

SHORT COMMUNICATION

Biological thin layer formation: interactions between the larval decapod, *Neotrypaea californiensis*, haloclines and light

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Received December 12, 2009; accepted in principle March 7, 2010; accepted for publication March 10, 2010

Corresponding editor: Roger Harris

Zoeae of the decapod *Neotrypaea californiensis* exhibited behavioural responses to a diel light cycle, consistent with vertical migration, and to the presence of haloclines, by forming biological thin layers.

KEYWORDS: biological thin layers; decapod behaviour; diel vertical migration; haloclines; pycnoclines; vertical distribution; zooplankton behaviour

As the average concentration of food in the ocean is often too low to support the growth observed in zooplankton, the ability to exploit patchily distributed resources is linked to zooplankton survival (Bainbridge, 1953; Mullin and Brooks, 1976; Daro, 1988; Tiselius, 1992; Leising, 2001). Biological thin layers of phytoplankton are often found at density discontinuities in the water column and can range in average thickness from tens of centimetres to several metres, can persist for several days, and span several kilometres horizontally (Nielsen *et al.*, 1990; Cowles and Desiderio, 1993; Dekshenicks *et al.*, 2001; Rines *et al.*, 2002; McManus *et al.*, 2008; Bochkansky and Bollens, 2009). Field observations demonstrate that planktonic grazers aggregate at thin layers (Castro *et al.*, 1991; Tiselius *et al.*, 1994; Holliday *et al.*, 1998), and several experimental studies have shown that zooplankton respond to thin layers of food (Bochkansky and Bollens, 2004; Clay *et al.*, 2004;

Ignoffo *et al.*, 2005; Bochkansky *et al.*, 2010). Other studies show that aggregations can occur at haloclines in the absence of food, suggesting that some species use physical cues to maintain position (Lance, 1962; Tiselius, 1992; Lougee *et al.*, 2002; Woodson *et al.*, 2007). Higher trophic levels aggregate at oceanographic discontinuities (Genin, 2004) and this can also occur at thin layers (Harder, 1968; Batty, 1994; Clay *et al.*, 2004). However, many questions remain as to how responses to thin layers and haloclines interact with predator avoidance behaviours, e.g. diel vertical migration (DVM; Bollens and Frost, 1989, 1991; and Hays 2003).

We investigated the effects of the presence of haloclines and diel light cycles on the vertical distribution of the first zoeae of the Callinassid decapod, *Neotrypaea californiensis*. Most previous behavioural research related to thin layers has focused on copepods (Saiz *et al.*, 1993; Leising and Franks, 2002; Lougee *et al.*, 2002; Bochkansky and

Bollens, 2004; Woodson *et al.*, 2005, 2007), with very few exceptions (Batty, 1994; Lougee *et al.*, 2002; Clay *et al.*, 2004; Ignoffo *et al.*, 2005). Decapod larvae are seasonally abundant members of coastal zooplankton communities (McConaughy, 1992), and, as meroplankton, their response to thin layers can be assumed to be independent from the benefit of reproduction via aggregation with conspecifics. Previous studies have investigated the behaviour of decapod larvae in response to salinity and density discontinuities (Lance, 1962; Roberts, 1971; Sulkin and Van Heukelem, 1982; O’Conner and Epifanio, 1985), however none have addressed the persistence of this response and its interaction with light. Our specific research questions were: How do zoeae of *N. californiensis* respond to the presence of physical stratification? How is this response modulated by light?

We conducted three laboratory experiments on the vertical distribution of first zoeae of *N. californiensis*. Our experimental apparatus consisted of two 2-m high columnar Plexiglas tanks (200 cm × 7.6 cm × 5.1 cm), each equipped with an overhead light source (65 watt GE Grow Bulb) and diffuser, a panning monochrome video camera (Cohu) and an infrared light emitting diode. As decapods are unable to perceive infrared light (Forward and Costlow, 1974), the video camera was able to record shadow images of the zoeae without disrupting their behaviour [for further details of this system see Speekmann *et al.* (2000); Lougee *et al.* (2002); Clay *et al.* (2004); Ignoffo *et al.* (2005)]. All experiments were conducted at 19°C in a temperature and light-controlled room.

