

Density regulation in *Sarsia tubulosa* (Hydrozoa)

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ABSTRACT: The majority of wild-caught *Sarsia tubulosa* M. Sars medusae are less dense than the surrounding water. The bell of *S. tubulosa* is the buoyant structure; the tentacles and manubrium sink if cut off from the bell. *S. tubulosa* individuals placed in dilute seawater sink initially but recover positive or neutral buoyancy and normal activity within a couple of hours. In all cases observed animals were able to achieve positive buoyancy in seawater of 20.25 ‰ S and some individuals were able to adjust to lower salinities. In most cases where positive buoyancy was not attained within two hours the animal did not achieve positive buoyancy within twelve hours and died within that period. While the mechanism of regulation is not known, ionic pumping, possibly involving the extrusion of sulphate ion, has been suggested to be responsible for the buoyancy of mesoglea in other jellyfishes.

INTRODUCTION

Only a few hydrozoans are known to be able to alter their density (Mackie, 1974). Some siphonophores which possess gas-filled floats are known to regulate their density by altering the amount of gas in the float (Jacobs, 1937, 1954). Jacobs (1937) also demonstrated that at least *Hippopodius* and *Diphyes*, among those siphonophores which do not possess floats, are able to change their density to become lighter or heavier than the surrounding seawater over a period of 30 min to one hour. Jacobs attributed this ability to properties of the mesoglea of the swimming bells because dismemberment of a floating animal always resulted in the bell floating and the rest of the animal sinking. The only other hydrozoans which have been previously reported to change their density are *Solmaris (Aegineta) flavescens* (Bethe, 1910) and *Pelagohydra*, which has a fluid-filled float (Pilgrim, 1967).

The mechanism of density regulation in coelenterates without gas-filled floats is as yet unknown. However, Denton & Shaw (1961) showed that the lower density of mesoglea relative to seawater, with which it is isosmotic, can be explained as being due to the lower concentration of sulphate ion in mesoglea. Mackay (1969) demonstrated that hydromedusae are able to pump sulphate ion and this provides support for the idea that hydromedusae may be able to change their density by changing the concentration of sulphate ion in the mesoglea.

In the course of a series of observations of swimming behavior in *Sarsia* it was observed that *Sarsia* which stopped swimming in the center of the tank almost always floated to the top (Leonard, unpublished). Animals put into dishes of dilute seawater as

part of a study of behavior under stress (Leonard, in preparation) sank initially but recovered buoyancy within a couple of hours. This study was conducted to quantify and confirm these observations since Bethe's (1910) is the only previous study of density change in a medusa.

MATERIALS AND METHODS

These experiments were conducted at the Friday Harbor Laboratories, Friday Harbor, Washington. All animals used were wild-caught adult *Sarsia tubulosa* M. Sars captured by being dipped up in a glass or plastic cup. Animals were caught by night lighting off the FHL dock or captured in the daytime in Parks Bay, Shaw Island. The animals were held in water from the FHL seawater system in glass jars submerged to the water line in a circulating sea table for several days. The seawater in which the animals were kept was not filtered but the animals were not fed otherwise.

Buoyancy tests were conducted on June 18, 20, 23 and 25, 1977. All animals used for the tests had been kept in FHL seawater for at least 24 h prior to testing. Each animal was dipped out of the home container individually and placed on a damp paper towel along with a small quantity of seawater. One cut was made in each quadrant in the bell margin between the tentacle bulbs. This operation prevents *Sarsia* from carrying out swimming contractions. Each animal was then dropped into a rectangular glass container, in such a manner that it fell below the water surface, and scored for buoyancy. The container was filled to a depth of 8 inches with fresh FHL seawater. Each animal was scored as positively, negatively, and neutrally buoyant according to whether it floated back to the water surface, continued sinking until it reached the bottom, or came to rest somewhere between the surface and the bottom, respectively. After half of the animals in each run were scored, the animals were removed and fresh water was put into the test container.

For the density change experiments in August 1978, five tall glass petri dishes were used to hold animals. Each dish was filled with 400 ml of seawater or appropriate volumes of seawater and tap water (Table 1). The dishes, including those for the controls were stirred vigorously with a glass rod to ensure good mixing. In the first series, four animals were put in each dish, five each in the second series except for the dish of 20.25 ‰ S seawater, which contained six animals.

