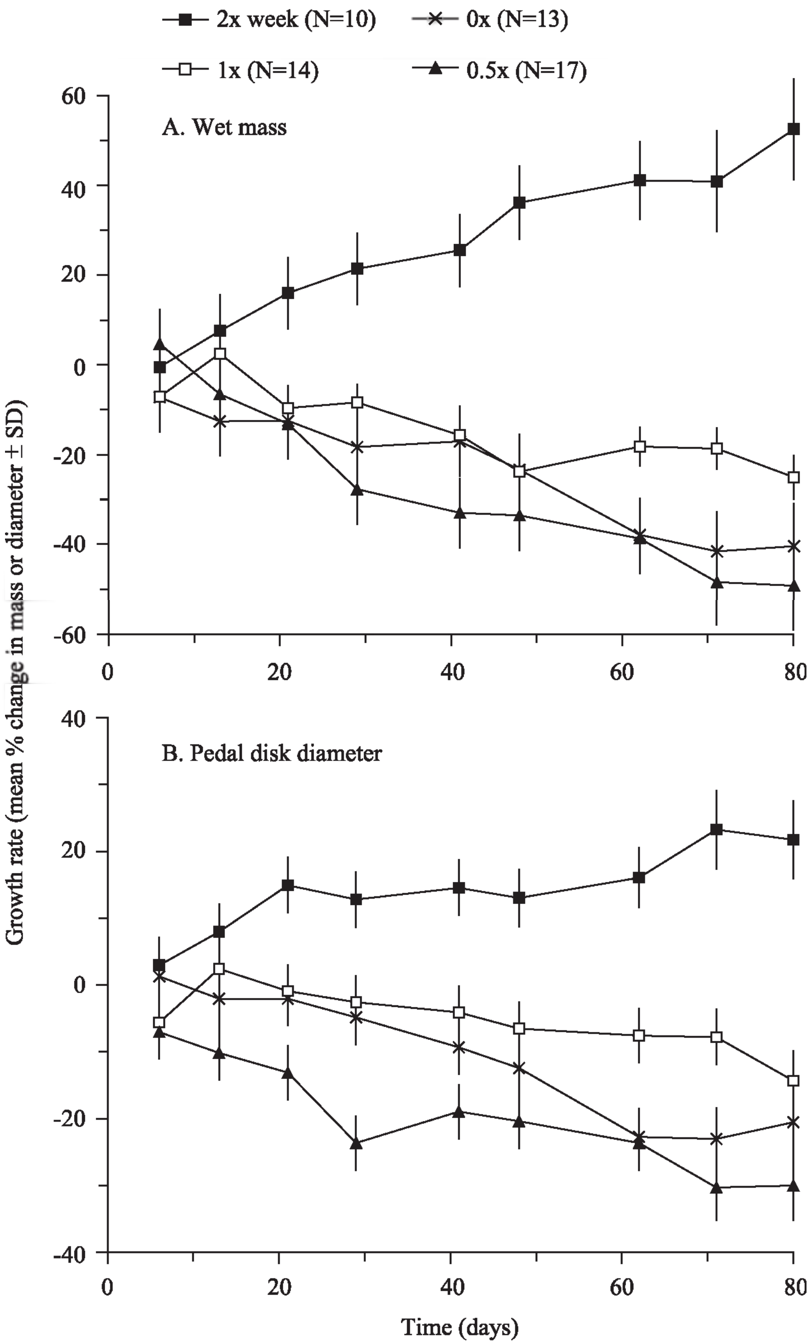

Fig. 3. Variation in percent growth rate among four feeding regimes in polyps of the sea anemone *A. equina* from the Mediterranean coast of Israel. Sample sizes are the number of polyps that survived all 80 days in each treatment. Note that in three of the treatments, the polyps lost mass (negative growth).

