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## Size–ascent rate relationships in positively buoyant marine diatoms

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### Abstract

Cell size and ascent rate were measured in individual short chains (2–8 cells) and single cells of positively buoyant marine diatoms from natural populations and cultures. Maximum ascent rates for *Rhizosolenia formosa*, *Rhizosolenia acuminata*, *Rhizosolenia castracanei*, *Rhizosolenia debyana*, and *Ethmodiscus rex* suggest an upper limit to diatom ascent rates on the order of 7–8 m h<sup>-1</sup>. Ascent rates were weakly correlated with cell diameter, volume, and surface : volume ratio across the pooled data for all species ( $n = 105$ ). Among *Rhizosolenia* spp., ascent rate was strongly correlated with size-related measures. The *Rhizosolenia* spp. average diameter was highly correlated with average ascent rate ( $r^2 = 0.99$ ,  $n = 4$ ). Calculated cell density was inversely related to cell diameter in *Rhizosolenia* spp. Cell diameter is a better predictor of ascent rate than volume in long, cylindrical cells owing to covariations of density and form resistance. The observed ascent rates are consistent with vertical migration by these large diatoms in oligotrophic seas.

Phytoplankton suspension has long been regarded as an important property influencing community losses, material flux, and successional characteristics (Hutchinson 1967). Although more recent work has indicated that accelerated transport rates and mass phytoplankton sinking are in large part due to flocculation processes (Allredge and Gotschalk 1989; Jackson 1990; Lampitt 1985), individual cell responses are still important for understanding how both size and physiological condition modify sinking characteristics. Diatom sinking rates are strongly related to cell quota (Bienfang and Harrison 1984), cell size, and nutritional state (Smayda 1970). In healthy, non-aggregated cells, sinking and ascent rates are generally described by Stokes' equation (Hutchinson 1967). Large, negatively buoyant cells have a slower sedimentation rate than is predicted based on densities derived from smaller cells, implying a lower density with increasing size (Smayda 1970).

Such empirical evidence implies that active density regulation must occur and that the size effect is related to the vacuole and changing surface : volume ratios. This observation was noted early on (Gross and Zeuthen 1948) and has led to several papers that examine the cell sap composition of both marine diatoms and buoyant non-motile dinoflagellates (Beklemishev et al. 1961; Kahn and Swift 1978; Smayda 1970). Active cellular regulation of cytoplasmic density is also implied by results of studies that use selective anesthetics and inhibitors in limnetic and marine diatoms (Smayda 1974; Waite et al. 1992).

Such mechanisms are required to lower density because eucaryotes do not possess gas vesicles as found in pro-caryotes such as *Trichodesmium* spp. (Walsby 1978). Both

inorganic ions and organic osmolytes are known to be important in buoyancy regulation in animals (Sanders and Childress 1988; Withers et al. 1994); however, organic osmolytes have not been measured in phytoplankton.

Recent studies have noted that the largest diatoms known, members of the genera *Rhizosolenia* and *Ethmodiscus*, are strongly positively buoyant and ascend at rates of several meters per hour (Villareal 1988, 1992; Villareal et al. 1993). Theoretical considerations suggest that positive buoyancy is a direct function of size and should not be found in diatoms below a critical minimum size because of the ballasting effect of the siliceous frustule (Villareal 1988). Positive buoyancy seems to be part of a generalized life-history strategy for migration to exploit subeuphotic zone nutrient pools. This vertical migration has been documented for the nonmotile dinoflagellate *Pyrocystis noctiluca* (Rivkin et al. 1984; Ballek and Swift 1986) and recently in *Rhizosolenia* mats (Villareal et al. 1993), and it seems likely to occur in a variety of other oceanic taxa as well (Moore and Villareal 1996; Villareal and Carpenter 1994; Villareal and Lipschultz 1995). Preliminary calculations suggest that vertical migration could be an important vector for new nitrogen flux (Villareal et al. 1993) or phosphate transport (Karl et al. 1992).

