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The effects of haloclines on the vertical distribution and migration of zooplankton

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Abstract

While the influence of horizontal salinity gradients on the distribution and abundance of planktonic organisms in estuaries is relatively well known, the effects of vertical salinity gradients (haloclines) are less well understood. Because biological, chemical, and physical conditions can vary between different salinity strata, an understanding of the behavioral response of zooplankton to haloclines is crucial to understanding the population biology and ecology of these organisms. We studied four San Francisco Bay copepods, *Acartia* (*Acartiura*) spp., *Acartia* (*Acanthacartia*) spp., *Oithona davisae*, and *Tortanus dextrilobatus*, and one species of larval fish (*Clupea pallasi*), in an attempt to understand how and why zooplankton respond to haloclines. Controlled laboratory experiments involved placing several individuals of each species in two 2-m-high tanks, one containing a halocline (magnitude varied between 1.4 and 10.0 psu) and the other without a halocline, and recording the location of each organism once every hour for 2–4 days using an automated video microscopy system. Results indicated that most zooplankton changed their vertical distribution and/or migration in response to haloclines. For the smaller taxa (*Acartiura* spp., *Acanthacartia* spp., and *O. davisae*), this behavior took the form of accumulating in or below the halocline, while the effects on the larger species (*C. pallasi* and *T. dextrilobatus*) were more subtle. *C. pallasi* yolk sac and 3- to 6-day-old larvae seemed to pause or remain in the halocline during their diel migration, while 14- to 17-day-old larvae appeared to avoid the halocline by remaining in deeper, more saline water. There were very few statistically significant effects of haloclines on the vertical distribution of *T. dextrilobatus*. Subsequent mortality experiments with *Acartiura* spp., *Acanthacartia* spp. and *T. dextrilobatus* indicated that the behavioral changes seen in the halocline studies were not associated with any salinity-induced mortality per se, although more subtle affects

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of physiological stress could not be ruled out. These results point to a high degree of flexibility in vertical migration behavior within a given species as well as large variation between species. Such behavioral flexibility is likely to be very important in allowing planktonic organisms generally, and estuarine organisms in particular, to maintain or alter position relative to currents, food, and predators.

Keywords: Fish larvae; Halocline; Mortality; Salinity; Vertical migration; Zooplankton

1. Introduction

Salinity has important biological implications for marine animals due to associated physical parameters including osmolality, relative proportions of solutes, absorption and saturation of dissolved gasses, density, viscosity, surface tension, absorption of radiation, and transmission of sound (Kinne, 1966). When a large volume of freshwater runoff meets the sea in areas such as estuaries, the salinity can vary dramatically in both the horizontal and vertical planes. Horizontal salinity gradients are very well studied and often determine the horizontal distribution and abundance of organisms throughout an estuary (e.g. Kinne, 1966; Ambler et al., 1985). Vertical salinity gradients, or haloclines, which can encompass salinity differences from nearly zero to 15 psu (practical salinity units) in just a few meters (e.g. Madirolas et al., 1997), are thought to control the vertical distribution of organisms in estuaries, but this phenomenon has only been studied for select taxa (e.g. Lance, 1962; Harder, 1968; Bjornsen and Nielsen, 1991; Vazquez and Young, 1996).

Zooplankton have been shown to respond in many different ways to haloclines, including residence in or near the halocline, below the halocline, above the halocline, and migrating through the halocline (Hansen, 1951; Williams, 1985; Morgan et al., 1997). Which type of behavior is exhibited can have important implications for the zooplankton. For example, a host of different biological, chemical, and physical conditions can vary between different strata of the water column, including food (Caffrey et al., 1994; Edmunds et al., 1995, 1997; Baylosis et al., 1997), temperature, which affects metabolic demand (McLaren, 1974; Caffrey et al., 1994; Edmunds et al., 1995, 1997; Baylosis et al., 1997), turbulence which affects feeding (Saiz et al., 1992), chemical contaminants (Flegal et al., 1996), predators and competitors (Ambler et al., 1985; Orsi and Mecum, 1986), light, and currents (e.g. susceptibility to flushing; Morgan et al., 1997). Therefore, an understanding of the behavioral response of zooplankton to salinity-stratified conditions, which are a regular feature of most estuaries including the San Francisco Bay (Cloern and Nichols, 1985; Peterson et al., 1996), is crucial to understanding the population biology and ecology of the zooplankton.

In the field, it is difficult to deduce the specific causes of zooplankton vertical distribution due to the many co-varying physical, chemical, and biological factors. Furthermore, field sampling to resolve the small-scale distribution of zooplankton is problematic because many zooplankton can avoid such samplers (Grindley, 1964; Williams, 1985; Tiselius et al., 1994). One way to obviate the confounding effects of multiple variables associated with field studies, as well as the problem of low-resolution sampling in the field, is to conduct

laboratory studies. For instance, both Lance (1962) and Harder (1968) studied the effect of haloclines on different zooplankton taxa by conducting a series of laboratory experiments in water columns 50 cm tall containing haloclines of various magnitudes. Lance (1962), using six species of copepods, one species of decapod zoea, and a series of surface seawater dilutions ranging from 5% seawater to 90% seawater, found that the percentage of organisms inhibited from entering the surface layer increased as the surface layer became less saline. The degree of inhibition in the intermediate surface salinity dilutions differed between species and, for some taxa, between sexes. Harder (1968) used a greater range of zooplankton taxa including protozoa, ctenophores, chaetognaths, polychaetes, copepods, amphipods, barnacle nauplii, brachiopods, mysids, mollusk larvae, appendicularians, and herring, to determine more precisely the minimum difference in salinity necessary to elicit a behavioral response. He found that haloclines comprising salinity differences as low as 0.23 parts per thousand (ppt) could elicit a response for some species. This response was commonly manifested as a slight aggregation of organisms in the halocline, with other members spread relatively evenly in the upper, lower, or both salinity layers; however, statistical analyses of these data were not performed.

More recent studies have focused almost exclusively with meroplankton rather than holoplankton. For instance, crab zoea (Roberts, 1971; O'Conner and Epifano, 1985), the larvae of three mactrid bivalves (Mann et al., 1991), ascidian larvae (Vazquez and Young, 1996), diadromous gobie larvae (Bell and Brown, 1995), and echinoid larvae (Metaxas and Young, 1998) have all been shown to respond in some manner to haloclines.

Further investigations could improve on existing work in several important ways. All previous studies with holoplankton and nearly all of those with meroplankton involved haloclines that spanned less than 1 cm. Although haloclines with this small of a vertical extent are possible, field studies typically show haloclines of several tens of centimeters to meters even for the sharpest haloclines (e.g. Richardson, 1985; Tiselius et al., 1994; Madirolas et al., 1997). Additional experiments involving haloclines spanning a greater vertical extent are needed.

Another limitation of previous experiments is the size of the experimental aquaria. The aquaria utilized were almost all less than 50 cm tall (e.g. Lance, 1962; Harder, 1968; Mann et al., 1991; Metaxas and Young, 1998), which could cause significant container effects on the behavior of the zooplankton. Experiments using larger aquaria may be more relevant to field conditions by reducing the chance of container effects and possibly revealing otherwise subtle vertical distribution patterns.

New experiments should also entail longer periods of observation. Only two of the experiments reviewed above involved observations for a full 24 h (Roberts, 1971; Bell and Brown, 1995) and most others involved observations of less than 3 h. Haloclines are a regular and persistent feature in some estuaries (Cloern and Nichols, 1985), suggesting that long-term observations of zooplankton behavioral responses to haloclines, including possible diel or tidal cycle vertical migrations, should be undertaken. Another important addition to previous studies should be the use of statistical analyses. Some previous studies of holozooplankton and haloclines, including those by Lance (1962) and Harder (1968), did not apply statistical analyses to the resulting data.