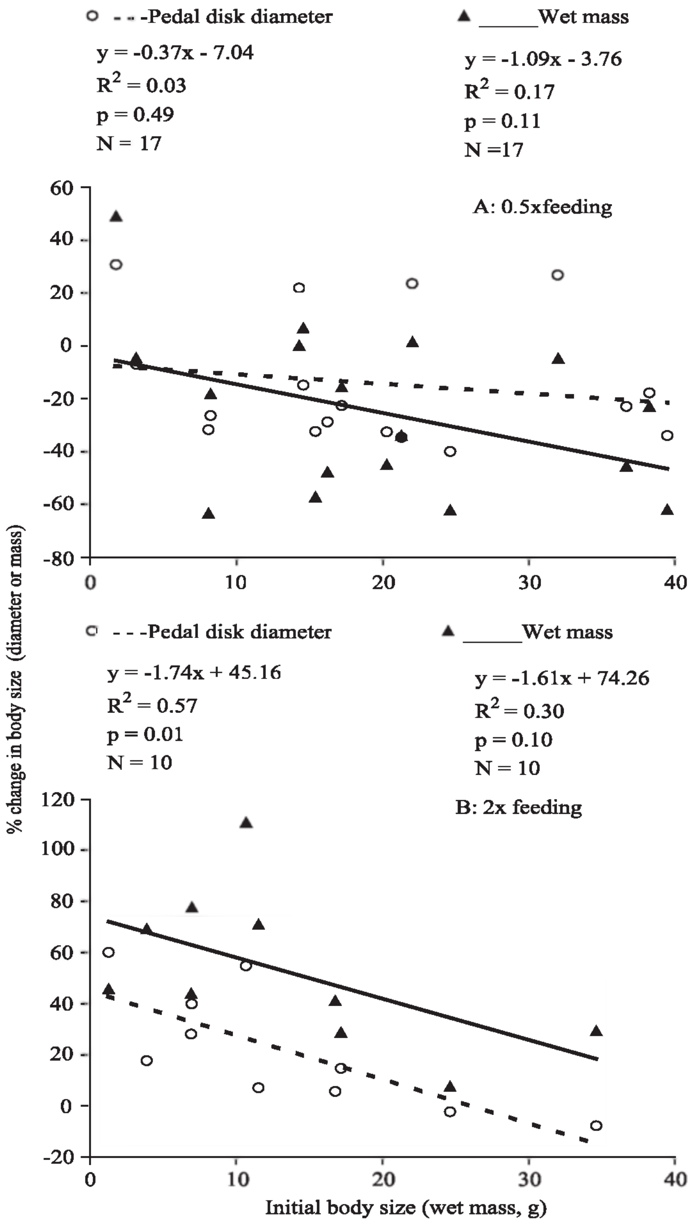

Fig. 4. Variation in percent growth rate with initial body size in the sea anemone *A. equina* from the Mediterranean coast of Israel, over 80 days. (A) Fed once every 2 weeks (= 0.5 × per week). (B) Fed 2 × per week.

group, large anemones (>15 g initial wet mass) lost significantly more in percent wet mass (on average 36%), than did small anemones (5%), but polyps in both groups lost on average 5% in diameter (*t*-tests, $t=2.181$ and $p=0.046$ for mass, $t=1.232$ and $p=0.237$ for diameter, Fig. 4A). In the 2 × feeding group, small anemones gained significantly more in percent mass (70%) and in diameter (35%) than did large anemones, which gained only 27% in mass and 3% in diameter (*t*-tests, $t=3.150$ and $p=0.014$ for mass, $t=2.825$ and $p=0.022$ for diameter, Fig. 4B).

## 4. Discussion

We show here that polyps of the sea anemone *A. equina* require a high rate of feeding in order to gain body mass, at average temperature along the coast of Israel. Changes in body mass at this temperature also vary widely with initial polyp size, in that small polyps appear to increase more in percent size if fed frequently, and to lose less in percent size if fed rarely, than do large polyps.

