RESEARCH ARTICLE

Temperature regulation of gliding motility in filamentous sulfur bacteria, *Beggiatoa* spp.

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Abstract

The response of gliding motility to changing temperatures was studied in filaments of the large sulfur bacteria *Beggiatoa* from arctic, temperate and tropical marine environments. The general shape of the gliding speed vs. temperature curves from all three locations was similar, but differed in the maximal gliding speed of the filaments, optimum temperature and the temperature range of motility. The optimum temperature and the overall temperature range of gliding motility accorded to the climatic origin of the filaments with a high temperature range for tropical, an intermediate range for temperate, and a low temperature range for arctic filaments. The temperature-controlled decrease in gliding speed at low temperatures was reversible while the decline in speed at high temperatures was due to irreversible thermal damage in individual filaments. Filaments from the Arctic and cold-acclimatized filaments from the temperate zone were unaffected by transient freezing of the surrounding seawater. At *in situ* temperatures, filaments glided at 17–55% of the gliding speed at the optimum temperatures, indicating that they were well adapted to the temperature regime of their origin. Our results point towards an enzymatic control of temperature-dependent gliding motility.

Introduction

Gliding motility is a characteristic property of filamentous sulfur bacteria of the genus *Beggiatoa*. *Beggiatoa* are widespread in sediments with steep concentration gradients of oxygen and sulfide. The gradients either overlap (Jørgensen & Revsbech, 1983) or are separated by a suboxic zone of varying depth (Sayama *et al*., 2005; Preisler *et al*., 2007). *Beggiatoa* are typically found at low concentrations of oxygen and sulfide, both of which provide stimuli for a negative chemosensory response (Møller *et al*., 1985; Nelson *et al*., 1986; Kamp *et al*., 2006; Preisler *et al*., 2007). The necessity to constantly reorient according to alterations in the chemical cues or to shuttle in the suboxic zone between the sulfide front and the oxic water column renders motility a crucial function in the ecology of *Beggiatoa*.

Beggiatoa filaments rotate around the long axis when gliding (Møller *et al*., 1985; Larkin & Henk, 1996), similar to members of the cyanobacterial family *Oscillatoriaceae* (Hoiczyk, 2000). The mechanism of gliding motility in *Beggiatoa* involves pores on the cell surface through which exopolymeric slime is extruded, which forms a mucilaginous trail as the filament proceeds (Larkin & Strohl, 1983; Larkin & Henk, 1996). A nozzle-like organelle through which the slime is extruded seems to be a general feature involved in the motility in gliding cyanobacteria (Hoiczyk & Baumeister, 1998) and in a variety of phylogenetically unrelated organisms (Pate & Chang, 1979; Wolgemuth *et al*., 2002; Robinson *et al*., 2007). It is not known whether the nozzle-like organelle is also present in *Beggiatoa*, but because cyanobacteria and *Beggiatoa* share many structural genes (Mussmann *et al*., 2007), it is likely that they glide by a similar mechanism. The propulsive force that drives the cells forward results from a combination of physicochemical factors and exopolymer production (Wolgemuth *et al*., 2002). Enzymatic reactions are necessary to produce the exopolymeric slime and to ultimately energize motility. Enzyme kinetics are highly temperature dependent (Russell, 1990; Somero, 1995; Feller & Gerday, 1997; Nedwell, 1999), and therefore the speed of gliding motility is a function of temperature (Crozier & Stier, 1926).

Biological temperature-dependent processes, such as growth, are generally described by cardinal temperatures. The optimum temperature (T_{opt}) is the temperature of the

maximum rate, while the minimum temperature and the maximum temperature (T_{max}) are the lowest and the highest temperatures, respectively, where activity is still detected. T_{opt} for growth is generally below T_{opt} for respiration or other energy-generating activities. T_{opt} for activities other than growth is commonly far from optimal for the organisms that then are on the verge of thermal damage, as evident from the steep decline in activity just above T_{opt}.