Ascent rates should be greater in larger organisms; however, there has been no formal examination of diatoms over a size range sufficient to encompass most positively buoyant species, nor is it clear what range of ascent rates is possible. The depth range of vertical migration and the zone where nutrient transport can be biologically influenced should be a function of ascent rate. Additionally, the postulated cell size–density relationship remains unconfirmed at the upper end of the size spectrum in marine diatoms. These issues are crucial for understanding the potential range of vertical migration as well as the time scale for the process to occur. To address some of these issues, we examined the ascent rates and sizes of individual short chains or single cells of *Rhizosolenia formosa* H. Peragallo, *Rhizosolenia acuminata* (H. Pera.) H. Per-

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agallo, *Rhizosolenia castracanei* H. Peragallo, and *Ethmodiscus rex* (Rattr.) Wiseman and Hendey in both field samples and laboratory cultures.

## Materials and methods

*Rhizosolenia* cultures were isolated from the Sargasso Sea near Bermuda in August 1993. *Rhizosolenia* chains were selected randomly from the top of low light (<40  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ ), nutrient-replete cultures. We used modified MET-44 medium (Villareal 1990) supplemented with K or K/20 trace metal/Fe/EDTA additions (Keller et al. 1987). These conditions are optimum for positive buoyancy in these species (Moore and Villareal 1996). *E. rex* ascent rates were measured on cells collected in horizontal and vertical net tows (0.5-m net, 303- $\mu\text{m}$  mesh) in the central North Pacific along a transect from Hawaii to California (June 1993). Included in the analyses are ascent rates (Villareal 1988) and unpublished size data for *Rhizosolenia debyana* H. Peragallo collected from the Sargasso Sea. Nutrient and light histories of the chains measured at sea are unknown.

Ascent rate measurements were conducted in a temperature-stabilized settling column (SETCOL, 45 cm high, 2.5-cm diam, Bienfang 1981) that contained 0.2- $\mu\text{m}$  pore-size filtered seawater. Cells or chains of cells were gently injected into the base of the SETCOL, and ascent time was measured against a series of lines spaced at 5-cm intervals. The slope of the time vs. distance plot yielded ascent rate (Villareal 1988). Chains were recovered from the top of the SETCOL column, and the chain length, diameter, and number of cells were measured with either an Olympus BZH compound microscope (*Rhizosolenia*) or an SZB stereoscope (*Ethmodiscus*). Volume was calculated assuming a cylindrical cell shape. Laboratory ascent rates were measured at 21°C. Flowing surface seawater was used in the outer jacket at sea (20–24°C).

The modified Stokes' equation (Smayda 1970) was used to calculate density and size-related effects on ascent rate:

$$\text{AR} = \frac{2gr^2(\rho - \rho_1)}{9\eta\phi_r}$$

AR is ascent rate ( $\text{cm s}^{-1}$ ),  $g$  is gravitational acceleration ( $980 \text{ cm s}^{-2}$ ),  $r$  is equivalent spherical radius (cm),  $\rho$  is seawater density ( $\text{g cm}^{-3}$ ),  $\rho_1$  is cellular density ( $\text{g cm}^{-3}$ ),  $\eta$  is kinematic viscosity ( $0.01 \text{ g cm}^{-1} \text{ s}^{-1}$ ), and  $\phi_r$  is the coefficient of form resistance (dimensionless).

A theoretical form resistance term,  $\phi_r$ , was calculated for the *Rhizosolenia* spp. as that of an ellipsoid equal in volume and axial ratios to the diatom chain (McNown and Malaika 1950; Davey and Walsby 1985; Davey 1986) and is a close approximation of the actual form resistance for short algal chains (Davey and Walsby 1985). Thus, the form resistance term is a function of chain volume, length, and diameter. Form resistance was calculated with the longest axis of the chain oriented in the vertical direction since chains in our study nearly always ascended with the longest axis at or near a vertical orientation. Similar orientations were observed by Lund (1959) for a

variety of limnetic taxa. *E. rex* cells had surface : volume ratios close to those of equivalent-sized spheres and therefore had a form resistance of unity. McNown and Malaika (1950) found that for such particles no serious error resulted from this simplification. The  $\rho - \rho_1$  term (hereafter referred to as the density difference, in units of  $\text{mg ml}^{-1}$ ) was calculated by means of Stokes' equation, with the theoretical form resistance (for *Rhizosolenia* spp.) and the measured chain size and ascent rate. The viscosity used is valid over the temperature range in this study with a salinity of 32–35 PSU (Sverdrup et al. 1942).

