REPRODUCTION AND SURVIVAL OF THE PILEWORM
NEREIS SUCCINEA IN HIGHER
SALTON SEA SALINITIES

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The Salton Sea is a large (200 square miles) closed salt lake in a below-sealevel depression in the Colorado Desert of southeastern California. The Sea was formed accidentally from 1905 to 1907 when flood waters of the Colorado River broke through poorly constructed headgates of an irrigation canal. Following repair of the break, the new Salton Sea evaporated to a low of 250 feet below sea level by 1925. Since then the Sea has gradually increased in volume and surface elevation because agricultural waste water inputs exceed the annual evaporation of about 6 feet. In 1977, surface elevation was -228 feet, highest since 1914, and salinities averaged about 37% in summer. Early history of the Salton Sea is given by McDougal (1914), and later history by Walker (1961).

The original biota of the Salton Sea, freshwater organisms from the Colorado River and a few species native to desert springs, died out by the mid-1920's. Attempts to introduce sportfishes did not succeed until the early 1950's, with the establishment of the croaker (Bairdiella icistia), sargo (Anisotremus davidsoni), and orange-mouth corvina (Cynoscion xanthalis), all from the Gulf of California. Several successful introductions of invertebrates have also occurred. The Salton Sea is eutrophic and highly productive (Walker, 1961), but as there are no planktivorous fishes, most plankton die and are converted to benthic detritus (Arnal, 1961). Nereis (Neanthes) succinea Leuckart, a polychaete annelid introduced in 1930, is the most important benthic detritivore and the most important food source for the sportfishes. The quasi-marine ecosystem of the Salton Sea is discussed by Walker (1961) and Young (1970). Ecology and reproductive biology of N. succinea in the Salton Sea have been discussed by Carpelan and Linsley (1961a, b) and Walker (1961).

With the salinity of the Salton Sea approaching 40% in the early 1970's, much concern has been expressed over the future of the sportshery, one of the most important in California (Hanson, 1972). Increasing development of local geothermal energy resources may result in spills of highly saline waste brines into the Sea, which may also affect the sportfishes or their food supply (Shinn, 1976). Reproduction by the three sportfishes is limited to salinities below 40% (Brooks and Cole, 1972; Lasker, Tenaza, and Chamberlain, 1972; May, 1975, 1976). There is little published information on high salinity adaptations in polychaetes (Bayly, 1972; Oglesby, 1978), and only one published study on the effects of higher salinities on N. succinea in the Salton Sea. Hanson (1972) observed that pileworms survived 96-hr exposures to salinities as high as 67.5%, but speculated

that "reproduction of the pileworm would probably be adversely affected at lower salinities."

It is the purpose of the present study to establish upper salinity limits for reproduction and survival of _N. succinea_ in Salton Sea waters, in order to assess the possibility that pileworm failure due to increased salinity from either evaporation or brine spills may adversely affect the sportfishery.

**Materials and Methods**

Pileworms were collected from the northeastern Salton Sea, at Mecca Beach in the Salton Sea State Recreational Area. Worms were picked by hand from shallow sediments, particularly from barnacle shell rubble cemented with gypsum crystals. While a few heteronereids could be collected from the benthos in this fashion, it was necessary to collect by night-lighting in order to secure adequate numbers for experiments on fertilization and development.

In the laboratory, worms were maintained in glass tubes in finger bowls, covered to reduce evaporation. For most experiments worms were maintained at 21 to 23° C; for some experiments, worms were kept at 34° C, somewhat warmer than summer water temperatures in 1976–77, but not as warm as maximum water temperatures of 36° C recorded by Walker (1961).

Salton Sea water was collected from Mecca Beach. Higher salinities were made by evaporating 36% Salton Sea water at about 50° C until it reached a concentration of about 90%. This was then mixed with 36% Salton Sea water to provide a full range of salinities. During the concentration process, calcium salts precipitated. Thus, in the final mixtures, calcium may have been somewhat undersaturated. For some experiments media were made up from Instant Ocean, an artificial salt mixture resembling ocean sea water in ionic ratios. All media were routinely filtered through activated charcoal in Whatman Grade 3 filter paper before use. Media were changed in the culture dishes daily. No antibiotics were used.