The effect of temperature on the metabolism and growth of microorganisms in the environment has been studied extensively (Thamdrup & Fleischer, 1998; Knoblauch & Jørgensen, 1999; Rysgaard *et al.*, 2004). These studies show that active organisms are adapted to the *in situ* temperature regime. Because of the slow growth of environmental organisms the adaptation does, however, not necessarily track seasonal temperature variations (Robador *et al.*, 2009). Temperature is an important characteristic of the microbial environment and some motile organisms have even been shown to orient in a thermal gradient by a thermotacic response (Maeda *et al.*, 1976; Paster & Ryu, 2008), but the regulation of microbial motility by temperature has widely been ignored. Few studies exist on the temperature dependence of motility of microorganisms and especially of gliding motility (Crozier & Federighi, 1924; Crozier & Stier, 1926; Halfen & Castenholz, 1971; Ridgway & Lewin, 1988). In our study, we compare the temperature-dependent gliding motility of *Beggiatoa* filaments from arctic, temperate and tropical marine environments. The aim of this study was to assess how gliding speed changes with temperature, and how the motility of filaments from the different climatic zones is adapted to the *in situ* temperature ($T_{in\ situ}$).

Materials and methods

All filament types used for this study had the typical morphology described for *Beggiatoa* (Teske & Nelson, 2006). They were colorless filamentous organisms with cylindrical cells and highly refracting sulfur globules in the cells (Supporting Information, Fig. S1a–c). All filaments moved by gliding and were visible to the naked eye.

Tropical filaments

The tropical *Beggiatoa* used for this study belong to the microbial consortium associated with the black-band disease of corals in the Florida Keys (Richardson, 1996). Water temperature at 15 m depth in the Florida Keys varies between 18 °C in winter and 32 °C in summer (Hudson & Anderson, 2007). The clonal culture originated from the laboratory of Douglas C. Nelson, where it was isolated as follows (D.C. Nelson, pers. commun.): single filaments of 6.3 μm diameter were isolated by allowing these to glide and spread on sterile agar plates and by repeated passages of single filaments to fresh agar plates (Nelson & Castenholz, 1981; Nelson *et al.*, 1982). After isolation, the culture was maintained in culture tubes with opposing gradients of oxygen and sulfide at room temperature (Nelson & Jannasch, 1983). The culture was used for various ecophysiological studies (Kamp *et al.*, 2008).

Temperate filaments

Temperate sediment was sampled in Knebel Vig (56°12.9′N, 10°27.9′E), a cove at the northern part of Aarhus Bay, Denmark (Troelsen & Jørgensen, 1982). Box cores were taken in April 2006 from 11 m water depth at 5.4 °C water temperature and transported to the laboratory. The sediment was carefully placed in a laboratory flume of 3 m length and 0.3 m width without disturbing the layering and kept in darkness. Seawater of *in situ* salinity (25‰), oxygen concentration (50% air saturation) and temperature (13 °C) circulated in the flume at a flow velocity of 1–2 cm s^{-1}. For the cold acclimatization of these temperate *Beggiatoa*, an intact box core from Knebel Vig was stored at 4 °C in the dark, covered with seawater. It was inoculated with tufts of filaments from the flume. The filaments were allowed to acclimatize and grow for 2 months before the experiment. The bottom water temperature in Aarhus Bay during the year of sampling ranged from 3 °C in February to 16 °C in August (Dale *et al.*, 2008). Cultivation of filaments at 13 °C represented the summer conditions, while cultivation at 4 °C adapted them to winter conditions. The *Beggiatoa* filament widths ranged from 5 to 35 μm. For gliding speed measurements, 20–25 μm wide filaments were used.

Arctic filaments

Arctic sediment was collected in August 2008 in the small lagoon of Ymerbukta (78°16.8′N, 14°03′E) on the west coast of Spitsbergen, one of the main islands of the Svalbard archipelago. The temperature of both the water and the surface sediment was 6.5 °C. Sediment cores of 80 mm diameter were sampled by hand from spots with partial white *Beggiatoa* coverage from 30 cm water depth. The cores were stored at 2–5 °C for 4 days before the measurement of gliding speed. The filaments were of two size classes of 2 μm and 8–10 μm diameter. The latter were used for gliding speed measurements.

