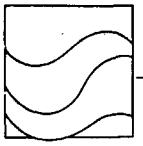

Amino acids
Carbohydrates
Microbial activity
Pycnocline boundaries
Sargasso Sea

Acides aminés
Glucides
Activité microbienne
Limites de la pycnocline
Mer des Sargasses

Dissolved free amino acids and carbohydrates at pycnocline boundaries in the Sargasso Sea and related microbial activity

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ABSTRACT

Measurements of dissolved free amino acids (DFAA) and carbohydrates have been combined with microbiological, inorganic and particulate parameters of water samples from a hydrostation in the Sargasso Sea.

Based on physical parameters (T, S, σ_t), the presence of sharp density gradients in the euphotic zone could be established. Free dissolved organic compounds were found to be enriched at the upper boundaries of these pycnoclines. This effect was attributed to the increased auto- and heterotrophic activity in these layers.

Measurements in deeper waters showed a drastic decrease in microbial activity (with respiration 0% and turnover times in excess of 5 000 hours).

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RÉSUMÉ

Relations entre l'activité microbienne et la distribution des acides aminés libres et des glucides dissous dans la Mer des Sargasses, au niveau de la pycnocline

Des mesures d'acides aminés libres et de glucides dissous ont été confrontées aux données microbiologiques, physico-chimiques, et à la composition du matériel particulaire, dans les eaux de la Mer des Sargasses.

La distribution des paramètres physiques (T, S, σ_t) a révélé l'existence de forts gradients de densité dans la couche euphotique. Aux limites supérieures de ces pycnoclines, les concentrations en matière organique dissoutes présentent un net enrichissement. Cette observation a été interprétée comme étant une conséquence de l'activité auto- ou hétérotrophique élevée à ces niveaux.

Dans les eaux plus profondes, l'activité microbienne décroît rapidement (avec 0% de respiration et un temps de recyclage supérieur à 5 000 heures).

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INTRODUCTION

Density gradients are frequent phenomena in natural waters. It has been shown by various investigators that organic particles including phytoplankton (Goering *et al.*, 1970), bacteria (Rheinheimer, 1974) and detrital material (Lenz, 1974) accumulate at halo- and thermoclines. Harder (1968) found that zooplankton are attracted to artificial haloclines. Chlorophyll *a* and phaeopigments contents increase with depth, their maxima lying within the thermocline or slightly deeper (Lorenzen, 1967; Goering *et al.*, 1970). Biggs and Wetzel (1968) found an enrichment of particulate carbohydrate at haloclines.

Variation in transport velocity of particles with depth (Lerman, 1979) or in the rate of decay or grazing (Jerlov, 1959), may be responsible for the observed accumulation of particulate organic matter in pycnoclines. Particles may also be trapped in convection cells (Stommel, 1949) or retarded at density interfaces (Lerman, 1979).

The increase in POM in pycnoclines should stimulate a greater rate of heterotrophic activity than in regions above or below these layers. Increased autotrophic activity may also occur. It is therefore likely that enrichment of dissolved organic compounds accompanies the enrichment of particles in regions of sharp density gradients. A similar phenomenon has been described to occur in fresh water lakes (Stabel, Steinberg, 1976).

In this paper we wish to report evidence for this hypothesis.

MATERIALS AND METHODS

Samples were obtained in two casts (surface, 200 m; 200-1 500 m) from a single profile on September 12th 1978. The hydrostation was 7 miles SE off Bermuda (64°39′N; 32°18′W) with a water depth of 2 200 m. For two days previous to the day of sampling, winds blew from E to SE at 8-12 knots (15-22 km/h). 1.7 l-Teflon^R lined Nansen and 5 l-Niskin-PVC-samplers were used, respectively. Amino acid analysis of the 200 m sample showed no difference between the two types of samplers used (see Table 3).

Temperatures from depths between 100 and 1 500 m were measured with reversing thermometers attached to the Nansen bottles. The temperature profile from the surface to 85 m was measured with a Montedoro Mark VB multiprobe, attached to the cable of the hydrowire. Roll of the research vessel caused an estimated uncertainty of depth of ± 1 m.

