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Density-Current Plumes

Abstract. *Diurnal solar heating produces an unstable warm zone just off the bottom of the inshore regions of a salt lake. The warm water rises in plumes in which brine shrimp become entrapped through apparently negative photokinetic behavior. The plumes of concentrated shrimp resemble those composed of insects in air.*

My observations of brine shrimp and their environment may increase our knowledge in two areas recently discussed in *Science*. The report of Peterson and Damman (*1*) and comments thereon (*2*) present two well-established observations: Visible plume-like formations occur over trees; and flying insects sometimes appear in plume-like formations, often over trees. From thermal considerations it has been inferred that these plumes may at times contain convectively rising warm air.

I have observed similar plumes of arthropods in an aquatic medium. In inshore waters of Mono Lake, California, when the population of brine shrimp (*Artemia salina*) is at maximum during the summer, concentrations of thousands of these plankton may be seen rising in graceful turbulent plumes from stones or calcium carbonate concretions. The plumes, varying in size from a few cubic decimeters to several cubic meters, may contain shrimp at more than 1000/dm^3. A similar phenomenon was observed in Great Salt Lake, Utah, in 1872 (*3*). The plumes appear to be closely associated with thermal and radiative processes of the inshore region, and I offer the following observations to support an explanatory hypothesis that may be relevant to both the convection plumes over trees and the density currents in aqueous media described by Bradley (see *4*).

The plumes of shrimp at Mono Lake appear only in shallow regions, to a depth of about 4 m, when direct sunlight enters the water; they appear most strongly developed soon after noon on calm, clear days; they are not seen when wind actively stirs the water.

The plumes often hover for long periods over a rock and always have their bases on the sunny side—never on the shady side; they slowly disperse when artificially shaded. Plumes may drift along the shore and move gradually upslope. The axis of the plume is frequently inclined away from the sun. Within the water of the plume, temperatures are several tenths of 1°C higher than in the adjacent strata.

Filtered plume water, when compared with filtered water from outside the plume, has a considerably higher energy absorption at several specific ultraviolet wavelengths and in the red region (Fig. 1); this fact suggests that the plume water may contain one or more dissolved organic compounds, possibly including certain breakdown products of plant pigments. Addition of 30 mg of vitamin-free casein to lake water produced an absorption peak at 230 nm comparable to the prominent peak found in natural waters. By wet-oxidation methods, the dissolved organic carbon of pelagic Mono Lake water was determined to be 62 mg/liter (*5*)—a very high value for natural media. The casein added to this water did not affect specific viscosity, which was 1.20 [considerably lower than that reported (*4*) for $NaHCO_3$ of comparable density]. Possibly, however, some of the naturally occurring organic compounds may reduce the viscosity (*6*) and "lubricate" the stream-tubes comprising the rising density currents. Garman (*3*) noted that breezes produced no ripples on water overlying swarms of shrimp; this fact suggests that plume water has a lowered surface tension—comparable to "slicks" at sea.

Dye-marker experiments and temperature observations indicate that just above the bottom in shallow regions there is a layer of water about 1 cm thick; it is warmer than the overlying water and presumably enriched with organic compounds from the mud (Fig. 2). This thermal layer causes a marked density instability, since the lake water expands considerably more per 1°C than pure water (*7*). The instability is apparently relieved by upward flows along warmed transisothermal surfaces (such as rocks) or in local up-funneling "thermals" that may travel along or across bottom contours, draining the warm water upward as they move. Grids of fluorescein dye laid by

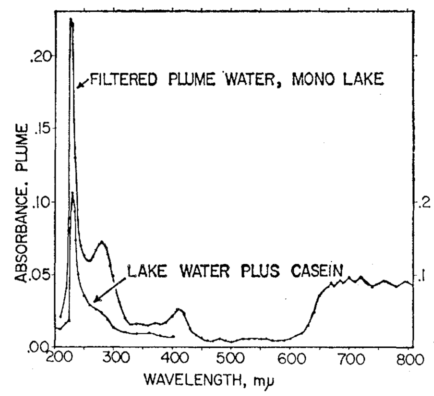

Fig. 1. Absorbance spectra of Mono Lake water from within a plume of shrimp (23 July 1964) and of pelagic water to which 30 mg of vitamin-free casein had been added (7 November 1964). The first measurement was made against water collected adjacent to the plane; the second was made against a normal pelagic-water blank; 1-cm quartz cells were used in a Beckman-DU spectrophotometer. All water had been filtered through a Whatman GF/C pad.