Measurements of gliding speed

Gliding speed was observed in a custom-made, thermostat-controlled polycarbonate chamber (Fig. 1) placed under a light microscope (Zeiss Axioskop). The chamber had two compartments separated by a glass slide. The upper compartment was made by a metal spacer cut out in the center. It had a capacity of 2 mL and was filled with sea water and

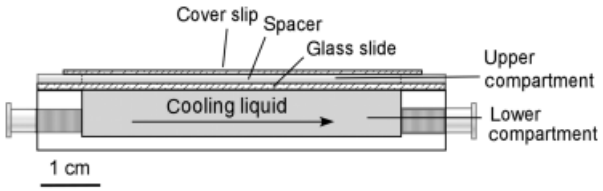

Fig. 1. Longitudinal section of the microscope chamber that provided defined temperatures during gliding speed recordings with *Beggiatoa*.

Beggiatoa filaments. Water of the desired temperature mixed with antifreeze fluid circulated through the lower compartment. Before each experiment, the water temperature in the upper compartment was measured at each temperature increment used in the experiment by inserting a thermocouple temperature sensor (NiCr-Ni, diameter 1 mm, Thermocoax, France). The small volume of the upper compartment and the continuous flushing of the lower compartment ensured fast heat exchange between the compartments.

For the experiments, the temperature was varied in 2–3 °C increments, starting at 20 °C for filaments from the tropics and from Aarhus Bay and 2–4 °C for arctic and cold-acclimatized filaments from Aarhus Bay. The gliding speed of the filaments at each temperature ($n = 1$–64) was recorded either by (1) simultaneous observation of the filaments through the microscope, timing of the speed with a stop watch and measuring the gliding distance using a calibrated ocular micrometer or (2) analyzing sequences of images taken by an attached digital camera (Canon Power Shot A 620) using an image analysis software (IMAGE J, National Institutes of Health). Measurements proceeded until the filaments stopped moving at each end of their temperature range or until the water in the chamber froze. After the filaments stopped, the temperature was reduced again from the high end or raised again from the low end to test whether the immobilization was reversible.

Arrhenius plots and Q_{10}

Activation energies (E_a) and temperature coefficients (Q_{10}) serve as indicators for the temperature response of biological processes. Here, the Q_{10} value is the factor by which the gliding speed increases when the temperature is increased by 10 °C. The activation energy can be calculated from the slope of the logarithmic form of the Arrhenius function

$$\ln \nu = \ln A - E_a/RT$$

where ν is the process rate or the speed, A is a constant, E_a is the activation energy, R the gas constant (8.31 kJ mol^{-1}) and T the absolute temperature (K). For each experiment, Arrhenius plots of $\ln(\nu)$ as a function of T^{-1} (K) were calculated. The slope of each Arrhenius plot (E_a/R) was determined from which E_a was calculated. The linear range of the slope was found by first calculating a linear regression and then omitting data points from the cold and warm extremes until the fit of the line had an R^2 value of ≥ 0.93.

Q_{10} values were calculated using the following equation:

$$Q_{10} = e^{E_a(T_2-T_1)/RT_1T_2}$$

where T_1 is the lower temperature and T_2 is T_1+10. Hence, in the linear range, Q_{10} values change slightly according to the temperature interval for which they were calculated, decreasing at high-temperature intervals.

Results

Gliding speed

There was no correlation between gliding speed and filament diameter. The wide temperate *Beggiatoa* glided at a maximum speed of 5.6 ± 0.6 and 6.0 ± 0.6 µm s^{-1} for filaments grown at 4 and 13 °C, respectively (Fig. 2b and c). The narrower arctic filaments glided much slower at 1.6 ± 0.2 µm s^{-1} at T_{opt} (Fig. 2d), but the yet narrower tropical filaments at 6.1 ± 0.6 µm s^{-1} (Fig. 2a) were as fast as the wide temperate filaments.

