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The gas vesicles, buoyancy and vertical distribution of cyanobacteria in the Baltic Sea

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The mean pressures required to collapse gas vesicles in turgid cells of cyanobacteria from the Baltic Sea were 0·91 MPa (9·1 bar) in *Aphanizomenon flos-aquae*, 0·83 MPa in *Nodularia* sp. collected from the main deep basins and 0·34 MPa in *Nodularia* from shallower coastal regions. The gas vesicles were strong enough to withstand the depth of winter mixing, down to the permanent halocline (60 m in the Bornholm Sea, 90 m in the Eastern Gotland Sea) or to the sea bottom (30 m or less in the shallow Arkona Sea and Mecklenburg Bight). The cyanobacteria had low cell turgor pressures, within the range 0·08–0·18 MPa. The colonies were highly buoyant: the *Aphanizomenon* colonies floated up at a mean velocity of 22 m per day and the *Nodularia* colonies at 36 m per day. The colonies remained floating when up to half of the gas vesicles had been collapsed. In summer the cyanobacteria were mostly restricted to the water above the thermocline and in calm conditions their concentration increased towards the top of the water column. A series of colony concentration profiles indicated that, following a deep mixing event, the population of colonies moved upward with a net velocity of 22 m per day, similar to the colony floating velocity. This demonstrated that the buoyancy provided by gas vesicles would give a selective advantage to populations of cyanobacteria by enabling them to float into the higher irradiance of the near-surface water.

Key words: Baltic Sea, buoyancy, cyanobacteria, gas vacuoles, waterblooms.

Introduction

In the Baltic Sea there are several types of filamentous cyanobacteria, notably species of *Anabaena*, *Aphanizomenon* and *Nodularia*, which produce populations that float near the water surface and form surface waterblooms under calm conditions (Geitler, 1932; Niemi, 1979; Hübel & Hübel, 1980; Šmarda *et al.*, 1986; Komàrek *et al.*, 1993). These populations may be so extensive that they can be seen in satellite photographs (Horstmann, 1983). Similar surface waterblooms are formed by planktonic cyanobacteria in freshwater lakes (Reynolds & Walsby, 1975; Reynolds, 1987) and by several species of *Trichodesmium* in tropical oceans (Carpenter *et al.*, 1992), where it has been shown that the cyanobacteria float up because they are rendered buoyant by gas vacuoles (Walsby, 1978). Gas vacuoles are known to be present in some of the cyanobacteria of the Baltic Sea (Gumpert *et al.*, 1987; Hübel & Hübel, 1980; Šmarda *et al.*, 1986; Komàrek *et al.*, 1993), but there has been no previous investigation of their role in providing buoyancy and influencing the vertical distribution of the cyanobacteria in these waters.

The gas vacuoles of cyanobacteria are formed from hollow cylindrical structures called gas vesicles (Bowen & Jensen, 1965). Gas vesicles are rigid and withstand application of moderate pressures with little shrinkage in volume (Walsby, 1982), but they collapse irreversibly when subjected to a certain critical pressure (Walsby, 1971). Inside cells they are subjected to cell turgor pressure, which varies from less than 0·1 MPa (1 bar) in halophilic cyanobacteria (Walsby *et al.*, 1983*b*) to as much as 0·55 MPa in freshwater cyanobacteria (Kinsman *et al.*, 1991). No direct measurements of turgor pressure have previously been made in cyanobacteria from marine or brackish waters.

In natural waters gas vesicles are also subjected to hydrostatic pressure, which increases with depth by approximately 0·01 MPa m^{-1}. Cyanobacteria from deep lakes tend to have stronger gas vesicles than those in shallow ones (Utkilen *et al.*, 1985; Walsby, 1994). The range of mean critical pressure for gas vesicles varies from less than 0·3 MPa for cyanobacteria from shallow brine pools (Walsby *et al.*, 1983*b*) to over 3·5 MPa in species of *Trichodesmium* in the deep oceans (Walsby, 1978); those in cyanobacteria from freshwater lakes usually range between 0·5 and 1·0 MPa (Hayes & Walsby, 1986; Walsby & Bleything, 1988). The waters of the Baltic range in depth from less than 10 m along the coastal shallows to more than 200 m in a number of "deeps", though circulation of cyanobacteria to depths greater than 60–90 m will normally be restricted by gradients of temperature and salinity (Kullenberg, 1981).

We investigated the gas vesicles, buoyancy and vertical distribution of planktonic cyanobacteria in parts of the Baltic Sea during the summers of 1992, 1993 and 1994. We related the critical pressure distribution of the gas

vesicles to depth and we obtained evidence for the role of gas vesicles in maintaining these organisms within the euphotic zone. Other factors that have been implicated in the success of cyanobacteria in these waters include their ability to fix nitrogen (Hübel & Hübel, 1980), the possibility that their growth is promoted by high phosphorus availability and a low N:P ratio (Niemi, 1979), and the possibility that they are subjected to less grazing than other groups (Hernroth & Ackefors, 1979). Factors leading to the formation of cyanobacterial waterblooms are discussed in detail by Reynolds & Walsby (1975), Reynolds (1987), and in the compendium edited by Vincent (1987).

