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Evidence for tidally-induced vertical migration of some gelatinous zooplankton in the Wadden Sea area near Sylt

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ABSTRACT: Gelatinous zooplankton is more abundant in the Wadden Sea area of North Sylt than in the adjacent North Sea. The hypothesis is tested that medusae maintain their position in the North Sylt Wadden Sea by ascending to the surface at flood tides and descending to the bottom during ebb tides, thus avoiding the strong ebb currents which could carry them out of this food-rich area. Surface sampling at a main tidal channel revealed great differences between high tide and low tide abundances of five species of medusae in the surface layer. *Rathkea octopunctata, Sarsia tubulosa, Eucheilota maculata* and *Pleurobrachia pileus* were all more abundant around high tide than during low tide. Bongo net sampling in different depth layers revealed that *Pleurobrachia pileus, Bougainvillia ramosa* and *Eucheilota maculata* showed a preference for the surface layers around high tide, whereas most of the individuals were found in the deepest layer around low tide. The results suggest tidally-induced vertical migration of medusae in tidal channels. This may assist maintenance of the populations in the Wadden Sea area near Sylt.

INTRODUCTION

The North Sylt Wadden Sea area is a bay enclosed by the islands of Sylt and Römö, the mainland of Schleswig-Holstein and Denmark and separated from the adjacent Wadden Sea areas by the Römö Dam and the Hindenburg Dam. Water exchange with the North Sea only occurs through a tidal inlet between the islands. Freshwater inflow is small (Hickel, 1975).

Gelatinous zooplankton is more abundant in the Wadden Sea area of North Sylt than in the adjacent North Sea area (Künne, 1952). There are three possible explanations for the high abundances of gelatinous zooplankton in the Wadden Sea. Firstly, the rate of reproduction in the Wadden Sea area of North Sylt may be higher than in the adjoining North Sea. Secondly, predation rate of Scyphomedusae in the Wadden Sea area is lower than in the adjacent North Sea area. Thirdly, physical processes as well as behavioural strategies may promote retention of the specimens in the Wadden Sea bay.

Although medusae are common, only small quantities of hydropolyps were found (Kopacz, unpubl.). Most of the medusae seem to be imported from the open sea, as indicated by a correlation between increasing salinity with inflowing water masses and the occurrence of the hydromedusa *Rathkea octopunctata* in the Wadden Sea area of North Sylt (Martens, 1980). This medusa and most of the other common species reproduce vegetatively by medusa buds in the investigated area. This may in part explain the high abundances. Also, predatory impact of Scyphomedusae may be higher in the North Sea than in the Wadden Sea (Künne, 1952). This predation may be avoided if the gelatinous zooplankton is retained in water masses which remain for some time within the Wadden Sea.

Hill (1991a) used a model which employs linear velocity shear in the vertical and sinusoidal vertical migration to discuss the kinematics of vertical migration in tidal currents. Selective tidal stream transport depends on exact timing of vertical migrations to match the tidal period. According to this model, zooplankton may maintain their position in a tidal basin if they ascend to the surface at flood tides and descend to the bottom during ebb tides. This hypothesis is the subject of the present investigation.

MATERIAL AND METHODS

A sampling programme was carried out in the Lister Ley, one of the three main channels of the North Sylt Wadden Sea (Fig. 1), to study the distribution and abundance of gelatinous zooplankton. A thermocline or different salinity layers were not observed in this tidal channel with a depth of up to 25 m. Only on a few days during summer, did temperature differences between the bottom and the surface occur. Most samples were taken from a ferry landing platform (Fig. 1).

Here the surface distribution of gelatinous zooplankton was investigated on May 21st, June 9th, 28th, August 4th, and September 2nd, 17th, 30th in 1991 and February 17th, March 11th, April 9th in 1992. Sampling extended over 24-h-periods. However, due to frequent arrivals and departures of the ferry in August and September, samples were only collected over 12-h-night periods. Zooplankton was collected with a hand net with an opening diameter of 50 cm and 500 µm mesh size. Sampling commenced around low and high tide, respectively. Six successive hauls were taken within 20 minutes. To avoid wind induced surface currents, the samples were taken 1 m below the surface. A flowmeter was used to estimate the volume of water flowing through the net.

