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Salinity effects on the growth, mortality and shell strength of *Balanus amphitrite* from the Salton Sea, California

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Abstract

The Salton Sea, the largest lake in California, has a salinity of around 43 g l^{-1} that is increasing by about 0.4 g l^{-1} y^{-1}. A 15 month microcosm experiment was conducted to determined the effects of salinity (30, 39, 48, 57, and 65 g l^{-1}) and tilapia (*Oreochromis mossambicus*) on an assemblage of benthic and planktonic Salton Sea algae and invertebrates, including the barnacle *Balanus amphitrite*. Eleven months after the microcosms were established, acrylic plates containing newly settled *B. amphitrite* collected at the Salton Sea were placed in the microcosms to determine the effects of salinity on their growth and shell strength. The Brody-Bertalanffy growth model was fitted to the *B. amphitrite* growth data. Growth was fastest at 48 g l^{-1} and slowest at 65 g l^{-1}. *B. amphitrite* grown at 39–48 g l^{-1} were the largest and required the greatest force to break, but the strength of the barnacle shell *material* declined steadily as the salinity increased. However, *B. amphitrite* at the higher salinities were shorter and had thicker walls relative to their diameters, which may have increased their structural stability.

The effects of salinity on the mortality of adult *B. amphitrite* was determined in laboratory aquaria set up at 43, 60, 70, 75, 80, 90, and 100 g l^{-1}. Salinities were achieved in two ways: by salt addition and by evaporation. Calculated 12-day LC_{50} values were 83 g l^{-1} when salinities were achieved through salt addition and 89 g l^{-1} when salinities were achieved through evaporation. Differences in *B. amphitrite* mortality between the two methods illustrate the importance of producing experimental salinity levels carefully. *B. amphitrite* is expected to become extinct within the Salton Sea when the salinity reaches 70–80 g l^{-1} and to show marked declines in abundance at salinities as low as 50 g l^{-1}.

Introduction

Probably introduced from the ocean into the Salton Sea by sea planes in the early 1940s (Raimonidi, 1992), *Balanus amphitrite* Darwin has successfully adapted to the non-marine ionic composition, 20 °C annual water temperature fluctuations and occasional summertime hypoxia. The salinity of the Salton Sea was 44 g l^{-1} in 1991 and is expected to increase to between 56 and > 91 g l^{-1} by 2010, depending on the extent of agricultural water conservation (Imperial Irrigation District 1986). *B. amphitrite* has been tested in laboratory experiments in salinities up to 48‰ (Vittor, 1968) and has been observed at field salinities as high as 75‰ (Simmons, 1957). These experiments were designed to determine how *B. amphitrite* growth, shell strength and mortality might be affected by the increasing salinity of the Salton Sea.

B. amphitrite, a fast growing, generally tropical barnacle, is capable of withstanding a wide range of environmental conditions, but its intertidal distribution is considered to be limited by predation and competition (Ortega, 1981). For the adults of *B. amphitrite* in the Salton Sea, however, interspecific competition and predation are virtually nonexistent. Here its horizontal distribution is mostly limited by the relatively small amount of hard substrate present around the lake (Linsley & Carpelan, 1961). In the absence of competitors and predators, and with daily settlement rates at times greater than 30 individuals cm^{-2} (Linsley

& Carpelan, 1961), dense aggregations of *B. amphitrite* quickly cover all hard substrates. The collapse of aggregations appears to be a major cause of adult mortality (Vittor, 1968). Aggregation collapse may be aggravated by the fact that the shell of *B. amphitrite* in the Salton Sea appears to be much weaker than that of *B. amphitrite amphitrite* in the ocean.

Despite its limited distribution, the contribution that *B. amphitrite* provides to the Salton Sea benthos is not insignificant. *B. amphitrite* aggregations provide living space for a substantial number of organisms including the amphipod *Gammarus mucronatus* Say and small individuals of the polychaete *Neanthes succinea* Frey & Leuckart. Barnacle contributions to infaunal diversity were demonstrated by Reimer (1967a, 1976b) in Panama, who found an average of 53 and 130 macrofaunal species associated with live and dead *Tetraclita stalactifera*, respectively. Within the Salton Sea, the extremely high productivity of *B. amphitrite* contributes to a new substrate: entire beaches have been formed from *B. amphitrite* shells (Linsley & Carpelan, 1961). These beaches are occupied by large numbers of *Neanthes* (Kuhl & Oglesby, 1979). *B. amphitrite* larvae form a major portion of the zooplankton, especially near shore (Carpelan, 1961), and are found in the plankton most of the year, except during summer.

The specific objective of this study was to determine the effects of salinity on the shell strength, growth and mortality of *Balanus amphitrite* from the Salton Sea population. The effects of salinity on the growth and shell strength was determined as a part of a microcosm experiment designed to test the effects of salinity and fish on a semi-natural assemblage of Salton Sea organisms (González et al., 1998a,b; Hart et al., 1998; Simpson et al., 1998). The effect of salinity on the short term mortality of *B. amphitrite* was determined in laboratory aquaria.

Methods

Growth and strength

The effects of salinity on the growth and strength of *B. amphitrite* were determined during a 15 month microcosm experiment. The establishment of these microcosms is detailed by González et al. (1998a), Hart et al. (1998) and Simpson et al. (1998), so an abridged description is provided here. The experiment used a 5 × 2 incomplete factorial randomized block design to test the effects of 5 salinity levels (30, 39, 48, 57, and 65 g l^{-1}) and 2 fish density levels (0 and 1 fish per tank) on an assemblage of organisms collected from the Salton Sea and other water bodies in the region. Microcosms with fish were set up only for the 39 and 57 g l^{-1} salinity levels. Thus there was a total of 7 treatment combinations, each replicated 4 times. The experiment used 380 l tanks with a sloped bottom maintained on the roof of the Life Sciences building at San Diego State University (32°46′ N lat., 117°05′ W long.).