At 5 °C and below, the arctic *Beggiatoa* glided almost as fast as the cold-acclimatized temperate filaments despite the lower maximal gliding speed at T_{opt} (Fig. S2). Hence, in the temperature range from 5 to −5 °C, gliding speed relative to the maximal speed was higher in arctic filaments than in cold-acclimatized temperate filaments. Below 6 °C, arctic filaments glided faster than the wider temperate filaments grown at 13 °C (Fig. S2).

Characteristics of the gliding speed–temperature relation

The shapes of the curves of the relation between temperature and gliding speed were similar for all filaments (Fig. 2a–d). They showed an increase in gliding speed with temperature until a maximum speed at T_{opt}, and just above T_{opt}, a sharp decline to T_{max}. This temperature-dependent response is familiar from other biologically catalyzed processes where T_{opt} is usually close to the T_{max} at which all activity comes to a halt.

The activity range occurred at the relatively highest temperatures for tropical filaments, intermediate temperatures for temperate filaments and coldest temperatures for arctic filaments. Arctic filaments had the narrowest temperature range for gliding while temperate Aarhus Bay filaments had the widest (shaded bars in Fig. 3). Cold acclimatization of Aarhus Bay filaments extended their temperature range of gliding by 7 °C towards lower temperatures relative to the nonacclimatized filaments, without affecting the T_{opt} or the T_{max}.

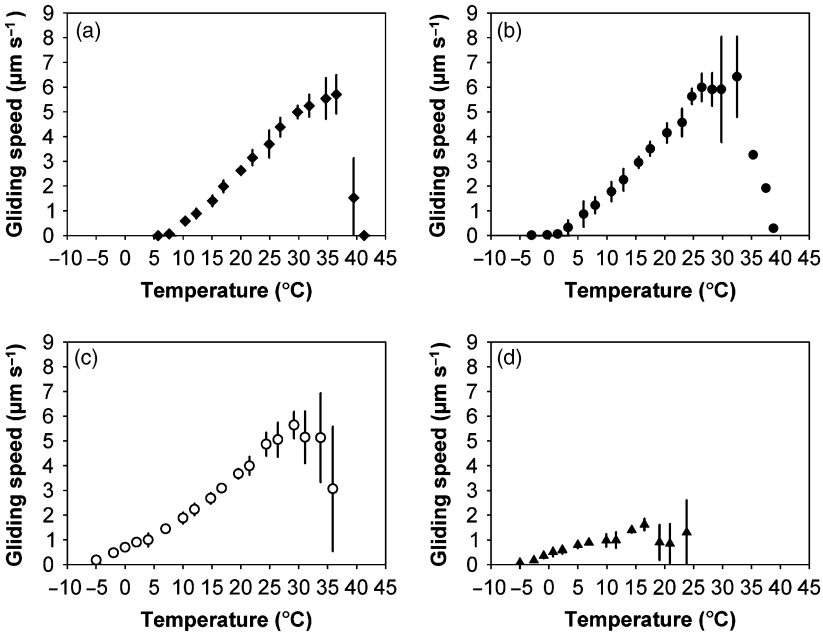

Fig. 2. Gliding speeds of *Beggiatoa* at different temperatures. Tropical filaments from the black-band coral disease grown at 20 °C (a), from a temperate environment, Aarhus Bay, grown at 13 °C (b), cold-acclimatized filaments from Aarhus Bay grown at 4 °C (c) and arctic filaments from Ymerbukta, Svalbard, growing at 6 °C (d). The vertical bars show the SDs.