The vertical distribution of gelatinous zooplankton in the Lister Ley was studied on June 29th and 30th, and July 5th, 6th, 12th, and 14th in 1993 using a Bongo-net with 60-cm mouth diameter fitted with 500-µm gauze. The samples were taken along a transect with a depth of up to 13 m (Fig. 1) at the surface and at depths of 6 m and 12 m, respectively. Sampling commenced around low and high tide, respectively. Six successive hauls at each depth were taken within a 1½ hour period. A flowmeter was used to estimate the volume of water flowing through the net.

All samples were fixed and stored in 4 % formalin. The distribution of replicates was not normal (Kolmogoroff-Smirnoff-test). Median and maximum values were calculated. Data from each series were tested on differences of medians by means of the median-test according to the four-fold table (Sachs, 1984).

RESULTS

The surface sampling of gelatinous zooplankton from the landing stage revealed marked differences in abundance between the high tide and low tide. *Rathkea octopunc-*

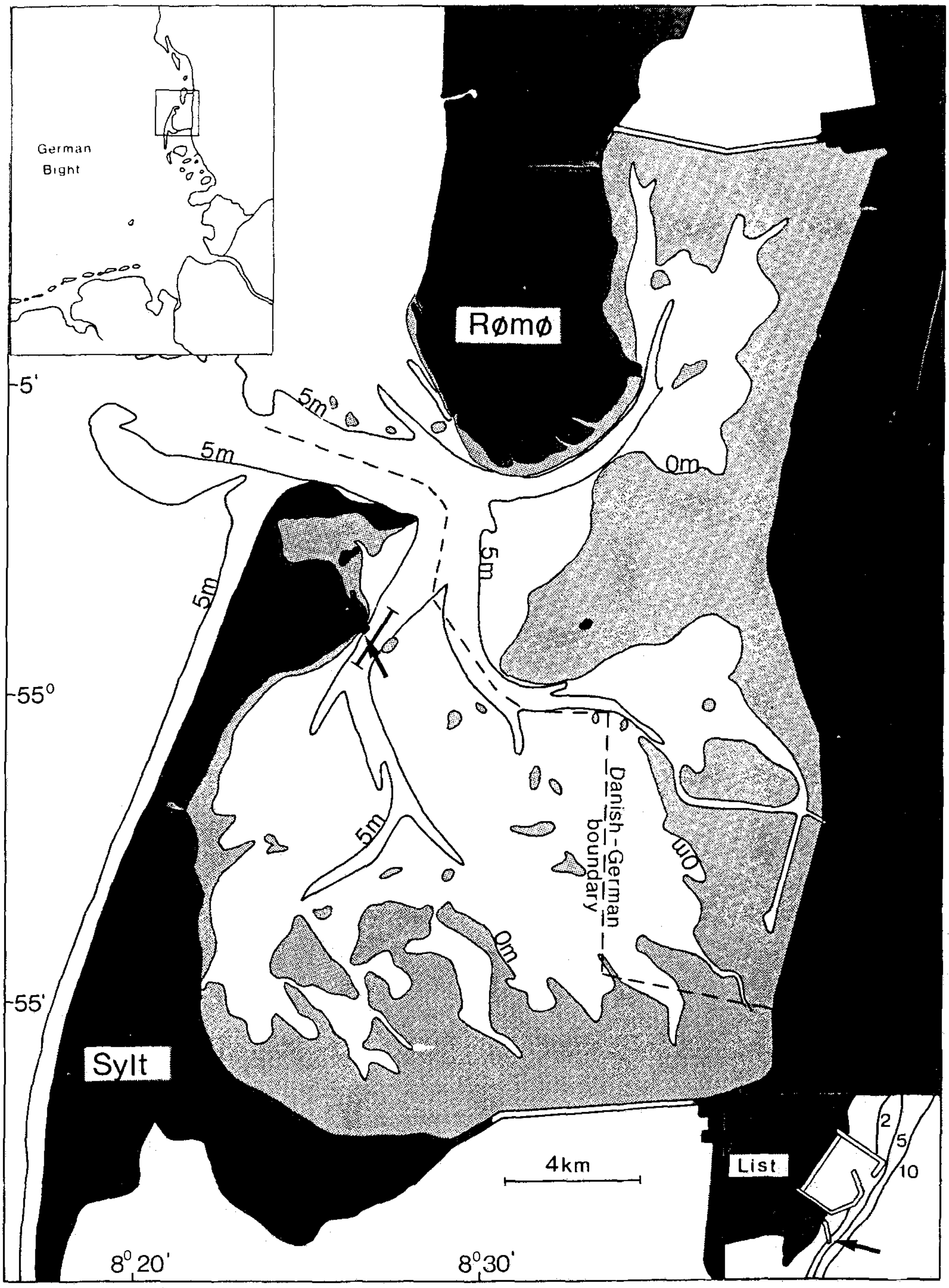

Fig. 1. Wadden Sea area of North Sylt with sampling transect (bar) in the Lister Ley and sampling station at List harbour (arrow, see inset). Depth refers to mean spring low tide level