Our results indicate that the 1 ×, 0.5 × and 0 × feeding regimes were not sufficient to support a positive growth rate in *A. equina* at the examined temperature of 23 °C (Fig. 3). Nutrition obtained directly from the water (i.e. dissolved organic matter) was not sufficient to compensate for metabolic losses in anemones in the three less-fed treatments. The high-feeding treatment (2 × ) was the only one resulting in substantial positive growth (Figs. 3 and 4B), but even in this treatment, the anemones did not reach a stable maximum mass or diameter by the end of the experiment. Previous experiments on aposymbiotic polyps of the sea anemone *Anthpleura elegantissima*, which are similar to polyps of *A. equina* in their morphology, habitat and diet (Shick, 1991), showed that when left unfed, they lost a similar percent of body mass over a 1-month period (Table 1). However, when fed, they gained more than twice the percent mass of *A. equina* in 1 month (Table 1). The *A. elegantissima* polyps had a more frequent feeding schedule (3 × per week versus 2 × in the present study), but even so their growth rate was much higher than that of the *A. equina* polyps. A possible cause of this difference may relate to differences in initial body mass. We used relatively large polyps, which tend to have slower percent growth rates than do small anemones (Ivleva, 1964; Sebens, 1980; Zamer, 1986; Tsuchida and Potts, 1994; Fig. 4). The size-dependent location of polyps on the exponential phase of a sigmoidal growth curve may in part explain the observed differences in growth rates. Other contributing factors may include inherent genetic differences between the two species, and differences in the experimental temperatures used. Ivleva (1964) also measured growth in *A. equina*, and found much higher percent growth rates, probably because she fed the polyps 3 × per day and grew them at relatively low temperatures (Table 1). Optimal temperatures for the growth of polyps of *A. equina* from the Black Sea appear to be 18.7–19.9 °C; their growth rates decline above and below this range (Ivleva, 1964). Sebens (1980) also has shown that body size in *A. elegantissima* decreases with increasing temperature, likely due to thermally enhanced respiration. Since the population of *A. equina* examined here occurs near the southern limit of the geographic range of this species in the northern hemisphere, these polyps likely exist at or near their maximum temperature tolerance.

Table 1
Summary of feeding experiments on the sea anemones *A. elegantissima* and *A. equina*

| Experimental conditions and results | Muscatine (1961) | Tsuchida and Potts (1994) | Ivleva (1964) | Present study |
|---|---|---|---|---|
| Species examined | *Anthopleura elegantissima*[a] | *Anthopleura elegantissima*[a] | *Actinia equina* | Actinia equina |
| Collection site | Pacific Grove, California, USA | Soquel Point, California, USA | Black Sea, USSR | Mediterranean Sea, Israel |
| Date of experiment | ND | October 1988 to January 1989 | ND | August to November 2000 |
| Duration of experiment | 77 days | 98 days | 1–70 days (variable) | 80 days |
| Water temperature | 14 °C | 10–17 °C | 14–23 °C | 23 °C |
| Food type | None | Frozen brine shrimp, several feeding groups | Mussel gonads, 3 times a day | Frozen brine shrimp, several feeding groups |
| Seawater filtration | Yes | Yes | ND | Yes |
| Seawater circulation | Standing | Flow-through | ND | Recirculated |
| Holding conditions | ND | Polyps in individual submerged cups | Polyps in individual submerged cups | Polyps in individual submerged Petri dishes |
| Weighing technique | Reduced mass in seawater (buoyant mass) | Wet mass | Wet mass | Wet mass and pedal disk diameter |
| Total number of polyps | 20 | 80 | 49 | 84 |
| Maximum wet mass | ND | 4.0 g | 4.3 g | 86.5 g |
| % Change in mass ($\bar{X} \pm$ S.D.) after 1 month when fed | ND | +55 ± 31 | +30–90[b] | +21 ± 22 |
| % Change in mass ($\bar{X} \pm$ S.D.) after 1 month when unfed | −27 ± 2 | −31 ± 10 | ND | −28 ± 40 |

ND = No data available.

[a] Aposymbiotic polyps were used (lacking zooxanthellae).