Because Stokes' equation is only applicable at low Reynold's numbers, we calculated the Reynold's number for each diatom chain with the equation

$$\text{Re} = \frac{\text{AR}d}{\eta/\rho}$$

Re is Reynold's number,  $d$  is chain diameter (cm), and AR,  $\eta$ , and  $\rho$  are as described above. Boundary layer interactions, which would increase drag and slow ascent rates, are possible in the SETCOL apparatus. According to McNown and Malaika's (1950) formulas for experimentally determined boundary effects of spherical particles moving in a cylinder, the *E. rex* cells (the largest species in this study) experienced negligible boundary layer effects (avg *E. rex* cell correction factor = 1.2%). However, the largest *E. rex* cells, with Reynold's numbers up to 2.01, may have been approaching the point at which inertial forces are no longer negligible and thus Stokes' equation is no longer applicable. If inertial forces were not negligible, the calculated density difference would be an underestimation. All *Rhizosolenia* spp. had Reynold's numbers appropriate for use in Stokes' equation (Table 1). McNown and Malaika (1950) found that the speed predicted by Stokes' equation of particles with  $\text{Re} < 0.1$  was very accurate and was within 10% when  $0.1 < \text{Re} < 0.5$ .

## Results

In our experiments, cell volume spanned 3 orders of magnitude from an average of  $9.37 \times 10^6 \mu\text{m}^3$  for *R. acuminata* to an average of  $1.26 \times 10^9 \mu\text{m}^3$  in *E. rex* (Table 1). Ascent rates ranged from 6 to 692  $\text{cm h}^{-1}$  across all species (Table 2); however, there was only limited correlation ( $r^2 = 0.42$ ) between cell (or chain) volume and ascent rate across the five diatom species (Fig. 1). The field-collected *R. debyana* (from Villareal 1988) had higher average (450  $\text{cm h}^{-1}$ ) and maximum ascent rates (692  $\text{cm h}^{-1}$ ) than did the much larger *E. rex* (avg = 196  $\text{cm h}^{-1}$ , max = 494  $\text{cm h}^{-1}$ ). Among the four *Rhizosolenia* spp., there was a positive although unimpressive correlation ( $r^2 = 0.53$ ) between chain volume and ascent rate (Fig. 1). Diameter and ascent rate were also poorly correlated across all five diatom species ( $r^2 = 0.33$ ). Within *Rhizosolenia* spp., there was a positive correlation ( $r^2 = 0.78$ ) between chain diameter and ascent rate (Fig. 2). There was also a high positive correlation between the *Rhizosolenia* spp. average ascent rate (AR,  $\text{cm h}^{-1}$ ) and

Table 1. The average (and range of) cell diameter ( $\mu\text{m}$ ) and length ( $\mu\text{m}$ ), chain volume ( $\times 10^6 \mu\text{m}^3$ ), number of cells per chain, and Reynold's number for *E. rex*, *R. formosa*, *R. acuminata*, *R. castracanei*, and *R. debyana*.

	Diam.	Length	Vol.	Cells	Re
<i>E. rex</i>	1,172	1,099	1,258	1.0	0.66
( <i>n</i> = 43)	(650–1,430)	(520–1,300)	(248–1,902)	(1)	(0.13–2.01)
<i>R. formosa</i>	132	661	20.36	2.5	0.035
( <i>n</i> = 24)	(112–162)	(238–976)	(9.49–41.4)	(1–6)	(0.007–0.136)
<i>R. acuminata</i>	119	561	9.37	1.5	0.008
( <i>n</i> = 13)	(112–124)	(408–800)	(4.41–26.2)	(1–3)	(0.002–0.017)
<i>R. castracanei</i>	120	657	23.60	3.2	0.008
( <i>n</i> = 14)	(120)	(453–800)	(13.9–45.2)	(2–6)	(0.004–0.016)
<i>R. debyana</i> *	227	527	119.9	5.6	0.288
( <i>n</i> = 11)	(214–250)	(478–593)	(51.7–175)	(3–8)	(0.178–0.383)

\* From Villareal 1988 and unpublished data.

the species average diameter ( $D$ ,  $\mu\text{m}$ ), with the linear-fit equation  $AR = 3.93 \times D - 441$  ( $r^2 = 0.99$ ,  $n = 4$ ).