Materials and methods

Sampling

This investigation was made in the Baltic Sea on the F.S. *Poseidon* from 2 to 14 August 1992, on the F.S. *Alkor* from 26 July to 6 August 1993, and on the F.S. *Littorina* from 31 July to 13 August 1994. Drift-stations were marked by a drogue, near the Eastern Gotland Sea (depth 210–240 m) and north-east of Bornholm Island (depth 90–100 m).

Cyanobacteria were collected from the sea with either 20 μm or 100 μm mesh plankton nets, drawn vertically from a depth of 10 m to the surface. Floating colonies of *Aphanizomenon* and *Nodularia* were drawn off from the surface of net samples left to stand for an hour. Drops of the suspension were placed on a polycarbonate Petri dish under a binocular microscope; the colonies, which floated to the centre of the convex drops, were withdrawn with a syringe and then cleaned by transfer through further drops of filtered seawater.

The vertical distribution of colonies in the seas was determined in samples collected at depth intervals of 5 m using General Oceanics 12-litre sampling bottles on a rosette array. Samples, usually of 2 l, were filtered through 2 cm diameter nylon filters of 20 μm mesh. These were mounted in filtered seawater under coverslips and the numbers of colonies or filaments of cyanobacteria were counted using a dissecting microscope.

Measurements on gas vesicles and buoyancy

The critical pressure distributions of gas vesicles in the cyanobacteria were determined using a portable pressure nephelometer (Walsby, 1973). Colonies were dispersed with a glass Potter homogeniser. The mean critical pressure (p_c or p_a) and median critical pressures (at which 50% of the gas vesicles collapsed) were calculated by the methods of Walsby & Bleything (1988). Figures are given as means $\pm$ standard deviations. Cell turgor pressure was determined as $p_t = p_c - p_a$, where p_c is the value obtained with cells suspended in seawater containing 0·5–1·5 M sucrose, and p_a is the value with cells suspended in seawater (Walsby, 1973).

The proportion of colonies floating in a water sample was determined by leaving 3 ml samples to stand in Utermöhl sedimentation chambers for 15 min and then counting those colonies floating under the coverslip and those sinking onto the base (Walsby & Booker, 1980).

To determine the proportion of colonies floating after collapsing different proportions of the gas vesicles, suspensions were placed in 1·5 ml Eppendorf tubes, inverted in the seawater-filled nephelometer tubes, and subjected to pressures of 0·4–1·3 MPa in steps of 0·1 MPa. The inverted tubes prevented colonies from floating near the gas–water interphase; without this precaution some gas vesicles become infiltrated with gas and survive the gas pressure rise (see Walsby, 1971, 1994). The pressure-treated samples were diluted and transferred to the Utermöhl chambers for analysis of the proportion of colonies floating.

The floating velocities of colonies were determined from the time taken to float up between gradation marks on a 50 ml measuring cylinder. The colony was expelled near the bottom of the water column from a 2 mm diameter cannula attached to a 5 ml syringe. The cylinder was secured in a gimbaled beaker containing a layer of cooled water to generate a temperature gradient that would prevent convectional mixing.