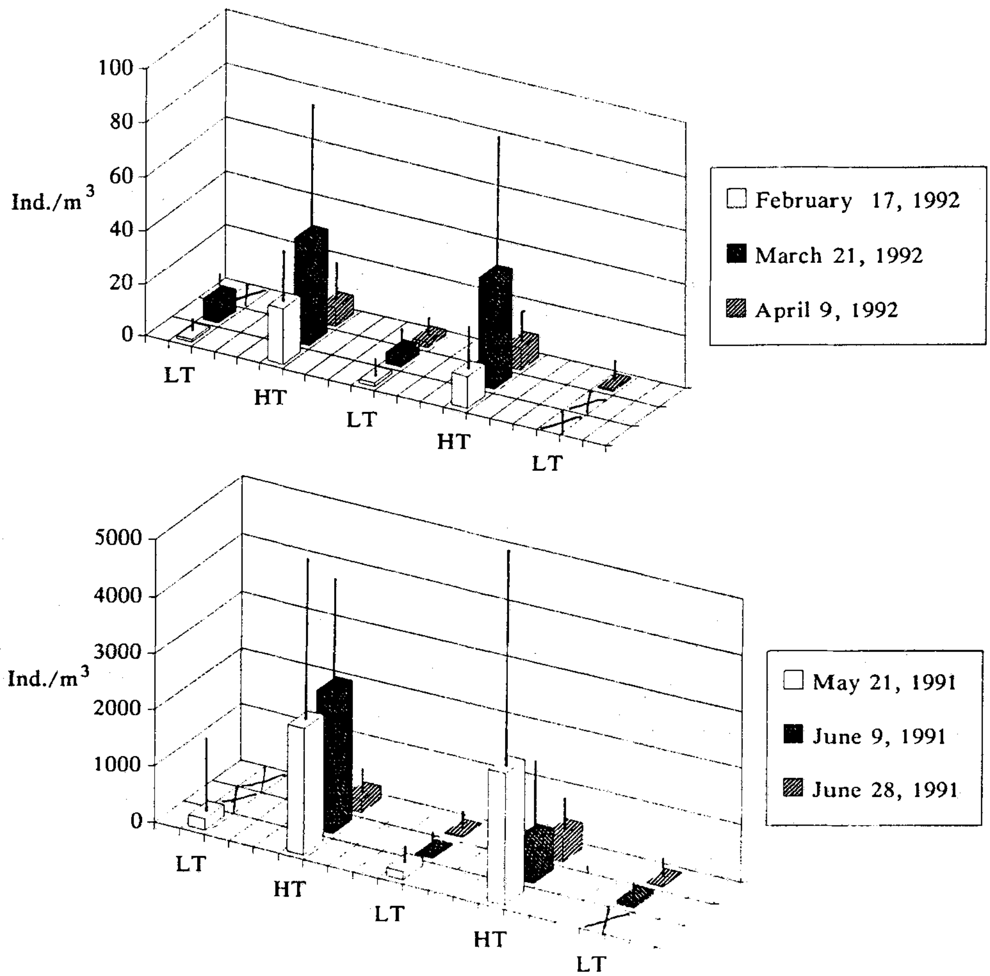

Fig. 2. Median (column) and maximum (bar) of abundance (individuals · m^{-3}) in *Rathkea octopunctata* at low (LT) and high tide (HT) in surface waters at the List landing stage. "x" denotes no samples

tata, Sarsia tubulosa, Eucheilota maculata and *Pleurobrachia pileus* occurred in significantly higher numbers (Table 1) around high tide than around low tide (Figs 2–5).

Although there were marked differences in abundance between the six sampling dates in *Rathkea octopunctata*, the tidal pattern remained the same (Fig. 2). In spite of the high variability observed within the sets of six successive hauls, the median values of abundances differed significantly (Table 1) between high tides and low tides.

