Revista Chilena de Historia Natural
69: 545-551, 1996

The photophysiology of surf diatoms - a review

La fotofisiología de las diatomeas de la zona de rompiente - una revisión

DEREK R. DU PREEZ[1] and EILEEN E. CAMPBELL

Department of Botany, University of Port Elizabeth, P.O. Box 1600, Port Elizabeth 6000, South Africa
[1]E-mail: superbt@upe.ac.za

ABSTRACT

The light environment in high energy surf-zones is extremely complex because of the periodic passing of waves, which cause the formation of foam and the suspension of sand. Despite high light attenuation, most of the surf-zone is euphotic. Surf diatoms, such as *Anaulus australis* Drebes et Schulz, *Attheya armatus* (West) Crawford, *Asterionella socialis* Lewin et Norris, *Asterionellopsis glacialis* (Castracane) Round and *Aulacodiscus kittonii* Arnott, are brought to the water surface by attachment to bubbles and are then returned to the water column by passing wave bores. This mechanism of flotation results in exposure to irradiances varying between full sunlight inhibitory to photosynthesis, and irradiances insufficient for photosynthesis, in a short space of time. The fluctuating light regime caused by the passing of the wave bores does not prevent photoinhibition. Three periods of photosynthesis can be identified: 1) photoinduction, 2) maximum photosynthetic rate (P_{max}), and 3) photoinhibition. The photoinduction phase is time-dependent, while photoinhibition is quantum-dose dependent. Inhibition of photosynthesis is associated with changes in the relative concentrations of diatoxanthin and diadinoxanthin. The xanthophyll cycle can be argued to play a role in photoprotection. However, photoinhibition still occurs *in situ*. Surf diatoms have high assimilation numbers and fix far more carbon than is required for their daily cell division cycle, even before photoinhibition occurs. This makes photoinhibition a protective rather than destructive phenomenon in surf diatoms.

Key words: photosynthesis, photoinhibition, photoprotection, xanthophyll cycle.

RESUMEN

El ambiente lumínico de la zona de rompiente de las olas es extremadamente complejo debido al paso periódico de las olas, lo que produce formación de espuma y suspensión de arena. Aun cuando existe atenuación de la luz, la mayor parte de la zona de rompiente es eufótica. Diatomeas de este hábitat, tales como *Anaulus australis* Drebes et Schulz, *Attheya armatus* (West) Crawford, *Asterionella socialis* Lewin et Norris, *Asterionellopsis glacialis* (Castracane) Round y *Aulacodiscus kittonii* Arnott, son llevadas a la superficie del agua por medio de la adherencia a burbujas de aire, para luego ser retornadas a la columna de agua por las olas que pasan. Este mecanismo de flotación resulta en exposición a la irradiación que varía en cortos períodos de tiempo entre plena luz del sol inhibitoria para la fotosíntesis e irradiaciones insuficientes para la misma. El fluctuante régimen de luz causado por el paso de las olas no previene fotoinhibición. Se pueden identificar tres períodos de fotosíntesis: 1) fotoinducción, 2) tasa fotosintética máxima (Pmáx), y 3) fotoinhibición. La fase de fotoinducción es dependiente del tiempo, mientras que la fotoinhibición es dependiente de la dosis de quantum. La inhibición de la fotosíntesis está asociada con cambios en las concentraciones relativas de diatoxantina y diadinoxantina. Se puede argumentar que el ciclo de la xantofila juega un rol en la fotoprotección. Sin embargo, la fotoinhibición aun ocurre *in situ*. Las diatomeas de la zona de rompiente tienen números altos de asimilación y fijan mucho más carbono que lo requerido para sus ciclos diarios de división celular aun antes que ocurra fotoinhibición. Esto hace de la fotoinhibición un fenómeno más protector que destructor en las diatomeas de la zona de rompiente.

Palabras clave: Fotosíntesis, fotoinhibición, fotoprotección, ciclo de la xantofila.