[b] Calculated from daily changes in the wet mass of adult polyps. The experiments varied in duration from 1 to 70 days.

Tissue hydration in sea anemones may vary due to ontogenetic and nutritional effects. Hydration level in a population of *A. equina* from the Atlantic shores of Spain (Ortega et al., 1988) was 80%, within the range reported by Ivleva (1964) for a Black Sea population of this species (79% and 86% for adult and juvenile polyps, respectively), and similar to that known for other anthozoans (Johnson and Shick, 1977; Hunter, 1984). In the present study, tissue hydration was 92.8% and 93.6% for freshly collected small (wet mass < 15 g) and large (>15 g) polyps, respectively ( = dry mass 7.2% and 6.4% of wet mass). The lower hydration values of Ivleva (1964) and Ortega et al. (1988) compared to ours may result in part from differences in polyp body size (mean dry mass = 0.1 g in Ivleva, and 0.01–0.5 g in Ortega, compared to 0.4–4.8 g in the present study). Differences in procedures used for removing excess water before wet weighing also may have affected outcome. The relatively large anemones in our population suffered mortality when we tried exposing them to the long period for removal of excess water that was used by Ivleva (1964). Thus, in our growth experiment, we dried the anemones only briefly before wet weighing, and therefore, the quantity of water retained by our animals may have been higher. Adult anemones maintained on high food rations during growth experiments also increase their dry mass relative to wet mass ( = lower their tissue hydration, Ivleva, 1964). Water temperature in our experiment (23 °C) was higher than in that of Ivleva (18 °C on average), so the energetic expenditure of our anemones likely was higher, possibly causing a reduction in polyp dry mass/wet mass ratios.

In our experiment, wet mass and pedal disk diameter appeared to be good indicators of changes in sea anemone body size (Fig. 3). Muscatine (1961) employed the buoyant weighing technique of Holter and Zeuthen (1948) for anemones suspended in seawater, which also has been used as an accurate method for determining skeletal growth rates in stony corals (Jokiel et al., 1978; Edmunds and Davies, 1986). We tried using the buoyant weighing technique for 1 month in our experiment, but did not detect any mass changes during this period. As in our study, linear measures of growth (i.e. pedal disk diameter) have proven adequate in long-term field studies of *A. tenebrosa* (Ottaway, 1980), *Anthopleura elegantissima*, and *A. xanthogrammica* (Sebens, 1983). Chadwick-Furman and Spiegel (2000) also used longest and shortest oral disk diameters as measures of growth rate in the ellipsoid corallimorpharian *Rhodactis rhodostoma*.

When feeding rate was minimized (0.5 × ), polyps of *A. equina* lost mass by reduction of column height, with little apparent decrease in their diameter (Fig. 4A). Thus, anemones fed only 0.5 × week retained maximal prey capture potential by maximizing their oral disk surface area relative to their body mass. When unfed, no significant difference in mass loss between small and large anemones was found, similar to results reported by Tsuchida and Potts (1994) for *A. elegantissima*.

Ivleva (1964) argued that rapid growth in juvenile polyps of *A. equina* is a consequence of a high rate of food ingestion at that age, and probably has been selected due to size-dependent mortality in the intertidal zone. In the antipodal congener *A. tenebrosa*, there is a negative correlation between size and mortality up to a basal diameter of 15 mm (Ottaway, 1979b). Similarly, individuals of *Anthopleura* spp. have higher rates of disappearance when small than when large (Sebens, 1983). Harris (1973) argued that rapid growth rate in the anemone *Metridium senile* may have been selected to provide an escape in size from predation. Rapid attainment of large size also may be favored due to the outcome of intraspecific agonistic encounters, where larger individuals prevail in *A. equina* (Brace and Pavey, 1978) and *Anthopleura xanthogrammica* (Sebens, 1984). In addition, large specimens of *A. elegantissima* are less susceptible to burial by shifting sand than are small individuals (Pineda and Escofet, 1989). The intertidal habitat of both *A. tenebrosa* and *A. elegantissima* is known to provide a refuge from predation by subtidal mollusks and sea stars (Mauzev et al., 1968; Sebens, 1983), so rapid growth rate may relate more to minimizing desiccation by achieving large size and small surface/volume ratio. Individuals also may grow quickly to avoid being screened from catching prey in dense aggregations. Coates and Jackson (1985) predicted that in solitary clonal forms (i.e. clonal products that are physiologically separated, as in *A. elegantissima*), the likelihood of ramet survival will increase with size, and there will be strong selective pressures for large size. Rapid growth of juvenile *A. equina*, and of other sea anemones, thus appears to minimize the period of vulnerability associated with small body size, and is part of a general phenomenon of rapid growth in juvenile marine organisms.

