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A look at the effect of sequence complexity on pressure destabilisation of DNA polymers

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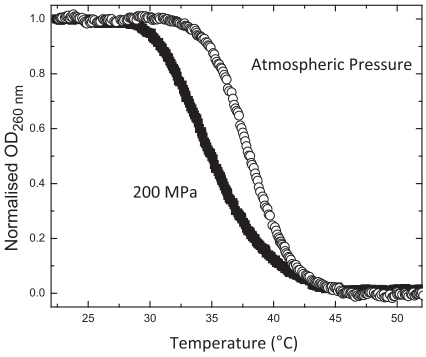
HIGHLIGHTS

- Under certain conditions synthetic nucleic polymers can be denatured with pressure.
- We show that the change of T_M of *Clostridium perfringes* DNA with pressure is negative.
- We were unable to induce a helix–coil transition *C. perfringes* DNA with pressure.
- The sequence complexity of this genomic DNA underlies its insensitivity to pressure.

GRAPHICAL ABSTRACT



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ABSTRACT

Our previous studies on the helix–coil transition of double-stranded DNA polymers have demonstrated that molar volume change (ΔV) accompanying the thermally-induced transition can be positive or negative depending on the experimental conditions, that the pressure-induced transition is more cooperative than the heat-induced transition [Rayan and Macgregor, *J Phys Chem B* **2005**, 109, 15558–15565], and that the pressure-induced transition does not occur in the absence of water [Rayan and Macgregor, *Biophys Chem*, **2009**, 144, 62–66]. Additionally, we have shown that ΔV values obtained by pressure-dependent techniques differ from those obtained by ambient pressure techniques such as PPC [Rayan et al. *J Phys Chem B* **2009**, 113, 1738–1742] thus shedding light on the effects of pressure on DNA polymers. Herein, we examine the effect of sequence complexity, and hence cooperativity on pressure destabilisation of DNA polymers. Working with *Clostridium perfringes* DNA under conditions such that the estimated ΔV of the helix–coil transition corresponds to −1.78 mL/mol (base pair) at atmospheric pressure, we do not observe the pressure-induced helix–coil transition of this DNA polymer, whereas synthetic copolymers poly[d(A-T)] and poly[d(I-C)] undergo cooperative pressure-induced transitions at similar ΔV values. We hypothesise that the reason for the lack of pressure-induced helix–coil transition of *C. perfringens* DNA under these experimental conditions lies in its sequence complexity.

1. Introduction

While the main aim of utilising elevated hydrostatic pressure is to gain additional information on the stability of the system being probed at atmospheric conditions, the fact that certain organisms can withstand

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pressures as high as 100 MPa (1 MPa = 10 bar = 9.678 atm) in the Mariana Trench (the deepest depression in the Pacific Ocean) makes this method particularly appealing to understanding the adaptations of those organisms to elevated pressures at the molecular level. A pioneering study conducted by Hedén, Lindahl, and Toplin [1] 50 years ago ushered in the era of investigation of high pressure effects on the stability of nucleic acids. This study, as well as most of the studies that followed [2–9] reported that elevated hydrostatic pressure led to the stabilisation of the helical from of DNA against the heat-induced transition, as witnessed by an increase in the melting temperature (T_M) of nucleic acids. With the exception of two studies, which showed that the molar volume change (ΔV) of the helix–coil transition of poly[r(A)]·poly[r(U)] (a synthetic double-stranded RNA homopolymer) can also be negative [10,11], the consensus was that pressure stabilises the helical state of DNA (hence a positive ΔV of the helix–coil transition). The temperature–pressure phase diagram for the helix–coil transition of double-stranded nucleic acids indicates that polymers with T_M values <~50 °C are destabilised by pressure (negative ΔV), while those polymers with T_M values >~50 °C are stabilised by pressure (positive ΔV) [12]. Consequently, the authors were able to perform the first pressure-induced helix–coil transition of a double-stranded nucleic acid polymer [12]. Following reviews summarise the studies on the effects of high pressure on the stability of DNA and other biopolymers [13–17].