In June and July 1993, Bongo-net samplings were carried out in different depth layers of the Lister Ley on 6 occasions. July 12th is chosen to demonstrate the distribution pattern (Fig. 6). *Pleurobrachia pileus* and *Bougainvillia ramosa* showed a preference for the surface layer during high tide, whereas the reverse was found during low tide.

For *Eucheilota maculata* a more complex pattern was derived, since highest abun-

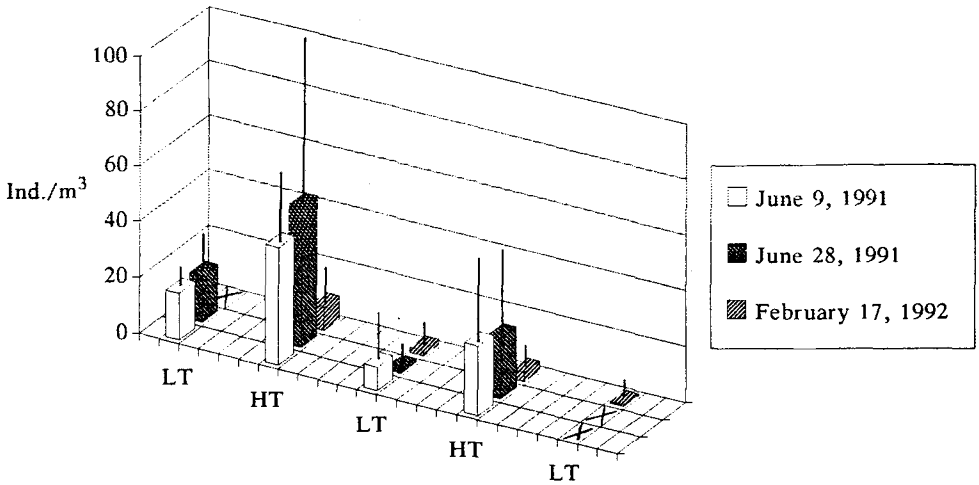

Fig. 3. Median (column) and maximum (bar) of abundance (individuals · m^{-3}) in *Sarsia tubulosa* at low (LT) and high tide (HT) in surface waters at the List landing stage. "x" denotes no samples