Regions of the San Francisco Bay contain haloclines throughout the year that regularly encompass salinity differences of several psu over only a few meters (Fig. 1) (Caffrey et

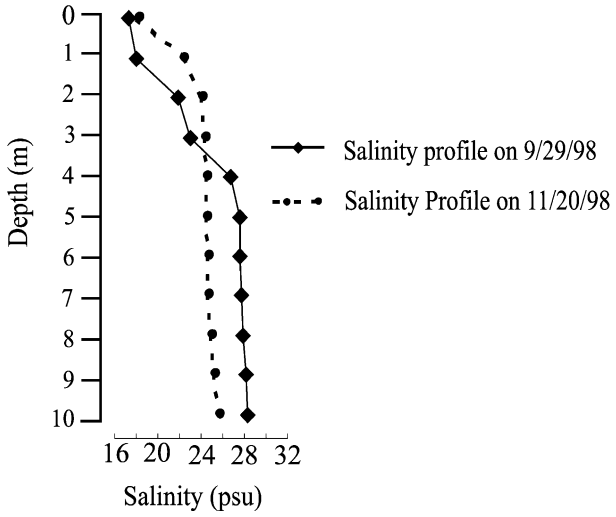


Fig. 1. Two examples of common salinity–depth profiles taken during collections from the San Pablo Bay within the San Francisco Bay estuary.

al., 1994; Edmunds et al., 1995, 1997; Baylosis et al., 1997). Typical estuarine circulation can occur where net non-tidal flow is seaward at the surface and landward at depth (Cloern and Nichols, 1985; Monismith et al., 1996). The San Francisco Bay is a shallow estuary, averaging only 6 m, which means even small amplitude migrations by zooplankton may result in their contact with a halocline.

The objectives of this study are to experimentally determine how and why haloclines affect the vertical distribution and migration of some of the dominant zooplankton of the San Francisco Bay estuary (i.e. the four copepods *Acartia* (*Acartiura*) spp., *Acartia* (*Acanthacartia*) spp., *Oithona davisae*, and *Tortanus dextrilobatus*, and the larval herring *Clupea pallasi*). More specifically, we intended to determine if these zooplankton change their location in a water column when a halocline is present and, if so, whether this change can be linked to salinity-induced mortality.

2. Materials and methods

2.1. Specimen collection

Copepods were collected from the channels (mean depth of stations = 17.4 m) of the northern end of the Central Bay (37°52.9′N, 122°25.6′W) to the northern end of San Pablo Bay (38°3.7′N, 122°15.8′W) within the San Francisco Bay estuary by conducting oblique tows from near bottom to the surface with a 0.5-m-diameter, 153-μm mesh plankton net. Salinity and temperature profiles of the water column were taken using a YSI model 85 CT meter. Specimens were immediately brought back to the laboratory and adult females of the desired taxa were sorted for each experiment. Adult female copepods are

easily identified by the presence of either a swollen urosomal segment (*Acartiura* spp., *Acanthacartia* spp., *T. dextrilobatus*) or egg sacs (*O. davisae*) and are ecologically important because of their contribution to reproduction and population growth. All experiments were initiated within 6 h of collection.

Herring eggs were obtained from adult *C. pallasi* from the San Francisco Bay by the Bodega Marine Laboratory, U.C. Davis, and eggs were held until hatching.

2.2. Halocline experiments

Twelve halocline experiments were undertaken on five taxa: *Acartiura* spp., *Acanthacartia* spp. (*Acartia californiensis* and *Acartia clausii*), *O. davisae*, *T. dextrilobatus*, and *C. pallasi*. These experiments entailed the direct observation of the vertical distribution of organisms in a tank with a halocline (halocline tank) and without halocline (control tank). These custom designed Plexiglas® tanks (200 cm × 7.6 cm × 5.1 cm) allowed the copepods sufficient room to migrate vertically. Details of the experimental vertical migration apparatus are given in Bollens et al. (in preparation). But briefly, an infrared light-emitting diode (LED) was used so that video could be recorded both during the day and at night without altering the organism's normal behavior. A plano-convex lens was placed in front of the light and behind the tank. The lens was used to convert the point light source of the infrared light into a columnated light source. A monochrome video camera (Cohu) with a macro/zoom lens was turned on once an hour and run up or down the length of the tank. The video was recorded on video cassette time lapse recorders (Panasonic, model AG-6124) with a date/time recorder. The whole system, which included the camera, lens, and LED, was mounted on a motorized linear bearing/rail system. The motor, camera, lights and VCR were all computer controlled. The system was programmed to turn on once an hour and it took 6 min for the camera to traverse and record the entire length of the tank. All tank and video systems were housed in a temperature-controlled cold room with the temperature set to that of collection (field) or culture conditions. A light diffuser was suspended above each tank and a 65-W GE grow bulb was turned off and on in concert with local times of sunrise and sunset.

The water used for the experiments was obtained by pumping San Francisco Bay water from 1 m depth off the seawall at the Romberg Tiburon Center (37°55.652′N, 122°35.303′W), filtering it through a 1-μm mesh screen, and allowing it to settle for at least 1 day. The salinity of this water was reduced as necessary with deionized water.

Haloclines were made by pouring saline water into the lower half of the tank and gently siphoning less saline water on top. This resulted in a mixed area (halocline) that spanned roughly 40 cm of the central portion of the water column. A control tank contained a water column of uniform salinity equal to one of the two salinities used in the halocline (treatment) tank, and was equal to that of the collection (field) site or culture condition. To confirm the location and magnitude of the experimental haloclines, the probe of the YSI CTD meter was lowered into each tank and the salinity was recorded every 5 cm before each experiment. Salinity readings were also taken at the end of several experiments, but this practice was halted after repeated measurements confirmed the stability of the haloclines (Fig. 2). A halocline encompassing a 4- to 5-psu change

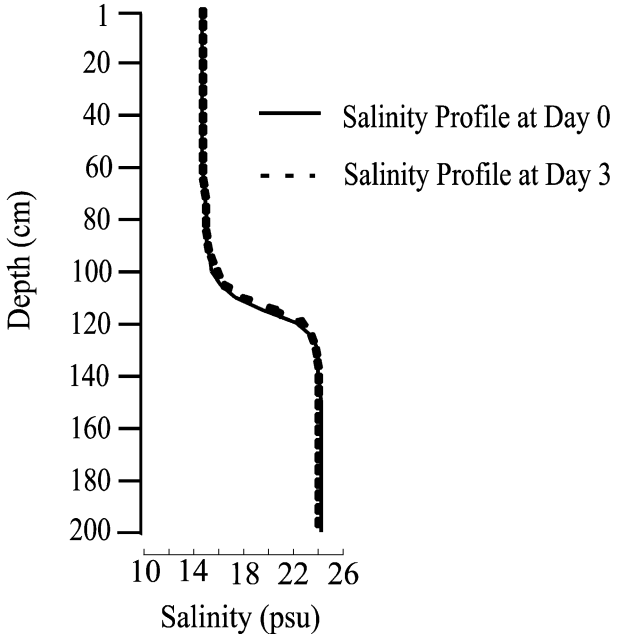


Fig. 2. Salinity–depth profiles taken from within the halocline (treatment) tank of *Acartiura* spp. experiment 2 at the beginning and end of the experiment.

over depth was used for each organism and when possible, haloclines of larger (9–10 psu) or smaller (1–2 psu) magnitude were also used. The salinity levels of the haloclines in each experiment (Table 1) are reflective of natural conditions each taxon would

Table 1
Halocline experimental conditions (organism used, experiment number, and salinity levels of each tank) and the percentage of organisms remaining suspended at the end of each experiment

Organism	Experiment number	Halocline tank (psu)	Control tank (psu)	Percentage of organisms suspended during the last experiment hour	
				Control	Halocline
Acartiura spp.	1	19.2–23.7	23.7	na	na
	2	14.0–24.0	24.0	84.0	22.2
	3	19.0–28.5	19.0	33.3	100.0
Acanthacartia spp.	1	12.8–17.6	17.7	60.0	36.8
O. davisae	1	14.2–18.9	18.9	100.0	93.1
	2	17.5–18.9	18.9	100.0	64.5
T. dextrilobatus	1	12.5–17.3	17.4	36.8	21.1
C. pallasi					
yolk sac	1	15.3–20.3	15.3	100.0	100.0
yolk sac	2	15.4–25.1	15.3	100.0	100.0
yolk sac	3	19.5–21.1	19.4	100.0	100.0
3–6 days old	4	16.5–20.8	16.4	100.0	60.0
14–17 days old	5	15.2–20.0	15.1	85.7	42.9

encounter in the Bay (Ambler et al., 1985; Kimmerer et al., 1999; Bollens et al., unpublished data); however, they are often greater in vertical extent than the 40 cm used in our tanks (Fig. 1) (Caffrey et al., 1994; Edmunds et al., 1995, 1997; Baylosis et al., 1997).

Food was added to all *Acartiura* spp., *Acanthacartia* spp. and *O. davisae* experiments in the form of phytoplankton (*Thalassiosira weissflogii*) at 15 μg l^{-1} chlorophyll *a*. The diatom density was deduced from chlorophyll analysis (Smith et al., 1981; Parsons et al., 1984) by taking 10 ml water samples from five to seven sampling valves that spanned the vertical extent of each tank. Chlorophyll samples were taken during the middle and end of the *Acanthacartia* spp. experiment and *Acartiura* spp. experiments 1 and 2, during the beginning and end of *Acartiura* spp. experiment 3, and during the middle of each *O. davisae* experiment. Rotifers were added as food to *C. pallasi* experiments 4 and 5 and their abundance and distribution were assessed using the video microscopy system.

