CHAIN-FORMING DINOFLAGELLATES: AN ADAPTATION TO RED TIDES

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ABSTRACT

Swimming speeds of two chain-forming dinoflagellates, the toxic Gymnodinium catenatum and the non-toxic Alexandrium affine, were measured as a function of chain lengths. Long chains swam faster than short chains. The increase in speed from a single cell to a chain of four cells for both species was about a factor of 1.5-1.6. Populations of both dinoflagellate species were coincident with red tides in areas of coastal upwelling relaxation and downwelling in the Ria de Vigo, northwest Spain. The higher swimming speeds of long chains may allow more cells to remain in the photic zone during downwellings or convergences. This may be a mechanism for local concentration of cells leading to a red tide.

INTRODUCTION

Two chain-forming dinoflagellates, Gymnodinium catenatum Graham and Alexandrium affine (Inoue and Fukuyo) Balech, bloomed simultaneously in the Ria de Vigo, NW of Spain, in 1985 [1] and again in 1986 (unpublished data) coincident with a relaxation in the persistent coastal upwelling that typifies that region. The upwelling relaxation was associated with areas of downwelling within the ria into which the dinoflagellate species were advected and concentrated in visible red tides. Chain-forming dinoflagellates are often responsible for red tide outbreaks throughout the world. This generalization, plus the simultaneous dominance of G. catenatum and A. affine in the downwelling regime suggests that chain formation may provide an evolutionary advantage leading to red tide formation in certain hydrographic environments.

The hypothesis being tested in this paper is that the drag force on cells in a long chain is less than that on those same cells if they were unattached. The chain should thus travel faster and remain in the photic zone when downwelling or other advective processes would remove non-motile cells or less-vigorous swimmers.

MATERIALS AND METHODS

Model

If we assume the shape of a single cell to approximate a sphere, Stoke's Law may be used to calculate the force required to propel a cell at a given swimming velocity (v). The total force applied by a chain during swimming (F_s) will be proportional to the number of cells in the chain (n):

$$F_s = n\ (6\pi\mu av)$$

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where a is the radius of a single cell and μ is the dynamic viscosity of the liquid. To propel a chain of cells at a given velocity, F_s must equal the total drag force:

$$F_d = 6\pi\mu A_s v$$

where A_s is the Stoke's radius of a sphere with the drag equivalent to a prolate spheroid oriented parallel to flow as given by Happel and Brenner [2]. We have interpolated values for F_s between those given by the latter authors assuming a linear relationship to exist.

Since the dynamic viscosity varies with temperature, we can construct a matrix of calculated swimming speeds as a function of chain length and temperature using the measured swimming speeds of single cells at given temperatures.

Measurements

Cultures of Gymnodinium catenatum (GC1V) and Alexandrium affine (PA5V) isolated in the Ria de Vigo during the 1985 bloom, were grown in "K/2" medium [3] at 20°C with a 14:10 L:D period. The last transfer of the cultures just before the experiments was to "K/2" medium without nitrate, with only ammonia as a nitrogen source.

Swimming speeds were recorded with the aid of a Zeiss light microscope fitted with a low-light video camera conected to a VCR. Swimming chambers were constructed with a coverslip separated from a microscope slide by four small pieces of modelling clay. Slides were held on an aluminum microscope stage that was cooled with circulating water from temperature controlled bath. Swimming velocities of chains of G. catenatum and A. affine were measured by frame analysis on a monitor. A more accurate method of measuring absolute swimming velocities of dinoflagellates was described by Kamykowsky [4], but in the present study we were interested in relative values as a function of the chain length more than in absolute values of swimming velocities per se.

RESULTS

Figure 1 shows the calculated swimming speeds of G. catenatum and A. affine as a function of chain length and seawater viscosity, using a single velocity of 247 μm/sec at 23 °C (average of 36 values) for G. catenatum and 410 μm/sec at 23 °C (average of 29 values) for A. affine. Greatest increase in swimming velocity as chain length extended was observed for relatively short chains of two to four individuals. As the length of the chain increased, the incremental advantage decreased. The advantage of swimming in a chain was greater at high rather than low temperatures.

Comparing curves of calculated and observed velocities (Fig.2), it was clear that the measured increase in swimming velocity was less than our simple model predicted. This may have been due to the effect of the flow field created by the anterior-most cells in the chain that may have forced trailing cell to swim less effectively.