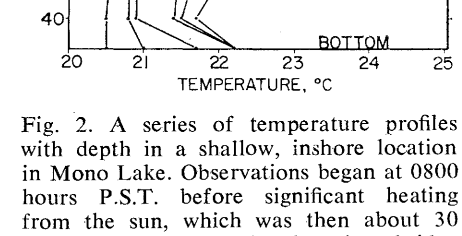

Fig. 2. A series of temperature profiles with depth in a shallow, inshore location in Mono Lake. Observations began at 0800 hours P.S.T. before significant heating from the sun, which was then about 30 deg above horizon. The thermistor-bridge circuit used, recently calibrated, was accurate within 0.01°C.

a capillary tube into this warm layer clearly showed these drainage patterns. The plumes of rising lighter water seem very similar, in reverse fashion, to the downward density currents so clearly figured by Bradley (*4*). Along ripple-marked bottoms the upwelling frequently takes a linear form, rising in sheets parallel with the ripple axes.

Within the plumes, shrimp appear to be borne upward in great concentrations by a rapid central stream; they become very active, thrashing about until they reach the top of the plume, at which point they are carried a short distance outward from the plume center. They then turn and swim downward vigorously just outside the central rising column; in downward movement they are less concentrated. At the base of the plume they are caught again by the currents and drawn upward. The shrimp thus trace a toroidal path of passive but agitated ascent and active descent. When swimming downward, the shrimp naturally reinforce the upward currents already present.

Unexplained are attraction of the shrimp by the thermal column and the subsequent maintenance of phenomenal numbers of animals within the system. Shrimp just above a shallow bottom would readily be caught up in a rising current; they may even prefer warm or near-bottom water, but I have not demonstrated this to my satisfaction in studies in an indoor aquarium, in which I used a column of artificially warmed water taken from just off the sediments. The shrimp concentrations themselves decrease the water density. [With a measured specific gravity of 1.01, one adult brine shrimp (6 mm^3) per cubic centimeter would cause 20°C lake water to decrease in density from 1.0560 to 1.0557 g/cm^3—equivalent to 1.0°C rise in temperature.] The shrimp become then analagous to the particles used by Bradley (*4*) to create downward density currents, and the plume certainly must derive some of its physical properties from the entrained shrimp. However, the shrimp are not inactive within this system, and three possible mechanisms of photo- and rheotaxes suggest themselves, all stemming from the observed fact that these shrimp are powerfully negatively photokinetic in the bright sunlight of shallow water (Fig. 3). The following hypothetical mechanisms concord with known facts of crustacean kinetic behavior (*8*).

A single shrimp, finding itself at the top of a rising column of water, seeks to avoid the high light by turning and swimming down. It is then faced by a gradient of current velocities along any radius of the toroid, varying from maximum upward velocity at the center to minimum outside. If the plume continues to approximate an inverted type of Bradley's "thermal cup" (*4*), there may be even a slight downward and inward (axial) movement of water. Uniform downward swimming in this radial velocity gradient inevitably causes a symmetric animal to be turned inward. A more elaborate explanation might postulate that medial or bilateral sensory feedback mechanisms detect the velocity gradient and subsequently alter swimming vigor. Such mechanisms would appear to have the same results upon a shrimp—to alter its course toward the center of the column. Finally, when a number of animals become trapped in the toroid, the effect of mutual shading may alter the mechanisms structuring the plume: now the animals preferentially may seek the shady side of the column, causing the frequently observed inclination of the plume away from the sun.

Occasionally I have seen portions of these plumes become detached from the bases by littoral currents; the isolated swarms of shrimp persist a few moments before dispersing. Apparently the initial motive force is the thermal-convection plume, which may be reinforced by the activity of the organisms in it. When the convective system goes, the organisms alone do not remain aggregated.