INTRODUCTION

Several surf-zones of larger sandy beaches are notable because surf diatoms such as *Anaulus australis* Drebes et Schulz, *Attheya armatus* (West) Crawford, *Asterionella socialis* Lewin et Norris, *Asterionellopsis glacialis* (Castracane) Round and *Aulacodiscus kittonii* Arnott accumulate into extremely high cell concentrations in the narrow strip along the shore (Lewin & Schaefer 1983, Sloff et al. 1984, Talbot & Bate 1986). Such accumulations of surf diatoms have been shown to occur along the west coast of the United States of America, New Zealand, much of the south coast of Africa, Tasmania,

(Received 1 December 1994; accepted 28 July 1996.)

the south and west coast of Australia, and the coasts of Brazil and Argentina.

These surf diatoms possess a mechanism that enables them to adhere to bubbles. As a result they float to the water surface between wave bores (Sloff et al. 1984). With each passing wave, the cells are tumbled into the water column and rise back into the surface foam again after the wave has passed. This results in the development of a unique light environment that is highly variable and characterised by strong attenuation of irradiance, but where the floating cells are periodically exposed to full sunlight.

Surf diatoms have a unique light climate to cope with and have adapted to this harsh environment in such a way that they effectively out-compete all other species and develop a complete dominance where they occur. The current state of our knowledge about this highly variable light climate and the photosynthetic characteristics of surf diatoms experiencing it are reviewed in this paper.

The light environment

Attenuation of light in surf-zones is almost entirely due to three factors: bubbles, sand and diatom pigments. Differences in turbulence result in different attenuation coefficients based on where waves are breaking. Surf-zones with diatom accumulations are typically in either a longshore bar-trough state or dissipative energy state (Campbell & Bate 1988). Attenuation coefficients where waves break are on average four times higher than in the trough where waves are reforming (Fig. 1) (Campbell et al. 1988a). Surf diatoms mostly accumulate on the beach terrace and always where waves are breaking. The light environment also changes as a result of the passing waves. After waves break the attenuation coefficient almost doubles (Fig. 1). This is because there are more bubbles both in and on the water surface than just before the next wave bore passes.

Once a wave passes, bubbles rise to the surface carrying surf diatom cells into the foam. This results in the high cell concentrations commonly recorded at the water surface. The pigment concentration in surface layers strongly attenuates the light (Campbell et al. 1988a) so that below a diatom accumulation aphotic conditions exist. Most of the cells are in the neuston just before a wave passes. The cells are dumped into the water column as the wave moves past the accumulation. The cells then rise with the bubbles to accumulate in the surface foam until the next wave breaks. Thus surf diatoms are exposed to a fluctuating light environment ranging from near aphotic conditions to full sunlight within an average of 10 seconds (Fig. 2).

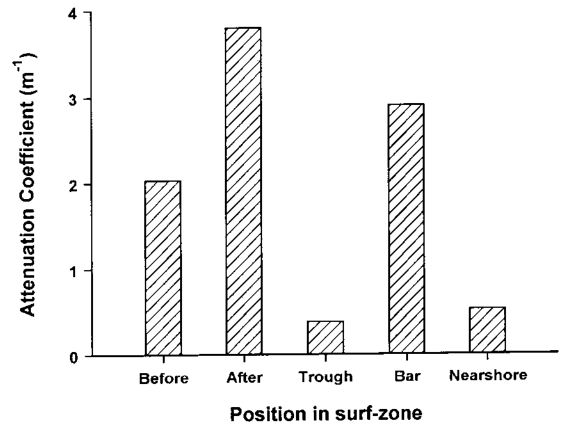

Fig. 1: Irradiance attenuation coefficients measured before and after the passing of wave bores on the beach terrace, in the trough and nearshore as well as an estimated value for the bar.

Coeficientes de atenuación de la irradiación medidos antes y después del paso de las olas sobre el fondo de la playa, en la zona de artesas, barras y sublitoral somero.