Salinity was determined with an inductive salinometer. Oxygen, ammonia, nitrite and nitrate analyses were performed in replicate by manual methods described by Strickland and Parsons (1972). The phenolhypochlorite as described by Solòrzano (1969) for the ammonia determination, was modified by the use of ferricyanide as catalyst (Liddicoat *et al.*, 1975).

o-phthaldialdehyde reactive substances, ORS, (i. e. all compounds containing an NH_2-group) were determined by a modified version of the method of Josefsson *et al.* (1977). The reagent consisted of 200 mg *o*-phthaldialdehyde (predissolved in 10 ml ethanol) and 0.5 ml mercaptoethanol made up to 1 l with 0.5 M boric acid, reagent grade. The reagent was adjusted to pH 10.5 with 8 N sodium hydroxide solution in order to reduce ammonia response to 5% of that of glycine, used a reference standard.

The native fluorescence of seawater at the wavelenghths employed (λ_{Ex} 340, λ_{Em} 455 nm), which may interfere in the ORS measurements, is generally low and lies around 0.01 µmoles glycine/l.

Neutral and acidic amino acids were determined within 15 hours after collection using a self constructed, single buffer programme analyser. Samples awaiting analysis were fixed with dichloromethane (1 : 1 000) and stored at 4°C. 2 ml of unfiltered sample, was acidified with conc. sulphuric acid to a pH of around 1.5 and immediately injected without further pretreatment. As filtration has been shown to cause cell destruction and therefore leads to an overestimation of the actual DFAA concentrations (Liebezeit, unpublished results), unfiltered samples were analysed.

For carbohydrate analyses, samples were filtered through 0.2 µm Nuclepore filters to exclude interactions between dissolved and particulate matter during desalting. The filters were prerinsed with doubly distilled water. 100 ml of sample, disinfected with dichloromethane (1 : 1 000), was desalted by electrodialysis according to Josefsson (1970). 100 µl glycerine/ethanol 1 : 1 (Dawson, Mopper, 1978) was added before lyophilisation to dryness. The residue was taken up in 500 µl 20% ethanol/water, and an aliquot was injected into a self constructed sugar analyser.

Separation of free monosaccharides was achieved by anion exchange chromatography of their borate complexes (Jandera, Churacek, 1974; Kennedy, 1974; Mopper, 1978). The reagent employed was Cu^{2+}-sodium bicinchoninnate-aspartic acid (Mopper, Gindler, 1973).

Quantitation of both chromatographic methods was by peak height times width at half peak height.

Relative standard deviations for both chromatographic methods ranged from 0.54 to 5.87% using standard mixture analyses in the case of amino acids and a Baltic surface sample in the case of carbohydrates.

Further details for the determination of the organic compounds are scheduled to appear elsewhere (Dawson, Liebezeit, 1980).

Material for the determination of particulate C and N was collected on precombusted Whatman GF/C filters from 2 l of sea water, and analysed with a Hewlett Packard 185 B CHN analyser. Seston content was determined gravimetrically on the same filters. No attempt was made to remove zooplankton prior to filtration.

The determination of total number and biomass of bacteria was carried out by using epifluorescence microscopy. The samples were fixed with formalin to give a final concentration of 1%. 3-6 ml of sample were filtered through prestained (Sudan black) Nuclepore filters and fluorochromed with acridin orange (1 : 10 000). The method of counting and factors for biomass estimations were taken from Zimmermann (1977).

Bacterial activity was measured without the use of a kinetic approach. The uptake of ^{14}C-(U)-glucose (NEN/200-350 mCi/mmole) was determined by measuring net uptake (incorporation), and respiration in duplicate after terminating incubation at ambient temperature with formalin after 15, 30, 45, 60 and 75 minutes. The variations in the results from duplicates were less than 1%. An amount of 0.014 5 µg ^{14}C-glucose was added to 10 ml of sample (8.05 nmoles/l), in order to minimise changes in the natural substrate concentration.

Linear regression analysis was used to determine the uptake rates and, taking into account the natural

substrate concentration, the actual uptake rates and turnover times (T_t). Respiration was measured by trapping $^{14}CO_2$ with ethanolamine, after addition of 14 % sulphuric acid. Liquid scintillation counting was performed with a Beckmann LS 100-C instrument.

RESULTS AND DISCUSSION

The general hydrography of the Sargasso Sea is well researched and has been summarised by Pocklington (1972) and Morris *et al.* (1977). The oceanic pycnocline extends from 1 200 m to about 400 m, above it lies what has been called the "18°" water (Worthington, 1959). During summer this layer undergoes density stratification during the development of seasonal pycnoclines by which the "18°" water is subdivided into three layers: a surface mixed layer, a thermocline region and the remaining "18°" water.