All organisms were added to the layer in each tank comprising their ambient salinity. Copepods, with the exception of those from *Acartiura* spp. experiment 3, were siphoned into the lower salinity layer (ambient) through a bottom sampling valve. *C. pallasi* larvae were gently placed in the surface layer (ambient) using a plastic spoon to prevent them from being damaged during the siphoning procedure. *Acartiura* spp. from experiment 3 were placed into the surface layer to see if they preferred their ambient salinity to the non-ambient, deeper, more saline water.

The video monitoring system was started immediately after the addition of the organisms and run for 2–4 days. The experiments were terminated after 4 days or when the number of suspended zooplankton within a tank was too low to offer reliable statistical analyses of the data.

Resulting data on vertical distributions were analyzed using two separate methods. The first method of analysis entailed comparing the variances of the depths of the organisms as a measure of dispersion between the control and halocline tanks on each hourly scan. Testing for differences in dispersion between treatments was done by calculating an *F*-value using a simple ratio of the variances (Zar, 1996). The second method involved calculating the depth of organisms (mean and variance) each hour in each tank and comparing these data every hour using independent samples *t*-tests in SPSS 9.0. Unequal variances were assumed and used to calculate *t*-values only when the *F*-tests for dispersion yielded significant differences. Statistical results are given for two *C. pallasi* larvae age groups (0- to 3- and 14- to 17-day-old groups) and once for each copepod taxon.

When chlorophyll measurements were taken on more than 1 day (*Acartiura* spp. and *Acanthacartia* spp. experiments), the weighted mean depths for any given tank were combined and then compared between the control and halocline tanks using a *t*-test. Chlorophyll *a* weighted mean depth was calculated using the following formula:

$$\text{Weighted mean depth} = \text{sum}\ (\text{valve depth} \times \text{chlorophyll}\,\mu\text{g}\ l^{-1}) \Big/ \text{sum valve depths}$$

2.3. Mortality experiments

Three mortality experiments involving three of the taxa used in the halocline experiments (*Acartiura* spp., *Acanthacartia* spp., and *T. dextrilobatus*) were performed to determine whether the observed reactions in the halocline experiments could be linked to salinity-induced mortality. Experiments involved placing 10 adult females of the target copepod species into 1-l containers of different salinities and observing copepod survival over time. The duration of each mortality experiment and the different salinity treatments, which encompassed the salinities used in the corresponding halocline experiment for each taxon, are shown in Table 2. Deionized water or Sweetwater artificial sea-salts were added to ambient salinity water to achieve the desired treatments. Four replicates of each treatment were used. Copepods were counted daily with the naked eye and mortality was confirmed by filtering the contents of the containers and counting the individual copepods under a dissecting microscope. Temperature, food, and lighting conditions for each taxon were identical to those used during the halocline experiments. Food was monitored and periodically added during the *Acartiura* spp. and *Acanthacartia* spp. experiments to maintain 15 $\mu g\ l^{-1}$ chlorophyll. Data (number of copepods alive on any

Table 2
Mortality experiment results: values in tables are the mean number of surviving copepods of four replicates for each salinity treatment

(a) *Acartiura* spp.

Day	Salinity treatment (psu)					*F*-value	*P*
	4	14	19	24	34		
0	0* * *	5.25	6.25	6.75	6.25	42.60	< 0.001
2	0* * *	5.50	6.25	6.25	7.25	35.00	< 0.001
5	0* * *	5.50	6.25	6.25	7.25	54.20	< 0.001
9	0* * *	4.75	5.75	5.50	4.75	22.00	< 0.001

(b) *Acanthacartia* spp.

Day	Salinity treatment (psu)			*F*-value	*P*
	4	14	19		
0	0* * *	4.75	5.75	97.10	< 0.001
2	0* * *	5.75	6.00	32.53	< 0.001
5	0 * *	4.75	3.50	10.00	0.005
9	0 *	4.30	2.30	7.50	0.024

(c) *T. dextrilobatus*

Day	Salinity treatment (psu)					*F*-value	*P*
	4	9	14	19	29		
0	6.25	7.50	7.50	7.50	6.75	0.96	0.45
2	1.00	2.50	3.50	3.75	2.25	2.84	0.062
4	0	0	1.25 *	0	0	3.95	< 0.05

Level of significant difference between salinity treatments on any given day indicated by *'s.

given day) from all treatments were analyzed by performing a one-way ANOVA on each day separately.

3. Results

3.1. Halocline experiments

The behavioral response of zooplankton to haloclines, as measured by dispersion values and mean depths, differed between species and with the strength of the halocline. Due to the large number of statistical tests, it should be kept in mind that a type 1 error will cause several test results (5%) to be spuriously significant.

3.2. 4–5 psu Haloclines

The presence of a 4- to 5-psu halocline resulted in significant behavioral responses for *Acanthacartia* spp., *O. davisae*, and 14- to 17-day-old *C. pallasi* larvae. The strongest responses were exhibited by the two copepod species which aggregated in and below the halocline (*Acanthacartia* spp., Fig. 3; *O. davisae*, Fig. 4). The 14- to 17-day-old *C. pallasi* larvae exhibited a moderate response by often remaining in the deeper, more saline water of the halocline tank (Fig. 5). The responses of the younger *C. pallasi* larvae and *T. dextrilobatus*, if present at all, were subtle.

Acanthacartia spp. were significantly deeper in the halocline tank during 24 of the 49 scans analyzed (Fig. 3). At no time were these copepods significantly deeper in the control tank. The dispersion of copepods was significantly less in the halocline tank than those in the control tank during 19 of 49 scans (Table 3). At no time was the dispersion of copepods significantly less in the control tank. The weighted mean depths of chlorophyll *a* were not significantly different between tanks.

O. davisae experiment 1 revealed copepods to be significantly deeper in the halocline tank during 9 of 47 scans and significantly deeper in the control tank during 2 of 47 scans (Fig. 4). The dispersion of copepods was significantly different between tanks during 32 of the 47 hourly scans (Table 3). In 31 of these 32 instances, the copepods in the halocline tank were significantly less dispersed than the copepods in the control tank. The single measure of weighted mean depth of chlorophyll *a* was similar between treatment tanks: 121 cm in the halocline tank and 112 cm in the control tank.

T. dextrilobatus did not respond in a strong and obvious manner to haloclines of a 4.8-psu magnitude (Fig. 6). Only 6 of 65 *t*-tests yielded significant results (Fig. 6), all of which occurred when the copepods were deeper in the halocline tank. Only 5 of 65 significant differences in dispersion were found (Table 3); in four of these, the dispersion of copepods in the halocline tank was less than in the control tank.

Only 2 of the 80 *t*-tests comparing the mean depth of yolk-sac *C. pallasi* larvae in experiment 1 revealed significant differences (Fig. 7). A significant difference in dispersion was seen during 8 of the 80 hourly scans (Table 3), all of which were cases where the dispersion of larvae in the halocline tank was greater than in the control tank.