The tanks were filled with Salton Sea water on November 20, 1990, diluted to 30 g l^{-1} by adding tap water and, by January 17, 1991, raised to the desired experimental salinities by the addition of pure salts (NaCl, $MgSO_4$, KCl, Na_2SO_4). Three liters of organically rich sediments collected from the Salton Sea shoreline were placed on the bottom of each tank as a nutrient source and substrate. A single juvenile tilapia (*Oreochromis mossambicus*) was successfully introduced to each of the 8 appropriate microcosms on September 28, 1991.

Evaporative water loss was compensated for by adding dechlorinated tap water, the upper portions of the tank walls were scrubbed every two weeks to prevent excessive build-up of attached organisms, and *B. amphitrite* were periodically removed from the interior of the airlift pipes to ensure wate circulation.

B. amphitrite from the Salton Sea were placed in the tanks and their growth was followed for 124 days, at which time the shell strength of the individuals that grew was measured. The barnacles were collected from the Salton Sea using 10.2 × 12.7 cm clear acrylic settling plates. On October 22, 1991, 48 plates were placed in the water on the pilings of a dock on the west shore of the lake. After 14 days the plates were recovered, placed in 20 l buckets full of Salton Sea water and returned to the laboratory at San Diego State University. The plates were placed in aerated plastic washtubs containing Salton Sea water collected from the same location.

The plates were cleaned of corixid (*Trichocorixa reticulata* Guérin-Menéville) eggs and corophiid amphipod tubes with a toothbrush. One plate with at least 10 *B. amphitrite* individuals on one side was randomly selected for placement into each microcosm. All organisms were removed from the back of each plate allowing the *B. amphitrite* bases on the front to be easily observed through the plate. The positions of the individual barnacles were mapped on acetate sheets and the maximum basal diameter of each individual

was measured using digital calipers. Measurements were made through the back of the transparent settling plate whenever neighboring barnacles prevented direct access to a barnacle.

One plate was placed against the southern wall of each tank, with the top of the plate 5 cm below the water surface, on November 11, 1991, six days after collection and 20 days after the plates had initially been placed in the Salton Sea. The *B. amphitrite* were remeasured at 7, 22, 50, 72 and 124 days after placement within the microcosms. The backs of the settling plates were cleaned and new acetate maps were made on each measurement date, including the positions and sizes of new recruits. The presence of dead or crowded individuals was also noted.

All *B. amphitrite* that showed detectable growth achieved a basal diameter of at least 7 mm, so only those individuals reaching this size were used for analyzing the changes of *B. amphitrite* growth with increased salinity. The Brody-Bertalanffy growth equation was fit to the growth of each *B. amphitrite* reaching 7 mm using Fabens (1965) method modified for Mathematica (Wolfram Research Inc. 1993) on a NeXT computer. Since the basal diameter of *B. amphitrite* upon settling could not be accurately determined using the Brody-Bertalanffy growth model, a value of 1.0 mm was arbitrarily selected for the model parameter b. This had no effect on the other model parameters. An overall Brody-Bertalanffy equation was also calculated for all fast growing barnacles in each tank. The Brody-Bertalanffy model was also fit to the growth of *B. amphitrite* in sea water as measured by Iwaki & Hattori (1987) and by Hirano & Okushi (1952) for comparison to *B. amphitrite* growth in the microcosms. In fitting the model to the *B. amphitrite* growth measured by Hirano & Okushi, we used only their data points collected from individuals older than 15 days.

Correlation analysis was performed to test the relationships between the final size of *B. amphitrite* predicted by the Brody-Bertalanffy growth model and the growth rate constant, between the final size and the size of the barnacles when initially placed in the microcosms, and between the growth rate constant and the initial size. The size of *B. amphitrite* on the settling plates was also contrasted with the size of the largest *B. amphitrite* on the wall of each microcosm, measured at the end of the experiment.

Regression analysis was performed to determine the effects of salinity of *B. amphitrite* wall strength, size (diameter, height, and wall thickness), size ratios (height:diameter and wall thickness:diameter ratios), and the maximum force withstood before breaking. Values for dependent variables were log transformed prior to analysis. Each regression analysis used only a single value, a mean, for each salinity level.

After 124 days in the microcosms, the settling plates were removed, placed in Salton Sea water of the same salinity as the microcosms from which they came, and transported to the mechanical engineering laboratory at San Diego State University. The fracture strength of the shell of each live, uncrowded *B. amphitrite* larger than 6 mm was tested using a Chatillon 1100 Universal Tensile Tester.

Prior to testing, the basal diameter and height of each *B. amphitrite* was measured. The settling plate was secured to the tensile tester as close as possible to the individual to be tested, with the lateral and carinolateral plates of the barnacle oriented toward the opposite side of the tensile tester. A steel plate was then brought into contact with the barnacle, and the distance between the steel plate and the settling plate was measured (Figure 1). Every attempt was made to make that distance equal to one half the height of the barnacle. The tensile tester was activated, and the force exerted on the barnacle was plotted. The maximum force attained was noted, as was the distance along which the force was applied. The settling plate was then removed and the width of the fractured barnacle shell wall was measured using digital calipers. The *B. amphitrite* wall fracture strength (σ_{wall}, measured as N/mm^2) was determined assuming that the force was applied mainly to the lateral and carinolateral plates. *B. amphitrite* wall fracture strength was calculated as:

$$\sigma_{wall} = R\,F\,D/I_{wall} \text{ (Wainwright et al., 1976)}$$

where R is the barnacle radius (mm), F is the maximum force (N or newtons) required to break the barnacle, D is the distance (mm) above the barnacle base at which the force was applied, and I_{wall} is a parameter related to the shape of the curved barnacle plates defined as the second moment of area. I_{wall} was calculated as $\pi\,R\,T^3/36$ where T is the wall thickness (mm).