Surface: volume ratio ( $\mu\text{m}^{-1}$ ) was a function of cell diameter, peralvar axis, and the number of cells in the chain. There was a negative correlation ( $r^2 = 0.79$ ) between surface: volume ratio and ascent rate among the four *Rhizosolenia* spp. (Fig. 3).

The theoretical form resistance used in density calculations varied considerably within species, with the highest average form resistance seen in *R. castracanei* (Table 2). There was no correlation between form resistance and ascent rate.

Density difference is a derived term and must be compared cautiously to the ascent rate and size data used in its calculation. In general, there was little relationship between the calculated density difference from seawater ( $\text{mg ml}^{-1}$ ) and ascent rate across all five species (Fig. 4). There was a strong positive correlation ( $r^2 = 0.82$ ) between the calculated density difference and ascent rate among only the *Rhizosolenia* spp. (Fig. 4). This correlation improved ( $r^2 = 0.94$ ) if only *R. acuminata*, *R. formosa*, and *R. castracanei* were considered. This higher correlation may be related to the relatively narrow range in diameter (avg 119–132  $\mu\text{m}$ , Table 1) among these three

Table 2. Summary of the average (and range of) calculated density difference from seawater ( $\text{mg ml}^{-1}$ ), ascent rate ( $\text{cm h}^{-1}$ ), and theoretical form resistance in *E. rex*, *R. formosa*, *R. acuminata*, *R. castracanei*, and *R. debyana*.

	Density difference	Ascent rate	Form resistance
<i>E. rex</i>	0.6	196	None
( <i>n</i> = 43)	(0.1–2.5)	(42–494)	
<i>R. formosa</i>	6.7	92	1.59
( <i>n</i> = 24)	(1.6–15.1)	(19–295)	(1.19–2.17)
<i>R. acuminata</i>	2.3	22	1.30
( <i>n</i> = 13)	(0.8–5.7)	(6–44)	(1.12–1.98)
<i>R. castracanei</i>	1.9	24	1.87
( <i>n</i> = 14)	(0.9–4.2)	(12–47)	(1.39–2.5)
<i>R. debyana</i> *	10.1	450	1.70
( <i>n</i> = 11)	(3.0–21.8)	(292–692)	(1.34–1.95)

\* From Villareal 1988 and unpublished data.

species; consequently, ascent rate variations were due mainly to variations in density. The *Rhizosolenia* spp. had larger and more variable density differences from seawater than did *E. rex* (Table 2). There was a positive correlation between the average density difference ( $\text{mg ml}^{-1}$ ) and average diameter ( $D$ ,  $\mu\text{m}$ ) among *Rhizosolenia* spp., with the equation density difference =  $0.0666 \times D - 4.69$  ( $r^2 = 0.78$ ,  $n = 4$ ).

## Discussion

As suggested by Stokes' equation, size and ascent rate were directly related. Larger diameter species had higher

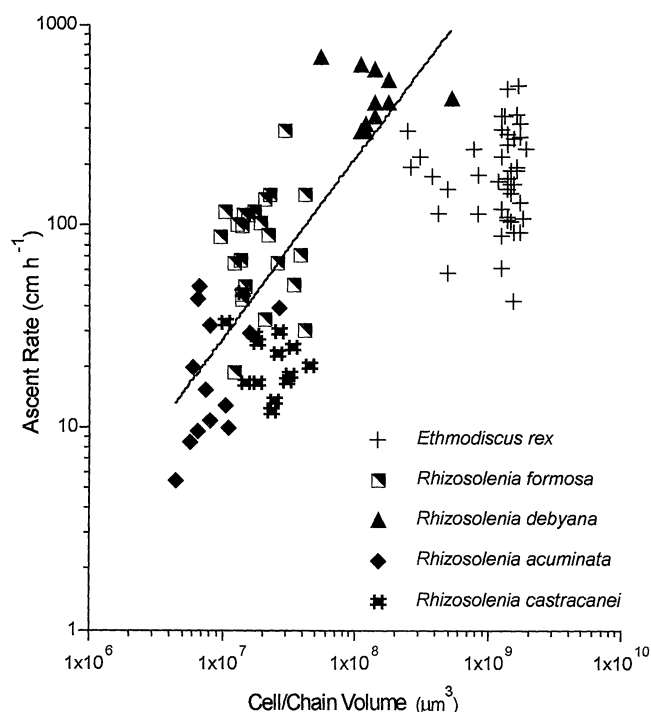


Fig. 1. The ascent rate of individual diatom chains (1–8 cells) plotted against chain volume. The line shows the curve fit of only *Rhizosolenia* species with equation  $AR = 1.55 \times 10^{-5} \times V^{0.893}$  ( $r^2 = 0.53$ ), where AR is ascent rate and  $V$  is chain volume.

