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The effect of salinity on larval survival and development in the sea urchin *Echinometra lucunter*

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Summary

Reductions in salinity can have adverse effects on larval development and larval survival in some invertebrate taxa but not others. Salinity tolerance of larvae may be particularly important in echinoderms because they are both poor ion regulators and stenohaline. I examined the effect of six levels of salinity (15, 18, 21, 24, 27 and 33 PSU) on survival and rate of development of larvae in the subtropical sea urchin *Echinometra lucunter*. In the short-term, mortality rate was significantly lower in 33 PSU than in all other salinities except 27 PSU, and it was significantly greater in 15 and 18 PSU than in all higher salinities. In the long-term, daily and cumulative mortality were significantly greater in 15 PSU than in most other salinities over 11 days of development (except for cumulative mortality in 18 PSU). They were significantly greater in 18 PSU than in 21 PSU or 33 PSU over a period of 13 days. Furthermore, daily mortality was significantly greater in 18 PSU than in 24 PSU or 27 PSU at 13 d after fertilization. Daily and cumulative mortality were significantly lower in 33 PSU than in 21, 24 or 27 PSU over a period of 17 days. Although in the control (33 PSU) 75% of larvae completed development to the 8-arm stage at 35 d, no larvae developed further than the 4-arm stage in 18, 21, 24 or 27 PSU; in 15 PSU, ~60% of larvae did not develop further than swimming blastulae. Since prolonged exposure to salinities as high as 27 PSU (frequently recorded in the adult habitat) can result in great larval losses, adaptive behaviours that prevent larvae from entering water layers of low salinity will enhance their chance for survival.

Key words: Development, larvae, mortality, salinity, sea urchin.

Introduction

The importance of salinity in determining rates of survival and development in larvae of marine benthic invertebrates has not been established clearly. Although several studies on different invertebrate taxa have shown that deviations in salinity from ambient values can result in increased mortality and/or delayed development (e.g. barnacles: Anil and Kurian, 1996; Crisp and Costlow, 1963; bivalves: Bayne, 1965; Calabrese and Davis, 1970; echinoderms: Roller and Stickle, 1985,

1994; polychaetes: Gray, 1976; Richmond and Woodin, 1996), others concluded that salinity is not an important factor in determining larval survival (e.g. Young and Hazlett, 1978; Greenwood and Bennett, 1981; Laughlin, 1983; Cameron et al., 1985; Pechenik, 1987).

The salinity tolerance of larvae can be affected by a number of factors, the most important being temperature (e.g. Gray, 1976; Watts et al., 1982; Anil and Kurian, 1996) but also by length and frequency of exposure to the altered level of salinity, larval stage and/or age, and food concentration (e.g. Costlow et al.,

1960; Roller and Stickle, 1993; Anil and Kurian, 1996; Richmond and Woodin, 1996).

Echinoderms are probably the most stenohaline of marine invertebrates (Stickle and Diehl, 1987) possibly because they are among the poorest ion regulators (Kinne, 1971). Larvae are less capable of ion regulation than adults (Kinne, 1971) and a few studies have demonstrated an adverse effect of decreased salinity on larval survival (e.g. Lucas, 1973; Watts et al. 1982; Roller and Stickle, 1985, 1993, 1994; but see Cameron et al., 1985). Stickle and Diehl (1987) suggested that the distribution of echinoderms along salinity gradients may depend upon the salinity tolerance of the larvae.

Echinometra lucunter is a subtropical sea urchin that has a wide distribution ranging from North Carolina, U.S.A., throughout the Caribbean, to Brazil. This species is found in intertidal and shallow subtidal habitats such as rocky areas, coral reefs and seagrass beds (McPherson, 1969; Hendler et al., 1995) and thus the adults are probably exposed to a wide range of salinities during their lifetime. In a previous study, Metaxas and Young (1998) showed that the larvae of this species did not cross haloclines into water layers of 21–27 PSU; but, they remained suspended immediately below the halocline in 33 PSU. In this study, I examined the effects of salinity on larval survival and development to assess whether the avoidance response of larvae to reduced salinity can be potentially adaptive by reducing the risk of osmotic stress and possibly death. I determined rates of mortality and development in salinities ranging from 15 to 33 PSU both in short- (24 h) and long-term (entire period of larval development –37d) experiments.