Laboratory fertilizations were carried out according to the procedures detailed in Costello, Davidson, Eggers, Fox, and Henley (1957) and Smith (1964). Water was changed daily, involving some loss of developmental stages by decanting. In some cultures, bacterial or protozoan contamination was present; however, this did not pose a severe problem experimentally. Since no supplemental food was supplied to the developing larvae, cultures died at a late trophophore or early 3-setiger stage.

Salinities in the field and during ordinary laboratory operations were measured with an American Optical total solids refractometer, calibrated against known solutions measured with a Hewlett-Packard vapor pressure osmometer and with a Buchler-Cotlove chloridometer. Chlorinities were converted to % Salton Sea water using the ion ratios given in Carpelan (1958), Walker (1961), and Young (1970).

**Results**

*Effects of higher Salton Sea salinities on survival of atokous worms*

Experiments on survival of large atokous (immature worms) involved either direct transfers to the full range of salinities, or gradual increases of salinity in increments of 5% for 50% survival time for 10 worms each of a given salinity. Graphs of the Critical Salinity showing survival in 36% of the concentration in which the mortality of worms was 50% were otherwise combined to establish the final salinity combined for the graph.
NEREIS SUCINEA IN HIGH SALINITIES

![Figure 1](image_url)

**Figure 1.** Survival time of *Nereis succinea* in increasing concentrations of Salton Sea water, expressed as average $ST_{50}$. Points are averages of all trays (initially 10 worms each) in each salinity, with the standard error indicated. Arrows indicate the Critical Salinity ($CS_{50}$) where survival is reduced to 50% of that in 36% Salton Sea water.

Increments of 10% until the final test salinity was reached. Calculation of the time for 50% survival ($ST_{50}$) of a test group of worms (usually four trays with 10 worms each) began with the day the worms first were placed in the final test salinity. Graphs of $ST_{50}$ as a function of the final salinity were used to determine the Critical Salinity ($CS_{50}$), the salinity where survival is reduced to 50% of the survival in 36% Salton Sea water. This calculation of $CS_{50}$ is possibly biased in those experiments involving graduated salinity increases, since it ignores the mortality of worms in lower salinities during the adaptation period. However, otherwise comparable experiments in which worms were transferred directly to the final salinities gave similar results. Results of both types of experiments are combined for the following analyses.

Results for all experiments on survival of atokes are summarized in Figures 1 and 2. These are averages and calculations based on over 280 worms in 36%, over 140 worms in each salinity between 45 and 60%, and between 50 and 100 worms in all higher salinities. Figure 1 shows the average survival time ($ST_{50}$) for all worms in all salinities, with the standard error indicated. Survival was high at salinities of 50% and lower, but declined in higher salinities. The critical salinity $CS_{50}$ is estimated to be slightly lower than 65%.

Figure 1 also provides the results of two related experiments: the effects of elevated temperature (34°C rather than the usual 21–23°C), and the effects of transfer to Instant Ocean. In both cases, overall survival seems to be diminished as compared with worms in...
Salton Sea water in 21 to 23° C, though the general pattern is similar. For worms in Instant Ocean, CS₅₀ is estimated to be somewhat higher than 65%. It was not possible to provide an estimate of CS₅₀ for the worms at 34° C, for it was higher than the highest salinity used in this experiment, 65%. It appears that the Critical Salinity is not lowered for Salton Sea pileworms exposed either to ocean sea water or to temperatures only slightly lower than maximum summer water temperatures in the Salton Sea.

Much of the variability in the estimates of average ST₅₀ (Fig. 1) is caused by the fact that in all salinities, all the worms in a given tray often would die soon after the first worm died, presumably because of the accumulation of toxic materials before the medium was changed. Not only is variability increased by this phenomenon, which may not be salinity-related, but also the average ST₅₀ is decreased. Die-off of entire trays of 10 worms was particularly a problem at 34° C, due to increased bacterial activity. In order to provide an estimate of survival that avoids this problem, Figure 2 shows the survival time for the longest surviving worm in each salinity. At least some pileworms survived longer than the length of the experiments in nearly all salinities of 65% and lower, over 4 weeks for the worms in Salton Sea water at 21 to 23° C, and over 2.5 weeks for the worms in Instant Ocean and in 34° C. At higher salinities maximum survival time declined rapidly. No worms survived even a day at salinities higher than 85% at 21 to 23° C, nor higher than 75% in Instant Ocean. In both these experiments, CS₅₀ was 70%. No salinities higher than 65% were used in the experiments at 34° C, and since at least one individual lived as long as 8 days in this salinity, it is not possible to estimate CS₅₀, which must be higher than 65%.