Measurements of physiochemical gradients

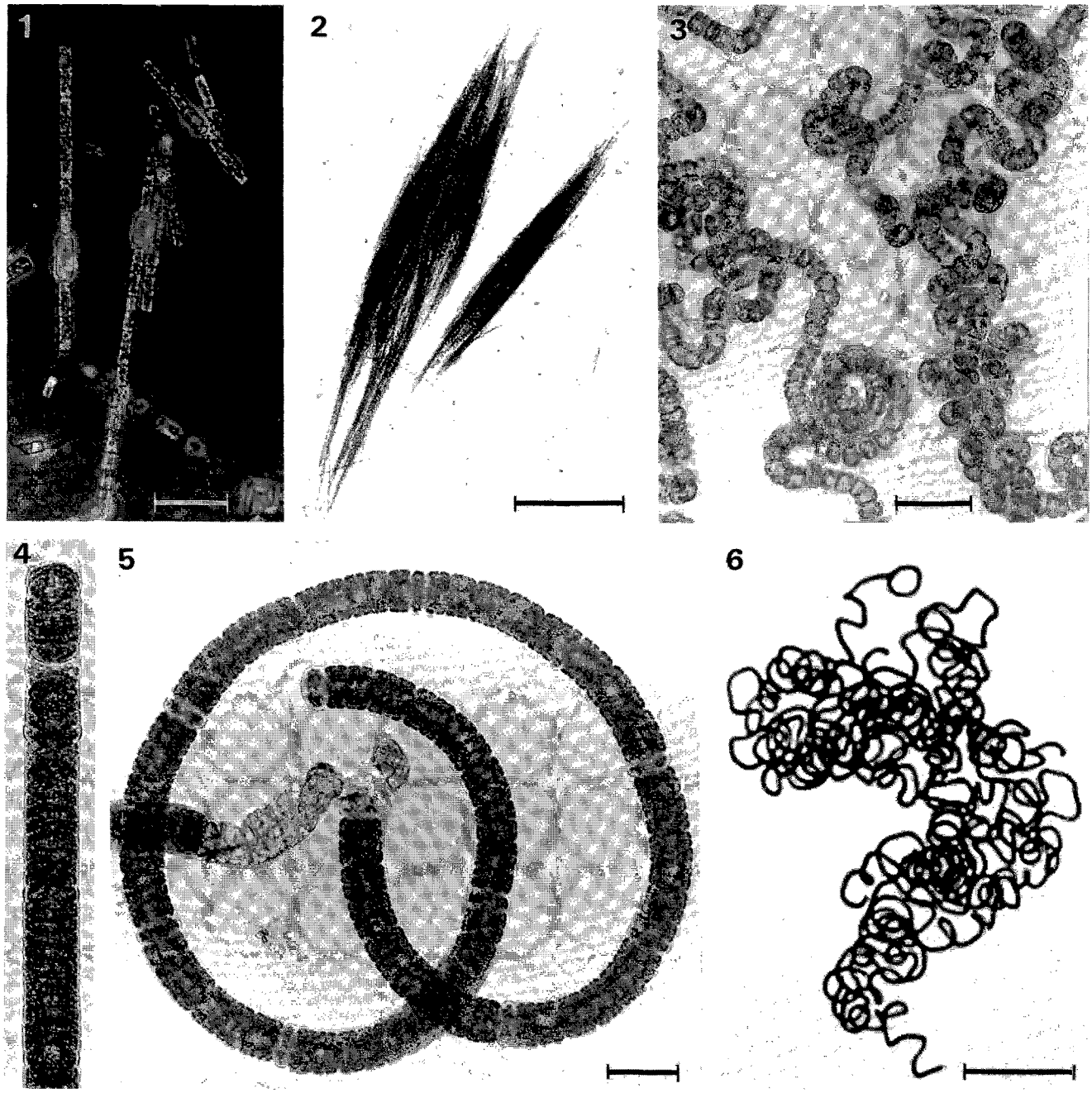
The vertical profile of photon irradiance in the water was measured with a 4π LiCor sensor. Other measurements of depth, temperature and salinity were made by instruments attached to the CTD rosette sampler.

Results

Description of cyanobacteria

Four morphological types of cyanobacteria could be distinguished at each of the Baltic sampling sites; the nomenclature of Komàrek *et al.* (1993) is followed for the *Nodularia* spp.

1. *Aphanizomen flos-aquae* (L.) Ralfs: cells cylindrical, 4·5 μm wide and 7–15 μm long; filaments arranged in parallel arrays, showing gliding movements over one another that cause colonies to change shape, from flat bundles (flakes) to elongate spears; either dark green or straw-coloured (Figs 1, 2).
2. *Nodularia litorea* Kützing: separate straight filaments; discoid cells 15–17 μm wide [i.e. at the upper size range given by Komàrek *et al.* (1993)] and 2–8 μm long (Fig. 4).
3. *Nodularia spumigena* Mertens: coiled filaments either singly or in tangled colonies; cells 11–12 μm wide and 3–6 μm long (Figs 5, 6).
4. *Nodularia* sp.: tightly coiled filaments; cells 6·5–8 μm wide and 2–5 μm long (Fig. 3). This organism resembled *N. spumigena* (Komàrek *et al.*, 1993, fig. 7Af). It occurred in low numbers, usually less than 1% of the total.



Figs 1–6. Light micrographs of cyanobacteria from the Baltic Sea. Fig. 1. Filaments of *Aphanizomenon flos-aquae* showing two heterocysts and cells with peripheral gas vacuoles (appearing light in phase contrast). Fig. 2. Two fusiform colonies of *Aphanizomenon flos-aquae*. Fig. 3. Tightly coiled form of *Nodularia* sp. Fig. 4. Filament of the straight form of *Nodularia litorea* showing spaced heterocysts. Fig. 5. Filament of the coiled form of *Nodularia spumigena*. Fig. 6. Colony of the coiled form of *Nodularia spumigena*. Scale bars represent 200 μm in Figs 2 and 6, and 20 μm in Figs 1, 3 and 5 (Fig. 4 is the same magnification as Fig. 5).

Critical pressure of the gas vesicles

The critical pressure distributions of mixed populations of *Aphanizomen* and *Nodularia* collected during August 1992, July 1993 and August 1994 from different sites showed wide variation (Table 1). The lowest mean apparent critical pressure (p_a) recorded was 0·34 ± 0·18 MPa for flocs of cyanobacteria floating in a loose surface scum in the Mecklenburg Bight (Fig. 7, curve a). The material had a pale-whitish coloration and contained some apparently senescent filaments.