Methods

Fertilization and larval culture

I collected adults of *E. lucunter* from the low intertidal and shallow subtidal zones of a rock jetty on the south side of Fort Pierce Inlet, Fort Pierce, Florida on 11 October 1996. Injection of ~2 ml of 0.55M KCl through the peristomial membrane induced spawning in the laboratory within 1–2 h after collection. For fertilization, I mixed sperm and eggs of five pairs of spawning adults and then combined the zygotes from all urchin pairs (fertilization success was 99.4–100%) to use in the experimental larval cultures. For all experiments, I reared the larvae under a high ration of a mixed microalgal species diet (*Isochrysis galbana*, *Dunaliella tertiolecta*, *Thalassiosira weissflogii*) known to result in rapidly-completed larval development (Metaxas and Young, 1998—see their Table 1 for a description of the composition of the diet). The larval cultures were in a

temperature-controlled room (23–24 °C) with fluorescent lighting (~50 $\mu\text{E m}^{-2} \text{s}^{-1}$) under a 12:12 h light:dark cycle. I changed the water in the culture jars and added exponentially-growing microalgae every two days.

Short-term effects of salinity on larval survival

I reared larvae in a 4-l culture jar at a density of 1 larva ml^{-1} of 0.45 μm -filtered seawater 33 PSU. I examined the effect of salinity on 24-h rate of mortality at 2, 5, 34 and 39 d after fertilization when >90% of the larvae in the culture had reached the 2-, 4-, 6- and 8-arm stages of development, respectively. On each experimental day, I introduced 50–75 larvae into finger bowls (three replicate bowls for each salinity) that contained 150 ml seawater at one of six salinities: 15, 18, 21, 24, 27 or 33 PSU. The different salinities were obtained by diluting full-strength (33 PSU), 0.45 μm -filtered natural seawater with 0.45 μm -filtered distilled water. After 24 h, I determined rate of mortality as the proportion of dead larvae (i.e. larvae not reacting to gentle prodding) in each replicate. I examined the effects of salinity (six levels) and developmental stage (four levels) on mortality rate using two-way ANOVA (fixed factors) and *a posteriori* multiple comparisons among means with Student-Newman-Keuls (SNK) tests.

Long-term effects of salinity on larval survival and rate of development

I introduced 150–250 zygotes and reared the larvae in finger bowls that contained 150 ml seawater at one of six salinities (three replicate bowls for each salinity): 15, 18, 21, 24, 27 or 33 PSU (see above for seawater preparation). After recording the number of live and dead larvae in each developmental stage, I removed all dead larvae from the bowls at 3 d after fertilization and at every 2 d thereafter, until no surviving larvae remained (or until 37 d in the control when >95% of larvae were in the 8-arm stage).

For each sampling date from 3 to 19 d after fertilization, I examined the independence in the number of live larvae between each developmental stage and salinity by two-way contingency tables using log-linear models (Sokal and Rohlf, 1981). Treatments are independent when a log-linear model fits the data well and the values of the G-statistic are low and therefore not significant. I examined the fit to the data of the model which contained the terms salinity and developmental stage but not the two-way interaction term (salinity \times developmental stage) because the full model yields expected values equal to the observed values (Fienberg, 1970). For a particular sampling date, the analyses

included each level of salinity with >10 surviving larvae. Because the sampling date at which there were <10 surviving larvae varied among salinities, the number of levels of salinity varied for each sampling date as follows: six levels (15, 18, 21, 24, 27 and 33) for 3, 5, 7, 9, 11 and 13 d; four levels (21, 24, 27 and 33) for 15 and 17 d; and three levels (24, 27, and 33) for 19 d. For all sampling dates, there were five levels for the factor developmental stage: swimming blastula, prism, 2-, 4- and 6-arm. For this analysis, I pooled replicates for each sampling date and level of salinity because analysis by two-way contingency tables (replicate with three levels and developmental stage with six levels) indicated homogeneity of replicates (Sokal and Rohlf, 1981).