We conclude that at mean annual temperature of the eastern Mediterranean Sea in Israel, individuals of the sea anemone *A. equina* were able to balance their metabolic needs only under the highest feeding regime of 2 × per week. With less frequent feeding, polyps of all sizes shrank, evidently because food intake was below that required to balance their basal metabolic rates. The only other feeding studies on this species have been conducted at lower ambient temperatures ranging from 14 to 23 °C (Ivleva, 1964). Past research has shown that when temperature increases by 10 °C, the respiration rate of sea anemones increases by about 2 × ($Q_{10} = 2$, Shick, 1991). Thus, we speculate that at 23 °C, these sea anemones require about twice as much energy intake as do colder-water conspecifics (at about 13 °C), which are able to gain substantially in mass even when fed only once each week (Ivleva, 1964).

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## References

Ashworth, J.H., Annandale, N., 1904. Observations on some aged specimens of *Sagartia troglodytes*, and on the duration of life in coelenterates. Proc. R. Soc. Edinb. 25, 295–308.

Ayre, D.J., 1984. Effects of environment and population density on the sea anemone *Actinia tenebrosa*. Aust. J. Mar. Freshw. Res. 35 (6), 735–746.

Brace, R.C., Pavey, J., 1978. Size-dependent dominance hierarchy in the anemone *Actinia equina*. Nature 273, 752–753.

Brace, R.C., Quicke, D.L.J., 1986. Seasonal changes in dispersion within an aggregation of the anemone, *Actinia equina*, with a reappraisal of the role of intraspecific aggression. J. Mar. Biol. Assoc. U.K. 66, 49–70.

Chadwick-Furman, N.E., Spiegel, M., 2000. Abundance and clonal replication in the tropical corallimorpharian *Rhodactis rhodostoma*. Invertebr. Biol. 119 (4), 351–360.

Chia, F.S., Rostron, M.A., 1970. Some aspects of the reproductive biology of *Actinia equina* (Cnidaria: Anthozoa). J. Mar. Biol. Assoc. U.K. 50, 253–264.

Chia, F.S., Spaulding, J.G., 1972. Development and juvenile growth of the sea anemone *Tealia crassicornia*. Biol. Bull. (Woods Hole, MA) 142, 206–218.

Chintiroglou, Ch., Koukouras, A., 1992. The feeding habits of three Mediterranean sea anemone species, *Anemonia viridis* (Forskal), *Actinia equina* (Linnaeus) and *Cereus pedunculatus* (Pennant). Helgol. Meeresunters. 46, 53–68.

Chintiroglou, C.C., Christou, I., Simsiridou, M., 1997. Biometric investigations on the cnidae of Aegean color morphs of *Actinia equina mediterranea* sensu Schmidt, 1972. Isr. J. Zool. 43, 377–384.

Coates, A.G., Jackson, J.B.C., 1985. Morphological themes in marine invertebrates. In: Jackson, J.B.C., Buss, L.W., Cook, R.E. (Eds.), Population Biology and Evolution of Clonal Organisms. Yale University Press, New Haven, pp. 67–106.