Samples collected off the islands of Gotland and Bornholm had stronger gas vesicles, usually with a mean p_a of 0·79–0·97 MPa; excluding samples showing bimodal distributions (see below), the mean p_a was 0·86 ± 0·05 MPa (n = 37). The example shown in Fig. 7 (curve c) is for a sample, consisting mainly of *Aphanizomenon* with some *Nodularia*, that was used to investigate the relationship between buoyancy and gas vesicle content (see below, and Fig. 9); p_a was 0·90 ± 0·30 MPa.

Some of the critical pressure curves obtained with colonies of *Nodularia* were bimodal, suggesting two

Table 1. Mean critical pressures of gas vesicles in colonies of *Nodularia* sp. and *Aphanizomenon* sp. collected from the Baltic Sea in August 1992, July 1993 and August 1994

Research vessel	Date	Latitude N	Longitude E	Mean p_a or [p_c]/MPa	Median p_a or [p_c]/MPa	Replicate samples	Cyanobacterium
F.S. *Poseidon*	3 Aug 92	54°34′	11°14′	0·415	0·411	2	m
	3 Aug 92	54°25′	11°48′	0·344	0·333	3	(*Aph*)
	5 Aug 92	57°18′	19°46′	0·922	0·975	3	*Aph*
	6 Aug 92	57°20′	19°50′	0·793	0·825	1	(*Aph*)
	6 Aug 92	57°20′	19°50′	*0·606*	*0·467*	1	*Nod*
	6 Aug 92	57°20′	19°50′	0·793	0·900	1	*Aph*
	6 Aug 92	57°20′	19°50′	[0·903]	[0·955]	1	*Aph*
	6 Aug 92	57°20′	19°50′	*0·784*	*0·881*	2	m
	6 Aug 92	57°20′	19°50′	[0·853]	[0·934]	2	m
	7 Aug 92	57°21′	19°56′	0·868	0·960	1	m
	7 Aug 92	57°21′	19°56′	[0·907]	[0·968]	1	m
	7 Aug 92	57°21′	19°56′	0·839	0·918	1	m
	8 Aug 92	57°22′	19°57′	*0·706*	*0·784*	3	m
	8 Aug 92	57°22′	19°57′	0·801	0·870	3	m
	8 Aug 92	57°22′	19°57′	0·888	0·933	3	m
	9 Aug 92	55°53′	17°23′	0·912	0·979	2	*Aph*
	9 Aug 92	55°15′	15°59′	0·891	0·928	1	m
	9 Aug 92	55°15′	15°59′	0·883	0·938	2	(*Aph*)
	9 Aug 92	55°15′	15°59′	[0·903]	[0·931]	2	(*Aph*)
	10 Aug 92	55°13′	15°56′	0·842	0·873	2	m
	10 Aug 92	55°13′	15°56′	0·932	0·978	3	m
	11 Aug 92	55°11′	15°51′	0·907	0·946	2	m
F.S. *Alkor*	26 Jul 93	54°26′	12°14′	0·810	0·895	1	m
	26 Jul 93	54°42′	12°38′	0·831	0·917	1	m
	27 Jul 93	54°48′	13°18′	0·859	0·923	1	m
	27 Jul 93	54°48′	13°18′	0·831	0·884	1	*Nod*
	29 Jul 93	55°09′	15°41′	0·807	0·871	3	m
	30 Jul 93	55°09′	15°44′	0·969	1·005	2	*Aph*
	30 Jul 93	55°09′	15°44	[0·807]	[0·859]	2	*Aph*
	31 Jul 93	55°12′	15°45′	0·853	0·931	3	m
F.S. *Littorina*	6 Aug 94	59°15′	19°54′	0·869	0·930	3	(*Aph*)

Numbers in *italics* indicate bimodal distributions (excluded from statistical analysis).
Square brackets indicate p_c of cells suspended in 0·5–1·5 M sucrose.
Nod, selected *Nodularia* filaments; *Aph*, selected *Aphanizomenon* colonies; (*Aph*), mostly *Aphanizomenon*; m, mixed *Nodularia* and *Aphanizomenon*.

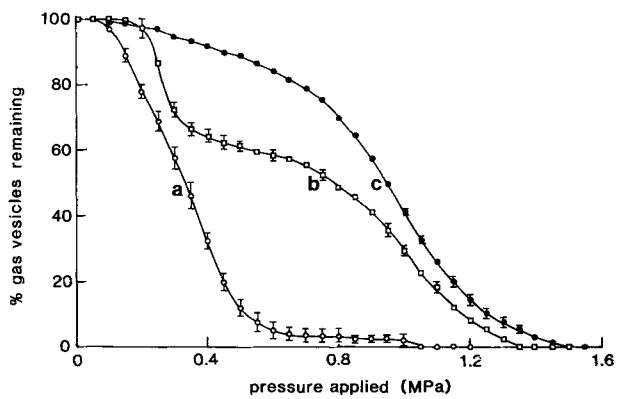


Fig. 7. Critical pressure distributions of gas vesicles in cyanobacteria: (*a*) in flocs of colonies from a surface waterbloom in the Mecklenburg Bight (open circles); (*b*) in a suspension of mixed *Nodularia* colonies (open squares); (*c*) in mixed cyanobacteria from a net tow in the Baltic Sea northeast of Bornholm (filled circles). Points shown are the means and standard deviations of three measurements.

populations of gas vesicles with mean p_a values of about 0·3 MPa and 1·0 MPa (Fig. 7, curve b). In one such sample removal of the bleached tangles of filaments resulted in a reduction in the proportion of the weaker gas vesicles. In August 1994, a year in which the surface water temperature was above 20 °C, much of the *Nodularia* was in a bleached condition and the critical pressure distributions were strongly bimodal.