I examined the effect of salinity on daily and cumulative mortality over the period of larval development. Because the sampling date at which cumulative mortality reached ~100% varied among salinities, it was not possible to do a single analysis with a balanced design using the entire data set. To maximize the information included in the analysis without using an unbalanced design, I did three separate ANOVAs by dividing the developmental period into three time intervals: interval 1 included days 3, 5, 7, 9 and 11; interval 2 included day 13; and interval 3 included days 15 and 17. I examined the effect of salinity on daily mortality (calculated as the percentage of live larvae at the end of a sampling day that died by the following sampling day) over each interval, but the ANOVA model varied among intervals. For intervals 1 and 3, it was a two-way ANOVA with salinity as a fixed factor (interval 1: six levels—15, 18, 21, 24, 27 and 33; interval 3: four levels—21, 24, 27 and 33) and repeated measures on the second factor time (interval 1: five levels; interval 3: two levels—see above). For interval 1, I adjusted p -values for sphericity with the Greenhouse-Geisser ϵ because of the five repeated measures in the ANOVA. For interval 2, the analysis was one-way ANOVA with salinity as a fixed factor (five levels: 18, 21, 24, 27 and 33). I also examined the effect of salinity on cumulative mortality (calculated as the percentage of the initial number of larvae in each replicate that died over a sampling period) using three separate one-way ANOVAs that covered the following periods: interval 1 (days 3–11), intervals 1 + 2 (days 3–13), and intervals 1 + 2 + 3 (days 3–17). Salinity was a fixed factor with the following levels: six levels for the 3–11 d period (15, 18, 21, 24, 27 and 33), five levels for the 3–13 d period (18, 21, 24, 27 and 33), and four levels for the 3–17 d period (21, 24, 27 and 33). I did not transform the percentage data for any analysis because Cochran's tests did not detect heterogeneity of variances (in all cases, $p > 0.05$). I did *a posteriori* multiple comparisons among means with SNK tests. All statistical tests were

significant when $p < 0.05$.

Results

Short-term effects of salinity on larval survival

In the control salinity (33 PSU), 24-h mortality decreased with stage from $16.5\% \pm 5.3$ (mean \pm SE, $N = 3$) in the 2-arm stage to $5.2\% \pm 0.8$ in the 8-arm stage (Fig. 1). Mortality after 24 h varied significantly with salinity ($F_{5,48} = 37.6$, $p < 0.001$), but did not vary among developmental stages ($F_{3,48} = 1.66$, $p = 0.187$) and there was no significant salinity \times developmental stage interaction ($F_{15,48} = 0.382$, $p = 0.978$). SNK tests showed that mortality was lower in 33 PSU than in all other salinities except 27 PSU. Also, mortality was greater in both 15 and 18 PSU than in all higher salinities. There was no difference in 24-h mortality among 21, 24 and 27 PSU.

Long-term effects of salinity on larval survival and rate of development

Larvae completed development successfully by reaching the 8-arm stage only in the control salinity. In this salinity, 100% of larvae were in the 2-arm stage at 2 d after fertilization and in the 4-arm stage at 3 d (Fig. 2). Although there were few larvae (<1%) in the 6-arm stage as early as at 19 d, ~90% of the larvae were in this stage at 33 d. At 35 d, 75% of larvae were in the 8-arm stage. In 18, 21, 24 and 27 PSU, ~100% of larvae were in the 4-arm stage at 3 d but did not develop further. In the lowest salinity (15 PSU), ~60% of the larvae had not developed further than swimming blastulae at 13 d. At 15 d, ~70% of larvae were in the 4-arm stage but this proportion is based on seven surviving individuals. Analysis by log-linear models showed that developmental stage was dependent on salinity for 3 to 13 d ($G_{13} = 726, 889, 686, 488, 240$ and 157, for each day respectively, $p < 0.001$ in all cases). At 15, 17 and 19 d, 100% of larvae were in the 4-arm stage in all tested salinities with >10 surviving larvae making analysis by contingency tables impossible.