Most worms in the laboratory did not survive more than a week or two, even when maintained in 36% Salton Sea water. Carpelan and Linsley (1961a) indicated that N. succinea takes over a month to reach sexual maturity in the Salton Sea, so presumably pileworms must live well over a month in their natural habitat waters. Diminished survival in the laboratory may be a consequence of accumulation of metabolites, to lack of adequate food, or to other artificial causes. For these reasons, the survival times of pileworms in these laboratory experiments should not be taken as an exact counterpart of survival in the Salton Sea as salinity increases. Rather, these laboratory results should be taken as an index of survival.

Both indices of survival (Figs. 1, 2) indicate that atokous pileworms survive increased Salton Sea salinities up to 60 to 65%. Survival is considerably diminished at salinities in excess of 70%, with no survival above 85%, a concentration which is well over twice the present concentration of the Salton Sea. Even high summer water temperatures of 34° C do not decrease the survival limits of the pileworms. There is no indication that pileworms live longer in ocean water than in Salton Sea water.

Effects of higher Salton Sea salinities on heteronereid development

Studies of sexual development and spawning indicate that while N. succinea breeds year-round in the Salton Sea, reproductive activity is somewhat depressed during the summer months of high water temperature (Carpelan and Linsley,
Nereis succinea in high salinities

Figure 2. Maximum survival time of *Nereis succinea* in increasing concentrations of Salton Sea water. Circled points are those where worms were still alive by the end of the experiment.

1961a, b). Nevertheless, heteronereids (sexually mature adult worms) were collected throughout the summers of 1976 and 1977. The sex ratio of worms collected from the benthos at Mecca Beach was about one-third males and two-thirds females. As noted by Costello, *et al.* (1957) and Carpelan and Linsley (1961a), the sex ratio of swarming heteronereids is strongly reversed, males outnumbering females by about 10 to 1. This was also the case in our own collections. Heteronereid development in the laboratory was strongly influenced by salinity...
(Fig. 3). About 15% of the pileworms maintained in low salinities (36 and 40‰) matured as heteronereids during the summer of 1977. A somewhat lower percentage (just under 12%) matured in 50‰, but in higher salinities maturation of heteronereids was greatly depressed, and there was no maturation in salinities of 70‰ or higher. There may be a differential effect of higher salinities on maturation of the two sexes, development of males being more strongly depressed than that of females. This observation may be an artifact of very small numbers of hetero-

\[\text{Nereis succinea} \]

Heteronereid development in higher Salton Sea salinities

\[\text{CS}_{50}\]

\[\text{Medium: } \% \text{salinity} \]

\[0 \quad 10 \quad 20 \quad 30 \quad 40 \quad 50 \quad 60 \quad 70 \quad 80 \quad 90 \quad 90\]

\[0 \quad 2 \quad 4 \quad 6 \quad 8 \quad 10 \quad 12 \quad 14 \quad 16\]

\[\% \text{ heteronereid development}\]

\[\begin{align*}
1 & \quad 11 \\
41 & \\
17 & \\
10 & \\
12 & \\
5 & \\
3 & \\
0 & 0
\end{align*}\]

**Figure 3.** Effect of increasing Salton Sea salinities on heteronereid production by *Nereis succinea*. Actual numbers of heteronereids produced are indicated. Arrow indicates CS$_{50}$ where heteronereid production is reduced to 50% of that in 36‰ Salton Sea water.

**Effects of higher salinities on heteronereid development.**

Laboratory studies of the Salton Sea heteronereids indicate that the development of the heteronereids is about 55% (Fig. 3). In all these studies,

**Fertilization**

be accomplished and the fertilizations varied from 5% successful fertilization to 95% successful fertilization. In these studies, eggs were transferred to culture dishes containing sperm from males of the heteronereids. The fertilization was particularly difficult, and it is possible that a small proportion of the eggs may not have been fertilized. This may be the case in which eggs were transferred to higher salinities after fertilization.

**Fertilization in the field.**

Smith (1964) described fertilization in the field and was less sensitive to the effect of salinity on the development of the heteronereids. In the first generation after fertilization, there were few abnormal cleavages, and the development of the embryos transferred to culture dishes containing normal trophic conditions resulted in successful development. However, these results were not significantly different from those obtained in the laboratory. This may be the case in which eggs were transferred to higher salinities after fertilization. These results are consistent with the laboratory studies of Smith (1964).