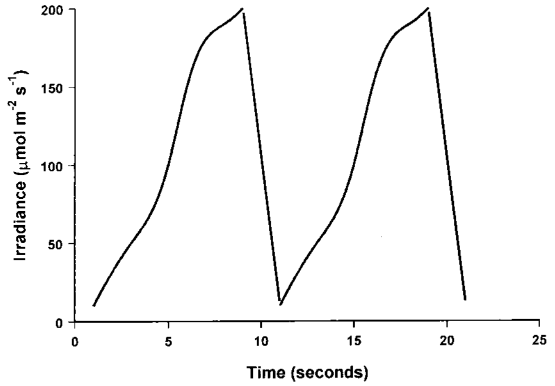

Fig. 2: The proposed irradiance regime experienced by surf diatoms while in accumulations.

Régimen de irradiación experimentado por acumulaciones de diatomeas de la zona de rompiente de las olas.

The photosynthesis-irradiance relationship

The photophysiology of *Anaulus australis* is the best described of the surf diatoms. Fig. 3 gives an average photosynthesis-irradiance curve based on measurements done at ambient temperature at fortnightly intervals over a year (Campbell 1987). The standard error bars include variation due to differences in water temperature. Because of the high cell numbers *in situ*, photosynthesis was measured on natural populations of diatoms using oxygen evolution. The chlorophyll-specific photosynthetic rate measured at saturating irradiance (P^{B}_{max}) is high at 16 g C g chl a^{-1} h^{-1} compared to that measured in other phytoplankton species. The average P^{B}_{max} for 188 other phytoplankton species was 5 g C g chl a^{-1} h^{-1} (references listed in Campbell 1987).

When this curve is compared with that of a mixed population of *Attheya armatus* and *Asterionella socialis* (Fig. 3) (Lewin & Schaefer 1983), the only difference is in the value of P_{max}. The initial slope is the same indicating similar ability to fix carbon at low irradiances. I_k (the irradiance of onset of light saturation, Talling 1957) is lower due to the low P_{max}. A high P_{max} and I_k is usually considered to be an indicator of high light adaptation. While it can be argued that the ^{14}C method used by Lewin & Schaefer (1983) resulted in the lower P_{max}, it was possible on one occasion during 1986 to measure the photosynthesis-irradiance relationship of *Asterionellopsis glacialis* (Fig. 3) using the same technique and equipment used in the work on *Anaulus australis*. As with the data of Lewin & Schaefer (1983) the Pmax is much lower than that of *Anaulus australis* at around 7.5 mg C mg chl a^{-1} h^{-1} and the light-limited slope is similar to that of *Anaulus australis*. No data is available for any other surf diatoms.

Anaulus australis is more high light adapted than the other three species. Both *Attheya armatus* and *Asterionella socialis*, are reported to have extensive mucilage and clay coats (Lewin & Norris 1970) as does *Asterionellopsis glacialis* (Du Preez & Campbell in press). These cell coverings most likely reduce the light received by the chloroplasts compared to that received by *Anaulus australis* for the same incident irradiance.

Photoinhibition

The photosynthesis-irradiance relationship for *Anaulus australis* presented by Campbell (1987) (Fig. 3) was determined using oxygen evolution with short incubation times. When long incubations are used, photosynthesis can be substantially reduced (Du Preez et al. 1990). Three hour incubations of *Anaulus australis* showed a reduction in photosynthetic rate of 20% at 800 µmol m^{-2} s^{-1} (less than half full sunlight).