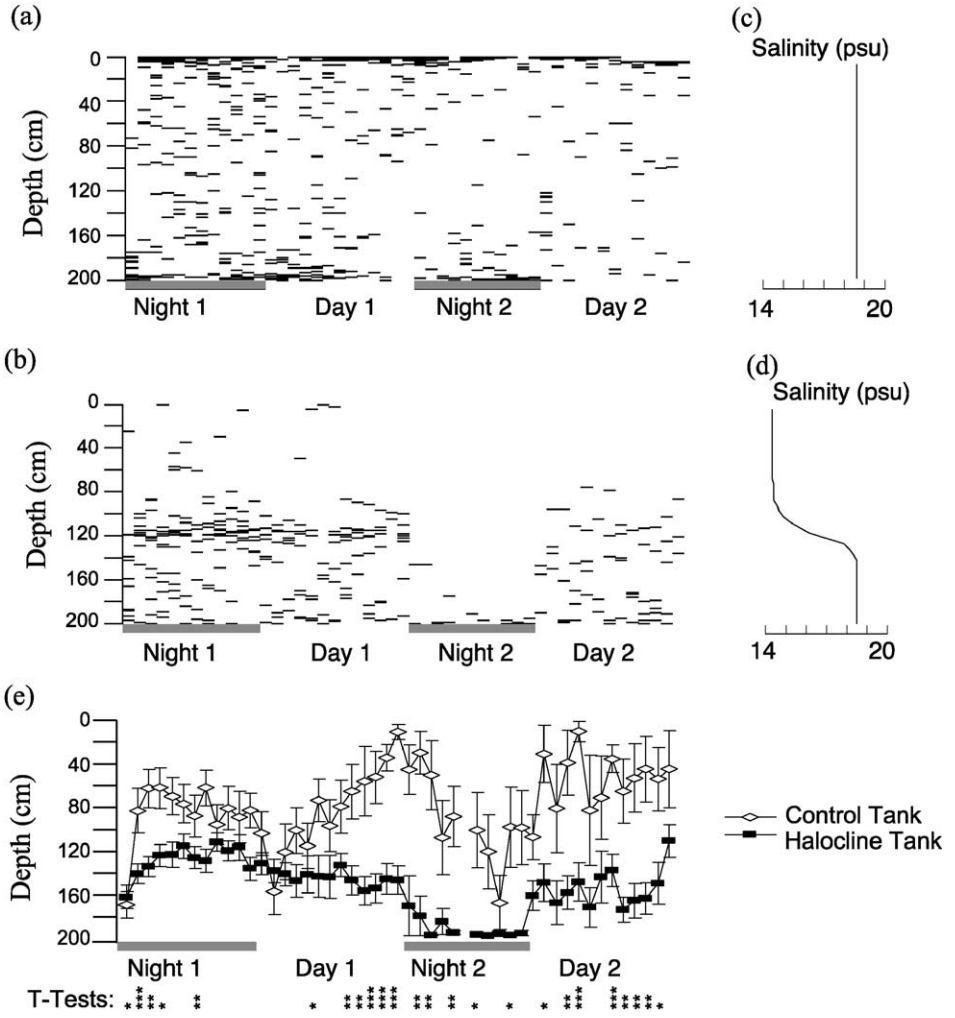


Fig. 3. Results of the *Acanthacartia* spp. halocline experiment. (a and b) The vertical position (*Y* axis) of each copepod for each hour scanned (*X* axis); (a) in a water column of uniform salinity (control) and (b) in a water column with a 4.8-psu halocline. Each small block (–) represents one copepod. Multiple observations at one depth during a single scan were plotted in adjacent (1 cm) vertical cells. (c and d) Salinity profiles for each tank [control tank (c); halocline tank (d)]. (e) The mean (± S.E.) depth (*Y* axis) of copepods in both tanks each hour scanned (*X* axis). The results of the *t*-tests comparing the mean depth of copepods between tanks are given directly under each scan (* = $P < 0.05$; ⁂ = $P < 0.01$; ⁂ = $P < 0.001$).

Three- to 6-day-old *C. pallasi* larvae exhibited a significant difference in mean depth during 10 of the 48 scans (data not shown). Seven of these 10 instances occurred when larvae were significantly deeper in the halocline tank. Data on the second and third days and nights of this experiment were lost. There was a significant difference in dispersion during 7 of 48 hourly scans. Six of these seven differences resulted when the

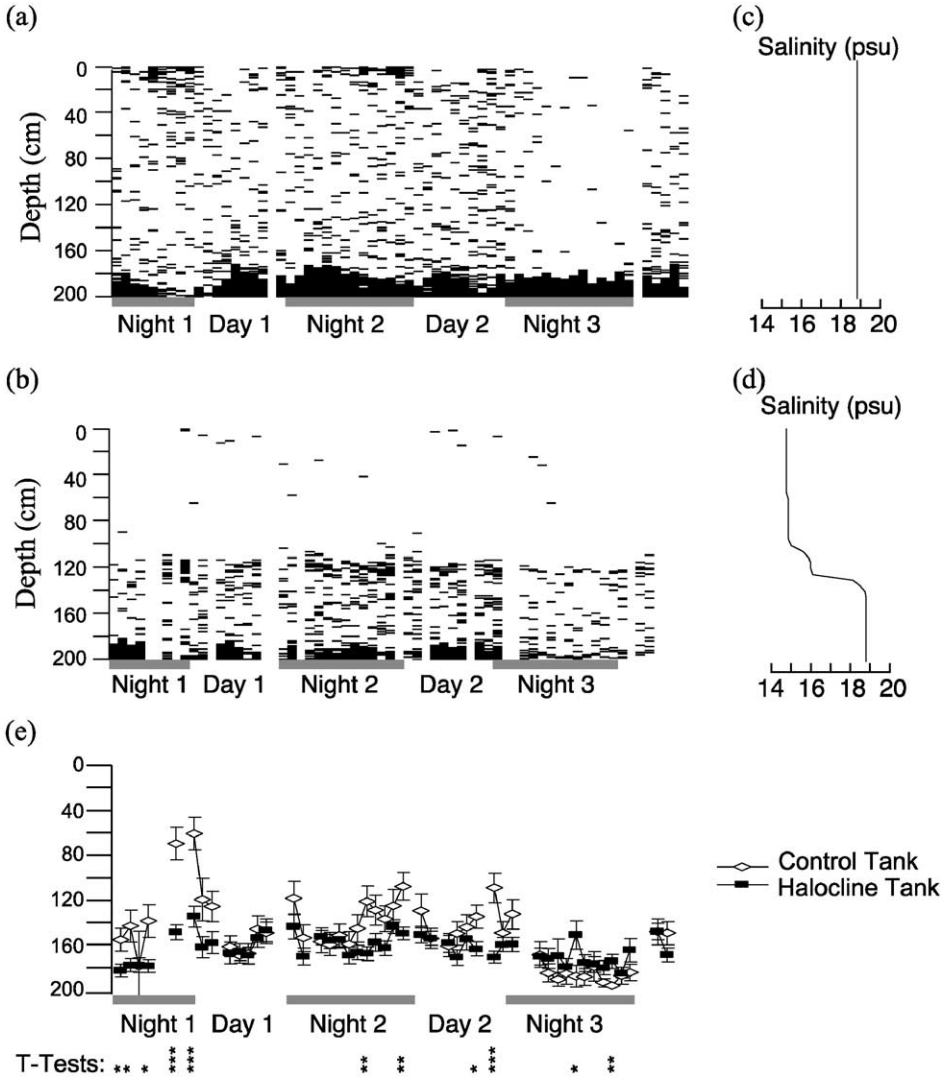


Fig. 4. Results of *O. davisae* experiment 1. (a and b) The vertical position (*Y* axis) of each copepod for each hour scanned (*X* axis); (a) in a water column of uniform salinity (control) and (b) in a water column with a 4.7-psu halocline. Each small block (–) represents one copepod. Multiple observations at one depth during a single scan were plotted in adjacent (1 cm) vertical cells. (c and d) Salinity profiles for each tank [control tank (c); halocline tank (d)]. (e) The mean (± S.E.) depth (*Y* axis) of copepods in both tanks each hour scanned (*X* axis). The results of the *t*-tests comparing the mean depth of copepods between tanks are given directly under each scan (* = $P < 0.05$; ⁑ = $P < 0.01$; ⁂ = $P < 0.001$).

dispersion of larvae in the halocline tank was greater than the dispersion in the control tank.

The 14- to 17-day-old larvae of experiment 5, in contrast to the younger *C. pallasi* larvae, appeared to show a preference for the more saline water in the bottom of the halocline tank,