**The effect of salinity on heteronereid development.**

In the laboratory studies, the effects of salinity on heteronereid development were investigated. The results are consistent with the hypothesis that heteronereids are more sensitive to higher salinities than other nemerteans. In the field, the development of heteronereids was less sensitive to salinity fluctuations than in the laboratory. These results are consistent with the hypothesis that heteronereids are more sensitive to salinity fluctuations than other nemerteans.
neroids in the higher salinities. The estimated CS₅₀ for heteronereid development is about 55% (Fig. 3).

Effects of higher Salton Sea salinities on fertilization and larval development

Laboratory fertilizations, using heteronereids either collected directly from the Salton Sea or produced in laboratory cultures, were readily accomplished. Development of larvae in 36% Salton Sea water appeared normal, and had the same time course as in previous studies on Salton Sea worms (Carpelan and Linsley, 1961a, b) and on this species at Woods Hole (Costello, et al., 1957). In all these studies, temperatures were similar, about 20 to 25° C.

Fertilization in various salinities. Fertilization of eggs of N. succinea could be accomplished at salinities as high as 50%, although the percentage of successful fertilizations was much reduced at 50%. In one experiment, there was less than 5% successful fertilization at 55%, and in a second experiment, no success at this salinity. In these experiments, eggs from females maintained in 36% were initially transferred to culture dishes containing 100 ml of the experimental salinity, and sperm from males opened in 36% added. Eggs transferred to salinities of 45% and higher shrank from osmotic water loss immediately after the transfer. Shrinkage was particularly noticeable in 50% and higher, many eggs becoming greatly distorted. It is estimated that the CS₅₀ for fertilization is 45%. While there was a small proportion of apparently successful fertilizations in 55% in one experiment, there was no further development even to the first cleavage. The highest salinity in which any development takes place following fertilization is 50%.

These results are summarized in Figure 4.

Fertilization in 36% Salton Sea water, followed by transfers to various salinities. Smith (1964) demonstrated that later developmental stages of N. diversicolor were less sensitive both to lower and to higher salinities than early stages. To determine if this is the case with N. succinea, several experiments were conducted in which eggs were fertilized in 36% Salton Sea water, and embryos transferred to higher salinities at several different times during development.

In the first group of experiments, eggs were transferred as soon as possible after fertilization into a full range of salinities. There was excellent survival and subsequent development in salinities up through 45%, although in 45% there was some evidence of shrinkage, and a few zygotes cleaved abnormally. These abnormally cleaving embryos (such as "dumbbells" which cleaved no further, and irregular cell clusters) did not develop successfully. There was poor survival of embryos transferred to 50%, with abnormal cleavages and much shrinkage, but a few normal trophophores developed at this salinity. At 55 and 60% there was temporary survival, a high proportion of abnormal cleavage patterns, and no successful development. Embryos transferred to salinities higher than 60% shrank excessively and showed no type of cleavage. These early cleavage stages seem as sensitive to higher salinities as fertilization itself; it is estimated that the CS₅₀ for early cleavage is 45%, with no successful development higher than 50%.

These results are summarized in Figure 4.

This same experiment was conducted at 34° C to determine if summer water temperatures were more stressful on development than 21 to 23° C. There were
no observed differences in survival and developmental success between 34° C and 21 to 23° C, other than a considerable acceleration of cleavage at the higher temperature. There seems to be no additional stress on development in temperatures as high as summer water temperatures in the Salton Sea. On the other hand, in either temperature regime, development in salinities of 45‰ was markedly delayed as compared with development at lower salinities.

In a second group of experiments, fertilized eggs were allowed to develop in 36‰ Salton Sea water until the early trophophore stage, about 8 to 10 hr. These early trophophore stages were then transferred to salinities up to 75‰. There was excellent survival and development at all salinities up through 50‰. No shrinkage of trophophores was noticed at 45‰. In 50‰ there was some shrinkage, and trophophore cilia ceased beating temporarily. At 55‰ these shock effects were more severe, but there was considerable survival and subsequent development. At 60‰ there was no recovery of ciliary motion following transfer, and while it was estimated that perhaps 5% of the early trophophores survived the transfer, there was no subsequent development. There was no survival at higher salinities. Thus, early trophophores are less sensitive to high salinities than earlier cleavage stages. The estimated CS50 is 50‰, but there was no development above 55‰. These results are summarized in Figure 4.