To determine whether the differences in critical pressure were associated with particular genera or species rather than regional populations, further measurements were made on samples of single colony types picked out by syringe. Suspensions of about 100 homogenised *Aphanizomenon* colonies gave curves almost identical with Fig. 7 (curve c), with a p_a of 0·91 ± 0·32 MPa. The critical pressure distributions were similar in *Aphanizomenon* colonies picked from samples taken east of Gotland Island in 1992 (p_a = 0·91 MPa) and east of Bornholm in 1993 (p_a = 0.97 MPa) and there was no evidence of populations of this cyanobacterium with much weaker gas vesicles.

Samples of *Nodularia spumigena* colonies indicated two types of gas vesicles. In August 1992, colonies in the

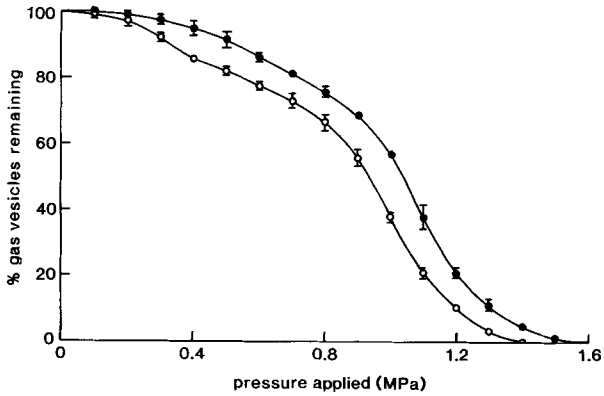


Fig. 8. Critical pressure distributions of gas vesicles in cyanobacteria suspended in seawater (open circles) and seawater containing 1·5 M sucrose (filled circles) to remove turgor pressure.

shallower water of the Arkona Sea has gas vesicles with a low mean critical pressure (p_a = 0·34 MPa) like that shown in Fig. 7 (curve a); those east of Bornholm in 1993 had stronger gas vesicles (p_a = 0·83 MPa). Bimodal curves (e.g. Fig. 7, curve b) were also obtained with *Nodularia* colonies from water samples in the Gotland sea.

Critical pressure determinations were also made on cultures of *Nodularia* spp., strains 279, 282, 297, 306, 307 and 311, from the Biological Station, Hiddensee, Culture Collection (E. M. Arndt University of Greifswald), established by Dr M. Hübel from seawater samples collected near the islands of Hiddensee and Rügen (Komàrek *et al.*, 1993). All these organisms possessed rather weak gas vesicles; for the six strains the mean value of p_a was 0·34 ± 0·04 MPa.

Turgor pressure

In a mixed sample of cyanobacteria from east of Bornholm, the mean critical pressures increased with the addition of sucrose from 0·85 MPa to 0·98 MPa. The highest value, found in 1·5 M sucrose (Fig. 8), indicated an average turgor pressure of 0·13 MPa in these samples. Previous analyses on filaments from *Aphanizomenon* colonies suspended in lower concentrations of sucrose (0·5 M) indicated turgor pressures of 0·08 MPa. In the six cultured strains of *Nodularia* spp., p_c, determined with the filaments suspended in 0·5 M sucrose, was 0·52 ± 0·04 MPa. The difference between p_c and p_a indicated a turgor pressure p_t = 0·18 ± 0·05 MPa, a little higher than in the material from the sea.

Buoyancy state of cyanobacteria

The majority of the colonies and filaments collected in the net tows from the top 10 m of the water column in the drift-station northeast of Bornholm were positively buoyant. In the sedimentation chambers 93% of the *Aphanizomenon* colonies (n = 260) and 95% of the straight *Nodularia* filaments (n = 57) floated. Only 67% of the coiled *Nodularia* filaments (n = 86) floated, but many of those that sank were entangled with long-spined cells of *Chaetoceros* sp., and other sedimenting organisms.

Buoyancy in relation to gas vesicle content

Application of a pressure of 1·6 MPa caused all floating cyanobacteria to sink, confirming that their buoyancy was solely due to their gas vesicle content. The pressures required to cause 50% of the cyanobacteria to sink were 0·91 MPa for *Aphanizomenon*, 0·94 MPa for the coiled *Nodularia*, and 0·88 MPa for the straight *Nodularia* filaments (Fig. 9).