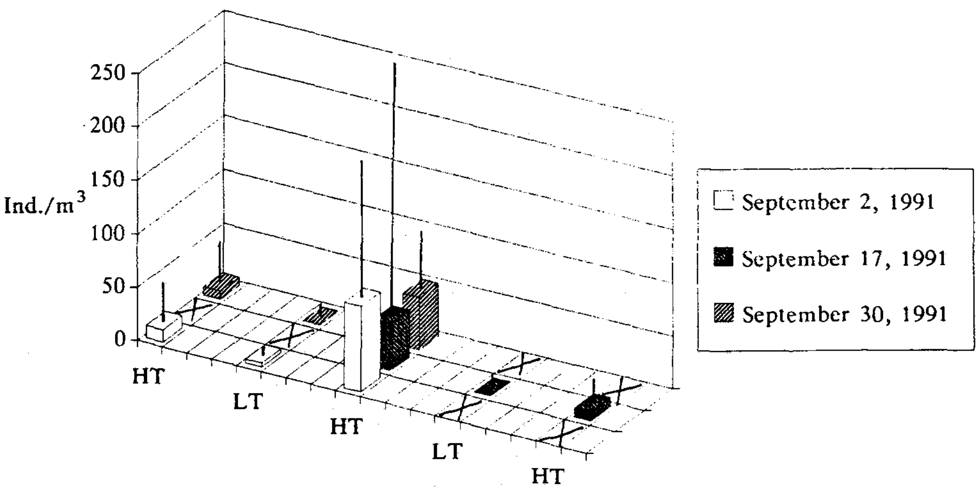

Fig. 4. Median (column) and maximum (bar) of abundances (individuals · m^{-3}) in *Eucheilota maculata* at low (LT) and high tide (HT) in surface waters at the List landing stage. "x" denotes no samples

dances during high tide were found near the surface and at 12 m depth with a minimum inbetween. However, during low tide most individuals were also found in the deepest layer. The significance of differences for all sampling dates is shown in Table 1.

DISCUSSION

Vertical migrations of marine plankton are influenced by behavioural and hydrographic factors (Longhurst, 1976). Hydrographic factors such as salinity or temperature

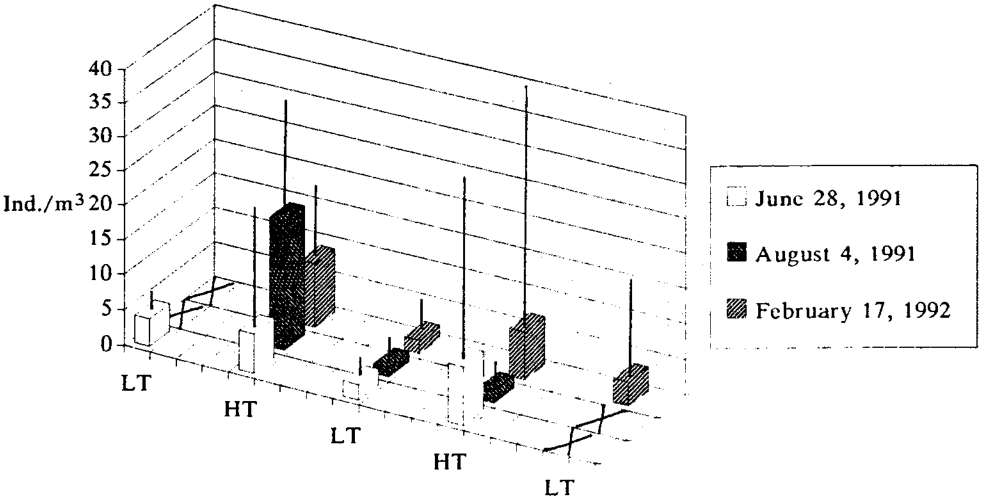

Fig. 5. Median (column) and maximum (bar) of abundance (individuals · m^{-3}) in *Pleurobrachia pileus* at low (LT) and high tide (HT) in surface waters at the List landing stage. "x" denotes no samples

affect the vertical distribution (e.g. Kramp, 1915; Greve, 1971; Moreira, 1973) as well as light intensity and pressure (Russell, 1927). All those factors, including the tidal current, affect the vertical distribution. The major controlling factor in the investigated Wadden Sea channel is supposed to be the tidal current.