Crisp, D.J., 1971. Energy flow measurements. In: Holme, N. A., McIntyre, A. D. (Eds.), Methods for the Study of Marine Benthos. I.B.P. Handbook, vol. 16. Blackwell, Scientific Publishers, Oxford, pp. 197–279.

Dalyell, J.G., 1848. Rare and remarkable animals of Scotland. Represented from Living Subjects: With Practical Observations on their Nature, vol. 2. Van Voorst, London.

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.

Donoghue, A.M., Quicke, J.L.D., Brace, R.C., 1985. Biochemical–genetic and acrorhagial characteristics of pedal disc color phenotypes of *Actinia equina*. J. Mar. Biol. Assoc. U.K. 65, 21–33.

Doumenc, D., Chintiroglou, Ch., Foubert, A., 1989. Variabilite du genre *Telmatactis graviar*, 1918 (Actiniaria, Acontiaria, Isophelliidae). Bull. du Museum National d'Histoire Naturelle Paris 4e ser 11 section A (3), 5–45.

Edmunds, P.J., Davies, P.S., 1986. An energy budget for *Porites porites* (Scleractinia). Mar. Biol. 92, 339–347.

Harris, L.G., 1973. Nudibranch associations. In: Cheng, T.C. (Ed.), Current Topics in Comparative Pathobiology, vol. 2. Academic Press, NY, pp. 213–315.

Holter, H., Zeuthen, E., 1948. Metabolism and reduced weight in starving *Chaos chaos* (L.). C.R. Lab. Carlsberg Ser. Chim. 26, 277–296.

Hughes, T.P., 1984. Population dynamics based on individual size rather than age: a general model with a coral reef example. Am. Nat. 123, 778–795.

Hunter, T., 1984. The energetics of a sexual reproduction: pedal laceration in the symbiotic sea anemone *Aiptasia pulchella* (Calgren, 1943). J. Exp. Mar. Biol. Ecol. 83, 127–147.

Ivleva, I.V., 1964. Elements of energetic balance in sea anemones. Trans. Sevastopol Biol. Sta., Acad. Sci. USSR 25, 410–428 (in Russian, translation available from the authors).

Jackson, J.B.C., Hughes, T.P., 1985. Adaptive strategies of coral reef invertebrate. Am. Sci. 73, 265–274.

Johnson, L.L., Shick, J.M., 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.

Jokiel, R.L., Maragos, J.E., Franzisket, L., 1978. Coral growth: buoyant weight technique. Monogr. Oceanogr. Methodol. (UNESCO) 5, 529–542.

Lipkin, Y., Safriel, U., 1971. Intertidal zonation on rocky shores at mikhmoret (Mediterranean, Israel). J. Ecol. 59 (1), 1–30.

Manuel, R.L., 1988. British Anthozoa, Rev. Ed. E.J. Brill, Leiden.

Mauzev, K.P., Birkeland, C., Dayton, P.K., 1968. Feeding behavior of asteroids and escape responses of their prey in the Puget Sound regen. Ecology 49, 603–619.

M'Bain, J., 1878. Notes on *Actinia mesembryanthemum*, taken from a rock pool at North Berwick by the late Sir John Graham Dalyell in August 1828. Proc. R. Soc. Edinb. 4, 280–288.

Muscatine, L., 1961. Symbiosis in marine and freshwater coelenterates. In: Lenhoff, H., Loomis, W.F. (Eds.), The Biology of Hydra. University of Miami Press, Miami, FL, pp. 255–268.

Norusis, M.J., 1999. SPSS 9.0 Guide to Data Analysis. Prentice-Hall, Upper Saddle River, p. 578.

Ormond, G.F.R., Caldwell, S., 1982. The effect of oil pollution on the reproduction and feeding behaviour of the sea anemone *Actinia equina*. Mar. Pollut. Bull. 13, 118–122.

Ortega, M.M., Lopez de Pariza, J.M., Navarro, E., 1988. Seasonal changes in the biochemical composition and oxygen consumption of the sea anemone *Actinia equina* as related to body size and shore level. Mar. Biol. 97, 137–143.