Over the developmental period, daily mortality was 2–10% in the control, but was much greater (reaching 100%) in lower salinities (Fig. 3). There were <10 surviving larvae per replicate at 13 d in 15 PSU, at 15 d in 18 PSU, and at 19 d in 21, 24 and 27 PSU. There was a significant effect of salinity on daily mortality at all intervals (interval 1: $F_{5,12} = 9.45$, $p = 0.008$; interval 2: $F_{4,10} = 9.16$, $p = 0.002$; interval 3: $F_{3,8} = 14.07$, $p = 0.001$), but there was no significant effect of time and no significant salinity \times time interaction for either interval 1 (Greenhouse-Geisser $\epsilon = 0.545$; time: $F_{4,48} = 2.64$, $p_{adj} = 0.086$; salinity \times time: $F_{20,48} = 1.85$,

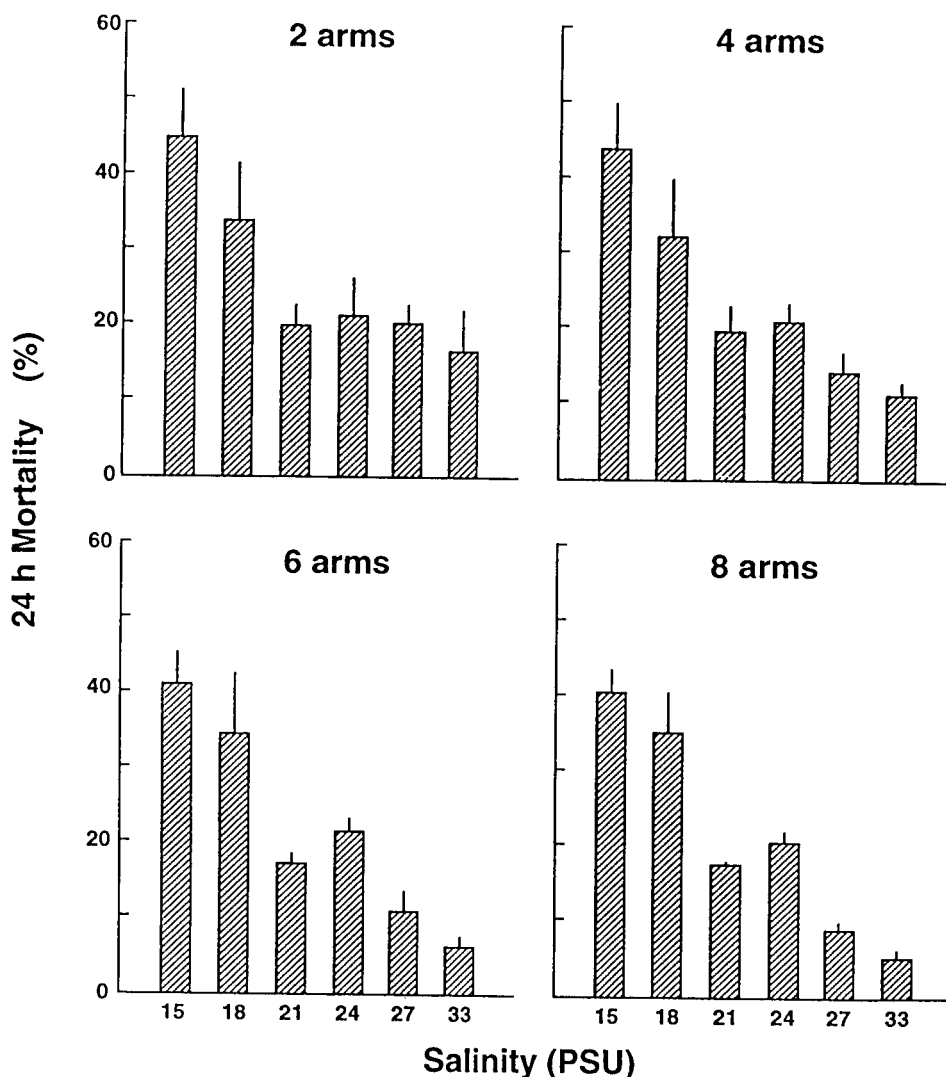


Fig. 1. 24-h mortality rate (mean \pm SE, $N = 3$) for four developmental stages of larvae of *E. lucunter* (expressed as percentage of dead larvae in each replicate) in six levels of salinity.