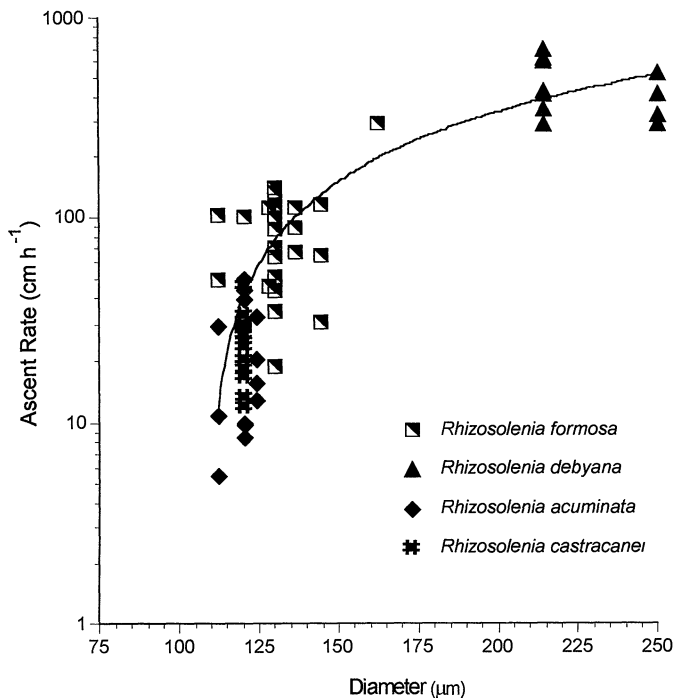


Fig. 2. Ascent rate–diameter relationships among *Rhizosolenia* spp. The linear fit for all *Rhizosolenia* spp. had the equation  $AR = 3.66D - 400$  ( $r^2 = 0.78$ ), where AR is ascent rate and  $D$  is chain diameter.

potential ascent rates; however, it is clear that both form resistance and internal cell density vary within and between species. Consequently, simple predictors of diatom ascent rates based on size-related parameters will yield only an approximation of individual cell ascent rates. Additionally, the observed buoyancy reversals in *Rhizosolenia* mats and *P. noctiluca* are related to nutrient status, not size, and underscore the absolute role that physiological processes play in controlling buoyancy in these species. Carbohydrate pools (which respond to nutrient and light fields) may be important in regulating the buoyancy of *Rhizosolenia* (Moore and Villareal 1996). Thus, our interpretations are limited to relationships between size, shape, and potential ascent rate limitations.

Several factors seemed to indicate an upper limit on marine diatom ascent rates between 7 and 8 m h<sup>-1</sup>. In this study, which included the largest known diatom species (*Ethmodiscus* and *Rhizosolenia* spp.), the maximum ascent rate observed was 695 cm h<sup>-1</sup>. Ascent rates increased rapidly with increasing cell size up to this maximum and then decreased slightly (Fig. 1). These latter numbers were from the *E. rex* cells, which appear to have Reynold's numbers approaching the point at which inertial forces are not negligible. At this point, inertial forces increase drag rapidly (Hutchinson 1967) and may set an upper limit on the ascent rate of large *E. rex* cells.