In the final experiment, fertilized eggs were allowed to develop in 36‰ Salton Sea water until the swimming trophophore stage, about 24 hr. Swimming trophophores were then transferred to salinities up to 75‰, and survival and subsequent development monitored to the beginning of segmentation about 18 hr later. Survival was not as good as in the experiments involving transfers at earlier stages, but there was some survival and development up through 55‰. Swimming trophophores transferred to 50 and 55‰ showed some shrinkage, and ciliary activity temporarily stopped. In 60‰ these shock effects were more severe, and survival was low; however, some trophophores were still alive after 18 hours, though development had not progressed. In higher salinities there was little or no survival following transfer, shock effects were very severe, and there was no subsequent development. It appears that swimming trophophores have about the same sensitivity to higher Salton Sea salinities as do early trophophores. These results are summarized in Figure 4.

DISCUSSION

The present experiments supplement and extend the results to Hanson (1972) in showing that atokous N. succinea can survive for extended periods of time in very high Salton Sea salinities, at least as high as 65‰, with perhaps some reduction of survival in 70‰. There is short term survival in salinities as high as 80‰, more than twice the present salinity of the Salton Sea. There are reports of nereid and other polychaetes in high salinities in lagoons and estuaries, but few reports are for salinities in excess of 50‰ (Bayly, 1972; Oglesby, 1978). There have been no experiments on any of these other polychaetes to determine actual upper salinity tolerances, or if they actually breed in such high salinities.

Hanson's (1972) prediction that reproduction of the pileworm in the Salton Sea would be adversely affected at salinities lower than the limit for adult sur-
between 34°C and 36°C and survived at the higher temperature. On the other hand, 8°C was markedly delayed survival. These eggs developed at 8 to 10 hr. These eggs developed to 75% survival at 50°C. No shrinkage occurred, and the shock effects were apparent at 55°C. Some eggs survived the transfer, but not at higher salinities. Early cleavage occurred in development above 55°C.

Survival at 36% Salton Sea salinity was about 18 hr later. Survival at 25°C was almost 100%, and ciliary activity was severe, and survival to 55°C was 18 hours, though embryonic survival was little or no survival occurred. There was no subsequent mortality. These results were confirmed by Hansen (1972) and Zingmark and Guzman (1978). There have been no reports of nereid development at salinities below 36%. There have been no reports of nereid development at salinities below 36%. There have been no reports of nereid development at salinities below 36%.

Figure 4. Salinity tolerance profile of development and survival of N. succinea in higher Salton Sea salinities. Stages and times are approximate for 21 to 23°C. The solid line indicates the Critical Salinity (CSmax), where survival and development are reduced to 50% of that at 36% Salton Sea water. The dashed line indicates the maximum salinity at which any survival or development occurred.

Survival is confirmed by these experiments, for there was no successful fertilization or cleavage in salinities higher than 50%, and reasonable success was limited to salinities of 45% and lower. Early and late trophophores could tolerate somewhat higher salinities, up to 50%. Assumption of the high salinity tolerance of the atokes must come later in development than the appearance of segmentation, the termination of the present experiments.

Table I summarizes the literature on the effects of low salinities on development of N. succinea. Taken together, these reports suggest that N. succinea, like many other estuarine and marine polychaetes, cannot reproduce at salinities below the horizalnicum of 5 to 8% (Oglesby, 1978), even though atokes N. succinea can...
survive at considerably lower salinities (Oglesby, 1965; Hogue and Oglesby, unpublished results). The report by Foster (1972) that *N. succinea* can survive in fresh water is not supported by published data (Oglesby, 1965, 1978). The studies summarized in Table I, combined with the present results, provide a picture that is comparable to *N. diversicolor* (Smith, 1964), showing a "bottleneck" of salinities above and below which cleavage is blocked (Fig. 4). That is, while adult and afove survival limits range from about 1% to as high as 80%, development is successful only between 10 and 45%.

It is premature to conclude that when the Salton Sea finally exceeds 45 to 50%, reproduction of *N. succinea* will be blocked. As Smith (1964, 1977) has discussed, at least some of the reason for lack of reproductive success at extreme salinities may be mechanical, due to osmotic swelling in low salinities and osmotic shrinkage in high salinities. Shrinkage was very apparent in the present experiments at 50% and higher in eggs and embryos transferred from 36%.