$p_{\text{adj}} = 0.096$) or interval 3 (time: $F_{1,8} = 1.73$, $p = 0.225$; salinity \times time: $F_{3,8} = 0.949$, $p = 0.462$). At interval 1 (3–11 d), daily mortality was greater in 15 PSU than in all other salinities, and also was greater in 18 PSU than when in 21 or 33 PSU (SNK tests). At interval 2 (13 d), daily mortality was greater when in 18 PSU than in 21, 24, 27 or 33 PSU (SNK tests). At interval 3 (15–17 d), daily mortality was greater in 21, 24 or 27 PSU than when in 33 PSU (SNK tests).

There also was a significant effect of salinity on cumulative mortality over each of the three sampling periods (3–11 d: $F_{5,12} = 6.52$, $p = 0.004$; 3–13 d: $F_{4,10} = 4.26$, $p = 0.029$; 3–17 d: $F_{3,8} = 41.09$, $p = 0.0003$). For 3–11 d, cumulative mortality was greater in 15 PSU than in all other salinities except 18 PSU (SNK tests,

Fig. 4). For both 3–11 d and 3–13 d, it was greater in 18 PSU than in 21 or 33 PSU (SNK tests). For 3–17 d, cumulative mortality was greater in 21, 24 or 27 PSU than in 33 PSU (SNK tests).

Discussion

There were strong short-term (24 h) and long-term (over the entire developmental period) effects of salinity on larval survival and rate of development. In the short-term, mortality never exceeded 55%, even when salinity was as low as 15 PSU, suggesting that a large proportion of larvae could survive brief periods of reduced salinity. Mortality might have been lower if I had acclimated the animals rather than introduce them directly to the ex-