The proportion of gas vesicles collapsed in a series of pressure steps in a mixed population of cyanobacteria (Fig. 7, curve c) was compared with the proportion of the filaments floating after each increment (Fig. 9*b*). It does

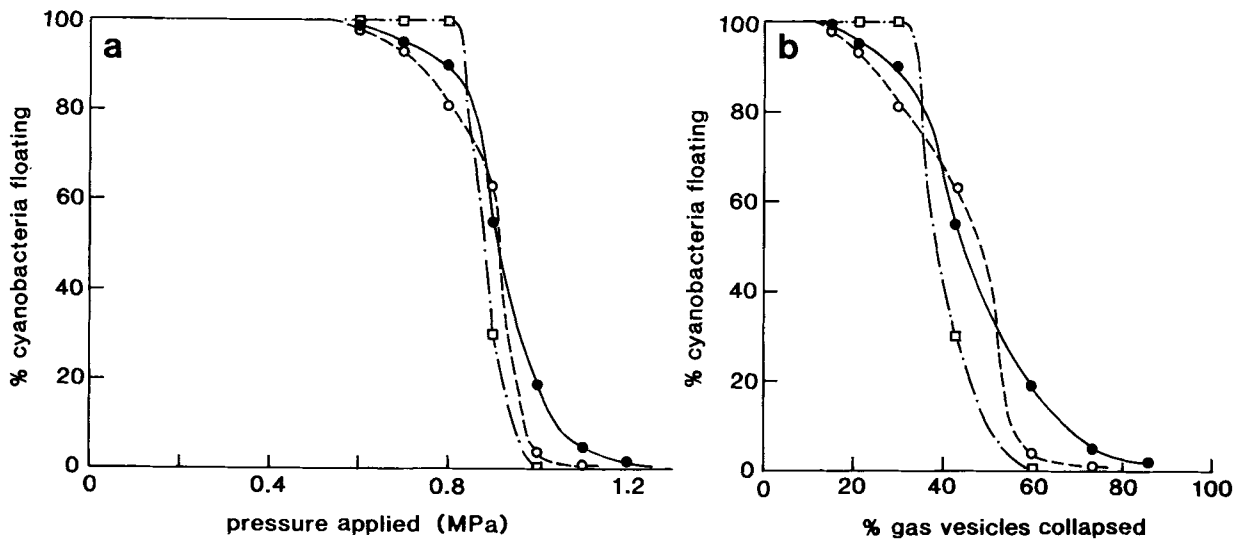


Fig. 9. (*a*) The buoyancy state of cyanobacteria after application of different pressures: filled circles, *Aphanizomenon flos-aquae*; open squares, straight *Nodularia litorea* filaments; open circles, coiled *Nodularia spumigena* filaments. (*b*) The same data on buoyancy state related to the proportion of gas vesicles collapsed in the mixed population of cyanobacteria, calculated from curve (c) in Fig. 7.

not necessarily follow that the proportion of gas vesicles lost was the same in each of the cyanobacteria, though comparison of the three curves in Fig. 9*a* supports the conclusion that the critical pressure distributions of gas vesicles in the three cyanobacteria were broadly similar.

Floating velocities of the cyanobacteria

For seven colonies of *Aphanizomenon* from surface-bucket samples taken from a calm sea containing a patchy surface waterbloom, the mean floating velocity (U_f) was 27 ± 4 m per day. For 14 colonies from 0–10 m net tows in the Gotland sea U_f was 20 ± 15 m per day. For a further 25 colonies from 0–10 m net tows from the sea near Bornholm, U_f was 21 ± 13 m per day. Hence the overall mean for the 46 *Aphanizomenon* colonies was 22 ± 13 m per day. Similar measurements made for 20 colonies of the coiled *Nodularia* gave a U_f of 36 ± 16 m per day.

These measurements, on colonies of various sizes, were made to determine whether the flotation velocities were high enough to affect the distribution of colonies under calm conditions (see below). No attempt was made to relate flotation velocity to the range of colony size present.

Vertical distribution of the cyanobacteria in the water column

Vertical profiles revealed a steep thermocline at 20–25 m between the surface at 17–19 °C and the deeper water at 6–7 °C, at all the sampling stations during the 1992 cruise. Within the surface layer shallow temperature gradients developed during times of relative calm. At the drift-station the salinity of the water above the thermocline remained constant at 8·7‰; the density of the water and stability of the water column were therefore determined solely by variations in temperature. The similarities of surface water salinity (Fig. 10*a–c*) indicate that the same water mass was followed at the drift station.

The concentrations of the cyanobacterial colonies were negligible at depths below 30 m, e.g. four *Aphanizomenon* colonies in 40 l of water from a depth of 50 m (0·1 colonies l^{-1} compared with between 2 and 72 l^{-1} above the thermocline). In seven depth profiles, the highest concentrations were always within the top 10 m of the water column.