Ottaway, R.J., 1979a. Population Ecology of the intertidal Anemone *Actinia tenebrosa*: II. Geographical distribution, synonymy, reproductive cycle and fecundity. Aust. J. Zool. 27, 273–290.

Ottaway, J.R., 1979b. Population ecology of the intertidal anemone *Actinia tenebrosa*: III. Dynamics and environmental factors. Aust. J. Mar. Freshw. Res. 30, 41–62.

Ottaway, J.R., 1980. Population ecology of the intertidal anemone *Actinia tenebrosa*: IV. Growth rates and longevities. Aust. J. Mar. Freshw. Res. 31, 385–395.

Pineda, J., Escofet, A., 1989. Selective effects of disturbance on populations of sea anemones from northern Baja California Mexico. Mar. Ecol. Prog. Ser. 55, 55–62.

Quicke, D.L.J., Brace, R.C., 1983. Phenotypic and genotypic spacing within an aggregation of the anemone *Actinia equina*. J. Mar. Biol. Assoc. U.K. 63, 493–515.

Quicke, D.L.J., Donoghue, M.A., Keeling, F.T., Brace, R.C., 1985. Littoral distributions and evidence for differential post-settlement selection of the morphs of *Actinia equina*. J. Mar. Biol. Assoc. U.K. 65, 1–20.

Rees, T.D., 1984. The population ecology and behaviour of *Actina equina*. PhD Thesis, University of Nottingham. United Kingdom.

Schmidt, H., 1971. Taxonomie, Verbreitung und Variabilitat von *Actinia equina* Linne 1766 (Actiniaria: Anthozoa). Z. Zoolog. Syst. Evol. Forsch. 9, 161–169.

Sebens, K.P., 1977. Habitat suitability, reproductive ecology, and the plasticity of body size in two sea anemone populations (*Anthopleura elegantissina* and *A. xanthogrammica*). PhD Diss., University of Washington, Seattle.

Sebens, K.P., 1979. The regulation of a sexual reproduction and indeterminate size in the sea anemone *Anthopleura elegantissima* (Brandt). Biol. Bull. (Woods Hole, MA) 158, 370–382.

Sebens, K.P., 1980. The control of body size and longitudinal fission in the sea anemone *Anthopleura elegantissima* (Brandt). Biol. Bull. 161, 152–171.

Sebens, K.P., 1983. Population dynamics and habitat suitability of the intertidal sea anemones *Anthopleura elegantissima* and *A. xanthogrammica*. Ecol. Monger. 53, 405–433.

Sebens, K.P., 1984. Agonistic behavior in the intertidal sea anemone *Anthopleura xanthogrammica*. Biol. Bull. 166, 457–472.

Sebens, K.P., 1987. The ecology of indeterminate growth in animals. Ann. Rev. Ecolog. Syst. 18, 371–407.

Sebens, K.P., Koehl, M.A.R., 1984. Predation on zooplankton by the benthic anthozoans, *Alcyonium siderium* (Alcyonacea) and *Metridium senile* (Actiniaria) in the New England subtidal. Mar. Biol. 81, 255–271.

Shick, J.M., 1991. A Functional Biology of Sea Anemones. Chapman & Hall. 395 pp.

Stephenson, T.A., 1928. The British Sea Anemones, vol. 1. Ray Society, London, p. 148.

Stephenson, T.A., 1935. The British Sea Anemones, vol. 2. Ray Society, London, p. 426.

Tsuchida, C.B., Potts, D.C., 1994. The effect of illumination, food and symbionts on growth of the sea anemone *Anthopleura elegantissima* (Brandt, 1835): I. Ramet growth. J. Exp. Mar. Biol. Ecol. 183, 227–242.

Zamer, W.E., 1986. Physiological energetics of the intertidal sea anemone *Anthopleura elegantissima*: I. Prey capture, absorption efficiency and growth. Mar. Biol. 92, 299–314.