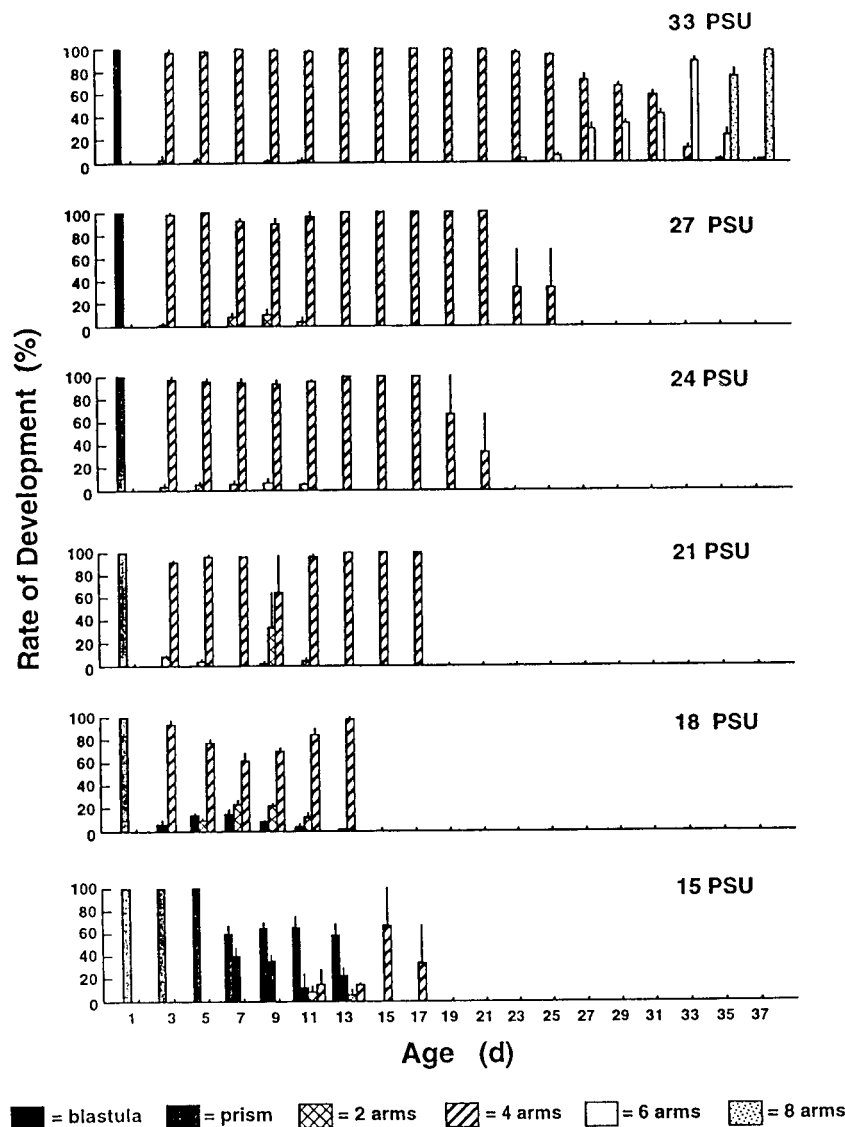


Fig. 2. Rate of development (mean \pm SE, $N = 3$) of larvae of *E. lucunter* (expressed as percentage of larvae in each of six developmental stages) reared in six levels of salinity, shown for different ages over 37 d.

perimental vessels. For echinoderms however, there is evidence that acclimation probably does not affect tolerance (Stickle and Diehl, 1987). In the short-term, reduced salinities also may result in altered larval behaviour such as reduced activity (Crisp and Costlow, 1963; Lyster, 1965; Yaroslavtseva and Sergeeva, 1993) but in this study all surviving larvae exhibited similar swimming behaviour and levels of activity in all salinities (personal observation).

In contrast to short-term effects, exposure to longer periods of reduced salinity had more adverse effects on larval survival and rate of development. Daily and cumulative mortality eventually reached 100% in all salinities except 33 PSU. The age of the cultures when 100% mortality occurred decreased with decreasing

salinity, ranging from 25-27 d in 27 PSU to 13-15 d in 15 and 18 PSU. In the long-term, development was also delayed or arrested with decreasing salinity as larvae did not develop further than the 4-arm stage in any salinity other than 33 PSU. This may be a critical stage in development since Roller and Stickle (1993) found that larvae of *L. variegatus* also died in the 4-arm stage in salinities <27.5 PSU. In this study, larvae reached the 4-arm stage at the same age in all salinities >21 PSU, were slightly delayed in 18 PSU, but most did not develop past the stage of swimming blastulae in 15 PSU.

Other studies have shown a weaker effect of reduced salinity on the survival and development of larvae in *Echinometra* than the one I observed. In a brief report,