A series of profiles made at the Bornholm drift-station showed that the vertical distribution of colonies was influenced by their flotation and by vertical mixing. At 1800 hours on 9 August a difference of only 0·3 °C between the surface and 15 m indicated there had been mixing to this depth. The next 24 h were calm (Beaufort 1–3); the depth of the surface mixed layer decreased to 7 m at 0800 hours next morning (Fig. 10*a*) and to 1 m by 1330 hours (Fig. 10*b*), indicating a stable water column. The profile of colony concentration indicated that the population had floated upwards, with the highest

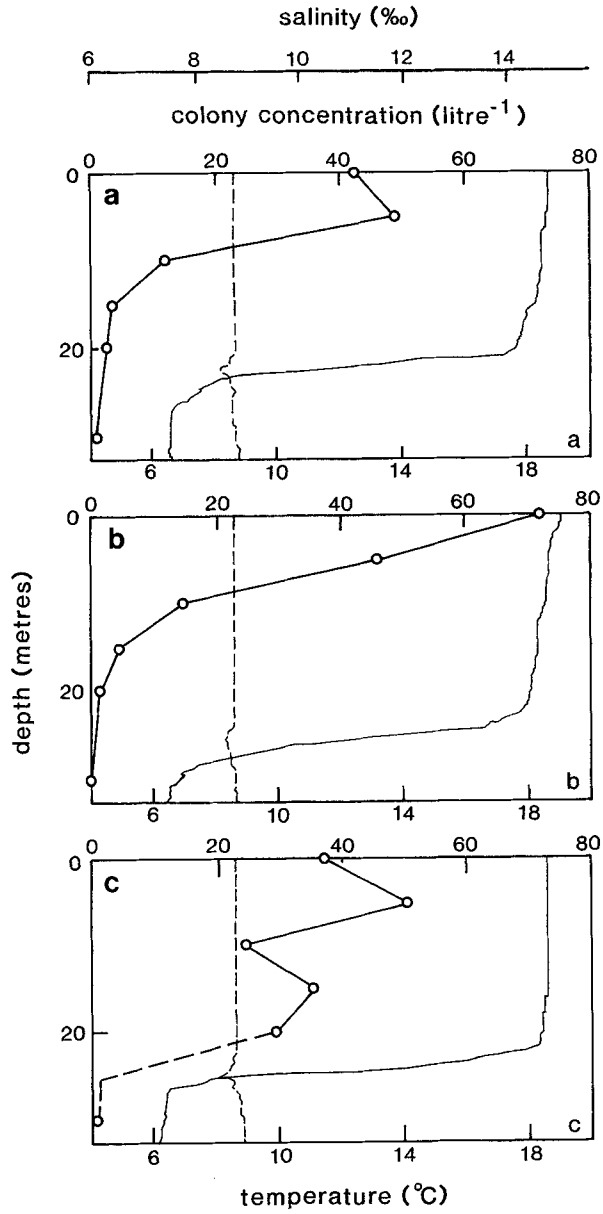


Fig. 10. Vertical profiles of *Aphanizomenon* colony concentration (open circles), temperature (continuous lines) and salinity (broken lines) in the Baltic Sea north-east of Bornholm Island (55°13′ N, 15°56′ E) at (*a*) 0800 hours (*b*) 1330 hours on 10 August, and (*c*) 1000 hours on 11 August 1992.

concentration, 72 colonies l^{-1}, near the surface (Fig. 10*b*). The wind speed rose from Beaufort 1 at 2000 hours to 7 at 2300 hours and remained at between 4 and 6 until the following day. At 1000 hours on 11 August the water temperature was uniform down to 20 m and the profile showed that the colony population had been mixed down to this depth (Fig. 10*c*).

Comparison of the colony concentration profiles in Fig. 10*a* and 10*b* indicates that some of the population had moved up by about 5 m in the 5·5 h between the time of these two samples. This suggests a net upward velocity of 22 m per day, which is the same as the mean floating velocity of the *Aphanizomenon* colonies (see above). The upward movement of the population can therefore be accounted for by flotation.

Discussion

Critical pressure of the gas vesicles in relation to depth of the Baltic Sea

A survey of planktonic cyanobacteria in various habitats suggests that the gas vesicles present are usually no stronger than is required to withstand the maximum pressures they experience (Walsby, 1994). This trend seems to hold for gas vesicles in the Baltic cyanobacteria.

Cyanobacteria in water samples from the shallow water of the Arkona Sea and Mecklenburg Bight had gas vesicles with a median p_a of 0·37 MPa, and a similar value, $p_a = 0{\cdot}34$, was found for cultures of *Nodularia* taken by M. Hübel from coastal waters around Hiddensee and Rügen. A majority of the cyanobacteria retained their buoyancy with 50% of gas vesicles collapsed (Fig. 9). This indicates that these organisms from coastal waters would remain buoyant after mixing to depths of 30 m.

Gas vesicles in *Aphanizomenon*, *Anabaena* and *Nodularia* from the major basin of the Baltic Sea, however, showed a much greater median p_a of 0·78–1·01 MPa. Over half the gas vesicles in the cyanobacteria investigated withstood a pressure exceeding 0·9 MPa (Table 1), which is the hydrostatic pressure developed by a water column of 90 m depth. This greatly exceeds the depth above which 99% of the summer population of cyanobacteria are found, i.e. the depth of the thermocline at about 25 m.