Inserting, the maximum diameter of *R. debyana* (310  $\mu\text{m}$ , Sundström 1986), our fastest rising species, into the linear equation that relates chain diameter to ascent rate (Fig. 2) gives an ascent rate of 735 cm h<sup>-1</sup>. If we consider chain surface : volume ratio and ascent rate among *Rhi-*

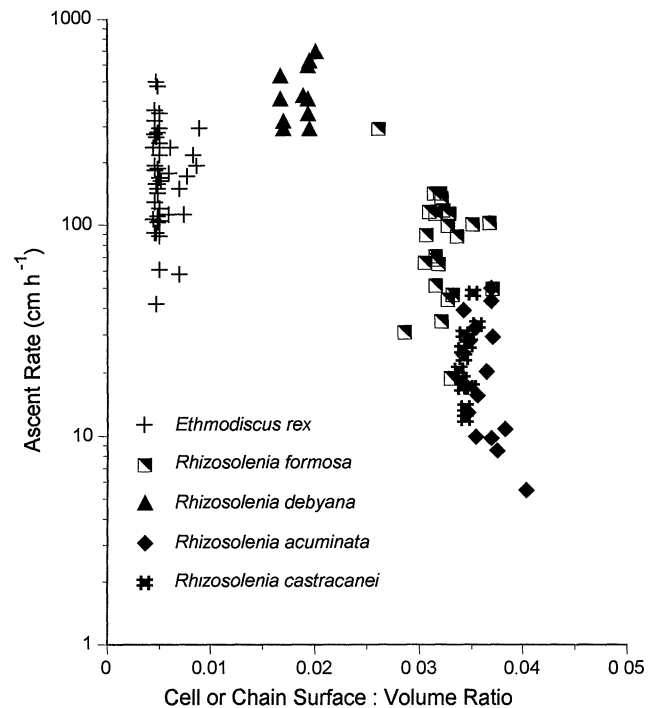


Fig. 3. Surface : volume ratio relationships to ascent rate in *Ethmodiscus* and *Rhizosolenia* spp. The best-fit curve of only *Rhizosolenia* spp. had the equation  $AR = -2.34 \times 10^4 \times SV + 854$  ( $r^2 = 0.79$ ), where AR is ascent rate and SV is the chain surface : volume ratio ( $\mu\text{m}^{-1}$ ).

*zosolenia* species (Fig. 3), the  $Y$  intercept of this equation (with the physically impossible surface : volume ratio of 0) was 854 cm h<sup>-1</sup>. Inserting the minimum surface : volume ratio seen in *E. rex* of 0.005 (this is probably below the minimum possible for *Rhizosolenia* spp., but represents single cell limitations) into the equation gives an ascent rate of 746 cm h<sup>-1</sup>. Lastly, the maximum observed ascent rate of even centimeter-sized *Rhizosolenia* mats is only 640 cm h<sup>-1</sup> (Villareal et al. 1996).

Among the *Rhizosolenia* spp. there were good correlations between measured ascent rate and chain diameter, surface : volume ratio, and density difference from seawater ( $r^2 = 0.78, 0.79,$  and  $0.82$ , respectively). However, because the average cell length was similar for each species (Table 1), the correlation between surface : volume ratio and ascent rate is primarily a function of changing cell diameter. Similarly, cell density is also strongly influenced by cell diameter (*see* Villareal 1988). Ascent rates were less well correlated with total chain volume ( $r^2 = 0.53$ , Fig. 1). These covariations between cell diameter, density, and form resistance imply that for solenoid, chain-forming diatoms, sinking or ascent rates estimated from chain volume will be less accurate than calculations based on the chain diameter. If the approximate size of the algal chains were known but the orientation was not, one could use the average of the vertical and horizontal orientations for calculating form resistance (Davey and Walsby 1985). Behavioral attributes must be considered as well since *Rhizosolenia* chains ascended with the long axis parallel