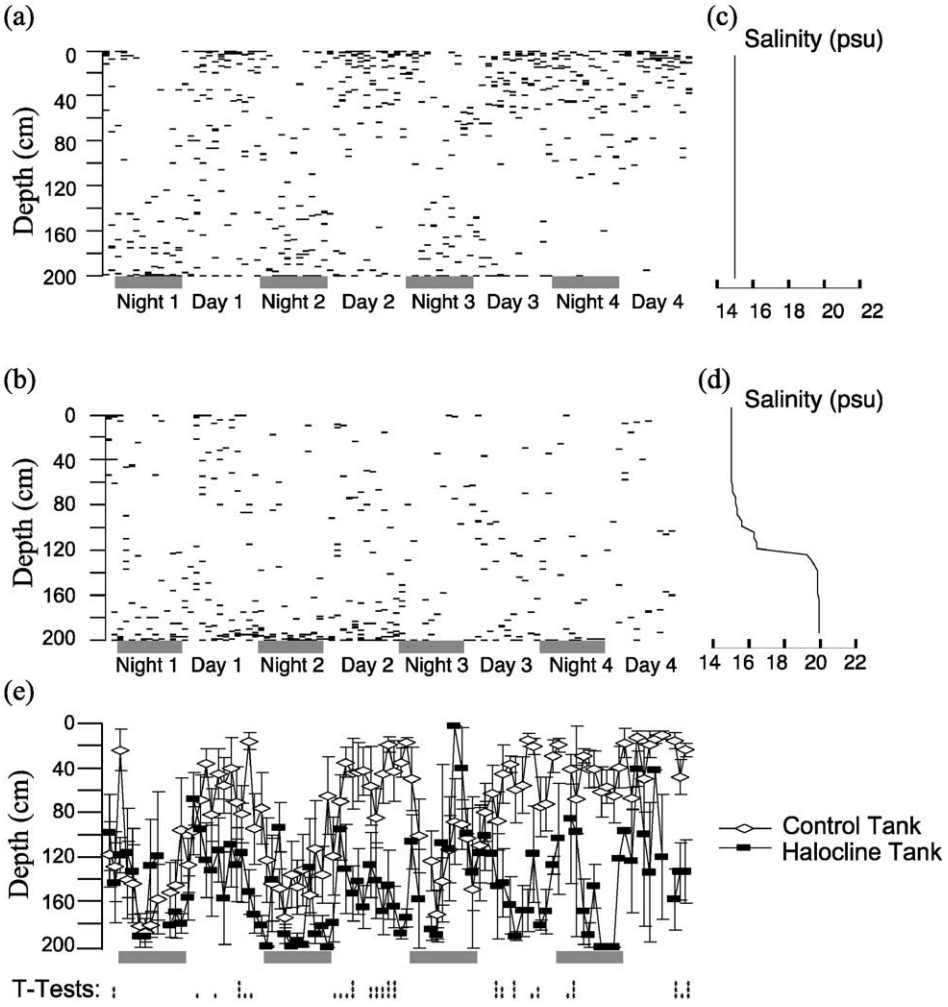
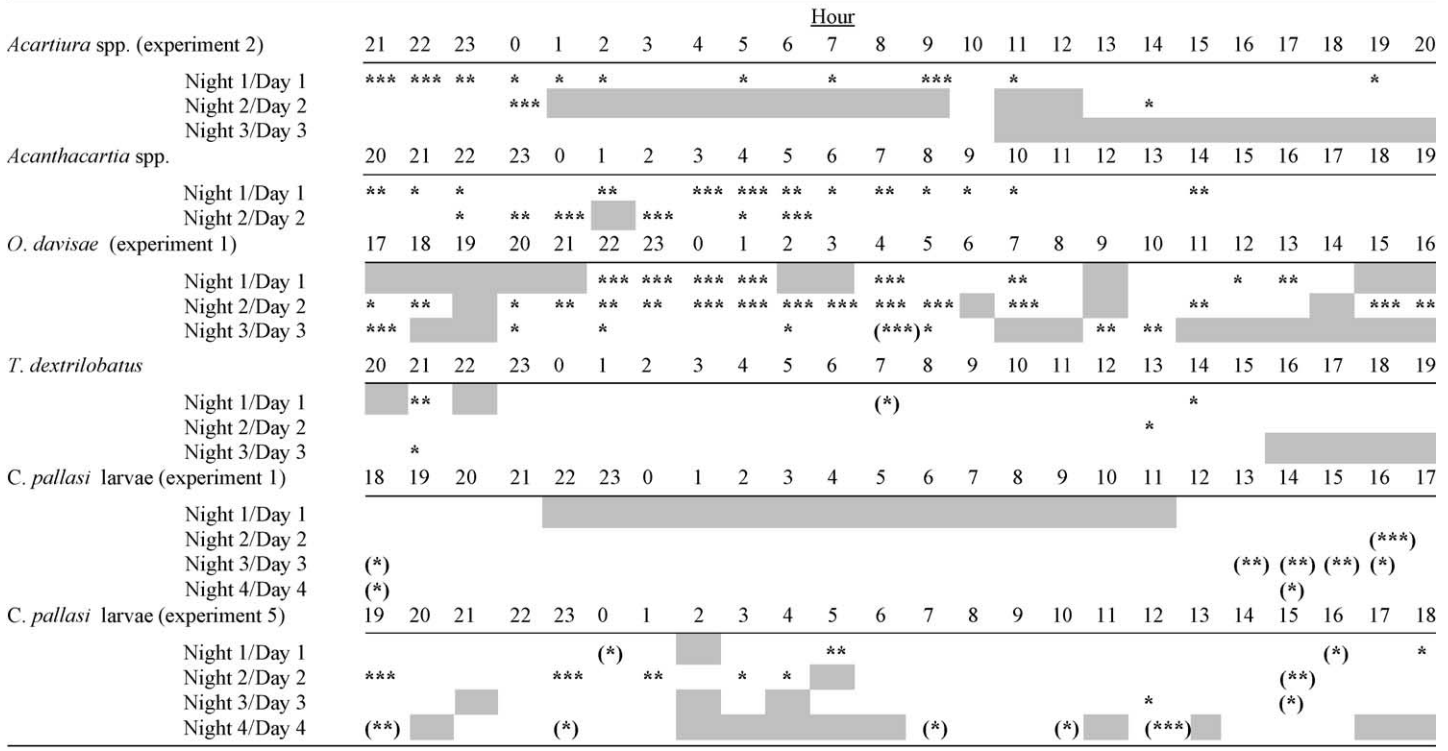


Fig. 5. Results of *Clupea pallasi* (14- to 17-day-old larvae) experiment 5. (a and b) The vertical position (*Y* axis) of each herring larva for each hour scanned (*X* axis); (a) in a water column of uniform salinity (control) and (b) in a water column with a 4.8-psu halocline. Each small block (–) represents one herring larva. Multiple observations at one depth during a single scan were plotted in adjacent (1 cm) vertical cells. (c and d) Salinity profiles for each tank [control tank (c); halocline tank (d)]. (e) The mean (± S.E.) depth (*Y* axis) of herring larvae in both tanks each hour scanned (*X* axis). The results of the *t*-tests comparing the mean depth of herring larvae between tanks are given directly under each scan (* = $P < 0.05$; ⁑ = $P < 0.01$; ⁂ = $P < 0.001$).

avoiding both the halocline and less saline surface water (Fig. 5). Analysis of these data revealed herring larvae to be significantly deeper in the halocline tank during 25 of the 82 scans (Fig. 5). At no time were the larvae significantly deeper in the control tank. The dispersion of *C. pallasi* larvae in the halocline tank was significantly greater than the dispersion in the control tank on 9 out of 82 scans and significantly less during 8 of 82 scans

Table 3
Results of the test for the difference in dispersion for each taxon



Significantly smaller dispersion value in the treatment tank is indicated by *(* = P < 0.05; * * = P ≤ 0.01; * * * = P ≤ 0.001). Significantly smaller dispersion value in the control tank is indicated by (*). Spaces left blank indicate no significant difference in dispersion. Gray areas indicate missing data.