At the end of the experiment in May 1992, after the tanks were emptied of water and sediment, all *B. amphitrite* on the tank walls were located and their basal diameters measured. The effects of salinity on the diameter of the largest *B. amphitrite* on each microcosm wall was tested using a 1-way ANOVA of the log transformed size data.

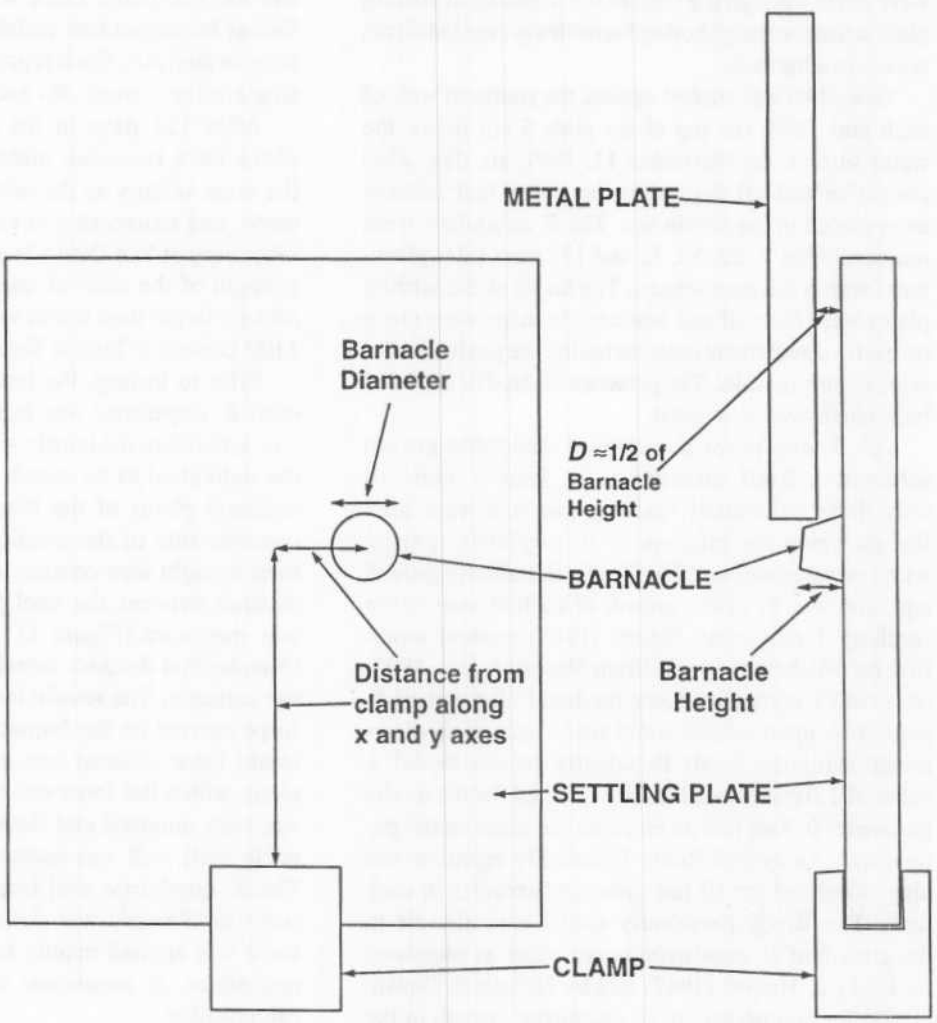

Figure 1. Placement and measurement of *Balanus amphitrite* on tensile tester. The clamp held the plexiglass settling plate in place while the metal plate moved down through the barnacle.

Salinity tolerance

The salinity tolerance of adult *B. amphitrite* was experimentally determined in the laboratory. The experiment used a 7 × 2 factorial design to test the effects of 7 salinity levels (100, 90, 80, 75, 70, 60, and 43 g l^{-1}) on *B. amphitrite* mortality. Two methods were utilized to achieve the 7 salinity levels: salt addition and evaporative concentration. The evaporation method consisted of filtering Salton Sea water through 35 μm-mesh netting, evaporating it to 100 g l^{-1} in outdoor containers, then diluting to the desired salinities using deionized water. The salt addition method consisted of adding to 43 g l^{-1} Salton Sea water pure salts to yield ionic proportions approximating those in the Salton Sea, until the desired salinities were attained. The salts added were, by weight, 63% NaCl, 18% Na_2SO_4, 17% $MgSO_4$, and 2% KCl. Each treatment combination had 2 replicates. Each replicate consisted of a 5 l plastic aquarium with 2 l of water. The aquaria were distributed in the laboratory utilizing a randomized complete block design. The water was aerated and salinities were maintained through daily additions of deionized water. The aquaria were maintained on a 16:8 hr light:dark regimen at 27–28 °C. *Nanochloropsis* sp. was maintained at at least 10^{12} cells l^{-1} as a food source.

Twenty-eight large clumps of live *B. amphitrite* were collected from the Salton Sea on July 13, 1991. The live *B. amphitrite* in each clump were counted on

July 18, 1991, and one clump was randomly assigned to each aquarium. Each clump initially contained 97–644 barnacles (mean = 248). The number of surviving *B. amphitrite* was determined 4 and 12 days later. A barnacle was considered alive if its operculum would not give when touched. While this method may have underestimated the number of dead barnacles, tissue decay was very rapid, and a barnacle would be unequivocally recognized as dead within 24 hours of death.