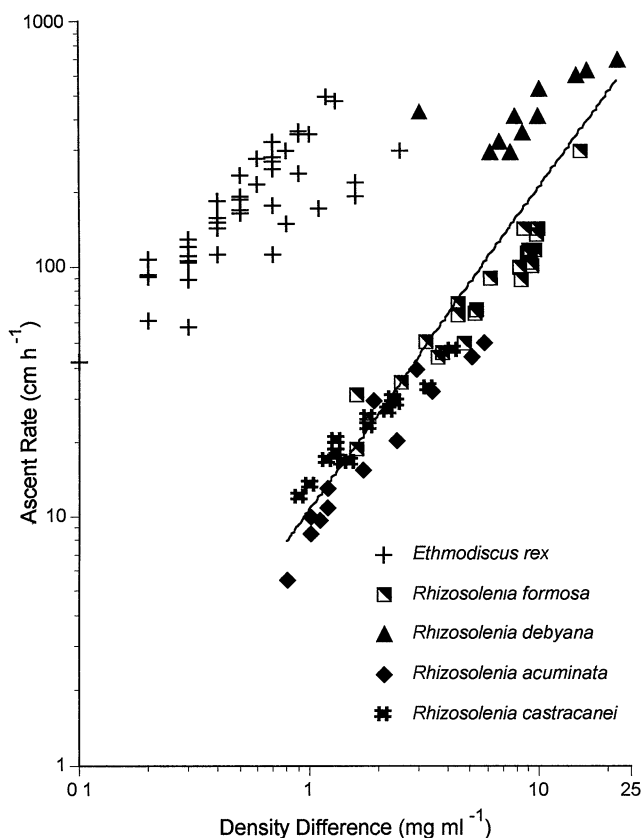


Fig. 4. The ascent rate of individual diatom chains (1–8 cells) plotted against their calculated density difference from seawater. Density difference was calculated from Stokes' equation by using the measured cell or chain size, ascent rate, and a theoretical form resistance. The line shows the best fit of only *Rhizosolenia* species with the equation  $AR = 10.6 \times P^{1.29}$  ( $r^2 = 0.82$ ), where AR is ascent rate and  $P$  is the density difference from seawater.

to the direction of motion, a behavior not predicted from simple resistance models. The reason for this vertical orientation of *Rhizosolenia* chains is not entirely clear. It may be due to variations in cell density among cells within the chain.

The model of Villareal (1988) suggested that there is a critical minimum size for positive buoyancy to be possible in diatoms. Our data show a clear decrease in the maximum ascent rate with decreasing size (regardless of the measure used). The best-fit curve for all *Rhizosolenia* data of ascent rate plotted against cell diameter had a  $y$ -axis intercept at 109- $\mu\text{m}$  diameter (Fig. 2). Similarly, the regression of *Rhizosolenia* spp. average ascent rate vs. average diameter ( $n = 4$ ) had a  $y$ -axis intercept at 112- $\mu\text{m}$  diameter. In general, positive buoyancy is observed only in these large oceanic taxa or in large post-auxospore cells (Smayda and Boleyn 1966; Waite and Harrison 1992). Villareal and Carpenter (1989) reported that when positively buoyant *Rhizosolenia* mats were broken up, the smallest species in the mats, *Rhizosolenia fallax* (diameter, 10–25  $\mu\text{m}$ ), was negatively buoyant, while the larger species present were positively buoyant. Thus, cells much smaller than those in this study may not be capable of

positive buoyancy, although the exact size limit remains unknown.

We think our results indicate that volume cannot be considered independent of morphology when factors determining ascent rate are considered. Although the calculated form resistance was not correlated with ascent rate, the chain or cell morphology can significantly modify ascent rates. For example, consider a single *R. castracanei* cell with 120- $\mu\text{m}$  diameter, 657  $\mu\text{m}$  long, and a density difference from seawater of 1.9  $\text{mg ml}^{-1}$  (average values from Tables 1 and 2); this single cell will have a theoretical form resistance of 1.26 and a Stokes' calculated ascent rate of 17.3  $\text{cm h}^{-1}$ . Increasing the chain length to four cells would quadruple the chain volume, increase the form resistance to 2.08, and increase the calculated ascent rate to 26.4  $\text{cm h}^{-1}$ . In contrast, a single cell with diameter doubled to 240  $\mu\text{m}$  and with the original length and density difference from seawater would also have a volume quadruple that of the original cell, but the form resistance would decrease to 1.06 and the calculated ascent rate would increase to 51.8  $\text{cm h}^{-1}$ . Thus, although total volume and density are identical, the short, fat single cell ascends at roughly twice the rate of the long, narrow chain of four cells.