At the time of sampling, the two boundaries of these layers occured at 30 and 80 m, respectively.

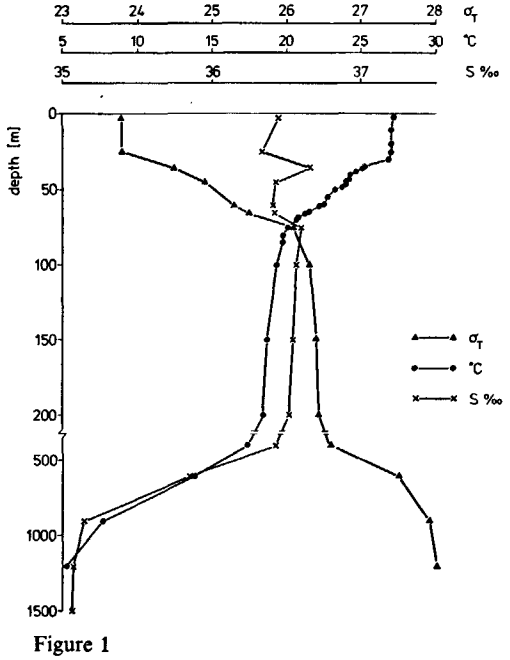

Figure 1
Physical parameters determined at hydrostation.

The development of thermoclines is a discontinuous process, a product of intermittent wind stress coupled with solar heating (Denman, Miyake, 1973). Within the seasonal layers, temperature and salinity may change significantly over short vertical distances and lead to microstructural stratification (Hogg *et al.*, 1978).

Within the seasonal pycnocline region, i. e. the layer between 30 and 80 m, this thermal fine-structure is evident and two sharp gradients were observed to occur at 45 and 60 m (Fig. 1). These could only have been established at or after the time of initial stratification in mid May. Therefore, the maximum age of these gradients is approximately four months, and thus represents the maximum possible residence time of particulates in the seasonal pycnocline.

Within the density layers of the euphotic zone, two oxygen minima occur at 25 and 75 m, respectively,

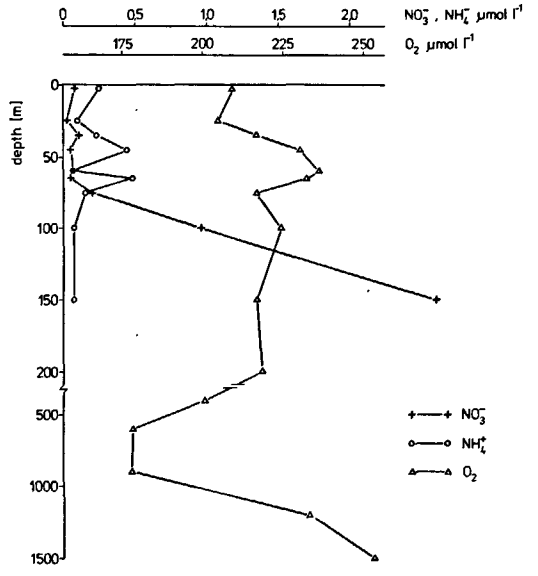

Figure 2
Inorganic nutrients and oxygen profiles of the Sargasso Sea water column.

together with a maximum at 60 m (Fig. 2). The low nitrate and ammonia values are in accordance with data reported by Morris *et al.* (1977). Nitrite values showed little fluctuations from an extremely low level. The oceanic oxygen minimum lies between 600 and 900 m.

Bacterial biomass (Fig. 3) showed high values at the surface and at 25 m. As biomass and activity data are lacking for the 600 and the 400 and 600 m stations respectively, no direct relationship can be derived between the oxygen minimum and the bacterial biomass maximum. However, as can be seen from Figures 2 and 3, relatively high biomass values are found in a region of beginning oxygen depletion although actual uptake rates remain almost constant. Karl *et al.* (1976) showed from ATP measurements that biomass maxima occurred within the oxygen minimum zone of the North Atlantic between 800 and 1 000 m. Holm-Hansen and Booth (1966) who calculated bacterial biomass from ATP determinations, found maxima at 25-50 and 300-500 m,