For each experiment, we stratified the water in the treatment tank by first filling the lower half of the tank with higher salinity water (made of Millipore filtered water and Instant Ocean sea salt) and then slowly pumping water of lower salinity (by 5) into the top half of the tank. The control tank was vertically homogeneous, containing the same salinity water as the top layer of the stratified tank. The salinity of the water at

the surface of the tanks differed between experiments, as it was made to match the salinity at which the zoeae were collected (Table I). No food was added to the tanks and zoeae were starved for several hours before the experiments began.

Neotrypaea californiensis first zoeae were collected (500 µm, 1 m diameter oblique net tows) from Willapa Bay, WA, USA (46°34’46’’N; 123°56’32’’W) within 24 h of each experiment, and were immediately placed into unfiltered seawater. Zoeae were kept in an aerated 20 L bucket under a diel light cycle. Zoeae were sorted using a pipette and observed under a dissecting microscope immediately prior to each experiment to ensure the inclusion of only individuals exhibiting normal motility. Equal numbers of zoeae (19–30) were placed into the top of each tank for each experiment.

Video cameras were programmed to record every hour, with each pan taking 6 min. The number of hourly video recordings varied between experiments (Fig. 1), however only data from those hours recorded in both paired control and stratified tanks were included in statistical analyses. Lights were programmed to turn on and off consistent with local sunrise and sunset. At the end of each experiment, we measured temperature and salinity at 20 cm increments using a YSI 85 salinity–temperature probe. Salinity stratification persisted throughout all experiments and the haloclines were restricted to a range of <40 cm. Videotapes were analysed visually and the depth of each zoea recorded to the nearest 5 cm.

The distribution of zoeae within the tanks was rarely normal and occasionally bimodal (Fig. 1). We therefore separated the tanks into three depth bins: surface (0–60 cm), middle (60–120 cm, containing the halocline) and bottom (120–180 cm) and compared the number of larvae between bins. To assess the extent of aggregation and biological thin layer formation, we calculated an index of mean crowding, m^* (Lloyd, 1967; Bez, 2000; Bochdansky and Bollens, 2004), for each camera

Table I: Summary of the duration (hours) and salinities (top-bottom) of the paired stratified treatment tanks (S) and the homogeneous control tanks (H), and the number and temporal order of the pans included in statistical analyses. If during the experiment any portion of the tank was obscured during the recording, that camera pan and its pair were excluded from statistical analyses. Also noted is the number of Neotrypaea californiensis zoeae included in each tank and the date they were collected

	Experiment 1		Experiment 2		Experiment 3	
	S	H	S	H	S	H
Duration	52	27	29	36	45	27
Pans (hours) analyzed	1–11, 13–24, 27	1–11, 13–24, 27	1–12, 14–27	1–12, 14–27	1–27	1–27
Salinity	22–27	22	27–32	27	24–29	24
Number of larvae	25	25	30	30	19	19
Collection date	9 May 2007		17 May 2007		23 May 2007	