We have shown that ΔV of the helix–coil transition of DNA polymers can be positive or negative, depending on the conditions, and that the pressure-induced and heat-induced transitions of DNA polymers appear to occur via different mechanisms, as the latter is more cooperative than the former [18]. As a follow-up to this study, we demonstrated that the pressure-induced helix–coil transition of DNA copolymers would not occur in the absence of water [19], much like the pressure-induced denaturation of proteins [20]. Furthermore, we have illustrated that ΔV values for the helix–coil transition of DNA as obtained from pressure-dependent studies are different than those obtained by methods that operate at nearly atmospheric conditions (such as pressure-perturbation calorimetry) thus providing additional insights into the effects of pressure on DNA polymers [21].

We would like to emphasise that the ΔV values are estimations obtained using the Clapeyron equation, which is applicable to reversible processes. Heat-induced denaturation of genomic DNA is not a reversible process, and consequently any thermodynamic parameter (such as ΔV or ΔH_{vH}) obtained using reversible thermodynamics is approximate. The fact that the dT_M/dP values are negative implies that the corresponding ΔVs are negative as well, and that elevated hydrostatic pressure should denature these polymers, as is the case with poly[d(A-T)] and poly[d(I-C)] under similar experimental conditions [18]. Here we report the first experimentally obtained negative ΔV for the helix-to-coil transition of genomic DNA (*Clostridium perfringes*). We chose this particular genomic DNA due to its low G-C content (28%), which renders it less stable than those biopolymers with a higher G-C content and consequently more amenable to studies exploring the pressure behaviour of low/negative ΔV (or dT_M/dP) values. Under the conditions used in these experiments, the ΔV equals −1.78 mL/mol (base pair), and the T_M is 38 °C at atmospheric pressure. Based on the sign and magnitude of the molar volume change, it is not unreasonable to expect this polymer to undergo a cooperative pressure-induced helix–coil transition. Indeed, we reported that synthetic DNA copolymers can undergo a pressure-induced helix–coil transition under the conditions where the magnitude of the negative volume change was less than the value of −1.78 mL/mol (base pair) obtained in this study [18]. We ascribe the inability of this genomic DNA to undergo the pressure-induced transition under these conditions to the greater sequence complexity of genomic DNA relative to that of the synthetic polymers poly[d(A-T)] and poly[d(I-C)]. We presume that this phenomenon arises because there are regions of the polymer that have sequences for which the dT_M/dP values are not negative, underscoring the role of the sequence complexity in the physical chemistry of DNA.

2. Materials and methods

2.1. Clostridium perfringes

DNA and sodium cacodylate trihydrate were purchased from Sigma-Aldrich Canada (Oakville, ON, Canada), while Na_2EDTA was obtained from Bio-Rad Laboratories (Hercules, CA). The DNA solution was dialysed 3× at 4 °C against an aqueous solution containing 1 mM sodium cacodylate and 0.1 mM Na_2EDTA, pH 6.7. The dialysis tubing with a molecular weight cut-off of 1000 Da was acquired from Genotech, Inc. (St. Louis, MO). The experimental DNA concentration was approximately 70 μM (base pair).

The melting experiments were performed using the temperature-regulated iso-hyperbaric spectrophotometer (TRIHBS), which has been described previously [22]. The sample is loaded into a 300-μL quartz cuvette that is placed in the optical high-pressure cell, which is positioned in the path of the spectrophotometer (Uvikon model 860). The spectrophotometer, the pressure pump and the thermometer are connected to a computer, enabling us to control absorption, pressure, and temperature in real time. The samples were heated at a rate of 0.1 °C/min and the helix–coil transition was monitored at 260 nm. Because the heat-induced denaturation of genomic DNA is irreversible a fresh DNA sample was used for each experiment. The measurements were performed in triplicate at constant pressures ranging from 5 to 200 MPa.