The effects of salinity and salt concentration method were tested using a 2-way ANOVA of the arcsine transformed values for percent mortality at 4 and 12 days. A separate probit analysis was performed to determine a 12-day LC_{50} value for each salt concentration method (Finney, 1971). The data for the lowest salinity (43 g l^{-1}) were not used in the probit analyses.

Results

As described below, barnacle mortality was high early in the experiment, and many of the barnacles that did survive grew almost not at all. These factors greatly reduced the power of the experiment to detect fish effects on the response variables of interest, and none were found. Thus the analyses for salinity effects presented here treated microcosms with fish as simply additional replicate microcosms for the salinities involved (39 and 57 g l^{-1}).

Growth and strength

The growth of a total of 387 *B. amphitrite* was followed on the settling plates, most of which recruited onto the plates after they were placed in the microcosms. Of the 387 barnacles, 255 did not survive long enough to be measured more than once (Figure 2). This early mortality was 100 percent in 13 of the 28 tanks and showed no apparent relation to salinity level. Mean percent mortality for the treatments, in order of increasing salinity, was 81, 94, 86, 92, and 84 (1-way ANOVA of arcsine-transformed data, $F_{4,23} = 0.31$, $P = 0.87$).

Of the 132 barnacles that survived, 106 either did not grow or grew extremely slowly throughout the experiment, none attaining a diameter of 5 mm (Figure 2). The data for the 15 microcosms having some survivors show that these slow-growers comprised a highly variable percentage of the survivors. This percentage averaged 85, 25, 50, 99, and 89 for the treatments in increasing order of salinity. For three of these treatments, values for replicate microcosms ranged from 0 to 100 percent. There was no clear evidence of a relationship between salinity and percentage of survivors that were slow growers (1-way ANOVA for arcsine-transformed data, $F_{4,10} = 0.86$, $P = 0.48$).

Twenty-six of the barnacles that survived grew rapidly, achieving basal diameters of at least 7 mm by the end of the experiment (Figure 2). These 26 were individuals which had settled on the plates while these were in the Salton Sea. These fast-growers were found in two microcosms at 39 g l^{-1} and in one microcosm at each of the other salinities.

The growth of the 26 barnacles which grew rapidly in the microcosms was similar to the growth of *Balanus amphitrite* measured in the field (Hirano & Okushi, 1952; Costlow & Bookhout, 1956; Iwaki & Hattori, 1987), and the growth of the slow growing barnacles was similar to that observed under laboratory conditions by Costlow & Bookhout (1956). Therefore all analyses of barnacle growth and shell strength were performed using only the 26 fast-growing barnacles. The slow-growers formed a distinct mode in the size-frequency distribution for all barnacles, and we presume they were individuals perhaps traumatized by some aspect of our procedures other than the salinity treatments.

The overall Brody-Bertalanffy growth curves for each salinity are in Figure 3. Although the Brody-Bertalanffy model fit the growth of all *B. amphitrite* individuals very well, there was a large amount of variability within microcosms in their size at the end of the experiment, i.e. at 145–165 days post-settlement. However, no correlations were found between initial size and predicted final size, between initial size and the calculated growth rate constant, or between the predicted final size and the growth rate constant (Simpson, 1994).

On the settling plates, *B. amphitrite* wall thickness was greatest at 39 and 48 g l^{-1} (Figure 4). The *B. amphitrite* with the largest diameters on the microcosm walls (Table 1) and on the settling plates (Figures 3, 4) were at 39 and 48 g l^{-1}. Relative to their diameter, however, the *B. amphitrite* grown at salinities above 39 g l^{-1} were shorter and had thicker walls (Figure 4). The force required to break *B. amphitrite* was greatest at 48 g l^{-1}, but the material strength of the wall declined steadily as the salinity increased.

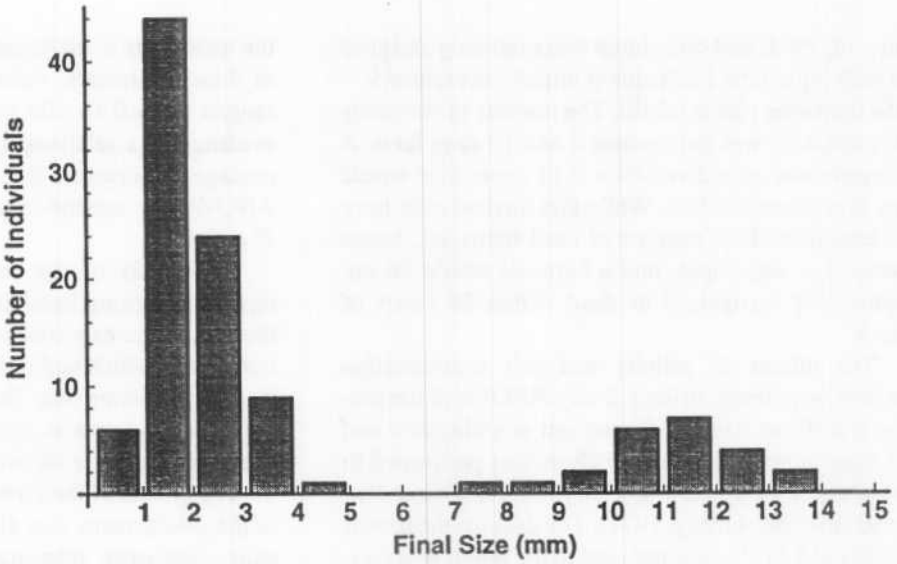

Figure 2. Frequency distribution of Balanus amphitrite size (basal diameter) at time of death or upon removal from the microcosm.