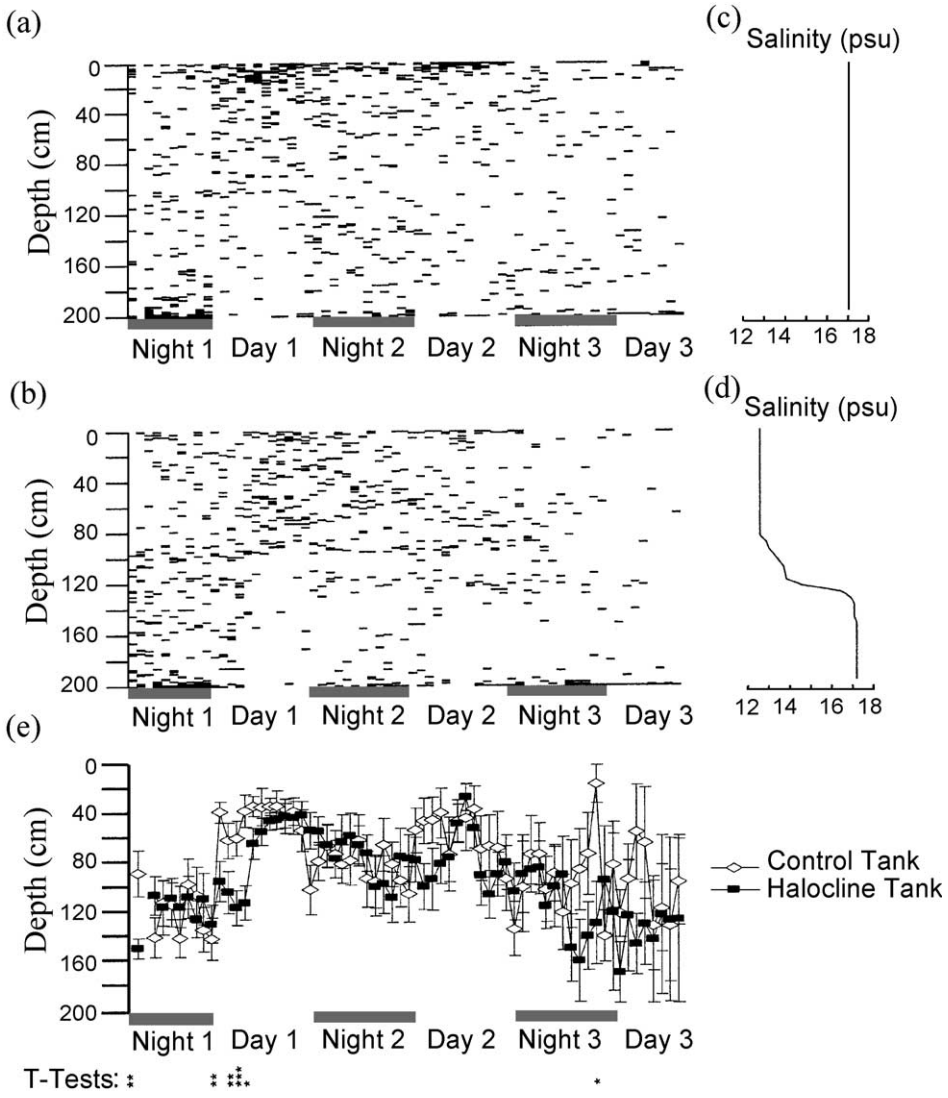


Fig. 6. Results of the *Tortanus dextrilobatus* halocline experiment. (a and b) The vertical position (*Y* axis) of each copepod for each hour scanned (*X* axis); (a) in a water column of uniform salinity (control) and (b) in a water column with a 4.8-psu halocline. Each small block (–) represents one copepod. Multiple observations at one depth during a single scan were plotted in adjacent (1 cm) vertical cells. (c and d) Salinity profiles for each tank [control tank (c); halocline tank (d)]. (e) The mean (± S.E.) depth (*Y* axis) of copepods in both tanks each hour scanned (*X* axis). The results of the *t*-tests comparing the mean depth of copepods between tanks are given directly under each scan (* = $P < 0.05$; ⁂ = $P < 0.01$; ⁂ = $P < 0.001$).

(Table 3). The distribution of food (rotifers) for all *C. pallasi* experiments, although not quantified, was seen on video to be present throughout the tanks during each experiment.

Data on all of *Acartiura* spp. experiment 1 were lost.

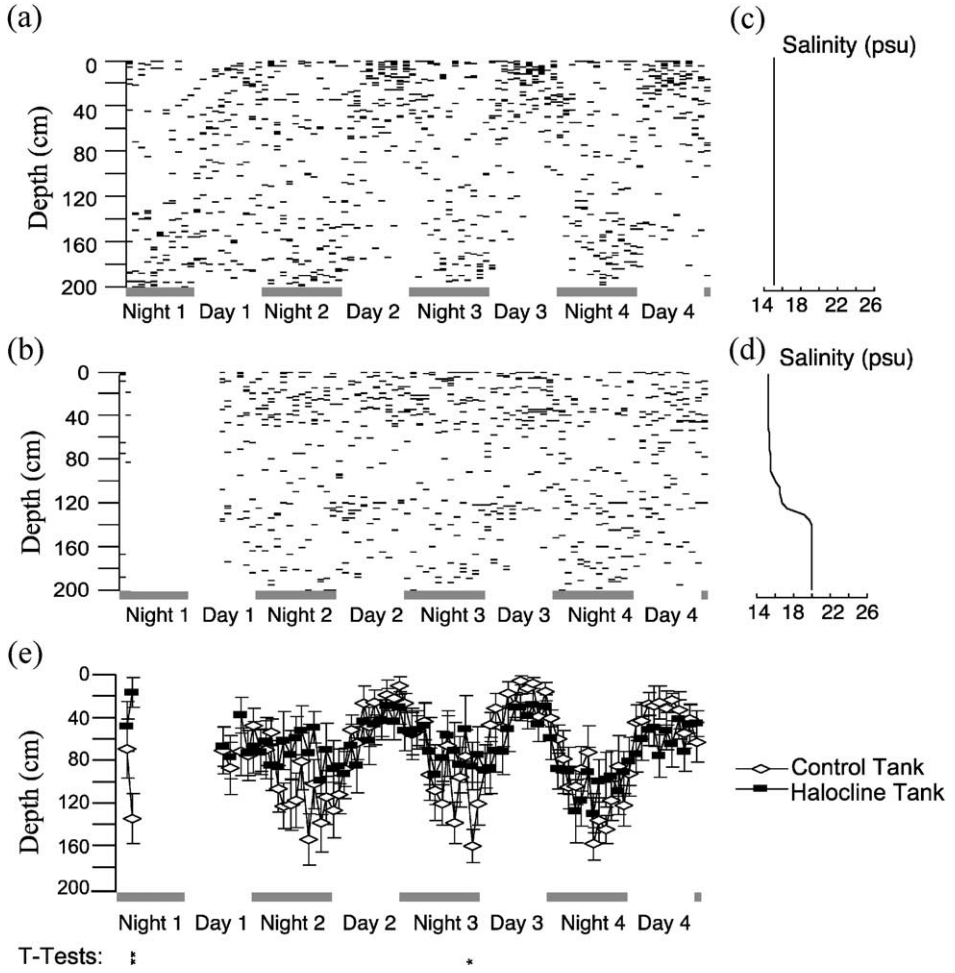


Fig. 7. Results of *C. pallasi* (yolk-sac larvae) experiment 1. (a and b) The vertical position (*Y* axis) of each herring larva for each hour scanned (*X* axis); (a) in a water column of uniform salinity (control) and (b) in a water column with a 5-psu halocline. Each small block (–) represents one herring larva. Multiple observations at one depth during a single scan were plotted in adjacent (1 cm) vertical cells. (c and d) Salinity profiles for each tank [control tank (c); halocline tank (d)]. (e) The mean (± S.E.) depth (*Y* axis) of herring larvae in both tanks each hour scanned (*X* axis). The results of the *t*-tests comparing the mean depth of herring larvae between tanks are given directly under each scan (* = $P < 0.05$; ⁑ = $P < 0.01$; *** = $P < 0.001$).

3.3. 9–10 psu Haloclines

The experiments involving a 9- to 10-psu halocline resulted in a strong response by *Acartiura* spp. (experiments 2 and 3) which aggregated in and below the halocline (Fig. 8) and a weak response by the *C. pallasi* yolk-sac larvae.

Acartiura spp. experiment 2 data revealed copepods to be significantly deeper in the halocline tank during 20 of the 48 scans (Fig. 8). At no time were copepods significantly