Our data support previous suggestions that increasing cell size and its influence on surface: volume ratios will lead to lower potential cell densities (Davey 1986; Eppley et al. 1967; Smayda 1970; Villareal 1988). *Rhizosolenia* spp. average density difference from seawater was positively correlated with diameter ( $r^2 = 0.78$ ,  $n = 4$ ). Note that the diameters of *R. castracanei* and *R. acuminata* were very similar (120 and 119  $\mu\text{m}$ , respectively), and their average (and the range of) ascent rates and density differences were also very similar (Table 2). In contrast, *R. formosa*, which had a larger average diameter (132  $\mu\text{m}$ ) but a chain volume and form resistance similar to *R. castracanei*, had significantly higher ascent rates and higher derived density differences (Table 2). Such relationships underscore the importance of cell cycle events (which alter diameter, surface: volume ratios, etc.) such as auxosporulation or vegetative cell enlargement to the overall buoyancy responses of a species. In at least two species, *Rhizosolenia setigera* and *Ditylum brightwellii*, positive buoyancy was seen only briefly, following cell enlargement (Smayda and Boleyn 1966; Waite and Harrison 1992). The density difference term, although more highly correlated with ascent rate than with diameter, is a derived measure and may have species-specific size relationships. *E. rex* cells had much larger volumes than the *Rhizosolenia* chains (Table 1), but did not show correspondingly higher ascent rates. The derived density difference term was considerably lower for *E. rex* than for *Rhizosolenia* spp. (Table 2). We infer from this that species-specific differences exist in strategies for achieving high ascent rates (size vs. low density), but direct measures of internal sap densities are required to validate this hypothesis.

Obviously, there must be a lower limit to cellular density. Our maximum observed density difference of 21.8  $\text{mg ml}^{-1}$  was seen in *R. debyana* (Table 2). This cellular

density value approaches that of distilled water and is counter-intuitive. However, there is evidence that *Halosphaera viridis* can have a density less than that of distilled water (Jenkinson 1986) and that *Rhizosolenia eriensis* approaches neutral buoyancy in limnetic systems (Jackson et al. 1989). Such densities cannot be supported by ion regulation mechanisms and suggest that organic compounds may play an important role in density regulation in phytoplankton, as noted in crustaceans (Sanders and Childress 1988) and elasmobranchs (Withers et al. 1994).

The ascent rates determined for single species chains of *Rhizosolenia* and *Ethmodiscus* were comparable to those of vertically migrating *Rhizosolenia* mats and *P. noctiluca* cells (Kahn and Swift 1978; Villareal et al. 1993). Recent work has shown that the buoyancy and growth characteristics of *R. acuminata*, *R. castracanei*, and *R. formosa* in laboratory cultures would lead to vertical migration if replicated in situ (Moore and Villareal 1996). The internal nitrate concentrations of *Rhizosolenia* and *Ethmodiscus* field populations are also consistent with vertical migration (Villareal and Carpenter 1994; Villareal and Lipschultz 1995). Thus, single species chains of *Rhizosolenia* and *Ethmodiscus* are capable of vertical migration in oligotrophic seas and would thus constitute a source of new nitrogen to the euphotic zone.

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## Errata

In a recent paper by K. Fabricius et al. (November 1995: Vol. 40, No. 7), we demonstrated the ability of several azooxanthellate soft corals to feed on phytoplankton and showed that their rates of feeding and growth were related to the speed of water flow. Erroneously, chlorophyll values in the gastrovascular cavities of the soft coral *Dendronephthya hemprichi* were reported in [ $\mu\text{g Chl } a \text{ polyp}^{-1}$ ] instead of [ $\text{ng Chl } a \text{ polyp}^{-1}$ ]. Consequently, the results describing the feeding on phytoplankton (p. 1294–1295) and the calculations of the coral's carbon budget (p. 1299) need to be corrected. As these corrections could change our conclusion with regard to herbivory in *D. hemprichi*, we have estimated the coral's feeding rate using a new approach, based on in situ measurements of chlorophyll removal from natural seawater. Chlorophyll *a* concentrations in seawater upstream of large *D. hemprichi* colonies were compared to those downstream of the corals with a time lag between pairs of samples equal to the water passage time through the coral thicket. On average, removal rates were equivalent to 2.5–3.6 times the corals' daily respiratory carbon demand (Fabricius et al. in prep.). The chlorophyll depletion of the water and recent electron microscopic documentation of digested algal cells within the endodermal tissue of the polyps suggest that our finding of herbivory in these soft corals is valid. However, our initial method of analyzing gut fluorescence underestimated the actual rates of intake and digestion of phytoplankton by *D. hemprichi*. —Katharina Fabricius, Yehuda Benayahu, Gitai Yahel, and Amatzia Genin.