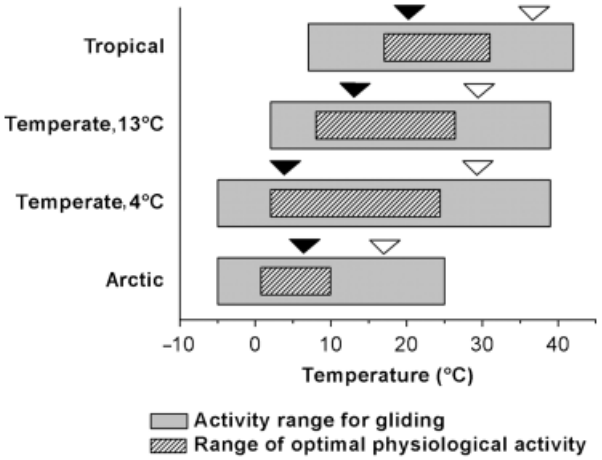

Fig. 3. Activity ranges of gliding motility in *Beggiatoa* filaments from different climatic origins. Filled triangles indicate the temperature, $T_{in\ situ}$, at which the *Beggiatoa* were growing; open triangles indicate T_{opt}. The shaded bars indicate the maximal range of gliding motility; the hatched bars indicate the range of optimal physiological activity. $T_{in\ situ}$ is always within the range of optimal physiological activity and T_{opt} is always outside of it.

The T_{opt} correlated with the climatic origin of the filaments. Tropical filaments exhibited the highest T_{opt} of 37 °C, temperate filaments an intermediate T_{opt} of 30 °C and arctic filaments a low T_{opt} of 17 °C (Fig. 2, open arrows in Fig. 3). According to the classification into thermal groups, which is actually based on growth (Morita, 1975), tropical and temperate filaments were mesophilic, cold-acclimatized temperate filaments showed a psychrotolerant response and arctic filaments were psychrophilic. In filaments from all tested locations, the T_{opt} for gliding was above the $T_{in\ situ}$. Yet, the gliding motility of the filaments from the respective origins was well adjusted to the prevailing $T_{in\ situ}$ despite the slower gliding speed at $T_{in\ situ}$ than at T_{opt}. At their $T_{in\ situ}$, arctic filaments reached 55% of the gliding speed observed at T_{opt}. At the minimum temperature for gliding at -5 °C they still maintained 11% of the gliding speed at T_{opt}. For temperate filaments grown at 13 and 4 °C, the gliding speed at $T_{in\ situ}$ was 35% and 17% of the T_{opt}, respectively. Tropical filaments glided at $T_{in\ situ}$ with 46% of the speed at the T_{opt}. Similar observations have been made for temperature-dependent metabolic rates. Metabolic rates and growth rates at $T_{in\ situ}$ were commonly 10–40% of those measured at the T_{opt} (Arnosti *et al.*, 1998; Knoblauch & Jørgensen, 1999; Rysgaard *et al.*, 2004).

Temperature range of physiological adaptation

The range of optimal physiological activity is narrower than the overall range of gliding activity. To illustrate this, we calculated Arrhenius plots for each temperature–speed curve (Fig. 4a–d). In the Arrhenius plots, an exponential dependence in the temperature–speed curves results in a linear relationship. E_a can be calculated from this exponential dependence. An exponential variation of a reaction rate with $1/T$ is commonly observed in enzymatically catalyzed reactions (Arrhenius, 1908). At the extreme low and high ends of the temperature range, the speed decrease deviates from linearity. Provided that enzymatic reactions control the decline in gliding speed with decreasing temperatures, the