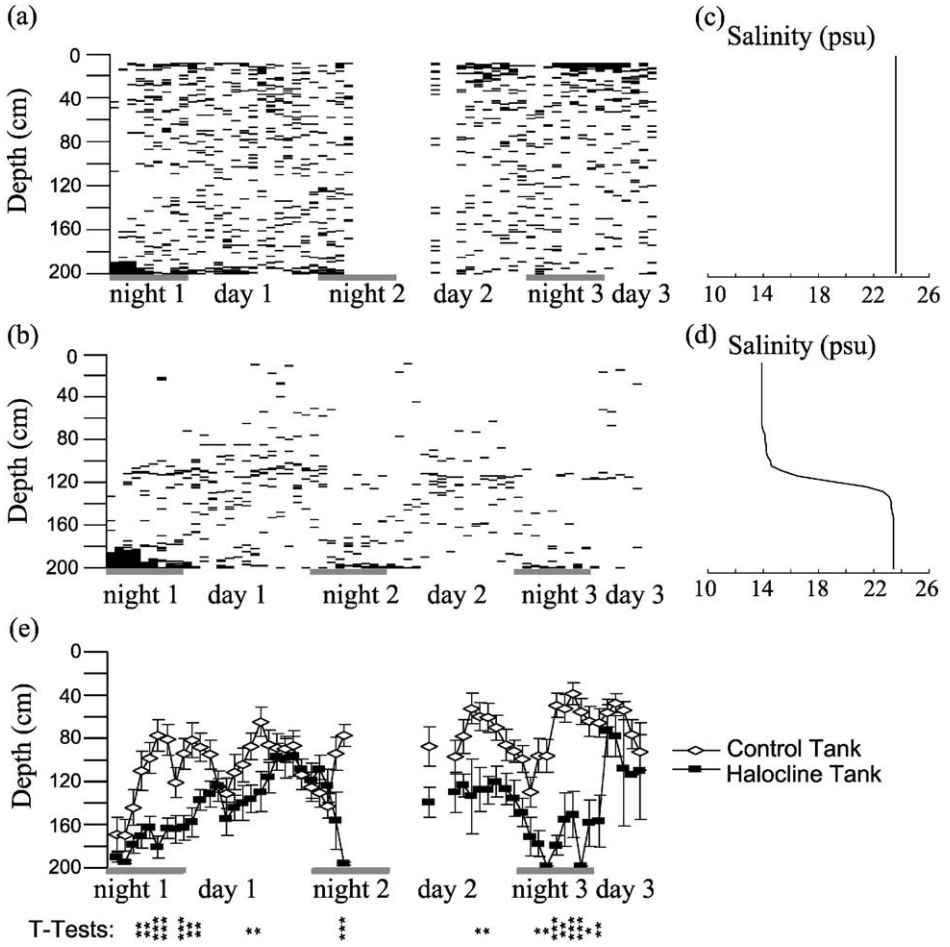


Fig. 8. Results of *Acartiura* spp. halocline experiment 2. (a and b) The vertical position (*Y* axis) of each copepod for each hour scanned (*X* axis); (a) in a water column of uniform salinity (control) and (b) in a water column with a 10-psu halocline. Each small block (–) represents one copepod. Multiple observations at one depth during a single scan were plotted in adjacent (1 cm) vertical cells. (c and d) Salinity profiles for each tank [control tank (c); halocline tank (d)]. (e) The mean (± S.E.) depth (*Y* axis) of copepods in both tanks each hour scanned (*X* axis). The results of the *t*-tests comparing the mean depth of copepods between tanks are given directly under each scan (* = $P < 0.05$; ⁑ = $P < 0.01$; ⁂ = $P < 0.001$).

deeper in the control tank. Data for most of night 2 are missing due to technical problems with the video equipment. The dispersion of *Acartiura* spp. in the halocline tank was less than the dispersion of copepods in the control tank in 48 out of 51 hourly scans during experiment 2, with 14 of these being significant (Table 3). The weighted mean depth of chlorophyll *a* in the halocline tank was significantly deeper than the control tank during experiment 2 ($P = 0.039$*).

Acartiura spp. experiment 3 yielded significant differences in mean depth of copepods on 24 of the 47 hourly scans (data not shown). Twenty-three of these 24 significant instances resulted when copepods were deeper in the halocline tank. The dispersion of copepods in the halocline tank was less than the dispersion of copepods in the control tank on 42 of 47 scans, and significantly so on 12 scans. The weighted mean depths of chlorophyll *a* were not significantly different between tanks.

The mean depths of *C. pallasi* yolk-sac larvae in experiment 2 (data not shown) were significantly different on 10 of the 91 hourly scans. Eight of these 10 instances resulted when larvae were significantly deeper in the halocline tank. There was a significant difference in dispersion during 9 of the 91 hourly scans. Seven of these nine differences resulted when the dispersion of the larvae in the halocline tank was greater than the dispersion in the control tank.

3.4. 1.4–1.6 psu Haloclines

The small-magnitude halocline experiments (1.4–1.6 psu) resulted in a weak response by *O. davisae* (experiment 2; data not shown) and *C. pallasi* yolk-sac larvae (experiment 3; data not shown).

The copepods did not greatly change their mean depth in response to the weak halocline but they did significantly change their dispersion patterns. The dispersion of *O. davisae* in the 1.4-psu halocline tank was significantly less than the dispersion of *O. davisae* in the control tank on 15 of 58 hourly scans and significantly greater during only 3 of these 58 scans. Copepods in the halocline tank appeared to aggregate more closely than those in the control tank by remaining in and below the halocline. *O. davisae* in experiment 2 were significantly deeper in the halocline tank during 2 of the 58 hourly scans and significantly deeper in the control tank during 3 of these 58 scans. The single measure of weighted mean depth of chlorophyll *a* during *O. davisae* experiment 2 was 115 cm in the halocline tank and 112 cm in the control tank.

The dispersion of *C. pallasi* yolk-sac larvae, unlike the dispersion seen with *O. davisae*, was regularly greater in the halocline tank than in the control tank; on 24 of 96 hourly scans, the dispersion of larvae in the halocline tank was significantly greater while on only 4 of these 96 scans was the dispersion of larvae significantly greater in the control tank. The mean depth of larvae was significantly deeper in the halocline tank during 15 of 96 scans and significantly deeper in the control tank during 2 of these 96 scans.

3.5. Mortality experiments

The 4 psu treatment caused near instantaneous death of *Acartiura* spp. and *Acanthacartia* spp. (Table 2). The mortalities of these taxa in all the remaining salinity treatments were not statistically different even after 9 days of exposure.

T. dextrilobatus did not suffer immediate mortality in any of the salinities to which it was exposed. However, by the fourth day, significantly greater mortality was seen in all salinity treatments versus the ambient (14 psu) control (Table 2).

4. Discussion

The responses of the smaller species (*Acartiura* spp., *Acanthacartia* spp., and *O. davisae*) to haloclines were stronger than the responses of the larger species (*C. pallasi* and *T. dextrilobatus*). The smaller species accumulated in or below the halocline while the effects on the larger species, if present at all, were more subtle and varied.

Acartiura spp. and *Acanthacartia* spp. appear to prefer the deeper, more saline water of a stratified water column to the less saline surface water thus making their mean depth greater and dispersion smaller than in the homogeneous tank (Figs. 8 and 3, respectively). *O. davisae* also aggregated in and below the halocline but, unlike the *Acartia* species, the comparison of mean depths of *O. davisae* between treatments was far less sensitive in supporting this interpretation than were the tests of differences in dispersion. This apparent discrepancy can be resolved by noting that the dispersion of copepods can be drastically different while their mean depth remains the same. For example, in *O. davisae* experiment 2, there is an aggregation of copepods in the center of the tank (at the halocline) and the bottom of the halocline tank while the control has an aggregation at the bottom of the tank and the remainder are spread relatively uniformly throughout the tank. This results in mean depths of copepods that are not statistically different between treatments and dispersion differences that are significantly less in the halocline tank.

Harder (1968) is one of the only investigators to conduct halocline studies with *Oithona*, but he showed only that an assemblage of mixed copepods, 10% of which were *Oithona similis*, reacted to a halocline with a salinity magnitude of 10.71 ppt. Although no statistical analyses were performed by Harder (1968), most of the organisms in his mixed copepod assemblage appeared to congregate at the halocline.

The behavioral response of *Acanthacartia* spp. to haloclines, although similar to the response of *Acartiura* spp., appeared to be slightly stronger. *Acanthacartia* spp. showed more significant differences in mean depth and more significant differences in dispersion in response to a lesser halocline (4.8 psu vs. 10 psu, respectively; Figs. 3 and 8). Reasons *Acanthacartia* spp. may have had a stronger response to haloclines than *Acartiura* spp. may be reflected in the natural distribution of these two organisms in the San Francisco Bay; although both species are relatively euryhaline and abundant in the salinity levels used in these halocline experiments, *Acanthacartia* spp. are not as dominant as *Acartiura* spp. in lower salinity waters (Ambler et al., 1985; Kimmerer et al., 1999; Bollens et al., 1999; Bollens et al., unpublished data).

Because *O. davisae* showed more significant differences in dispersion but fewer differences in mean depth than *Acartiura* or *Acanthacartia*, it is difficult to say which species is more sensitive to haloclines. Visually, however, it appears *O. davisae* (Fig. 4) is as sensitive (if not more so) to haloclines as both *Acanthacartia* and *Acartiura* species (Figs. 3 and 8). However, caution should be used in comparing the strength of the response of different species of zooplankton to haloclines because our experiments were performed at different times at slightly different salinity levels.

Although the number of significant statistical results for the yolk-sac and 3- to 6-day-old *C. pallasi* larvae experiments was low, there still may have been a subtle behavioral effect. It appears that the larvae, upon migrating up through the halocline, pause or remain in the halocline while those in the control tank remain tightly grouped either on

the top or bottom of the tank (i.e. Fig. 7). This pattern explains why the dispersion of larvae in the halocline tanks is typically greater than those in the control tanks for all experiments with young *C. pallasi* (*C. pallasi* experiments 1–4). However, because this behavior is so subtle, more experiments would need to be performed to determine the validity of this conclusion.