The greater increase in velocity associated with longer chains A. affine compared to G. catenatum agree well with the idea that fast swimmers benefit more from long chain formation than do slow swimmers.

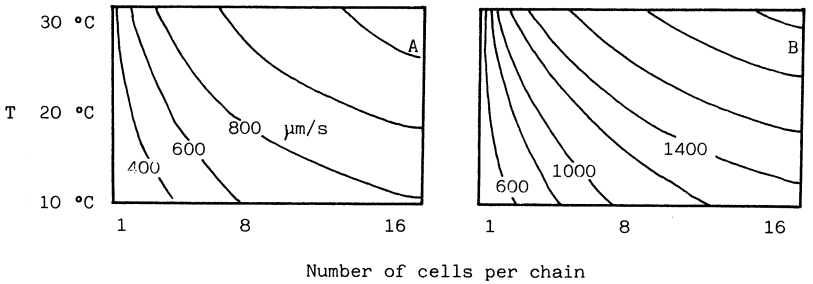

FIG. 1. Calculated swimming velocities of G. catenatum (A), and A. affine (B), as a function only of chain length and temperature.

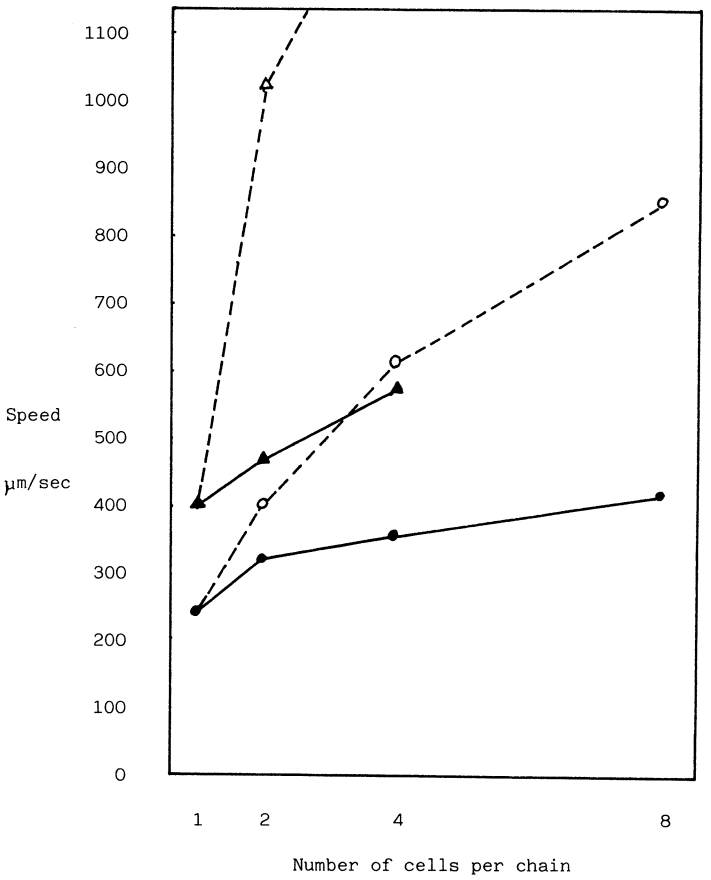

FIG. 2. Calculated (- - - - - - -) and observed (————————) swimming velocities of G. catenatum (o ●) and A. affine (△ ▲).

DISCUSSION

The fact that chains of cells swim faster than single cell is an important concept in the development of red tides in areas of convergences or downwelling. When chain forming species have to compete with non-chain formers, an advantage accrues to those requiring the least amount of energy to stay within the photic zone. This may be true even when the energy needed for motility is a small fraction of total metabolic requirements [5]. Another important fact is that variation in swimming speed may be due to changes in seawater viscosity as a function of temperature. The differences in swimming speeds between chains of different lengths increases with temperature. As cells swim towards the surface, they encounter warmer temperatures which may favor the presence of long chains over individual cells. Non-motile species, like diatoms, will sink from the water column faster at warmer temperatures. This may explain why rapid changes from diatom-dominated populations to single-cell dinoflagellates and to chain-forming dinoflagellates have been observed in the Ria de Vigo when a change of wind direction has caused a relaxation in coastal upwelling ([1] and unpublished data). We have not considered in our simple model physiological factors that clearly play a decisive role in determining the shape of the curves of speed vs temperature shown in the literature [4,6].

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