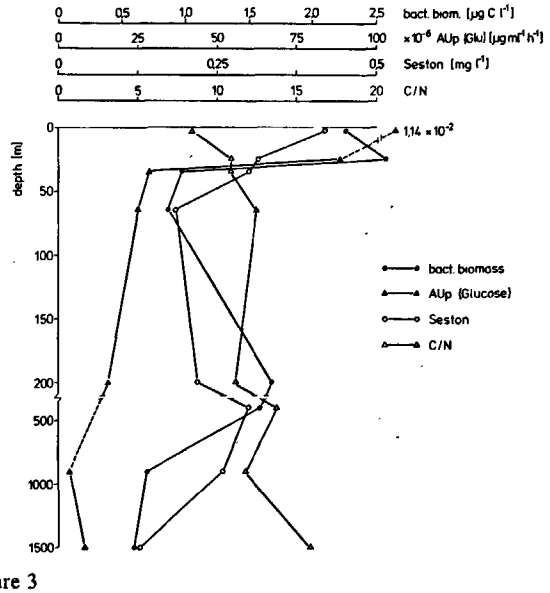

Figure 3
Profiles of bacterial biomass, actual uptake rates (AU_p), seston dry weight and particulate C/N ratios.

Table 1

Seston and particulate organic carbon and nitrogen in Sargasso Sea water column. POC, particulate organic carbon; PON, particulate organic nitrogen.

Depth (m)	Seston (mg/l)	POC (µg/l)	PON (µg/l)	C/N
3	0.42	57.4	6.8	8.44
25	0.32	44.1	4.0	11.00
35	0.30	74.8	6.9	10.84
65	0.19	63.8	5.1	12.51
200	0.22	45.4	4.1	11.07
400	0.30	51.7	3.8	13.61
900	0.26	61.1	5.2	11.75
1 500	0.13	28.8	1.8	16.00

respectively, in the North Pacific. In the Central Pacific, the same pattern was found by Sorokin (1971). However, as these determinations were carried out using the total particulate fraction, plankton activity is included as well.

Actual uptake (Fig. 3) had the highest values in the surface samples and decreased with depth. Turnover times (Table 2) showed a marked increase with depth.

Particulate C/N ratios (Fig. 3, Table 1) increase from a typical phytoplankton value of 8.5 to 16.0, indicating preferential degradation of nitrogen containing compounds which is supported by findings of Handa and Yanagi (1969), who found the same pattern in the Pacific. Cauwet (1980) reports values of 20-200 µg POC/l in the surface layers and 10-60 µg POC/l for underlying and deeper waters in the ocean, but states that these values may be slightly overestimated. The results obtained in this study lie around the upper limits of these values, probably due to the fact that zooplankton has not been removed.

Amino acid content is relatively low (Fig. 4, Table 3) and ranges from trace amounts (<1 nmole/l) to not more than 30 nmoles/l for individual acids. Lee and Bada (1977) reported similar values for total dissolved free amino acids in the Sargasso Sea.

Free monosaccharides range from trace amounts (<5 nmoles/l) to 660 nmoles/l, the greatest portion of them being hexoses with a predominance of glucose and fructose (Fig. 4, Table 4). The same pattern has been found in near shore and interstitial waters (Mopper, Ittekott, Dawson, Liebezeit, in prep.). Arabinose and melibiose were present only in a few samples. The amount of oligosaccharides was low in all samples, and has therefore not been included in the calculations.

Total values are considerably lower than those reported by Walsh and Douglass (1966), but show the same pattern. Their higher values may be attributed to hydrolysis of polysaccharide material thus leading to an overestimation (Josefsson *et al.*, 1972; Burney, Sieburth, 1977).

Both compound classes investigated show different behaviour. Amino acid values are low at the surface and enriched at the upper boundary of the seasonal pycnocline (25 m), and within the 60-80 m thermocline. No increase with depth could be observed, except for

Figure 4

Dissolved free amino acids and carbohydrates in the Sargasso Sea water column. Notations as in Tables 3 and 4.