Fourteen- to 17-day-old *C. pallasi* larvae preferred the deeper, more saline water but, unlike the small copepods and perhaps the younger herring larvae, they did not appear to aggregate at the halocline. Regarding the different behaviors in different age classes of *C. pallasi*, it may be that these larvae select an increasingly saline area in the water column as they age; this phenomenon has been seen with other species of diadromous fish, such as the larvae of some diadromous gobies (Bell and Brown, 1995). Harder (1968) states that *Clupea harengus* larvae and postlarvae avoid haloclines (exact age of the larvae and strength of haloclines are not stated), which is in agreement with our results on older larvae, but not yolk-sac or 3- to 6-day-old larvae.

The strength of the behavioral response of zooplankton to haloclines appeared to be directly related to the strength of the halocline to which they were exposed. Both *O. davisae* and *C. pallasi* yolk-sac larvae (*C. pallasi* experiments 1 and 2) exhibited a greater change in depth and/or dispersion when exposed to a halocline of greater magnitude. Time is not a confounding factor to this conclusion because all treatments were run under identical conditions (except for magnitude of haloclines) and at the same time. In addition to our findings, evidence of an increasingly strong response of zooplankton to an increasingly strong halocline has been seen in some past studies (Lance, 1962; Harder, 1968; Roberts, 1971; Vazquez and Young, 1996; Metaxas and Young, 1998).

The food in our experiments did not likely affect the mean depth of organisms. For *Acartiura* spp., the significantly deeper weighted mean depth of chlorophyll *a* correlates with a significantly deeper mean depth of copepods in the halocline tank in experiment 2, but in experiment 3, the copepods are significantly deeper in the halocline tank despite the insignificant difference in weighted mean depth of chlorophyll *a* between tanks (weighted mean depth significantly greater in halocline tank of experiment 2 by 10.5 cm; weighted mean depth insignificantly greater in control tank of experiment 3 by 5.0 cm). Furthermore, halocline effects on the mean depth and dispersion of copepods revealed immediate and significant differences, that is, before the phytoplankton could have had a chance to become distributed differently between tanks. For experiments with *O. davisae*, the small difference in weighted mean depths of chlorophyll *a* between treatments (magnitude = 9 cm) is unlikely the cause of the observed differences in copepod behavior because, again, differences between tanks were seen immediately. Furthermore, the differences between tanks of *O. davisae* involved dramatic differences in dispersion. *Acanthacartia* spp. showed significant differences in mean depth between tanks despite the chlorophyll *a* depth remaining statistically unchanged.

Although salinity-induced mortality is a possible selective pressure associated with our halocline experiments, our mortality studies for *Acartiura* spp., *Acanthacartia* spp., and *T. dextrilobatus* lead us to rule this possibility out. The mortality experiments revealed that salinity levels equal to those in the halocline experiments did not cause significant mortality. Although no mortality studies were conducted on our other study

organisms, other research attests to the euryhaline nature of both *O. davisae* (Kimmerer et al., 1999; Bollens et al., unpublished data) and *C. pallasi* larvae (Holliday and Blaxter, 1960; Alderdice et al., 1979; Alderdice and Hourston, 1985; Griffin et al., 1998) and shows they are able to thrive in the variety of saline waters used in these halocline experiments.

Salinity-induced stress, caused by any change in salinity from ambient (Kinne, 1966), is another selective pressure that remains a possible explanation for the observed zooplankton behavior. Stress is commonly manifested as a change in rates and efficiencies in metabolism, activity, growth, and reproduction (Kinne, 1966), none of which were directly measured in this study. Some evidence of zooplankton responding to haloclines for reasons other than salinity-induced stress is present in *Acartiura* experiment 3; these copepods showed a preference for the high-salinity water over their ambient surface water. In addition, Harder (1968) showed that salinity-induced stress was not likely a factor affecting the distribution of *Temora longicornis* in haloclines.

Other selective pressures could involve retention in an estuary, predation, or food. The waters of the San Francisco Bay can exhibit typical estuarine circulation (Cloern and Nichols, 1985; Monismith et al., 1996) and by staying at depth or in an area of the halocline where there is zero net horizontal movement, the zooplankton would be less subject to advection out of the bay (Carriker, 1951; Bousfield, 1955; Cronin, 1982; Morgan et al., 1997). With regard to predation affecting the vertical distribution of zooplankton (e.g. Bollens and Frost, 1989), it is noteworthy that in this study, the obligate carnivore *T. dextrilobatus* spent at least half its time in the surface layer under stratified conditions, while its potential prey species, *Acartiura* spp., *Acanthacartia* spp. and *O. davisae*, all tended to remain in the deep layer. Alternatively, a refuge from predators could result from the often large amount of other particulate matter accumulating at the halocline interface (Bjornsen and Nielsen, 1991; Morgan et al., 1997). Food can vary in abundance between different water strata in the Bay (Caffrey et al., 1994; Edmunds et al., 1995, 1997; Baylosis et al., 1997) and the taxa in this study may be responding to haloclines by moving to areas in the water column where food is typically more abundant, as has been seen in past studies with some *Acartia* species (Tiselius, 1992; Avent et al., 1998; Bollens et al., in preparation).

Physical barriers, rather than selective pressures, may be the cause of some of the observed distributions of organisms. Two physical parameters associated with salinity that may also be acting as physical barriers are density and viscosity. Less saline water is less dense and less viscous which may make it harder to swim in and easier to sink out of (Harder, 1968) thus acting as a physical barrier to organisms attempting to migrate up through it. Each of these possible barriers could result in the observed accumulation of organisms in and below the halocline (Harder, 1968). Because these organisms thrive in the lower salinities and densities used in our halocline experiments (Ambler et al., 1985; Kimmerer et al., 1999; Bollens et al., unpublished data), these barriers alone seem like unlikely causes for the observed zooplankton distribution. It is possible that density and viscosity act as selective pressures because less energy may be required for zooplankton to remain suspended in the more saline dense water.

Although we have assumed that salinity is the proximate cue that elicits selective responses, it is equally possible that changes in a salinity-associated physical parameter,

such as density, is responsible for cueing these responses. In our experiments, in which temperature was uniform, the halocline was also an area of a rapid change in density over depth (pycnocline). Harder (1968) manipulated density in a water column with sucrose and was thus able to construct a salinity gradient without a density gradient and, conversely, a density gradient without a salinity gradient, and found that the copepod *T. longicornis* reacted to changes in density rather than salinity. In estuaries, salinity, rather than temperature, is the dominant force that drives the density gradient and a halocline spanning greater than 1 psu will almost always result in a proportionally strong density gradient (Caffrey et al., 1994; Edmunds et al., 1995, 1997; Baylosis et al., 1997). Thus, in estuaries, density gradients in the absence of salinity gradients are rare, and while either salinity or density could be the proximate cue eliciting changes in zooplankton vertical distribution, the consequence for the zooplankton would usually be the same.

The *C. pallasi* larvae exhibited a clear diel vertical migration behavior in concert with the presence of the daily light source at the top of each tank. All other organisms changed their distribution over time as well but the migration pattern, if present, was less clear. In all cases, the change in the vertical distribution of organisms over time in the stratified water columns (Figs. 3–8) underscores the importance of extended periods of observation for halocline studies such as these.

The number of organisms observed in the halocline tanks often became less than those in the control tanks during our experiments (Table 1). We are not sure whether the reduced numbers over time are due to mortality or that the animals are simply remaining still at the bottom of the tank where they cannot be observed by our methods. We do not think that mortality, if it occurred, was the result of the haloclines per se; indeed, our mortality experiments and an abundance of literature attest to the euryhaline nature of our study organisms. If some of the study organisms were simply resting on the bottom where we could not observe them, this would reduce the magnitude of the halocline effect on the entire population, but not that portion of the population actually observed to reside in the water column. In other words, the halocline effects we observed in these experiments are real, even if the proportion of the population affected is somewhat reduced.

Future studies, similar to those done by Harder (1968) and Tiselius (1992), should test for the effect of other factors, including food, predators, and stress, in conjunction with haloclines, to see how these variables further affect the distribution of zooplankton. Field studies to determine the fine scale distribution of zooplankton in relation to haloclines using either the Optical Plankton Counter (Herman, 1992) or Video Plankton Recorder (Davis et al., 1992) would be very useful in linking zooplankton behaviors observed in the laboratory to behaviors seen in nature.

Our results point to a high degree of flexibility in vertical migration behavior within a given species of zooplankton, as well as large variation between species; these species are not fixed to a single distribution or migration pattern, but change their behavior in relation to changes in their external environment (i.e. salinity). Such behavioral flexibility is very important in allowing planktonic organisms to maintain or alter position relative to currents, food, and predators, especially for those organisms living in dynamic environments such as estuaries.

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