It has been suggested (Lewin & Schaefer 1983) that the ability of surf phytoplankton species to float would be of benefit to them in two ways. Firstly, flotation maintains the cells within the surf-zone as they are carried towards the beach by wave action. Secondly, flotation exposes the cells to high irradiances near, or equal to that of full sunlight and the cells are in a position to photosynthesise maximally. Teleologically, it makes sense for

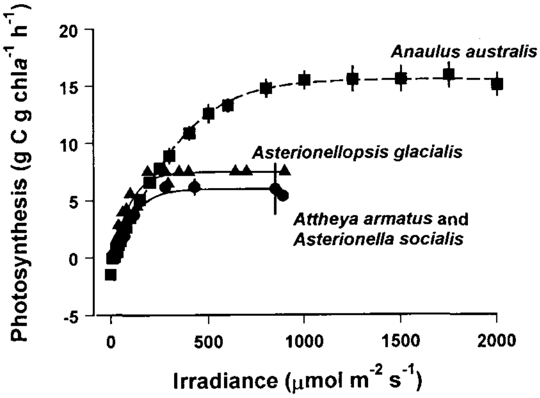

Fig. 3: The photosynthesis-irradiance relationships of the surf diatoms *Anaulus australis* Drebes et Schulz (dots, annual mean ± 1 SE, taken from Campbell 1987), a mixture of *Attheya armatus* (West) Crawford and *Asterionella socialis* Lewin et Norris (squares; taken from Lewin & Schaefer 1983) and *Asterionellopsis glacialis* (Castracane) Round (triangles). In each case a hyperbolic tangent form of the P - I relationship is fitted (Harrison et al. 1985).

Relaciones fotosíntesis-irradiación de las diatomeas *Anaulus australis* Drebes et Schulz (annual mean ± 1 DE, tomado de Campbell 1987), mezcla de *Attheya armatus* (West) Crawford y *Asterionella socialis* Lewin et Norris (tomado de Lewin & Schaefer 1983) y *Asterionellopsis glacialis* (Castracane) Round. Para cada relación P - I se ajustó una tangente hiperbólica (Harrison et al. 1985).

phytoplankton that accumulate at the water surface to make optimal use of the available light, or at the very least, to be adapted to withstand high irradiances. Yet it is apparent that surf diatoms are photoinhibited by high irradiances.

The photosynthetic capacity (the chlorophyll specific rate of photosynthesis measured at saturating irradiance, P^B_{max}) of cells kept in low light conditions showed two phases (Du Preez et al. 1990). The P^B_{max} increased following exposure to light. This was interpreted to be a photoinduction phase. Thereafter P^B_{max} levelled off to remain at a fixed rate for the remainder of the light period. By contrast, cells kept in full sunlight showed an additional phase (Fig. 4) (Du Preez et al. 1990). After a very short photoinduction and constant photosynthetic rate phase, cells became photoinhibited to a quarter of the initial rate within 1 hour. Photoinhibition was reversible in that the cells recovered fully following a 14 hour dark period to a P^B_{max} similar to that of the cells kept in low light.

High cell concentrations resulted in a substantial reduction in the extent of photoinhibition (Du Preez et al. 1990). At a concentration of a million cells ml^{-1}, no photoinhibition could be demonstrated after 8 hours incubation at 800 $\mu mol\ m^{-2}\ s^{-1}$. At 50 000 cells ml^{-1}, the measured rate of photosynthesis decreased by 80% after an incubation of 1 hour. Intermediate cell concentrations resulted in intermediate responses. At high cell numbers (i.e. in dense accumulations) photoinhibition will be delayed substantially.

Photoinhibition was observed in our experiments as a reduction of the assimilation number (carbon fixed per unit chlorophyll per hour) *in situ* at the Sundays River beach (Campbell 1987). This suggests that the cells derive some advantage, other than optimal photosynthesis, by rising into the surface foam. It is possible that there is insufficient light in most of the surf-zone to saturate photosynthesis as the water is relatively turbid. By accumulating at, or near, the water surface, the cells would be exposed to high irradiances, sufficient to saturate photosynthesis, but also sufficient to cause photoinhibition.