It would have been desirable to attempt fertilizations with eggs and sperm taken from adults adapted to much higher salinities, to avoid the initial osmotic problem. However, even though hetrocoroids were produced in the laboratory in salinities as high as 65% (Fig. 3), never were a male and a female mature at the same time in a salinity higher than 36%. Smith (1964) reported that some populations of *N. diversicolor* in northern Europe reproduce in salinities greater than the upper salinity limit for reproduction of other populations of the same species. It may

**Table 1**

<table>
<thead>
<tr>
<th>Stage and treatment</th>
<th>Observed effects on development</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unfertilized eggs</td>
<td>Survival down to 9.6%.</td>
<td>Just (1928)</td>
</tr>
<tr>
<td>Fertilized eggs</td>
<td>Very low resistance to dilute sea water.</td>
<td>Just (1928)</td>
</tr>
<tr>
<td>Development in 91% SW after 1 hr exposure to dilute SW</td>
<td>Normal development above 16%; diminished success at 11–14%, though some eggs develop normally.</td>
<td>Just (1930a)</td>
</tr>
<tr>
<td>Development in varied SW after fertilization in 91% SW</td>
<td>Normal development above 16%; diminished success at 14%, some normal development; cleavage but not trophophores in 11, 13%.</td>
<td>Just (1930b)</td>
</tr>
<tr>
<td>Development in varied SW after fertilization in 100% SW</td>
<td>Normal development of nectochaeta larva in 14–35%; normal development of trophophore in 8%; no cleavage in 2–6%.</td>
<td>Kinne (1954)</td>
</tr>
<tr>
<td>Development in varied SW and temperatures after fertilization at 20%</td>
<td>Development at 10, 15, 20%, except none at 10% at 10°C. Development accelerated at higher salinity and higher temperature.</td>
<td>Dean and Mazurkiewicz (1975)</td>
</tr>
</tbody>
</table>

*Nereis limbata* Ehlers, the name used by Just (1928, 1930a, b) is synonymous with *N. succinea* Leuckart. Just (1928, 1930a, b) did not provide the actual concentration of his "100% SW." Salinities presented in this table are based on data of Cole (1940) for summer water salinities at Woods Hole. Since there are no significant fresh-water inflows in the area, it is reasonable to assume that Woods Hole summer sea water averages about 32%, or 91% of 35% salinity.

be that as the result of selection for *N. succinea*. Development may be below 45 to 50% in low salinities and below 36% in the Salton Sea.

The present study has any marked adaptations for life in the present time. The present saline pattern should continue to be as it is now.

Interestingly, salinities in Salton Sea afove 36% are found that eggs and embryos transferred from 36% can live but had very poor development. This suggests that this is the position of the upper limit of life in the Salton Sea.

Spills of geothermal waters from the Salton Sea (California) would be expected to eliminate the afove 36% in the afove 36% in the Salton Sea. Even if geothermal waters are available source, the low salinity of the geothermal waters would be expected to reduce oxygen levels. Water of all year (Carper, 1974) would be expected to reduce oxygen levels of the water of the Salton Sea.

The present study indicates that salinities of the Salton Sea will not exceed 45%, and perhaps 50%, salinities of the Salton Sea. The data presented indicate that salinities of the Salton Sea will not exceed 45%.

It is a pleasure to acknowledge the assistance of the Soil Conservation Service, and to thank R. J. Hargreaves, J. E. Fitch, R. R. Ireland, and J. E. Fitch, R. R. Ireland, who provided technical assistance. We are particularly grateful to Dr. Alice Shoemaker, Area Manager, U.S. Bureau of Mines, for making her laboratory available for this study, as well as for her encouragement and cooperation. We are also grateful to R. J. Hargreaves, J. E. Fitch, R. R. Ireland, and J. E. Fitch, R. R. Ireland, who provided technical assistance.
be that as the salinity of the Salton Sea gradually rises, there will be genetic selection for *N. succinea* with higher limits for reproductive success.

Developmental events were somewhat slowed at higher salinities, but at salinities below 45 to 50%o development was otherwise normal. Smith (1964) observed that low salinities also delayed development, particularly cleavage, in *N. diversicolor*.

The present experiments indicate that temperatures as high as 34°C do not have any marked effect on adult survival and reproduction in *N. succinea*. At the present time there is year-round reproduction in the Salton Sea, and this pattern should continue as long as the overall salinity itself does not become too high.