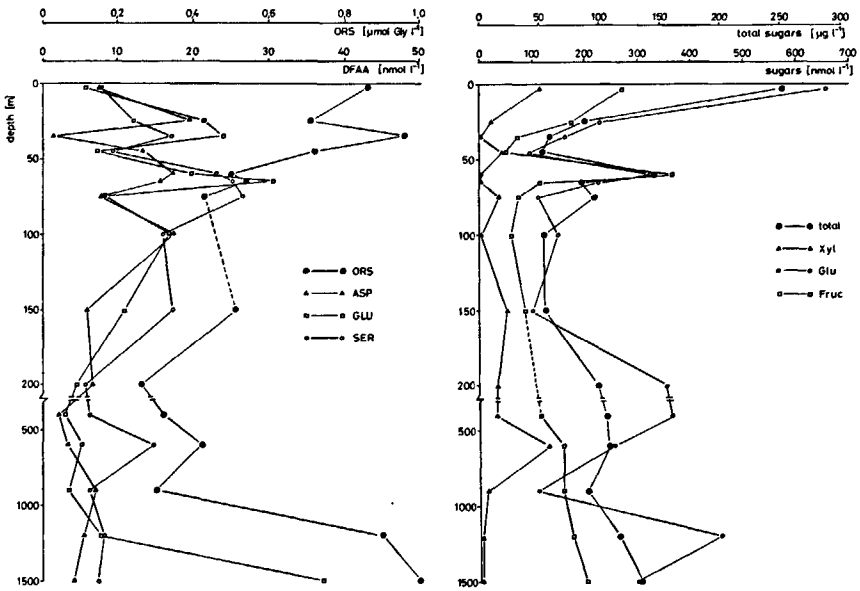

Table 2

Microbiological parameters in Sargasso Sea water column. Tot. count, total counts of acridin orange stained cells; incorp., incorporation; resp., respiration; % resp., % respiration; AU_p, actual uptake; T_t, turnover time.

Depth (m)	Biomass (ng C/ml)	Tot. count ($ml^{-1} \times 10^4$)	Incorp. (µg/ml × h × 10^{-6})	Resp. (µg/ml × h × 10^{-6})	% resp. (%)	AU_p (µg/ml × h × 10^{-6})	T_t (h)
3	2.26	2.8	116.5	21.5	15.6	11 417	10.5
25	2.58	3.1	2.5	0.5	16.6	88.7	482.3
35	0.97	1.9	0.7	0.7	49.7	28.6	1 076.9
65	0.87	2.0	0.8	0.1	11.6	25.3	1 671.9
200	1.69	4.9	0.4	–	–	15.9	4 133.4
400	1.59	4.7	n. d.	n. d.	n. d.	n. d.	n. d.
900	0.71	1.1	0.3	–	–	3.8	5 677,4
1 500	0.61	0.9	0.2	–	–	8.5	6 487.7

Table 3

Dissolved free amino acids in Sargasso Sea water column. ASP, aspartic acid; THR, threonine; SER, serine; GLU, glutamic acid; GLY, glycine; ALA, alanine. All concentrations given in nmoles per litre. ORS, o-phthaldialdehyde reactive substance; n. d., not determined.

Depth (m)	ASP	THR	SER	GLU	GLY	ALA	ORS (moles Gly/l)
3	7.5	tr.	7.8	5.8	7.8	3.3	0.85
25	19.3	6.3	12.1	21.4	29.5	5.4	0.71
35	1.4	9.4	17.1	24.0	20.7	4.6	0.96
45	13.2	5.2	9.4	7.2	11.4	6.0	0.72
60	17.3	18.5	22.1	19.8	17.4	14.7	0.50
65	15.6	28.1	25.2	30.6	23.7	22.5	0.54
75	9.7	10.0	26.5	8.1	19.0	8.3	0.43
100	17.3	9.6	15.9	16.8	8.3	15.2	n. d.
150	5.9	9.1	17.2	10.8	21.4	5.5	0.51
200	6.6	2.9	5.6	4.6	3.1	1.4	0.26 Nansen
200	6.6	2.8	5.8	4.6	3.3	1.3	0.28 Niskin
400	2.1	5.2	6.2	2.9	5.4	1.4	0.32
600	3.3	9.8	14.6	5.2	19.9	5.0	0.42
900	7.0	3.1	6.2	3.4	11.0	1.8	0.30
1 200	5.4	tr.	8.1	7.9	9.8	4.5	0.90
1 500	4.1	tr.	7.3	37.0	8.7	5.5	1.00

glutamic acid, whereas ORS values increase considerably, probably due to the fact that basic amino acids, oligopeptides and dissolved proteins with positive *o*-phtaldialdehyde response comprise a greater part of the total than in the upper layers (Garrasi *et al.*, 1979).

Carbohydrate values are high at the surface, and enriched only at the upper boundary of the 60-80 m thermocline. Only glucose and xylose show any significant enrichment above the oceanic density layer.