Table 1. Basal diameter of the largest barnacle on the floor of each microcosm at the termination of the experiment. One microcosm at 65 g l^{-1} contained no barnacles. One-way ANOVA, $F_{4,22} = 8.01$, $P < 0.001$

Salinity (g l^{-1})	Basal diameter (mm) Mean	Range	*n*
30	17.4	15.1–20.3	4
39	18.5	16.3–22.7	8
48	18.5	16.5–22.4	4
57	13.5	10.7–16.0	8
65	13.4	11.9–14.5	3

Balanus amphitrite salinity tolerance

In the laboratory salinity tolerance experiments, few *B. amphitrite* died within the first 4 days. After 12 days, however, mortality was usually greater than 50 percent at salinities of 80 g l^{-1} or greater (Figure 5). The 12-day LC_{50} in evaporated water was 89 g l^{-1} (95% Cl: 65–144), and that in salt-added water was 83 g l^{-1} (95% Cl: 57–133). There was no strong evidence the difference was real ($P > 0.3$). A 2-way ANOVA did suggest, however, a real effect of salinity manipulation method on other aspects of the pattern of mortality rate over the tested salinity range ($F_{1,14} = 5.13$, $P < 0.05$). The laboratory containers prepared with evaporated water developed much higher concentrations of *Nanochloropsis* than did those prepared by salt addition. This or some other difference in microbial populations may account for the different patterns of mortality increase with salinity increase for the two methods of producing the salinities.

Discussion

Balanus amphitrite growth

The 48 g l^{-1} treatment produced the highest *B. amphitrite* growth rate (Figure 3), the largest final basal diameter (Figure 4, Table 1), the second largest final height, the thickest walls, and the highest nauplius production (Hart et al., 1998). As a result of their large size, the *B. amphitrite* at 48 g l^{-1} also required the greatest force to break. The strength of the shell material declined, however, and the barnacles became shorter and developed thicker walls relative to their diameters as the salinity increased. The shorter, thicker walls increase stability, i.e. their ability to withstand forces based on their architecture, and may partly compensate for the reduced material strength, such that the hardest individuals to break are at 48 g l^{-1}, not at 30 g l^{-1} where the walls are strongest. Since it is not the strength of the wall *per se* which is of ultimate importance, but the survival of the individual, *B. amphitrite* that grew at 48 g l^{-1} seemed best able to withstand physical stress.