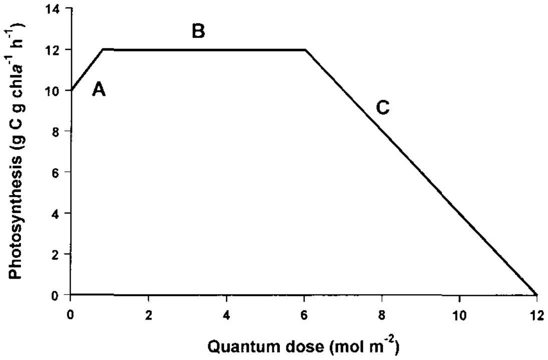

Fig. 4: A representation of the phases of photosynthetic activity related to photon dose in *Anaulus australis* Drebes et Schulz.

Representación de las fases de actividad fotosintética relacionada a dosis de fotones en *Anaulus australis* Drebes et Schulz.

Photoinhibition may be reduced, on occasion, by the accumulation of the cells in the foam in numbers high enough to shade each other.

Surf diatoms may accumulate at the water surface in order to maintain themselves within the surf-zone as suggested by Talbot & Bate (1987). If the cells do not accumulate at, or near the water surface they will be lost from the surf-zone by the prevailing water circulation patterns. Surface accumulation ensures that the cells are retained within the surf-zone, but with resulting photoinhibition.

Fluctuating light

It has been suggested (Gieskes et al. 1979, Harris 1978) that diatoms *in situ* will not be photoinhibited as the cells move vertically in the water column resulting in a short residence period in that part of the water column receiving photoinhibitory irradiances.

The movement of cells in the water column occurs in a rhythmic fashion. This can be demonstrated by an increase in foam chlorophyll *a* concentration and a proportionate decrease in water chlorophyll *a* concentration with time after the passing of a wave bore (Fig. 5). This movement of the cells, together with a rhythmic increase and decrease in irradiance due to wave passage results in a fluctuating light regime.

The elimination of high irradiance photoinhibition is one of the most commonly reported effects of fluctuating irradiance

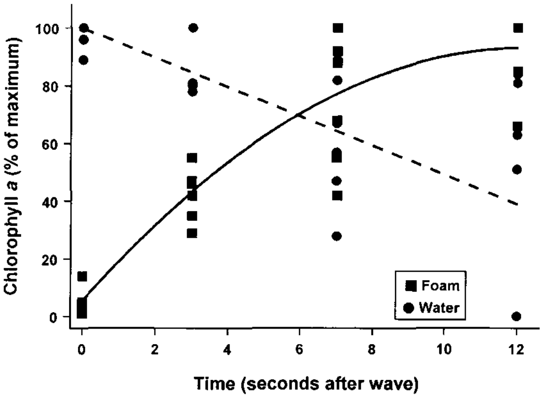

Fig. 5: The chlorophyll *a* concentration of the foam and water sampled in a diatom accumulation at the passing of a wave bore (t = 0 s), at 3 and 7 seconds after a wave bore and just before the next wave (t = 12 s) showing the location of the cells with time relative to the water surface.

Concentración de clorofila *a* en la espuma y agua muestreadas en una acumulación de diatomeas durante (t = 0 s), 3 y 7 segundos después del paso de una ola y justo antes de la ola siguiente (t = 12 s), mostrando la localización temporal de las células en relación a la superficie del agua.

(Harris 1978). This is because photoinhibition is a time-dependent process and relatively short exposures to high irradiance do not depress photosynthesis to the extent that it does when phytoplankton are kept in full sunlight for several hours (Harris 1978, Marra 1978).

Anaulus australis cells became photoinhibited under a range of fluctuating light regimes, provided the quantum dose was high enough (Campbell et al. 1988b). Photosynthetic rates under fluctuating light were not significantly different from an average of the photosynthetic rate measured at the constant maximum irradiance and the constant minimum irradiance of the fluctuating light regime (Fig. 6). Because the relationship is near to 1:1, it can be seen that there is also no enhancement of photosynthesis in a fluctuating light field for this diatom.

The photoinduction phase lasted equally long at all quantum dose treatments (17 minutes ± 2 minutes) (Du Preez et al. 1990). However, photoinhibition was found to be quantum dose dependent for a given cell concentration.