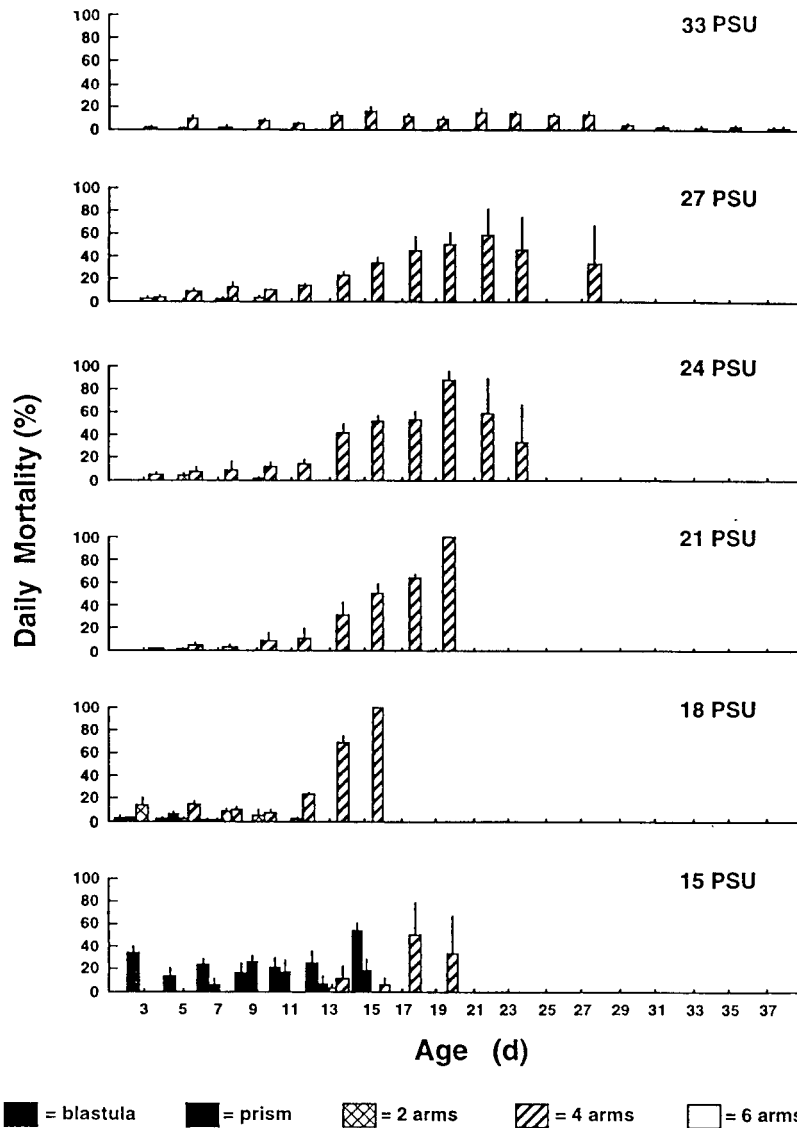


Fig. 3. Daily mortality (mean \pm SE, $N = 3$) of larvae of *E. lucunter* (expressed as percentage of dead larvae in each replicate at a sampling day—see Methods for calculation) for each of six developmental stages reared in six levels of salinity, shown for different ages over a developmental period of 37 days.

Petersen and Almeida (1976) suggested that plutei (of unspecified developmental stage) can tolerate salinities as low as 26 PSU for at least 8–10 d and development of larvae can be completed in this salinity. Cameron et al. (1985) did not find an effect of salinity on either the survival rate of plutei or on larval development in *E. lucunter* but they only used a range in salinity of 31.5–38.5 PSU. In support of my results, studies on other echinoderms have provided evidence that the lower limit of salinity which larvae of most species in this group can tolerate is 20–25 PSU. Such evidence of increased mortality and delayed development by exposure to reduced salinity exists for the sea urchins *Arbacia*

lixula (<18 PSU; Petersen and Almeida, 1976), *Litochinus variegatus* (<26 PSU; Petersen and Almeida, 1976; <27.5 PSU; Roller and Stickle, 1993; but see Cameron et al., 1985), *Strongylocentrotus droebachiensis* (<20 PSU; Roller and Stickle, 1994), *S. nudus* (<20 PSU; Yaroslavtseva and Sergeeva, 1993), *S. pallidus* (<27.5 PSU; Roller and Stickle, 1985; <25 PSU; 1994), and *S. purpuratus* (<27.5 PSU; Roller and Stickle, 1985); and the sea stars *Acanthaster planci* (<35 PSU; Lucas, 1973) and *Pisaster ochraceus* (<20 PSU; Roller and Stickle, 1985).