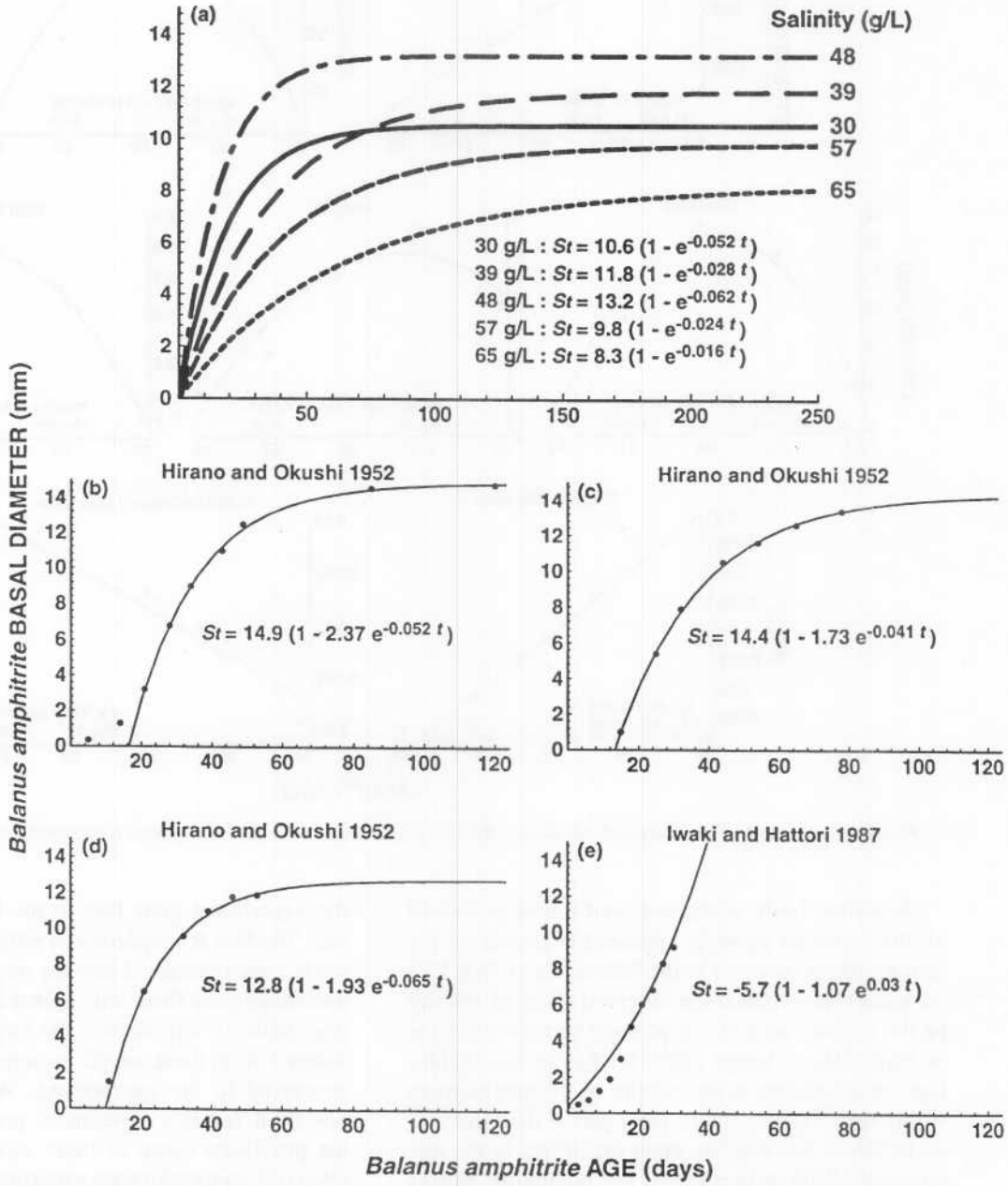

Figure 3. Brody-Bertalanffy curves fit to *Balanus amphitrite* growth data. (a) Mean growth curves of *B. amphitrite* grown on microcosm settling plates for each salinity. *B. amphitrite* measured by Hiranco & Okushi (1952) in (b) May–September, (c) June–September, (d) July–September. Points in plots b–e represent the individual barnacles measured in those studies. Data from barnacles younger than 16 days not used for curve fit (see text). Equations are Brody-Bertalanffy curves fit to *B. amphitrite* growth data and take the form: $S_t = S_{max}\ (1 - be^{-kt})$ where S_t is the size at time t, S_{max} is the maximum size possible, K is the growth rate constant and b is related to the size at recruitment (S_0) via the equation $b = 1 - S_0/S_{max}$. b was set to 1 for B. amphitrite grown on settling plates (see text).

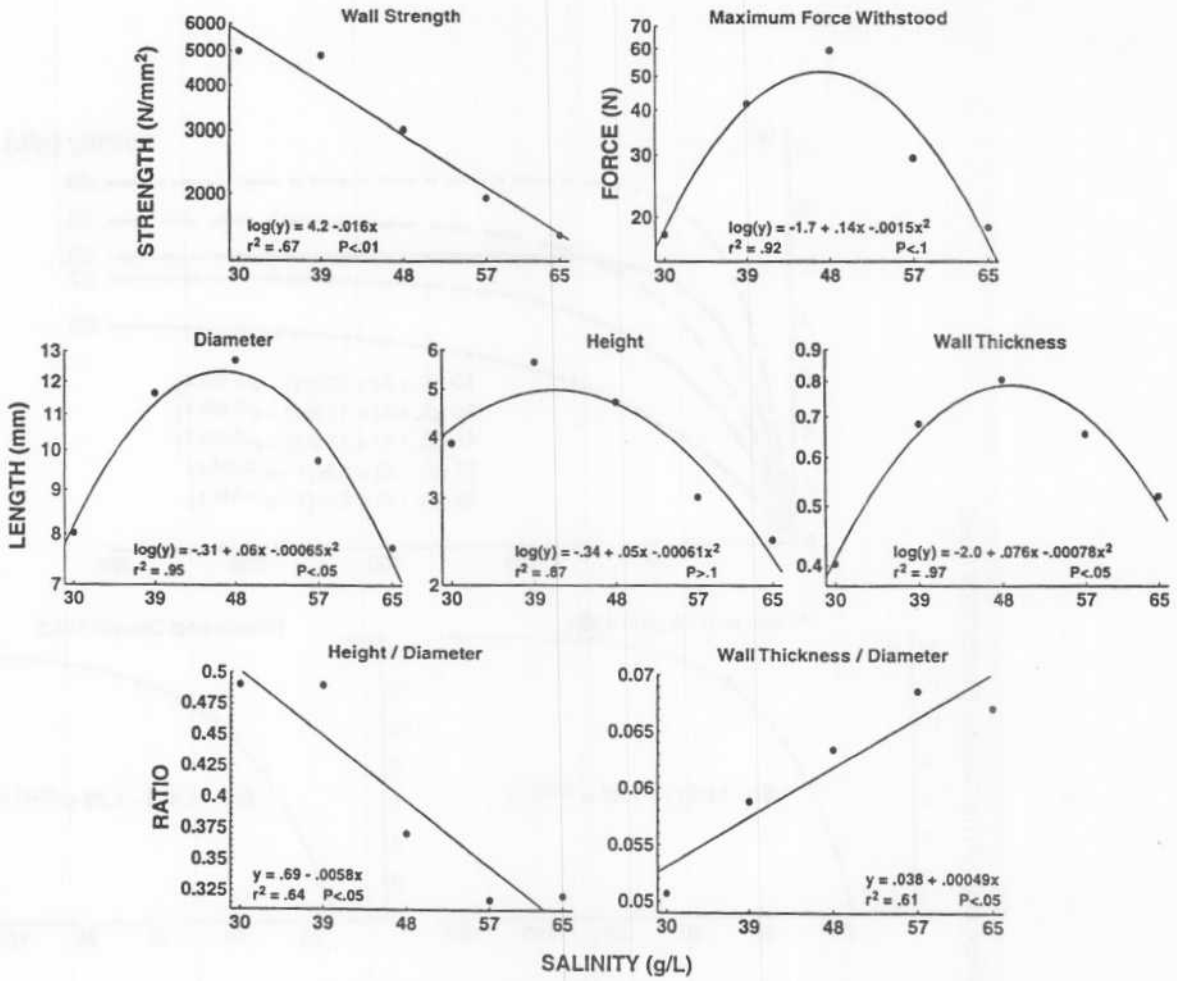

Figure 4. Regressions of strength and dimensions of *Balanus amphitrite* on salinity. Values plotted are treatment means at each salinity.

Since the birth, settlement, and initial growth of all the barnacles showing appreciable growth on the settling plates occurred in the Salton Sea at 44 g l^{-1}, we cannot say whether the observed effect of salinity on the growth rate and size of these barnacles reflects an evolutionary change within the Salton Sea population, an adaptation to the salinity of the environment within which they spent the early part of their lives, or an influence mediated by other organisms in the microcosms. With respect to this last possibility, slower growth at the highest salinity may have reflected a lower food supply. During most of the experiment, grazing by *Artemia* caused phytoplankton density to be 50–95 percent lower at 65 g l^{-1} than at other salinities (González et al., 1998b).