Xanthophyll cycle

Because surf diatom cells are exposed to very high irradiances, close to full sunlight for at least part of the time, it is reasonable to assume that they must have photoprotective mechanisms to prevent light-induced damage to the cells. The xanthophyll cycle, which is generally accepted to be a mechanism by which excess light energy is dissipated by photosynthetic organisms (Foyer et al. 1989), has been demonstrated to occur in *Anaulus australis*. This cycle in diatoms, involves an interconversion between two xanthophyll pigments, namely diatoxanthin and diadinoxanthin (Olaizola et al. 1992). The conversion only occurs under high light conditions and has only been measured in cells that exhibit photoinhibition (Fig. 7). Rapid recovery from photoinhibition, shows that the photosystems are intact and are not permanently damaged by high light. Prolonged periods of high light can lead to irreversible photooxidation and cell death (Demmig-Adams 1990).

The light energy absorbed by the cells has to be dissipated in order to prevent photooxidation. The xanthophyll cycle is one mechanism by which this occurs. More important however is dissipation of light energy in photochemistry, or in other words photosynthesis, leading to the production of carbohydrates. *Anaulus australis* has been shown to divide only once per day (Talbot &

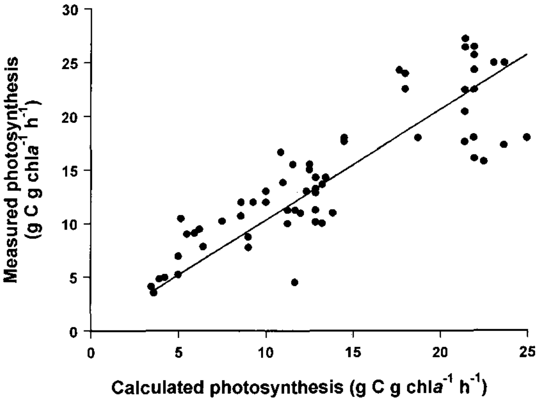

Fig. 6: The correlation between measured photosynthetic rate under fluctuating irradiance and calculated photosynthesis (an average of the rate measured in constant maximum and minimum irradiances used in the fluctuating light measurements).

Correlación entre tasa de fotosíntesis medida bajo irradiación fluctuante y fotosíntesis calculada (en las medidas de luz fluctuante se usó una media de la tasa medida en irradiaciones constantes máximas y mínimas).

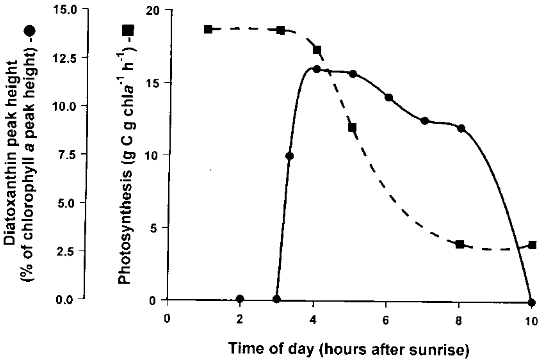

Fig. 7: The production of diadinoxanthin and coincident decrease in photosynthetic rate after exposure to high light in *Anaulus australis* Drebes et Schulz.

Producción de diadinoxantina y coincidencia en la disminución de la tasa de fotosíntesis después de exposición a luz intensa en *Anaulus australis* Drebes et Schulz.

Bate 1986). They can fix enough carbon for this single cell division in about 4 hours (calculated from carbon content and photosynthetic rate reported in Campbell 1987). During this period they will dissipate energy very efficiently. After this it appears as if the cells continue to dissipate energy through photosynthesis, but now exude much of this carbon. Estimates indicate that about 50% of the carbon fixed by the cells is exuded (also calculated from Campbell 1987). It is also during this latter part of the day that the surf accumulations have been observed to dissipate and it has been suggested (Talbot & Bate 1986) that the cells sink out of the foam and attach to sand grains. Here the cells would be exposed to a much lower light environment and no longer subject to photodamage. In high light the production of extracellular mucilage (polysaccharide) would help the diatoms to adhere to sand grains and hence sink out of the high light. In the lower light near the bottom, the polysaccharide would gradually break down releasing the diatom from the sand grains. The cells would then be free to be carried up to the high light by turbulence.