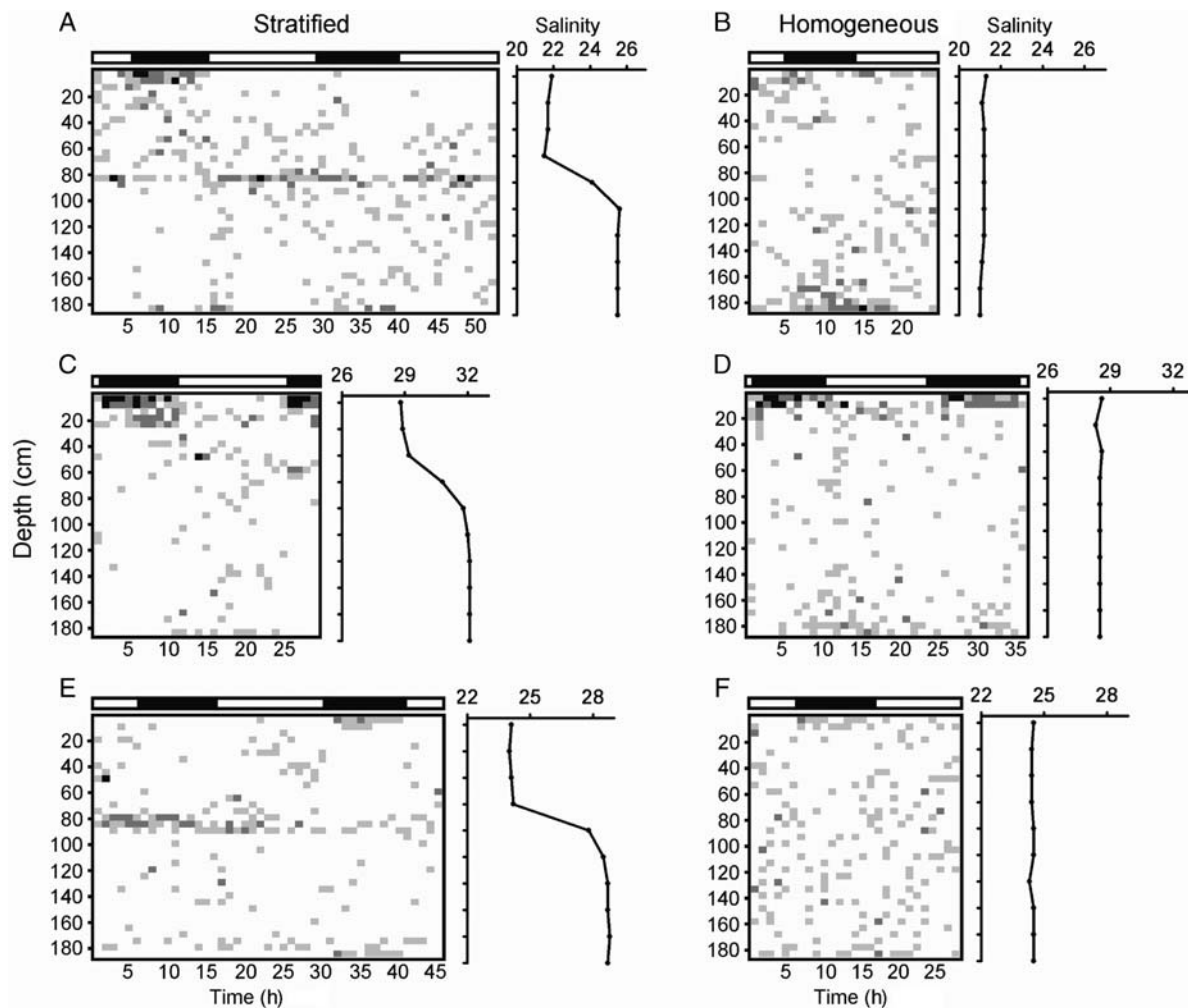


Fig. 1. Vertical distribution of *N. californiensis* over time in salinity stratified and homogeneous tanks. (**A** and **B**) Experiment 1, (**C** and **D**) experiment 2 and (**E** and **F**) experiment 3. Bars indicate the presence of zoeae. Pale grey, one zoea; dark grey, two to three zoeae; black, four or more zoeae. Each column represents the distribution of individuals during one camera pan. Note that not all zoeae were visible in each camera pan. To the right of each figure is a panel showing the measured salinities at the end of each experiment and indicating the position of the halocline. The bars on top of each figure indicate periods of darkness (black) and light (white).

pan from the raw counts of zoeae in each 5 cm depth increment:

$$m^* = m + \left(\frac{\sigma^2}{m} \right) - 1$$

where m is the mean number of individuals per increment and σ^2 the variance. To avoid biasing these indices, we omitted larvae from the top and bottom 5 cm of the tanks because the presence of a surface (air or bottom) might cause a natural aggregation (Bochdansky and Bollens, 2004).

We performed similar analyses for both depth distribution and m^* . The effects of stratification and light were analysed in ANOVAs using general linear models,

along with the repeated measure, hour. Depth bin was included as a factor for the analyses comparing numbers of zoeae in the top and middle of the tank (the bottom depth bin was excluded to meet ANOVA's assumption of independence). Where data did not meet the assumption of equality of variance they were square-root transformed, which normalized the variances in all cases. *Post hoc* comparisons were made using Tukey simultaneous tests. Statistical analyses were performed using Minitab v.15 ($\alpha = 0.05$).