The observed helix–coil transition curves were analysed using the following equation:

$$\theta(T) = \frac{OD(T) - L(T)}{H(T) - L(T)}$$

where θ(T) corresponds to the fraction of polymer in the coil form at a temperature T, OD(T) is the optical density at temperature T, L(T) is the equation of the line for the low-temperature baseline, and H(T) is the equation of the line for the high-temperature baseline. When $\theta = 0$, the polymer is assumed to be in the native, double stranded state, while $\theta = 1$ signifies that the polymer is in the denatured, single-stranded state. The helix–coil transition temperature (T_M) is the temperature at which $\theta = 0.5$.

The model-dependent, van't Hoff enthalpy change (ΔH_{vH}) of the transition was calculated using the following equation and under the assumption that the helix–coil transition is a single-step, reversible, bimolecular transition: [8,23]

$$\Delta H_{vH} = 6RT_M^{\,2}(d\theta/dT)_{T=T_M}$$

where R is the gas constant and $d\theta/dT$ is the slope of a θ versus T curve at T_M [23]. As already mentioned the ΔH_{vH} values we report here are apparent values because the heat-induced helix–coil transition of genomic DNA is not a reversible process.

The calorimetric enthalpy change (ΔH_{cal}) of the transition was taken from the following reference [24]. The ratio of the van't Hoff enthalpy change to the calorimetric enthalpy change was used to calculate the cooperative melting unit (N):

$$N = \frac{\Delta H_{vH}}{\Delta H_{cal}}$$

where N is the number of base pairs that melt as one.

Isothermal pressure-induced denaturation experiments were attempted at the pressurisation rate of 1.0 MPa/min, at several temperatures ranging from 30.8 to 38.1 °C by monitoring the absorption at 260 nm (data not shown).

3. Results and discussion

In general, elevated hydrostatic pressure stabilises double-stranded DNA polymers, that is dT_M/dP (and ΔV) is positive. While a few studies have shown that ΔV of the helix–coil transition can also be negative [10,11], the first pressure-induced helix–coil transition of DNA polymers was presented just over a decade ago [12]. Working with a synthetic DNA-RNA hybrid, poly(dA)·poly(rU), the authors showed that pressure can stabilise, destabilise, or have no effect on a double-stranded nucleic acid polymer, and that this is contingent on the T_M at atmospheric pressure [12]. Polymers whose T_M values are ~>50 °C are expected to be stabilised by pressure, while those whose T_M values ~<50 °C are going to be destabilised by pressure. In agreement with this study, we showed that pressure can stabilise or destabilise the double-stranded synthetic DNA polymers, poly[d(A-T)] and poly[d(I-C)], depending on their respective helix–coil transition temperatures at atmospheric conditions [18].

We have also shown that the cooperative unit of the heat-induced and pressure-induced helix–coil transition of double-stranded DNA polymers differs, suggesting that the transitions occur via different mechanisms, although the mechanistic details remain unknown [18]. Comparison of the ΔV values for the helix–coil transition of poly[d(A-T)] obtained by pressure-dependent UV spectroscopy, and pressure perturbation calorimetry (PPC), which operates at nearly atmospheric pressure, showed that the respective ΔV values differ in magnitude. We attributed the difference in the volume changes to the effect of elevated pressure on both double- and single-stranded polymers [19]. Pressure increases hydration of the native/helix state of DNA [25,26], and penetration of water molecules [27]. At the temperatures where we can search for a pressure-induced strand separation, i.e., near the T_M, we hypothesise that the first step along the path leading to denaturation is the incorporation of water molecules between the hydrogen bonded bases on the two interacting strands at elevated pressure. Support for this idea, and that the pressure- and heat-induced helix–coil transition of DNA polymers occurs via different mechanisms was provided by our recent work, which illustrated that the pressure-induced helix–coil transition of DNA does not occur in the absence of water [19]. As our previous studies have investigated pressure-destabilisation of synthetic DNA copolymers, this study was undertaken to look at the effect of sequence complexity on this process.