Surf accumulations only occur during conditions of high wave activity. During conditions of low wave activity accumulations do not form. During calm conditions, surf diatom cell numbers are very low (Talbot & Bate 1988). The cells therefore must be in or on the sediments and/or be behind the breaker zone. Wherever they are within the system, they will be exposed to relatively low light conditions or even complete dark. That they survive is evidenced by the formation of accumulations once turbulent conditions return.

Experiments done with *Anaulus australis* have shown that the chlorophyll *a* concentration in cells kept in the dark initially increases due to low light acclimation and then decreases gradually (Du Preez & Bate 1992). When returned to the light the chlorophyll *a* concentration increases rapidly.

The cells kept in the dark do not look like those that are normally found in the light and take on a resting form. Based on the data presented by Du Preez & Bate (1992), it can be estimated that *Anaulus australis* cells are capable of surviving for at least 75 days in complete dark and recover within 10 days (Fig. 8). It is highly unlikely that more than two months of calm weather will prevail and so the cells should be able to survive the dark conditions to which they are periodically subjected.

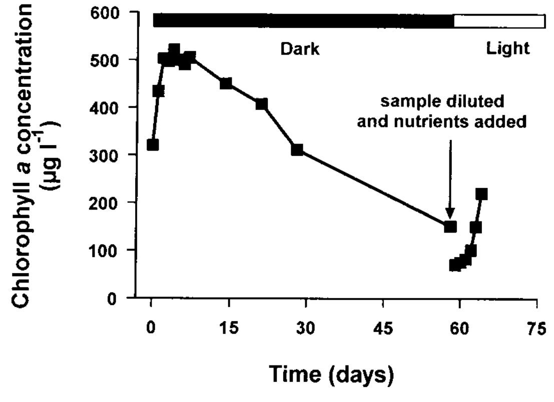

Fig. 8: The change in the chlorophyll concentration of *Anaulus australis* Drebes et Schulz cells kept in complete darkness.

Cambios en las concentraciones de clorofila de células de *Anaulus australis* Drebes et Schulz mantenidas en completa oscuridad.

CONCLUSIONS

Surf diatoms, being exposed periodically to high irradiances, have developed several photoprotective mechanisms. They are 1) a high chlorophyll *a*-specific photosynthetic rate, i.e. they complete their daily photosynthetic requirement for division in the first four or five hours of the day; 2) by accumulating into high cell concentrations, the cells shade each other; 3) surf diatoms dissipate excess energy by xanthophyll cycling (producing diatoxanthin from diadinoxanthin under high light conditions) in *Anaulus australis* and this presumably also occurs in other surf diatoms; 4) excess energy may also be dissipated in production of a mucilage coat in *Attheya armatus*, *Asterionella socialis* and *Asterionellopsis glacialis*; or as exuded polysaccharides in *A. australis*; 5) the cells may sink out of the accumulations in the late afternoon in order to avoid prolonged exposure to the very high irradiances at the water surface; and 6) photoinhibition is not permanent as full photosynthetic activity is restored by the next morning.

Anaulus australis has been demonstrated to have the ability to survive long periods in complete darkness by changed into a resting state. The cells may remain in a resting state until a high wave event returns them to the high light environment in the surf-zone.

ACKNOWLEDGMENTS

This study was funded by the South African National Committee for Oceanographic Research (SANCOR) and the Research Committee of the University of Port Elizabeth.

LITERATURE CITED

CAMPBELL EE (1987) The estimation of phytomass and primary production of a surf- zone. Unpublished PhD thesis, University of Port Elizabeth, South Africa. 429 pp.