Vertical migration, as a form of behaviour, is important for planktonic organisms. The vertical migration provides a means to effect transport to specific locations, or conversely to promote retention in particular areas (Sinclair, 1988). The transport of zooplankton and the utilization of tidal currents by plankton are mentioned in two studies. Gagnon & Lacroix (1983) investigated the transport and retention of zooplankton in the vicinity of a sill. They found two contradictory flow modes. It is assumed that the maintenance of zooplankton is affected by a mean flow mode, the magnitude and direction of which depends on the mean flow of water at the depth where the organisms are concentrated, and a turbulent mode which is independent of water exchange, and varies considerably on a species basis. Wooldridge & Erasmus (1980) found several species of copepods avoiding or using inflowing and outflowing surface currents to maintain position in an estuary or to migrate during slack water. One of the copepod species avoided inflowing and outflowing surface currents, but migrated towards the surface at slack water. Two other copepod species remained in greater numbers near the bottom during ebb tide, moving laterally into areas of slowest current velocity. This behaviour is supposed to be similar to that of medusae in a tidal channel.

Hardy & Bainbridge (1954) considered that vertical migration of plankton is predominantly a direct up-and-down swimming. The hypothesis should be considered that the medusae are able to migrate upward and downward around slack water in the Lister Ley within one hour's time. This would allow the medusae to experience a longer low current regime near the bottom of the tidal channel, compared to higher current velocities near the surface. Migration-induced motion may also interact with flow components such as

Table 1. Median-tests for the significance of differences in abundances (individuals $\cdot m^{-3}$) at high tide (HT) and low tide (LT)

Species	HT Quartile 25	HT Median	HT Quartile 75	HT samples (n)	LT Quartile 25	LT Median	LT Quartile 75	LT samples (n)	Chi-square	Probability level
Rathkea octopunctata	16.0	44.0	133.0	72	2.0	9.5	20.0	72	21.8	<0.001
Sarsia tubulosa	4.5	12.0	16.0	72	0.0	1.0	3.5	72	46.7	<0.001
Eucheilota maculata	9.0	19.0	25.0	72	0.0	0.0	1.0	42	63.1	<0.001
Pleurobrachia pileus	8.5	14.0	18.5	72	0.5	2.0	9.0	72	36.0	<0.001
Pleurobrachia pileus										
0 m	1.1	2.4	3.8	36	0.3	0.7	1.2	36	22.2	<0.001
6 m	0.0	0.9	1.9	36	0.5	0.9	1.4	36	0.2	not sign.
12 m	0.9	1.0	1.5	36	1.3	2.5	4.1	36	18.0	<0.001
Bougainvillia ramosa										
0 m	6.5	8.3	23.6	36	0.1	0.7	1.3	36	50.0	<0.001
6 m	1.0	1.6	2.5	36	0.5	1.1	3.1	36	5.6	0.01
12 m	0.6	1.0	2.3	36	3.0	5.5	10.7	36	26.9	<0.001
Eucheilota maculata										
0 m	0.3	1.3	2.0	36	0.0	0.0	1.0	36	50.0	<0.001
6 m	0.1	0.3	0.5	36	0.3	0.5	0.8	36	6.9	0.001
12 m	1.0	1.0	1.5	36	0.7	1.3	2.5	36	8.1	0.001