It is similarly uncertain why the barnacles measured on the walls of the microcosms at the end of the experiment grew best at the intermediate salinities. The first *B. amphitrite* to settle on the microcosm walls were inoculated into the microcosms as nauplii when they were filled with Salton Sea water. Thus it is impossible to tell whether the largest individuals developed from these nauplii or represented individuals conceived in the microcosms. Although the methods used for this experiment preclude determining the proximate cause of these salinity effects, a few relatively straightforward experiments might.

Linsley & Carpelan (1961) thought that *B. amphitrite* from the Salton Sea was broken easily because faster growth in the Salton Sea resulted in thinner shells. However, the lateral shell walls of *B. amphitrite* weakened as salinity increased (Figure 4), despite having faster growth at salinities below 57 g l^{-1} (Figure 3). The weakened shells may be due to either

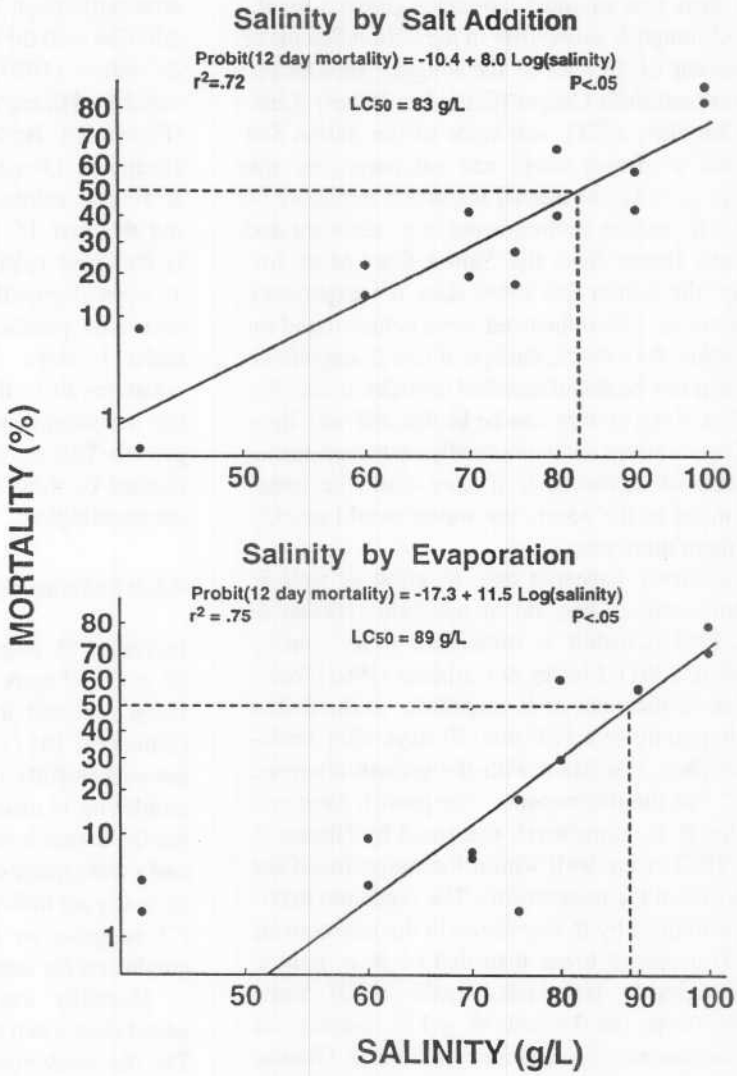

Figure 5. Effects of salinity and salt concentration method on 12 day mortality of *Balanus amphitrite*. 43 g L^{-1} values are not included in calculation of probit regressions. P values under equations are for regression slopes. Dashed lines indicate LC_{50} predicted by probit regression. P values for 2-way ANOVA at 12 days were: Salinity: $P < 0.001$; Salt concentration method: $0.01 < P < 0.05$; Interaction: $P > 0.1$.

structural or chemical changes within the shell wall. *B. amphitrite* has relatively large parietal pores, compared to other marine barnacles (Barnes et al., 1970). If the pores become larger with salinity, the integrity of the shell would be compromised. All treatments appeared to be saturated with $CaCO_3$ (González et al., 1998a) so the necessary ions were probably available to the barnacles at all salinities. However, trace elements incorporated into the walls might have affected wall strength. Both the substitution of Ca^2 by Mg^2 during wall mineralization as well as the prevalence in the shell matrix of other trace elements which do not substitute for Ca^2, such as boron, tend to increase as salinity increases (Lowenstam & Weiner, 1989).

The experiment has demonstrated that the walls of *B. amphitrite* become weaker as salinity increases, but that changes in the wall morphology can compensate for the reduced material strength. The perception of weak shells and easy breakage in the Salton Sea may reflect the tendency of *B. amphitrite* to settle near conspecific adults (Clare et al., 1994) and their ability to develop larger clumps in the Salton Sea than they normally can in the ocean, as well as their having an adult shell wall apparently inherently

weaker than that of most barnacles (Barnes et al., 1970). Although *B. amphitrite* in the Salton Sea make up 5 percent of the diet of the longjaw mudsucker, *Gillichthys mirabilis* Cooper (Gobiidae: Pisces) (Linsley & Carpelan, 1961), and some of the Salton Sea birds such as diving ducks can eat barnacles, the organisms usually considered important predators of barnacles in marine environments, e.g. sea stars and snails, are absent from the Salton Sea. More importantly, the Salton Sea shore does not experience the continuous, tide influenced wave action found on ocean shores. As a result, clumps of live *B. amphitrite* 10 cm deep can be found attached to rocks around the Salton Sea. Such clumps can be broken off with little effort. These clumps are undoubtedly destroyed during the occasional storms and, if they could be transplanted intact to the ocean, the waves would quickly destroy them there too.