Fig. 1 illustrates normalised heat-induced helix–coil transition curves of *C. perfringes* DNA in 1.2 mM Na^+ at 5 and 200 MPa. The mid-point of the transition (T_M) at 5 MPa is 38.1 °C, and at 200 MPa it is 34.8 °C, clearly showing that elevated hydrostatic pressure led to destabilisation of this biopolymer. The value of ΔT_M over this pressure range is around 4 °C, which is significantly greater than those of poly[d(A-T)], poly[d(I-C)] [18] and poly[d(G-C)] [19] under similar conditions. While the transition is cooperative, it is less cooperative than those seen with synthetic alternating DNA copolymers [8,9,18]. This is not unexpected, as greater sequence complexity of the genomic DNA results in a lower degree of cooperativity of the transition.

Fig. 2 displays the T_M of *C. perfringes* DNA as a function of hydrostatic pressure. We calculated the molar volume change (ΔV) of the transition using the Clapeyron equation:

$$\frac{\Delta T_M}{\Delta P} = T_M \frac{\Delta V}{\Delta H_{cal}}$$

where ΔH_{cal} is the calorimetric (model-independent) enthalpy change of the helix–coil transition. Table 1 lists the thermodynamic parameters associated with the transition. The pressure dependence of T_M, dT_M/dP, is negative; consequently, the helix should be destabilised by hydrostatic pressure. Using dT_M/dP and the Clapeyron equation we calculated the volume change accompanying the heat-induced transition from a helix to a coil form (Table 1). However, the Clapeyron equation is strictly valid only for reversible phase transitions, which is not the case for the genomic *C. perfringes* DNA. Thus, the value of ΔV given in the table is an approximation. The calculated/estimated molar volume change (ΔV) of the transition equals −1.78 mL/mol (base pair). Under similar experimental conditions the ΔV of poly[d(A-T)] equals −1.39 mL/mol [18]. According to Le Chatelier's principle, elevated pressure will favour the species with a smaller partial volume, the coil state in this case. One would anticipate a pressure-induced helix–coil transition under these conditions as we have observed with poly[d(A-T)] and poly[d(I-C)] [18]. We attempted to induce a helix–coil transition of *C. perfringes* DNA by increasing the pressure from 3 to 220 MPa at a rate of 1.0 °C/min at several temperatures near the atmospheric T_M (30.8 to 38.1 °C); we were unsuccessful (data not shown). It has been demonstrated that the mid-point of the pressure-induced helix–coil transition (P_M) of DNA copolymers is temperature dependent, decreasing with increasing

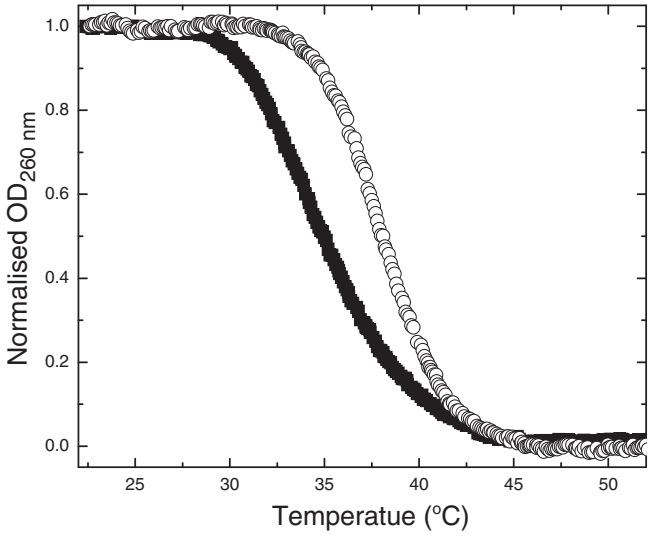

Fig. 1. Representative, normalised, heat-induced, helix–coil transition curves of *Clostridium perfringes* DNA in aqueous solution containing 1.2 mM Na^+ at 5.0 MPa (○) and at 200 MPa (■). The heating rate was 0.1 °C/min. The melting temperature (T_M) is 38.1 °C at 5 MPa and to 34.8 °C at 200 MPa.