Our experiments yielded significant effects both on crowding and vertical distribution. Zoeae were more likely to aggregate in tanks containing a halocline (Figs 1 and 2; ANOVA $F_{(1,131)} = 12.60$, $P = 0.001$), however this aggregation occurred in the area of the halocline only in

experiments 1 and 3 (Depth*Treatment*Experiment: $F_{(2,315)} = 11.75$, $P < 0.001$).

In the analysis of vertical distribution, the effect of the halocline interacted with that of light in both experiments 1 and 3 (Fig. 3; Depth*Treatment*Light: $F_{(1,315)} = 6.87$, $P = 0.009$). In experiment 1, in the stratified tank, the number of zoeae was greater near the surface during darkness (Tukey's HSD, all $P < 0.001$). While this trend is apparent during the first period of darkness, during the second, zoeae appeared to disperse to areas above and below the halocline (Fig. 1A and B). Results from experiment 3 indicate that zoeae remained primarily in the area of the halocline with a more dispersed distribution during periods of light (Tukey's HSD, $P < 0.05$). Note, however, that due to the shortened recording length for the control tank in experiment 3, the second period of darkness was not analysed statistically. In the stratified tank of experiment 3, we saw a

dispersal of zoeae during darkness to areas above and below the halocline similar to that seen in experiment 1 (Fig. 1E and F). While in the control tanks of experiments 1 and 3, light had no detectable effect on the vertical distribution of zoeae, in experiment 2 light was its primary driver (Tukey's HSD, all $P < 0.0001$). In experiment 2, zoeae exhibited the typical DVM pattern of aggregating towards the surface during periods of darkness in both stratified and control tanks (Fig. 1C and D).

Haloclines are often associated with high concentrations of phytoplankton and zooplankton (see references above) and residence within these layers would increase rates of encounter of *N. californiensis* with prey items. Haloclines also indicate the interface between two water masses and may, particularly for estuarine species such as *N. californiensis*, be an important cue used in horizontal transport or position maintenance (Seuront, 2006). Willapa Bay is a partially mixed, coastal plain estuary (Banas *et al.*, 2004). Over the period when *N. californiensis* first zoeae are abundant (April–July) (Graham and Bollens, 2010) and when salinity stratification occurred, the average difference between surface and bottom salinity was 5.4. Observed haloclines had a median rate of change of 8 m^{-1} and a maximum rate of change of 30 m^{-1} . As is common among estuarine decapods, *N. californiensis* possesses behaviours which promote export of first zoeae to coastal waters (Johnson and Gonor, 1982; Pimentel, 1983).

That individual *N. californiensis* crossed the halocline in experiment 3 indicates that aggregation of *N. californiensis* into thin layers was not due to the halocline acting as a physical barrier. In our first experiment, we saw an

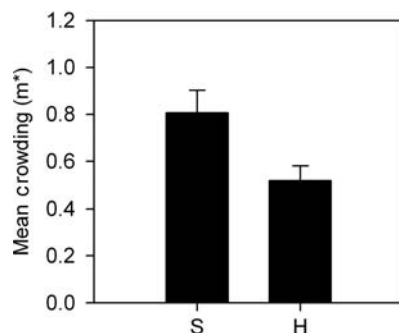


Fig. 2. The effect of treatment on mean crowding (m^*) of *N. californiensis* zoeae in salinity stratified (S) and homogeneous (H) tanks. Error bars represent +1 SE.