Some studies have shown that more developed and/or older larvae can be either more (e.g. Costlow et al.,

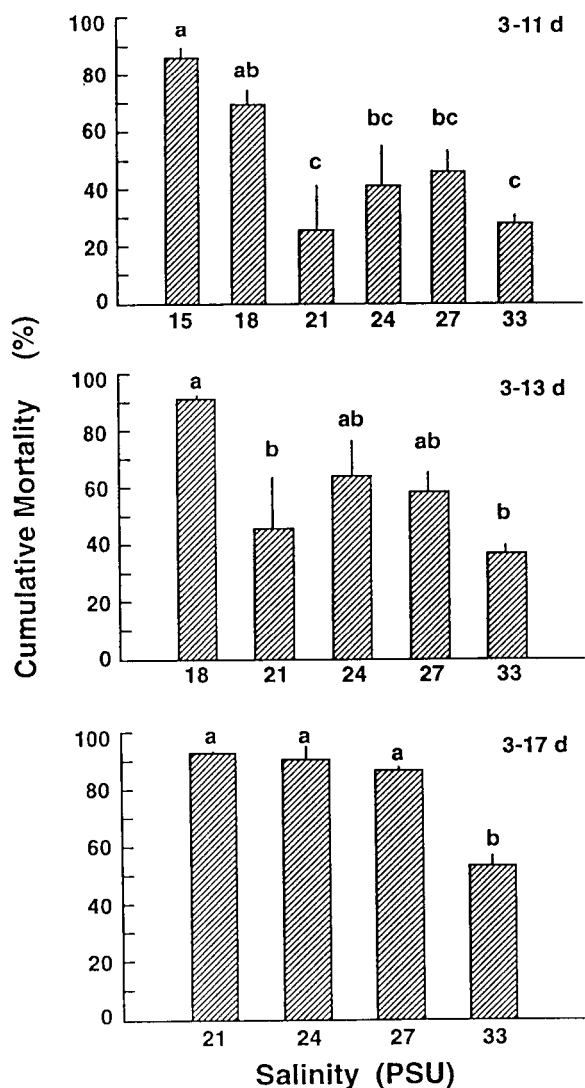


Fig. 4. Cumulative mortality (mean \pm SE, $N = 3$) of larvae of *E. lucunter* (expressed as percentage of dead larvae in each replicate over each of three sampling period during larval development, 3–11 d, 3–13 d, and 3–17 d—see Methods for calculation) reared in six levels of salinity. Within each period, same letters above different bars illustrate that there was no significant difference between these means as indicated by SNK tests at $p > 0.05$.

1960; Gray, 1976; Yaroslavtseva and Sergeeva, 1993; Anger, 1996) or less (e.g. Bayne, 1965; Richmond and Woodin, 1996) sensitive to decreases in salinity than earlier stages, whereas others found no change in tolerance with stage and/or age (e.g. Scheltema, 1965). In this study, the effect of salinity on larval survival after 24 h did not vary among developmental stages.

The range in salinity that larvae can tolerate may be

wider (e.g. Hendler, 1977; Laughlin, 1983), narrower (e.g. Lyster, 1965; Little et al., 1984) or similar to the range that adults can tolerate. Although to my knowledge their tolerance has not been measured directly, adults of *E. lucunter* can probably tolerate salinities < 30 PSU since there are frequently such reductions in salinity at Fort Pierce Inlet, particularly between June and September (Metaxas and Young, 1998). Thus, the observed sensitivity of larvae to salinities as high as 27 PSU suggests that the larvae of this species probably have a narrower range of tolerance to salinity than the adults.

The period of great salinity fluctuations (from 15 to 42 PSU) in the adult habitat coincides with the period of reproductive maturity in *E. lucunter* (McPherson, 1969; Metaxas and Young, 1998) and thus the period that larvae are in the plankton. My results suggest that persistence of these conditions for long periods can result in larval loss, but such losses probably are avoided because salinity is restored to oceanic levels by the incoming tide (Metaxas and Young, 1998). However, since echinoid larvae in the early stages of development swim upwards, they may enter a water layer of reduced salinity during their ascent; if trapped there their development may cease and they may eventually perish. Metaxas and Young (1998) showed that larvae avoided crossing haloclines in which the salinity of the top water layer was 21–27 PSU. Thus, it appears that larvae may develop adaptive behaviours that prevent them from being introduced into water layers of low salinity which may be unfavourable to their survival and development.

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