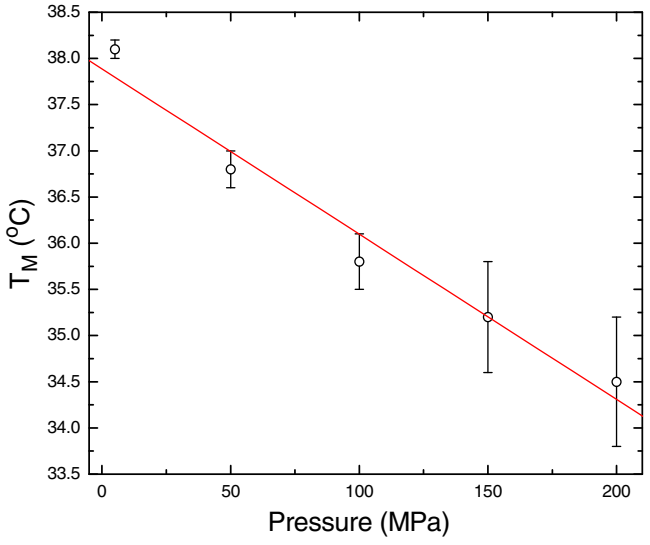

Fig. 2. Helix–coil transition temperature of *Clostridium perfringes* DNA as a function of pressure in aqueous solution containing 1.2 mM Na^+. The solid line is the least-squares fit to the data. The value of dT_M/dP is listed in Table 1.

Table 1
Thermodynamic parameters for the helix–coil transition of *C. perfringes* DNA in a 1.2 mM Na^+ aqueous solution and at atmospheric pressure.

T_M (°C)[a]	$100 \times dT_M/dP$ (°C/MPa)	ΔH_{cal} (kJ/mol)[b]	ΔV (mL/mol)
38	-1.79 ± 0.19	30.9	-1.78 ± 0.23

[a] Extrapolated to atmospheric pressure from the dTm/dP plot. A linear fit gives a T_M of 37.9 ± 0.2 °C, while a second order polynomial fit gives a T_M of 38.2 ± 0.1 °C. Consequently, we use the value of 38 °C as the melting temperature at atmospheric pressure.
[b] Obtained from reference [24].

temperature [18]. Consequently, we expected to see pressure-induced denaturation at a temperature near the T_M at atmospheric pressure. However, in the pressure range from 3 to 220 MPa, we did not observe any pressure-induced transition. This indicates that these DNA polymers do not undergo a pressure-induced transition even under conditions at which the ΔV is negative.

Previously, we showed the pressure-induced helix–coil transition to be more cooperative than the heat-induced transition [18]. Hence, it seems reasonable to assume that the pressure-induced transition is more likely to occur with those polymers exhibiting a greater degree of cooperativity. Thus, under experimental conditions employed in this study, we suspect that the lack of pressure-induced transition of *C. perfringes* DNA stems from its lower cooperativity compared to that of synthetic DNA copolymers, such as poly[d(A-T)] and poly[d(I-C)]. Evidently, the sequence complexity of genomic DNA results in regions that are GC-rich and that consequently undergo the transition at higher temperatures than the AT-rich regions. We would like to emphasise that the pressure–temperature phase diagram of nucleic acids predicts that those polymers whose melting temperature is lower than about 50 °C are destabilised by elevated hydrostatic pressure and can be pressure-denatured [12]. The present data imply that this is not the case for genomic DNA, presumably due to its sequence complexity, which gives rise to the irreversibility of the transition and its deviation from the phase diagram.