In both series the animals were put into the dishes at 03:00 PDT and the number of

Table 1. Number of positively buoyant animals in each treatment (14 °C, 10 animals at 20.25 ‰ S; 9 animals in other cases)

Experimental time (min)	Salinity (‰)				
	27	23.6	20.25	16.9	13.5
15	8	0	0	0	0
30	9	0	1	0	0
45	9	4	4	0	0
60	9	7	6	1	0
75	9	8	8	3	0
90	9	9	9	4	0
120	9	9	10	4	1

positively and negatively buoyant animals was recorded from each dish every 15 min (Tables 1 and 2). The criteria for negative buoyancy were: (1) the animal was lying on the bottom of the dish with the bell resting on the glass, or (2) the animal sank when it stopped swimming (tentacles outspread). The criteria for positive buoyancy were: (1) the animal was floating stationarily at the surface, (2) the animal floated upward (bell first and tentacles trailing) when it stopped swimming, or (3) the animal, if tethered by its tentacles to the glass on the bottom or sides of the dish, floated with its bell upward and away from the bottom or parallel to the sides. Neutrally buoyant animals would have been scored as positive if they were at the surface and probably would also have been recorded as being positive, depending on their position, if they were lying on the bottom.

RESULTS AND DISCUSSION

Sarsia tubulosa held in deep containers floated motionless at the water surface for long periods of time. When animals stopped swimming they usually floated bell first to the surface. *Sarsia* which had been swimming downward turned over after swimming had stopped so that they arrived at the surface bell first. This righting appears to be entirely passive. The apex of the bell has the thickest mesoglea, and the heavy tentacles and manubrium trail behind the bell when the animal is swimming. The tentacles and manubrium sink turning the bell right side up. Buoyancy testing after surgical paralysis showed that the majority (82.8 %) of adult *Sarsia* are lighter than the seawater in which they have been kept (Table 2). The only cases in which apparently healthy *Sarsia* are consistently heavier than the surrounding water occur when the animal has large or numerous prey items attached to the tentacles or when there is a large bulge of food in the manubrium.

Although *Sarsia* has been the subject of experimental work since at least Romanes' paper in 1876, I have been unable to find any mention in the literature of *Sarsia* or any other medusa being positively buoyant. This oversight is actually quite easy to understand. *Sarsia* are very small, transparent animals and are hard to see in large containers. In small containers *Sarsia* become tethered to the bottom by their long extensible tentacles. Then the tentacles usually contract so that the animal becomes so firmly fixed to the bottom that they have difficulty rising from the bottom even by means of vigorous swimming contractions. Some other anthomedusae such as *Bougainvillia* spp. and *Euphysia flammea* also seem to be positively buoyant.

Sarsia put into dilute seawater were observed to regain positive buoyancy after a period of hours. The results of the two series of experiments designed to confirm and

Table 2. Results of buoyancy tests

Buoyancy	Run 7	Run 2	Run 3	Run 4	Total	%
Positively buoyant	34	34	19	19	106	82.8
Negatively buoyant	8	1	5	7	21	16.4
Neutrally buoyant	8	1	0	0	1	.8
Total	42	36	24	26	128	100

quantify this observation are summarized in Table 1. In all cases the jellyfish in salinities higher than 20.25 were able to regain positive buoyancy within the 2-h experimental period. In the second series, four out of five animals were able to achieve positive buoyancy in 16.9 ‰ S and one recovered in 13.5 ‰ S seawater. This last observation was very unusual since all other *Sarsia* placed in 13.5 ‰ S seawater remained negatively buoyant even after 12 h and most of them were dead by that time. Those animals which regained positive buoyancy remained buoyant and seemed in most cases healthy 12 h later.

In all the experimental, but not the control, dishes, the animals initially sank to the bottom, their bells became swollen and distorted and they tended to lie on their sides, swimming in place or along the bottom if at all. The animals in dilute seawater seemed to be, at least initially, less active, an observation which agrees with that of Arai (1973). This made it quite easy to distinguish between negatively and positively buoyant animals since few, except the controls, swam for very long. The recovery of normal bell shape, normal activity, and positive buoyancy were all gradual and appeared to follow a similar time course.

Some of the variability in the the time required to attain positive buoyancy within a treatment may be attributable to size differences, with smaller animals becoming buoyant faster. In the 20.25 ‰ S dish of the second series the first animal to become positively buoyant was an extremely small (ca. 2-mm bell height) individual which had apparently been introduced into the dish unobserved in a dipper with a larger individual. It would be logical for density changes to occur more rapidly in smaller animals because of their larger surface-area to volume ratio, if the mechanism is something like the active movement of ion(s) across a membrane to change the concentration in the mesoglea.

In conclusion, *Sarsia tubulosa* medusae are able to adjust their density to achieve positive buoyancy in a dilute medium. The physiological mechanism for this is not known, but the work of Denton & Shaw (1961) and Mackay (1969) makes it seem likely that changes in sulphate ion concentration in the mesoglea are involved. *Sarsia* have not yet been shown to change their density actively while remaining in one medium. *Sarsia* in behavioral experiments are occasionally observed to become negatively buoyant without feeding, over the course of a few hours, but it is not known whether this process is reversible. Dead and dying *Sarsia* tend to sink. The demonstration of density changes in *Sarsia* provides a new approach for further work on density regulation and vertical migration in hydrozoans.

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