From the data given above, it may be concluded that different planktonic populations, bacteria, osmotrophic and autotrophic phytoplankton as well as zooplankton, at the surface and the two seasonal pycnoclines exist.

At the surface, the high actual uptake rate together with low dissolved free amino acid, and high carbohydrate values indicates that DFAA are more rapidly turned over. The low particulate C/N value and the relatively high seston content show that a phytoplankton community attributes to a protein enrichment in the particulate fraction. On the other hand, the high carbohydrate contents may be caused by excretion of these materials by phytoplankton (Fogg, 1966; see however Sharp, 1977!).

At the upper boundary of the seasonal pycnocline (25 m), bacteria contribute significantly to the seston, as reflected by the high biomass value and the oxygen minimum.

Within the 60-80 m pycnocline the enrichment in DFAA (65 m) and carbohydrates (60 m) together with the oxygen maximum suggest this region to be of high autotrophic activity. The high C/N value and the low seston content, however, indicate that a considerable portion of the particulate fraction may be detrital material.

As the involved processes in all three layers discussed above are highly complex, no distinct separation can be made between either auto- or heterotrophic processes. The sum of these, however, may lead to the observed production of dissolved organic compounds at the upper boundaries of pycnoclines and in the surface mixed layer.

It should be pointed out that as long as sufficient data on auto- and heterotrophic activity in connection with pycnoclines are lacking, the results given above remain hypothetical.

The one-dimensional nature of this study did not allow any investigations of lateral variability of enrichment at pycnoclines. Lateral advection, eddy diffusion and patchniness in the plankton community will further affect the vertical distribution of dissolved and particulate organic matter in the ocean. The picture would be further complicated by the possibility of diurnal variations in planktonic activity (Meyer-Reil *et al.*, 1979; Ferguson, Palumbo, 1979).

CONCLUSION

The data given above support the hypothesis whereby free dissolved organic compounds such as amino acids and carbohydrates, are enriched at the upper boundaries of pycnoclines. This phenomenon may be attributed to the enrichment of particulate organic matter such as phytoplankton and bacteria, and the resulting auto- and heterotrophic activities.

Measurements from Bermuda inshore waters and the Skagerrak/Kattegatt region (Liebezeit, Dawson, unpublished results) suggest that this process is a widespread occurrence.

These findings have far reaching consequences in modelling the vertical flux of particulate and dissolved organic matter, since the assumption that there is a constant flux to the sea bottom no longer holds true if density layers are involved.

A considerable amount of organic carbon produced within the euphotic zone will also be remineralised in concentrated zones in the upper water column. Similar conclusions have been drawn from the work on the particulate fraction (Menzel, Ryther, 1970; Bishop *et al.*, 1977, 1978; Knauer *et al.*, 1979).

Table 4

Dissolved free carbohydrates in Sargasso Sea water column. GLU, glucose; FRUC, fructose; MAN, mannose; GAL, galactose; XYL, xylose; ARA, arabinose; MEL, melibiose. All concentrations given in nmoles per litre; n. d., not determined.

Depth (m)	GLU	FRUC	MAN	GAL	XYL	ARA	MEL	Total (µg/l)
3	658.0	270.4	45.5	320.1	114.2	tr.	–	250.4
25	229.7	175.6	6.9	52.8	22.5	tr.	–	87.1
35	163.3	70.4	24.7	63.1	tr.	tr.	–	57.9
45	95.5	49.6	43.9	25.0	43.0	44.8	–	52.0
60	319.6	364.9	11.6	104.0	tr.	tr.	+	144.0
65	226.7	113.9	9.3	117.0	tr.	tr.	+	84.0
75	110.9	72.7	130.3	65.6	29.7	146.3	–	95.2
100	147.9	60.8	9.2	tr.	tr.	86.5	+	52.5
150	99.5	85.6	31.4	61.1	50.6	94.3	–	87.4
200	358.3	n. d.	tr.	160.4	35.3	tr.	+	98.8
400	345.5	116.6	tr.	97.3	33.3	tr.	–	105.7
600	254.6	160.4	11.8	60.1	133.1	tr.	–	108.0
900	112.6	159.6	18.6	34.8	15.4	192.8	–	90.5
1 200	458.4	183.5	tr.	tr.	tr.	tr.	++	115.5
1 500	297.1	201.7	tr.	236.4	tr.	tr.	+	132.3

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