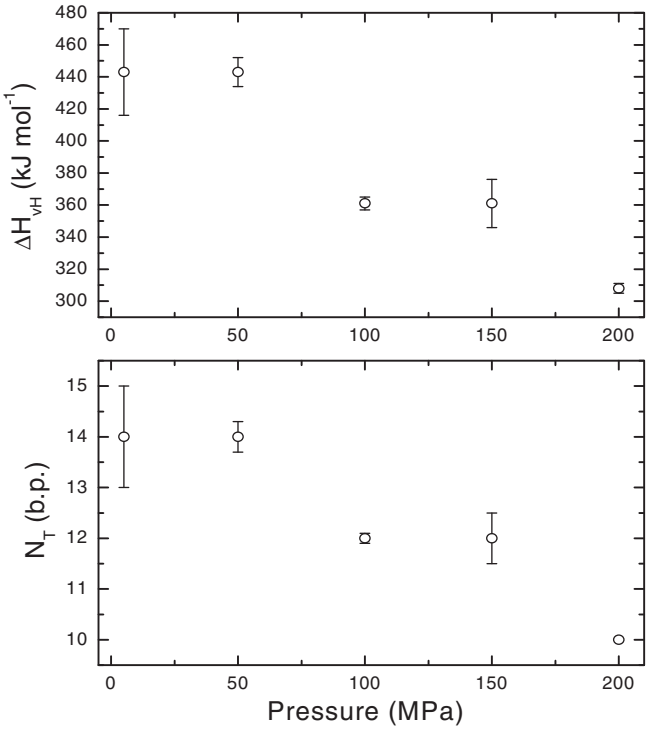

Fig. 3. Two-state (or van't Hoff) enthalpy change (ΔH_{vH}) (top panel), and the cooperative melting unit (N) (bottom panel) for the heat-induced helix–coil transition of *Clostridium perfringes* DNA as a function of pressure in an aqueous solution containing 1.2 mM Na^+.

In the top panel of Fig. 3 we show the effect of pressure on the van't Hoff (two-state model) enthalpy change of the helix–coil transition. The cooperative melting unit (N) or the number of base pairs that melt in tandem is defined as:

$$N = \Delta H_{vH}/\Delta H_{cal}$$

Since N is the ratio of the model-dependent to model-independent enthalpy change, its pressure dependence (Fig. 3 bottom) will be directly related to the pressure dependence of the van't Hoff enthalpy change (Fig. 3 top). These two parameters exhibit evident pressure dependence, the magnitude of both decreasing with increasing pressure. These results contrast with those we obtained with poly[d(A-T)], poly[d(I-C)], and poly[d(G-C)], which exhibited no apparent pressure dependence [8,9,18]. Conceivably this difference is due to sequence complexity and hence reduced cooperativity of genomic DNA, relative to that of synthetic DNA copolymers. The pressure dependence of ΔH_{vH} and N for the helix–coil transition of genomic DNA has also been reported in the past. Working with calf thymus DNA, Nordmeier showed that the ΔH_{vH} and N were pressure dependent, increasing with pressure [5]. His results as well as those from this study corroborate the idea that hydrostatic pressure affects the helix–coil transition of genomic DNA in a different manner than synthetic DNA polymers. We would like to point out that whereas the present study was carried out under conditions at which the ΔV of the helix–coil transition is negative, Nordmeier's study was done under conditions at which the ΔV of the helix–coil transition was positive. While the ΔH for the transition of DNA polymers appears to be pressure dependent for genomic DNA, this parameter (ΔH of the helix–coil transition) depends strongly on temperature for genomic and synthetic polymers alike [28,29]. The ΔV of this transition is also strongly temperature dependent, as demonstrated by several studies employing different techniques [18,21,30]. The temperature dependence of ΔV, that is the expansivity change (ΔE) accompanying the transition, is always positive for nucleic acid polymers [16,18,21]. The interpretation of this finding is that the coil state is more extensively hydrated than the helix state [16,21].

In conclusion, we present the first report of a negative molar volume change (ΔV) for the helix–coil transition of genomic DNA. Working with *C. perfringes* DNA under conditions such that the change in the T_M as a function of pressure (dT_M/dP) is negative, the ΔV of the transition equals -1.78 mL/mol (base pair) at atmospheric pressure; however, at hydrostatic pressures up to 220 MPa we were unable to observe a pressure-induced helix–coil transition of this DNA polymer. Presumably this is due to sequence complexity and reduced cooperativity of genomic DNA, thus showing further importance of sequence complexity in the physical chemistry of DNA.

Acknowledgements

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