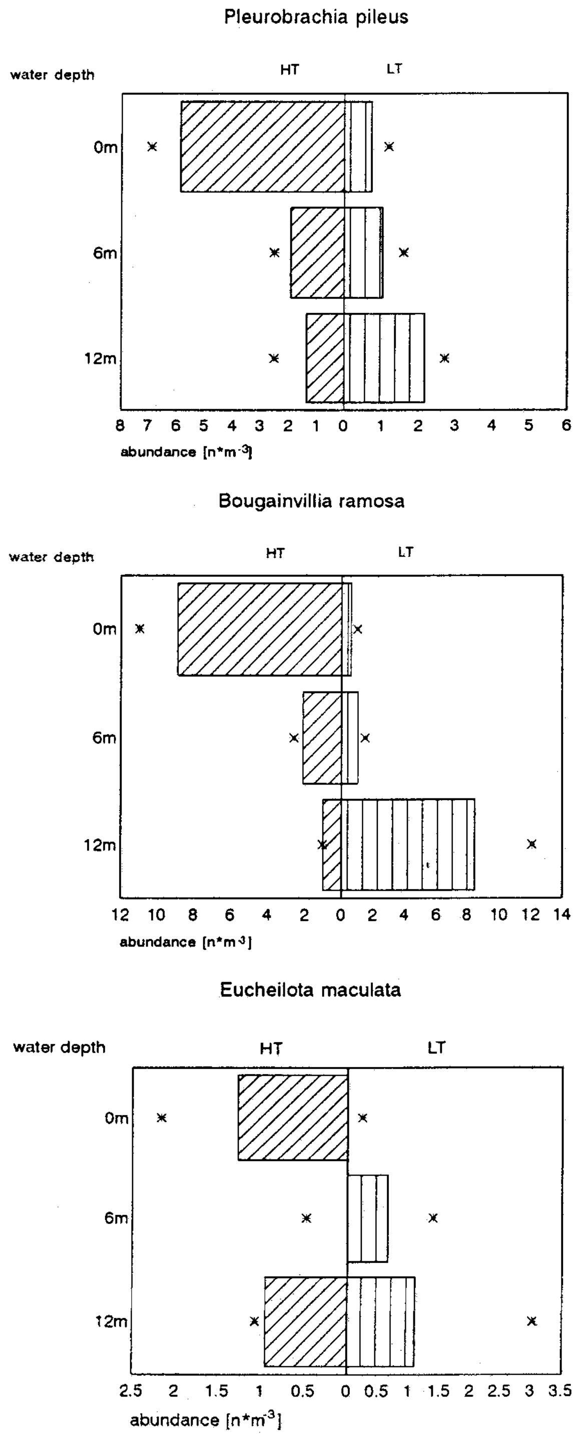

Fig. 6. Median (column) and maximum (asterisk) of abundance (individuals $\cdot$ m^{-3}) in three depth layers of the Lister Ley on July 12th, 1993. *Pleurobrachia pileus* and *Bougainvillia ramosa* were most abundant at the surface during high tide. *Eucheilota maculata* was more abundant at the surface and at the bottom during high tide with a minimum inbetween. During low tide, most individuals prefer the bottom layers

tidal and non-tidal residual currents, enabling an organism to maintain position in a given location against prevailing mean flow (Hill, 1991b).

In the North Sylt Wadden Sea, high abundances of gelatinous zooplankton were recorded during high tide at a near-shore, shallow site and also at high tide in the surface waters of a deep tidal channel. During low tide, abundances at the shallow site were low and at the tidal channel they were high close to the bottom. This suggests transport of the medusae with the flood current towards the shallow intertidal, while the ebb current transports these medusae towards the bottom of the tidal channel. It is assumed that downward movement of the medusae augments this transport. From the bottom of the channel, active upward migration must occur for them to arrive back in the surface waters. From here they may be again transferred with the next flooding tide towards the shallows.

Over many tidal cycles, other flow components such as wind-driven residual currents may influence the surface distribution of the plankton, disabling the organisms to oscillate back and forth with more or less constant displacement in the same Wadden Sea channel. Five species of gelatinous zooplankton rising to the surface on successive high tides but descending to near the bed on each low tide might provide evidence for such interaction with tidal currents enabling them to promote retention in the Wadden Sea area. This may help the small medusae to avoid predation by Scyphomedusae and also maintain position in a food-rich area.

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