Other instances of shrimp-concentration forces are seen at Mono Lake in the form of freshwater springs rising to the surface near shore; in calm weather they may be visually located from a distance, not only by the different rippling properties of the fresh water, but also by the congregations of birds feeding on the shrimp concentrations. The same mechanisms of convection and shrimp concentration seem to

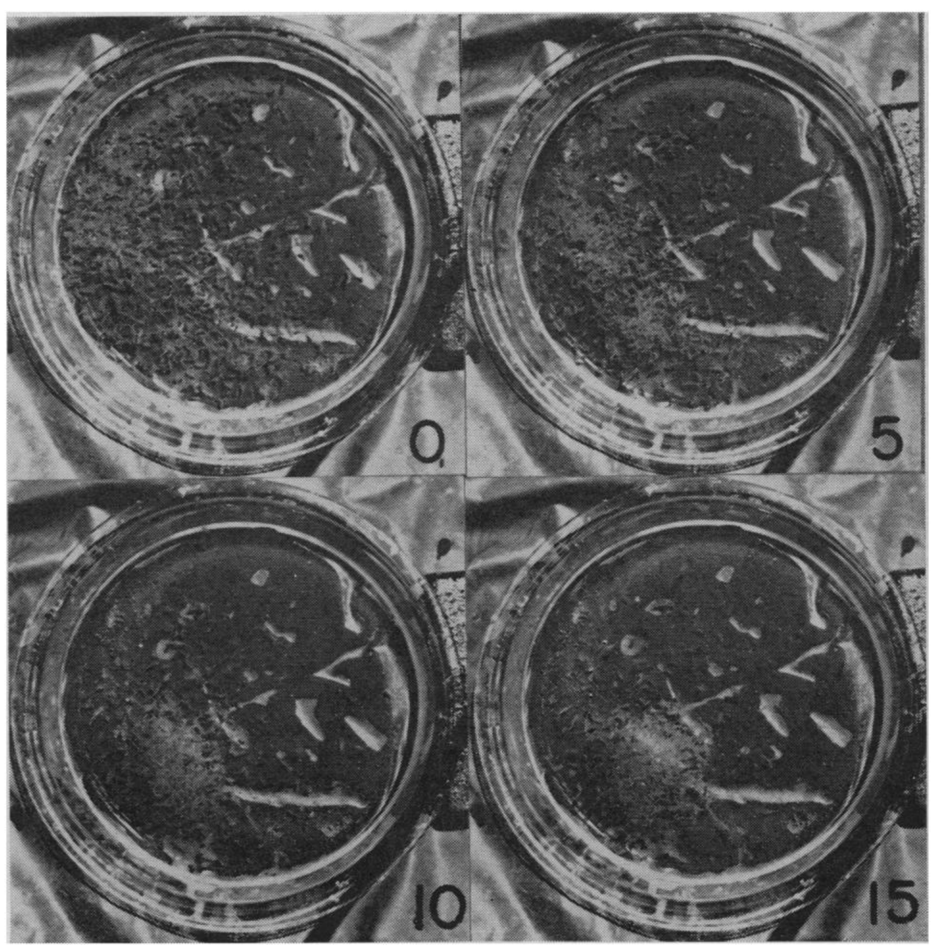

Fig. 3. Negative photokinetic response of brine shrimp to bright light. Shrimp from a convective plume were placed at 1100 hours P.S.T. in a shallow (2-cm) dish of lake water and covered for several minutes with an opaque cloth. The series of photographs began when the cloth was removed; it was taken at 0, 5, 10, and 15 seconds. The angular sides of the dish reflect light toward the center.

apply to these springs as to the rising thermals. Shrimp appear less concentrated over the springs in cloudy weather or at night.

Populations of migrating phalarope stop at the lake, and a bird frequently swims in a tight circle, occasionally pecking at shrimp drawn into the vortex created by it. The concentration mechanisms suggested above may also aid this process.