Although the population of planktonic cyanobacteria reaches its maximum during the summer months when the water is thermally stratified, it must develop from an inoculum that survives over winter, either suspended in the water column or on the shallower parts of the sea bottom. The upper 60–90 m or so of the Baltic basin turns over in the winter. Below the halocline at 60–90 m is a layer of more saline water (Kullenberg, 1981) which does not usually mix with the overlying layers. For much of the period from winter to early spring the planktonic cyanobacteria will circulate down to the depths of the halocline, but not deeper. It would appear, therefore, that the considerable strength of the gas vesicles in these organisms is an adaptation for maintaining buoyancy through the winter period of circulation. A similar argument has been used to explain the occurrence of strong gas vesicles in species of *Oscillatoria* from deep Norwegian lakes (Walsby *et al.*, 1983*a*).

Some species of both *Aphanizomenon* and *Nodularia* produce akinetes (Rippka *et al.*, 1979). During their differentiation the akinetes of gas-vacuolate species lose their gas vesicles and sink to the bottom sediments, where they may overwinter (but see Livingstone & Jaworski, 1980; Rother & Fay, 1977). The filaments that germinate from the akinetes must form new gas vesicles in order to regain buoyancy; they can do this only if sufficient gas vesicles withstand the pressures generated by the overlying water column.

Effect of buoyancy on vertical distribution

The buoyancy provided by gas vesicles in the cyanobacteria of the Baltic Sea enables colonies of these organisms to float upwards at velocities of about 20 m per day relative to the water mass. Even in light winds this velocity is likely to be exceeded by the vertical shear velocity (u_*) in the surface mixed layer of the water column. The shear velocity can be calculated from the equation

$$u_*^2 = (\rho_a/\rho)C_d U_w^2$$

where ρ_a is the density of air ($1{\cdot}2\ \mathrm{kg\,m^{-3}}$), ρ is the density of the Baltic seawater ($1005\ \mathrm{kg\,m^{-3}}$), C_d is the neutral drag coefficient ($1{\cdot}3 \times 10^{-3}$) and U_w is the wind speed (Spigel & Imberger, 1987). It can be calculated that u_* exceeds the mean floating velocity of the cyanobacterial colonies ($0{\cdot}23 \times 10^{-3}\ \mathrm{m\,s^{-1}}$) when the wind speed exceeds $0{\cdot}21\ \mathrm{m\,s^{-1}}$, and that u_* exceeds the velocity of the fastest floating colonies ($0{\cdot}7\ \mathrm{m\,s^{-1}}$) at wind speeds greater than $0{\cdot}63\ \mathrm{m\,s^{-1}}$ (cf. 0·3–1·5 $\mathrm{m\,s^{-1}}$ at Beaufort 1). This explains why surface waterblooms do not form unless the water column is stabilised by thermal density gradients that reach very close to the water surface.

In very windy conditions the water column became mixed down to the region of the seasonal thermocline and the colonies were dispersed throughout the water above the thermocline (Fig. 10). Buoyancy would still have been of value in preventing colonies from sinking through the thermocline. It would therefore have guaranteed a longer residence time within surface waters. During this investigation the depth of the mixed layer (z_m = 20–23 m) did not greatly exceed the depth of the euphotic zone (z_{eu} = 15 m) and colonies circulating within the mixed layer would therefore have exhibited net primary production (Reynolds, 1984).

During calm conditions (Beaufort 1–2) the decrease in the depth of the surface mixed layer would have enabled the cyanobacteria to float up and become concentrated further up the vertical light gradient (Humphries & Lyne, 1988). This would have provided an advantage not obtained by phytoplankton that remained in suspension by having low sedimentation velocities (Ibelings *et al.*, 1991). The faster the cyanobacteria float up the closer they will approach the water surface and the more time they will spend in the euphotic zone (Reynolds & Walsby, 1975). Since the speed of flotation increases with the square of radius (Stokes's equation) there will be selection for cyanobacteria with large filaments (the straight *Nodularia litorea* filaments) or those that aggregate in colonies (formed by the coiled *Nodularia* filaments and by *Aphanizomenon*). Large size and colonial habit hold disadvantages for nutrient uptake and light absorption (Raven, 1986; Fogg, 1991); these must therefore be outweighed by advantages provided by buoyancy discussed here.

We suggest that the buoyancy provided by gas vesicles is advantageous to the planktonic cyanobacteria of the Baltic in two respects. The first is that it enables

those which have survived the winter to float up into the surface waters when the seasonal thermocline is established in the spring; it is now necessary to obtain information on the vertical distribution of these organisms throughout the annual cycle. The second is that it enables the cyanobacteria to move up the vertical light gradient during periods of calm throughout the summer season. A quantitative assessment of the advantage this provides can be made by calculating the extra amount of light the cyanobacteria would intercept by successive migrations to the water surface.

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