CAMPBELL EE & GC BATE (1988) The estimation of annual primary production in a high energy surf-zone. Botanica Marina 31: 337-343.

CAMPBELL EE, DR DU PREEZ & GC BATE (1988a) Photosynthetic rates and photoinhibition of surf diatoms in fluctuating light. Botanica Marina 31: 411-416.

CAMPBELL EE, DR DU PREEZ & GC BATE (1988b) The light environment in a high energy surf-zone with high phytoplankton biomass. Botanica Marina 31: 329-335.

DEMMIG-ADAMS B (1990) Carotenoids and photoprotection in plants: A role for the anthophyll zeaxanthin. Biochimica et Biophysica Acta 1020: 1-24.

DU PREEZ DR & GC BATE (1992) Dark survival of the surf diatom *Anaulus australis* Drebes *et* Schulz. Botanica Marina 35: 315-319.

DU PREEZ DR & EE CAMPBELL (in press) Cell coatings of surf diatoms. Revista Chilena de Historia Natural.

DU PREEZ DR, EE CAMPBELL & GC BATE (1990) Photoinhibition of photosynthesis in the surf diatom, *Anaulus australis* Drebes *et* Schulz. Botanica Marina 33: 539-543.

FOYER CH, M DUJARDYN & Y LEMOINE (1989) Responses of photosynthesis and the xanthophyll and ascorbate-glutathione cycles to changes in irradiance, photoinhibition and recovery. Plant Physiology and Biochemistry 27: 751-760.

GIESKES WWC, GW KRAAY & MA BAARS (1979) Current 14C methods for measuring primary production: gross underestimates in oceanic waters. Netherlands Journal of Sea Research 13: 58-78.

HARRIS GP (1978) Photosynthesis, productivity, and growth: the physiological ecology of phytoplankton. Archiv für Hydrobiologie 10: 1-171.

HARRISON WG, T PLATT & MR LEWIS (1985) The utility of light-saturation models for estimating marine primary productivity in the field: A comparison with conventional "simulated" in situ methods. Canadian Journal of Fisheries and Aquatic Sciences 42: 864-872.

LEWIN J & RE NORRIS (1970) Surf-zone diatoms of the coasts of Washington and New Zealand (*Chaetoceros armatum* T. West and *Asterionella* spp.) Phycologia 9: 143-149.

LEWIN J & T SCHAEFER (1983) The role of phytoplankton in surf ecosystems. In: McLachlan A & T Erasmus (ed) Sandy beaches as ecosystems: 381-389. Dr Junk Publishers, The Hague.

MARRA J (1978) Phytoplankton photosynthetic response to vertical movement in a mixed layer. Marine Biology 46: 203-208.

OLAIZOLA M, PK BIENFANG & DA ZIEMANN (1992) Pigment analysis of phytoplankton during a subarctic spring bloom: xanthophyll cycling. Journal of Experimental Marine Biology and Ecology 158: 59-74.

SLOFF DS, A MCLACHLAN & GC BATE (1984) Spatial distribution and diel periodicity of *Anaulus birostratus* Grunow in the surf zone of a sandy beach in Algoa Bay, South Africa. Botanica Marina 27: 461-465.

TALBOT MMB & GC BATE (1986) Diel periodicities in cell characteristics of the surfzone *Anaulus birostratus*: their role in the dynamics of cell patches. Marine Ecology Progress Series 32: 81-89.

TALBOT MMB & GC BATE (1987) Distribution patterns of rip frequency and intensity in Algoa Bay, South Africa. Marine Geology 76: 319-324.

TALBOT MMB & GC BATE (1988) The response of surf diatom populations to environmental conditions. Changes in the extent of the planktonic fraction and surface patch activity. Botanica Marina 31: 109-118.

TALLING JF (1957) Photosynthetic characteristics of some fresh water plankton diatoms in relation to underwater radiation. New Phytologist 56: 29-49.