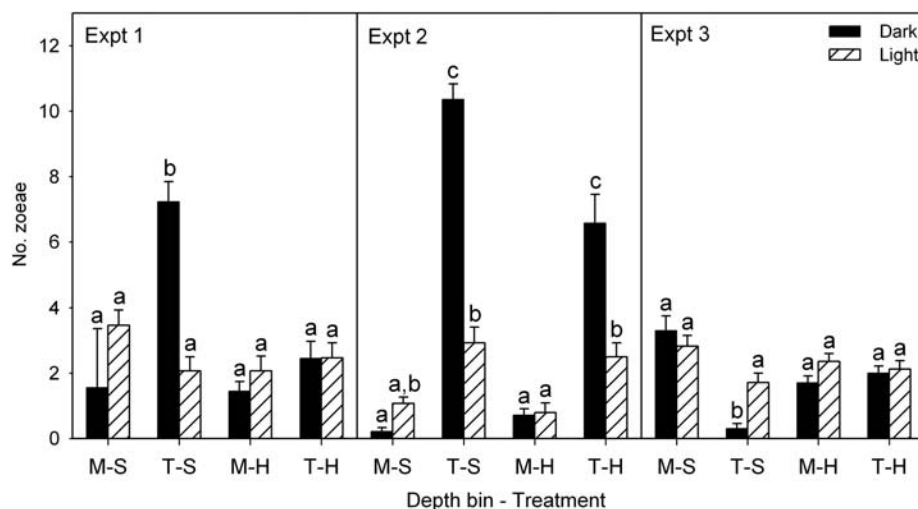


Fig. 3. The effect of a stratified (S) or homogeneous (H) water column and light on the number of *N. californiensis* zoeae in the top (T) and middle (M) depth bins in experiments 1, 2 and 3 compared between light (light bars) and dark (dark bars) conditions. Each bar represents the mean number of zoeae in a depth bin over the course of the experiment in one tank. Letters above each bar indicate groupings from Tukey's HSD. Error bars represent +1 SE.

aggregation at the surface during darkness and at the halocline during light (Fig. 1A), whereas in our third experiment aggregation at the halocline persisted during both light and dark conditions (Fig. 1E). Some zooplankton have been found to avoid aggregating at thin phytoplankton layers (Bjornsen and Nielsen, 1991; Alldredge *et al.*, 2002; McManus *et al.*, 2005), possibly to avoid exposure to toxic species, pathogens or predators. We had predicted that *N. californiensis* would disperse from the layer during light so as to reduce susceptibility to visual predators. Aggregation at a halocline during higher levels of ambient light may be affected by starvation (which was beyond our capability to assess), where the benefit of being positioned in a location with increased likelihood of food outweighs the increased risk of predation. Hunger has been found to induce vertical migration or to cause vertical migrators to spend longer periods in surface waters (Hays *et al.*, 2001; Pearre, 2003).

It is interesting that zoeae showed a somewhat differential response to the presence of haloclines across our three experiments. The only differences between these experiments were the date of collection of the zoeae and differences in the salinities of the water used. Larval behaviour may be influenced by absolute salinity (Latz and Forward, 1977) and it is possible that zoeae search for a gradient or alter their vertical position only in salinities above or below a certain threshold. Alternatively, zoeae themselves may have differed between dates, i.e. that three different “cohorts” may have differed in terms of age (though all were first zoeae), location of release or past experience with predators and prey. Behavioural plasticity is necessary to maximize foraging success while minimizing the risk of predation in a changing environment. In a study similar to ours on copepods, Lougee *et al.* (Lougee *et al.*, 2002) also observed considerable within-species variability in vertical migration patterns in response to thin layers. The variety of behavioural responses seen in this and in our study illustrates the benefit of including field caught organisms in experiments. By not controlling the pre-conditioning of these larvae, we gained ecologically relevant information on the range of potential responses to thin layers, from which we can form more directed research questions. For instance, how does variable exposure to different predator and prey communities influence the strength of larval response to either light or physical thin layers?

In summary, we found that the first zoeae of *N. californiensis* altered their vertical distribution and aggregated in the presence of haloclines, but that this response was variable. *Neotrypaea californiensis* zoeae also responded to a diel light cycle in a manner consistent with DVM. The interplay between these two responses appears plastic and is possibly dependent on pre-conditioning.

ACKNOWLEDGEMENTS

We are grateful to Ian McComas and Rian Hooff for experimental assistance and to Brian Tissot and Gretchen Rollwagen-Bollens for manuscript review.

FUNDING

This work was supported by an ONR grant N000140610200 to S.M.B. and G.R.-B.

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