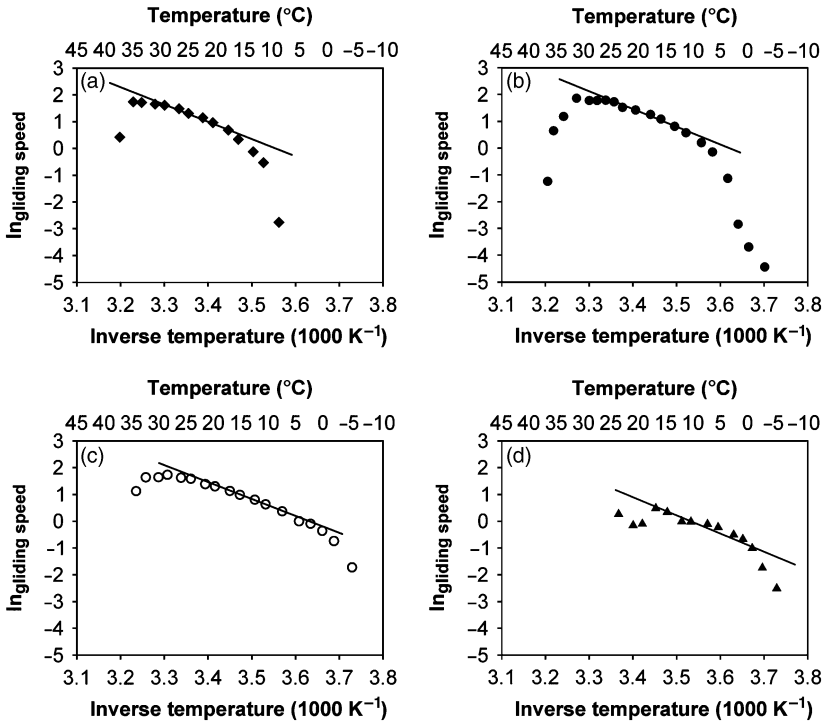

Fig. 4. Arrhenius plots of graphs in Fig. 2 that correspond to the *Beggiatoa* types (a)–(d).

temperature range with a constant and low E_a should be the temperature range to which the filaments are physiologically optimized (hatched bars in Fig. 3). Corresponding to the overall activity range of gliding, the temperature range in which the Arrhenius plot was linear was the narrowest for the arctic filaments (Figs 3 and 4d), indicating that they were physiologically optimized to a narrow range around $T_{in\ situ}$. The linear range for tropical filaments (Figs 3 and 4a) was slightly broader. Aarhus Bay filaments had the broadest range of optimal physiological activity (Figs 3 and 4b, c). Their optimal range was further shifted downward by cold adaptation. The range of optimal physiological activity always included $T_{in\ situ}$, but never T_{opt} (compare open triangles and hatched bars in Fig. 3). The $T_{in\ situ}$ that arctic filaments experience during winter is not known, but it is definitely $< -5\,^{\circ}C$. During the freezing period in winter, they might thus survive in an immobilized state.

Response to extreme temperatures and freezing

The reduction in speed at the low end of the temperature range occurred simultaneously in all individual filaments from each climatic origin as evident from the small error bars at the low end of the temperature range. The speed decrease with decreasing temperature at the low end of the temperature range was fully reversible in these experiments (Fig. S3). The arctic and the cold-acclimatized *Beggiatoa* community from Aarhus Bay were even unaffected by transient freezing of the surrounding seawater and still glided at $-5\,^{\circ}C$ in unfrozen water (Fig. 2c and d). Upon sudden freezing of the super-cooled water at $-5\,^{\circ}C$, the filaments immediately stopped gliding. Microscopic observation did not reveal whether the cytosol of the cells was also frozen. After thawing, the filaments did not show visible damage under the light microscope and they resumed gliding at their temperature-dependent speed unaffected by the previous freezing (Fig. S3a, b).

At the high end of the temperature range, above T_{opt}, an increasing number of cells in the individual filaments appeared damaged when observed under the microscope. Increasingly large error bars illustrate a variation in lethal temperature between filaments. The speed reduction above T_{opt} was irreversible in all filaments tested, indicating permanent cell damage.

Discussion

Temperature response and dependence of gliding motility

To evaluate the temperature response of the filaments from the different climatic origins, we analyzed the temperature range of optimal physiological adaptation. The steepness of the slope of the Arrhenius plots, as calculated from this range, is an indicator of the adaptedness to this temperature (Fig. 4). All filaments roughly doubled their gliding speed

when increasing the temperature by 10 °C (Table 1). The E_a value of 58 kJ mol^{-1} for Aarhus Bay filaments adapted to summer conditions was slightly higher that than for tropical, cold-acclimatized Aarhus Bay filaments and arctic filaments (49, 50 and 46 kJ mol^{-1}). The E_a value of tropical filaments was comparable to that of cold-acclimatized Aarhus Bay filaments.