B. amphitrite appeared able to grow as well in the microcosms as they do in the field (Hirano & Okushi, 1952; Costlow & Bookhout, 1956; Linsley & Carpelan, 1961). Linsley & Carpelan (1961) found that the basal diameter of *B. amphitrite* in the Salton Sea during summer was 9 mm 30 days after settlement, which is consistent with the growth observed at 39 g l^{-1} in the microcosms. The growth rates calculated for *B. a. hawaiiensis* measured by Hirano & Okushi (1952) were well within the range found for *B. amphitrite* in the microcosms. The predicted maximum size attained by *B. amphitrite* in the microcosms (Figure 3) averaged lower than that of *B. a. hawaiiensis* measured by Hirano & Okushi (1952). Some *B. amphitrite* in the 39 and 48 g l^{-1} microcosms were in the size range measured by Hirano & Okushi, however, and, at salinities below 57 g l^{-1}, many *B. amphitrite* larger than 20 mm were found attached to the microcosm floors.

B. amphitrite in the microcosms approached their maximum size by 30 to 50 days. Hirano & Okushi (1952) found that *B. a. hawaiiensis* approached their maximum size by 40–50 days, and that nauplius release began at that time regardless of the actual size achieved. Costlow & Bookhout (1956) found that *B. a. niveus* growth slowed after 35 days, although their data were admittedly inconclusive.

The Brody-Bertalanffy growth model described very well the growth of *B. amphitrite* within the microcosms as well as the growth of *B. a. hawaiiensis* measured by Hirano & Okushi (1952) beginning in June (Figure 3c) and in July (Figure 3d). All these data are limited to barnacles first measured 15 days after settlement. The Brody-Bertalanffy model did not describe well the short term growth measured by Iwaki & Hattori (1987) (Figure 3e) nor the growth measured by Hirano & Okushi (1952) beginning in May (Figure 3b). Both the early growth data collected by Hirano & Okushi and the data collected by Iwaki & Hattori suggest an exponential growth curve during the first 15 days of growth. A different model is therefore required for data that includes the first 15 days of growth, and the Brody-Bertalanffy growth equations produced here cannot be extrapolated to under 15 days. This is why the Brody-Bertalanffy equations fit to the Hirano & Okushi data used only the measurements collected after at least 16 days of growth. This also means that the sizes at settlement estimated by these Brody-Bertalanffy growth equations are meaningless.

Adult Balanus amphitrite salinity tolerance

Increased *B. amphitrite* mortality at salinities above 75 g l^{-1} (Figure 5) corresponds with *B. amphitrite* being reported in water no more saline than 75‰ (Simmons, 1957). It is possible that *B. amphitrite* cannot successfully reproduce at 75 g l^{-1}. However, *B. amphitrite* is usually considered an intertidal and estuarine barnacle that naturally experiences desiccation and a wide range of salinity (Newman, 1967). Survival of nearly all individuals for 4 days in as high as 100 g l^{-1} suggests an ability to tolerate very hypersaline conditions for short periods.

Mortality was slightly higher when salts were added than when the water was evaporated (Figure 5). The *Nanochloropsis* bloom that occurred in the evaporatively concentrated treatments suggested the presence of increased nutrients in that water, and food availability may have been responsible for the difference in mortality. This demonstrates the potential consequences of the method chosen for achieving experimental salinity levels. By adding salts to the lowest salinity level, all treatments had the same dissolved nutrient concentration, at least initially. By evaporating the water to the highest salinity level and diluting with deionized water, treatments were produced that differed not only in their total ionic strength, but also in the concentration of dissolved nutrients. The nutrient levels at 100 g l^{-1} were initially about 2.5 times those at 43 g l^{-1}. Therefore, if *B. amphitrite* mortality is affected by the nutrient concentration then that effect will vary across treatment levels in the evaporated water, but not in the salts-added water.

The salinity levels produced through evaporation are likely to differ from the salts-added water in some other basic ways. By evaporating the water to 100 g l^{-1}, it is likely that some salts, especially $CaCO_3$, precipitated out of solution prior to dilution with deionized water. Ca^2 levels were therefore lower in these treatments than in the salts added water. $CaCO_3$ is a buffer, so its loss may have resulted in different pH and alkalinity levels in the evaporated treatments than in the salts added treatments. Finally, the process of evaporation took some time as it was accomplished using only solar radiation. Although the water was coarsely filtered prior to evaporation, bacteria and much phytoplankton would not have been removed by the filter, and these could have altered the nutrient conditions of the water.

The results presented here suggest that *B. amphitrite* will most likely disappear from the Salton Sea when its salinity reaches 70–80 g l^{-1}. However, unless further adaptation to the increasing salinity occurs, the Salton Sea population will begin to decline as the salinity increases much above 50 g l^{-1} as individual growth rates decline making reproduction begin at a smaller size, and as the shell walls weaken making the barnacles more susceptible to physical disturbance. The loss of *B. amphitrite* will result in lost habitat for the organisms associated with them, and the eventual loss of the *B. amphitrite* shell beaches and any faunal assemblage especially associated with them. Further, these results raise some interesting questions regarding the optimization of the barnacle wall structure. How do the mechanisms resulting in a more stable shape relate to the mechanisms resulting in a weaker shell material, or is the apparent balance between wall shape and material strength merely a coincidence?

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