It appears, then, that littoral solar warming of the near-bottom water causes it to rise in localized convective density currents, often along natural barriers that provide easy upward paths —for example, ripple marks and rocks. The water is warmer, less dense, and, coming from intimate sedimentary contact, probably richer in dissolved organic compounds than the main water mass. In these rising plumes brine shrimp become trapped in a revolving toroid through exercise of a negative photokinesis, which may be combined with one or more hypothetical mechanisms causing an apparent positive rheokinesis. The presence and activity of the shrimp may decrease the density and augment the upward flow of the current. It should be recognized that according to this model the shrimp will circulate within the plume, while the water is continually drawn from below and released above.

Application of portions of this model to aerial swarms of insects in thermally convective air requires only ethological treatment of the kinetic behavior of the organisms involved in plumes.

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Progesterone Retards Postpartum Involution of the Rabbit Myometrium

Abstract. *Postpartum involution of the uterus was significantly reduced in rabbits by immediate and repeated injections of progesterone. Progesterone had no effect if the injections commenced 24 hours after delivery. The decrease in concentration of progesterone that accompanies birth results in release of proteolytic and other degradative enzymes from subcellular particles; these enzymes cause the involution, and, once the enzymes are released into the cellular milieu, progesterone has no effect.*

The mechanism by which involution, or decrease in size and weight of the mammalian uterine myometrium, occurs after termination of pregnancy is poorly understood. Histological study (*1*) has shown little cell autolysis, and that loss of weight by the myometrium reflects decrease in size of individual cells in the tissue. It has been proposed (*2*) that proteolytic enzymes may participate in this process, but the "trigger mechanism" that begins postpartum involution is not known. Csapo *et al.* (*3*) recently suggested that the loss of chronic stretch, which occurs after expulsion of the fetal mass during delivery, may initiate postpartum involution in the rabbit, since maintenance of this stretch appears to prevent complete involution of the tissue.

A recent report (*4*) is that estradiol-17β stimulates increased synthesis of several degradative enzymes in the uterine myometrium of ovariectomized rabbits; the same enzymes are also much more abundant in the myometrium of pregnant than of nonpregnant rabbits. Of particular interest is the increase in proteolytic enzyme activity in the myometrium during these periods; it was proposed that this increase is important for the process of postpartum involution.

It was also reported (*4*) that these degradative enzymes, including the proteolytic enzyme activity, can be isolated in a subcellular particulate fraction from homogenates of pregnant-rabbit myometrium. It was proposed that progesterone may participate in growth and involution of the rabbit myometrium by interaction with the subcellular particles in the following manner. Although exogenous estradiol-17β stimulates increased synthesis of the proteolytic enzymes, concurrently with the stimulation of growth of the uterine myometrium of ovariectomized rabbits, a source of exogenous progesterone is needed for continued growth of the tissue. During normal pregnancy, a source of progesterone, either ovary or placenta, is needed to ensure continued growth of the uterus and maintenance of the pregnancy until term. In either case, loss of the source of progesterone results in cessation of tissue growth and the beginning of tissue involution.

Progesterone could prevent involution by stabilizing the subcellular particles so that their content of proteolytic enzyme is not released into the cellular milieu, or by inhibiting the proteolytic enzymic activity after the enzymes had been released from the particles. These two possibilities could combine. Removal of the source of progesterone, which occurs with the loss of the placenta at birth, would then allow the particulate-bound degradative enzymes to become active. Involution of the tissue would result from activity of these degradative enzymes.

These propsals can be tested very simply. The concentration of progesterone in the circulating blood can be maintained in animals postpartum by administration of exogenous hormone. If progesterone either stabilizes the particles or inhibits the enzymic activity, the weight of the uterus should not decrease rapidly as it does during normal postpartum involution. A test of these proposals entailed consideration of the following points: The daily production rate of progesterone during pregnancy is very high and the turnover rate is very rapid (*5*). The concentration of progesterone in the circulating blood of the rabbit falls very rapidly following the birth process (*6*). These facts mean that large amounts of progesterone must be administered daily, with the total amount divided into frequent injections throughout the experimental period. Secondly, it must be assumed that enough of the injected hormone reaches the cells of the uterus to maintain the intracellular content of progesterone after the termination of pregnancy. Thirdly, the decrease in chronic tension in the uterus, which results from loss of the fetal mass at birth, should not by itself result in some uterine change that would mask an effect of the hormone.