Our results were similar to the Q_{10} and E_a values of enzymatic processes in other bacteria from cold climatic regions (Thamdrup & Fleischer, 1998; Knoblauch & Jørgensen, 1999; Rysgaard *et al*., 2004). Enzymatic processes from cold environments are often less temperature dependent than those from temperate or warm environments in that the reaction rates are not affected as strongly by changes in temperature (Somero, 1995; Feller & Gerday, 2003). This results from a lower reaction enthalpy $\Delta H^{\#}$ and thus low E_a and Q_{10} values in cold-adapted enzymes (Low *et al*., 1973; Lonhienne *et al*., 2000). Gliding motility in *Beggiatoa alba* and in an *Oscillatoria* strain also had a low E_a of 35 and 39 kJ mol^{-1}, respectively (Crozier & Federighi, 1924; Crozier & Stier, 1926, Table 1). Yet, it cannot be generalized that gliding motility is an activity of low temperature dependence. The E_a estimated for gliding motility in *Oscillatoria princeps* from a hot spring (Halfen & Castenholz, 1971) is, at 144 kJ mol^{-1}, much higher than in the other organisms, which is probably due to the constantly high temperature of the spring water.

A low E_a for gliding motility was also found in *Flexibacter polymorphus* (Ridgway & Lewin, 1988). The E_a for respiration is very similar to that of gliding motility (Table 1). The correlation between E_a values for gliding motility and for metabolic rates that energize motility points towards a direct relation between gliding motility and energy metabolism. In this case, the temperature-controlled gliding speed decrease at the cold end of the temperature range could be related to the increasingly slow kinetics of enzymatically catalyzed metabolic processes. This argument is further supported by the temperature-dependent gliding speed curves that had shapes similar to those often observed in temperature–metabolism curves. The E_a values were constant over a wide temperature range as apparent from the Arrhenius plots (Fig. 4a–d). Similar observations have been made for *B. alba* and *Oscillatoria* (Crozier & Federighi, 1924; Crozier & Stier, 1926).

Both these findings suggest that the speed of gliding depends on the rate of chemical (enzymatic) reactions rather than on physical factors such as the viscosity of the ambient medium or on the cell membrane fluidity and permeability of *Beggiatoa*. Additionally, the temperature response at the extreme ends of the temperature range points to an enzymatic speed control. Highly reversible cold denaturation, as observed for some globular proteins (Privalov, 1989), could have played a role in the reversibility of the gliding speed of the filaments. Impaired protein and membrane integrity due to high temperatures was probably the main reason why filaments stopped gliding at the high end of the temperature range. Thermally induced cell lysis cannot be stopped (Morita, 1975), which explains why the filaments did not resume motility when cooling down again after having exceeded the T_{max}.

Our hypothesis of an enzymatic control of gliding speed might be tested further by observation of filaments in media

Table 1. Upper part: temperature responses, *in situ* and optimum temperatures for filaments from the different climatic origins and the corresponding activation energies and Q_{10} values. Lower part: activation energies and Q_{10} values of gliding motilities and respiration of gliding bacteria. Temperature ranges for which Q_{10} values were calculated are in parentheses

Origin of filaments	*T* response of gliding speed	$T_{in\ situ}$ (°C)	T_{opt} (°C)	E_a (kJ mol^{-1})	Q_{10}	Sources
Tropical	Mesophilic	20	37	49	2.1 (19–29 °C)	This study
Temperate	Mesophilic	13	30	58	2.3 (12–22 °C)	This study
Temperate (cold acclimatized)	Mesophilic	4	30	50	2.1 (8–18 °C)	This study
Arctic	Psychrotolerant	6.5	17	46	2.0 (0–10 °C)	This study
Gliding motility of *Beggiatoa alba*	–	–	–	35.2	–	Crozier & Stier (1926)
Gliding motility of *Oscillatoria*	–	–	–	38.7	–	Crozier & Federighi (1924)
Gliding motility in *Oscillatoria princeps*	–	30–40	42	144*	–	Halfen & Castenholz (1971)
Gliding motility of *Flexibacter polymorphus*	–	–	35	61.13	2.06 (15–35 °C)	Ridgway & Lewin (1988)
Respiration of *Flexibacter polymorphus*	–	–	40	58.62	2.64 (15–35 °C)	Ridgway & Lewin (1988)