Interestingly, Salton Sea pileworms do not seem to have reduced survival in Salton Sea water as compared with ocean water (Figs. 1, 2). May (1976) found that eggs and larvae of the croaker *Bairdiella* survived well in salt water, but had very poor survival in Salton Sea water of the same salinity. He suggested that this poor survival of the fish was related to the unusual ionic composition of the Salton Sea. This seems not to be a problem with *N. succinea*.

Spills of geothermal waste brines of 5 to 10 times the salinity of the Salton Sea (California Department of Water Resources, 1970; Shinn, 1976) would be expected to eliminate pileworms from the affected area, as well as other benthic and pelagic organisms. These adverse effects could be caused not only by the excessively high salinity per se, but also by concomitant elevated temperatures or reduced oxygen concentrations. Pileworm larvae are in the Salton Sea plankton all year (Carpelan and Linsley, 1961a, b), and so there would be a constantly available source for recolonization. Only if there were contamination by heavy metals would there be a long-term problem (Reish and Carr, 1978). Thus, it is unlikely that a spill of even highly saline geothermal waste brines would have any more than a temporary and localized effect on the population of *N. succinea* in the Salton Sea.

The present experiments indicate that reproduction of *N. succinea* in the Salton Sea will continue with undiminished success at salinities at least as high as 45%, and probably as high as 50%. This means that gradually increasing salinities of the Salton Sea will not adversely affect the pileworm until some years after the collapse of the sportfishery, which seems sensitive to salinities no higher than 40%.

It is a pleasure to thank Pomona College students Charles Anderson, William R. Hargreaves, E. Wayne Hogue, and Jan Low, who have assisted in various aspects of this study, as well as many other students and faculty who helped with the collections. We appreciate the helpful discussions and assistance of C. A. Engle, Area Manager, and R. C. Johnson, of the Salton Sea State Recreational Area; J. E. Fitch, Research Director of the California Department of Fish and Game; R. R. Ireland of the Imperial Valley Environmental Project, Lawrence Livermore Laboratory; Dr. Ralph I. Smith, University of California at Berkeley; and Dr. Alice Shoemaker Osletby. This research was supported in part by Subcontract #345003 from the Lawrence Livermore Laboratory, University of California, Imperial Valley Environmental Project, supported by the U. S. Department of Energy under Contract No. W-7405-ENG-48.
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SUMMARY

The polychaete annelid *Nereis (Neanthes) succinea* is the major benthic detritivore in the Salton Sea, an inland salt lake in southeastern California, and is critical in the trophic chain leading to the sportfishery. In view of the increasing salinity of the Salton Sea, laboratory experiments were conducted to determine critical upper salinity limits for reproduction and survival of pileworms. Atoxous (immature) pileworms can survive for extended periods in Salton Sea salinities at least as high as 65‰, with some reduction of survival in 70‰, and with only short term survival in 80‰, more than twice the present salinity of the Salton Sea (36‰). Heteronereid production is depressed by salinities higher than 50‰. Reproduction of *N. succinea* is successful at salinities at least as high as 45‰, and probably as high as 50‰. Fertilization and early cleavage stages are less tolerant of elevated salinities than later development stages such as trophophores.

LITERATURE CITED


the major benthic organism of the Salton Sea, California, and is affected by the increasing salinities to determine the survival of worms. Atokous larvae of the Salton Sea salinities are higher than 70%, and with salinity of the Salton Sea as high as 45%, survival stages are less common as trophophores.


**Nereis succinea** (Frey and Koste) is a common worm Neanthes succinea, from the benthic animals and of the Salton Sea. Pages 171-197

**Verterbrate Animals.**

**Biota of Freshwater Environmental Protection**

**Neathes succinea**, from the benthic animals and the effect of extreme salinity. Pages 24-32.

The fertilization of eggs. Pages 33-40.

**Trophic Adaptation of Nereis succinea**

**Response of Salton Sea Ecosystem**

to changes in zooplankton, the Geology,


**Smith, R. I., 1977.** Physiological and reproductive adaptations of *Nereis diversicolor* to life in the Baltic Sea and adjacent waters. Pages 373-390 in D. J. Reish and K. Fauchald, Eds. *Essays on Polychaetous Annelids in Memory of Dr. Olga Hartman,* University of Southern California, Allan Hancock Foundation Special Publication.