*E_a was calculated from the published plot.

of different viscosities but at the same temperature. Gliding speed in *O. princeps* and *F. polymorphus* was found to decrease with increasing viscosity of the medium, but showed a linear decrease instead of a curve with a skewed slope towards the maximal gliding speed as found for temperature-dependent gliding speed (Halfen & Castenholz, 1971). We would expect a similar result for viscosity-dependent gliding speed in *Beggiatoa* because of the structural similarities of the motility apparatus of filamentous cyanobacteria and *Beggiatoa* (Larkin & Strohl, 1983; Larkin & Henk, 1996; Mussmann *et al.*, 2007).

Adaptation potential in *Beggiatoa* from the temperate zone

After an acclimatization period of 2 months, the community of *Beggiatoa* from Aarhus Bay had expanded the low temperature range of gliding from $+1\,^{\circ}C$ to $< -5\,^{\circ}C$, i.e. to below the freezing point of seawater (Fig. 3). The range of optimal physiological activity was also extended towards lower temperatures so that the winter temperature of $3\,^{\circ}C$ was within the range of optimal physiological activity (longer linear range in the corresponding Arrhenius plot as compared with filaments from Aarhus Bay that were not cold acclimatized, Fig. 4b and c). T_{opt} and T_{max} were unaffected by the cold acclimatization (Figs 2c and 3).

The shift towards a more cold-adapted population could be due to either (1) a physiological acclimatization in individual filaments or (2) an undetected shift in the community composition from mesophilic to psychrotolerant forms (Sieburth, 1967; Thamdrup & Fleischer, 1998). There is a continuous range of filament diameters in natural *Beggiatoa* communities (Jørgensen, 1977), and each size class can contain multiple taxonomic units based on 16S rRNA gene phylogeny (Mussmann *et al.*, 2003). Thus, it is possible that cold- and warm-adapted species that cannot be distinguished in the microscope could coexist in temperate sediments. If the cold acclimatization was due to a gradual shift in species composition rather than a physiological adaptation, we would expect to see the gliding pattern of both the mesophilic and the psychrotolerant individuals at a low temperature in our experiments. However, all the filaments tested showed the same shift in temperature dependence as evident by the low statistical variance of the data. Additionally, it appears unlikely that a different community would have the same T_{opt} and T_{max} for gliding. Phylogenetic analyses would, however, be required to clarify this question.

Temperature response of a mixed community vs. a clonal culture

The arctic and the temperate filaments were from mixed samples with a variety of filament diameters and hence were presumably phylogenetically more diverse than the clonal tropical culture. Tropical filaments had the most sharply defined T_{opt} and showed less variance in gliding speed at the high end of the temperature range than temperate and arctic filaments (Fig. 2a). The T_{opt} of the tropical filaments was closest to the T_{max} for gliding of all tested filament types. We attribute this to the clonal nature of the tropical strain. However, the homogeneity of the speed vs. temperature curves of the temperate and arctic community, expressed in small error bars, comes close to that of the tropical strain. Thus, the temperature response of filaments of one size class from a natural community is surprisingly close to that of a single strain.

Conclusions

The motility of *Beggiatoa* communities is adapted to the prevailing temperatures in their habitat with distinct temperature responses for arctic, temperate and tropical populations. Temperate populations that experience high seasonal temperature fluctuations are able to adapt to the range encountered throughout the year. Our results suggest that temperature-dependent gliding speed is mainly enzymatically regulated. Therefore, *Beggiatoa* filaments can unequivocally be placed into thermal groups without the need to test the growth or the metabolic response to temperature. Our results show that a single size class from a specific habitat shows an equally homogeneous behavior towards temperature change as a clonal culture.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Light micrographs of (a) a tropical filament, (b) a filament from Aarhus Bay and (c) an arctic filament.
Fig. S2. Gliding speeds of *Beggiatoa* filaments from all climatic regions plotted with expanded scales between -5 and 15 °C.
Fig. S3. Reversible temperature control of gliding speed in (a) filaments from Aarhus Bay cultivated at 4 °C and (b) arctic filaments.

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