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SPATIAL AND TEMPORAL VARIABILITY IN CHLOROPHYLL-*a* AND DIATOM DISTRIBUTION IN THE SOUTH-EAST INDIAN OCEAN

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DIATOMS
BIOGEOGRAPHY
SUBTROPICAL CONVERGENCE
CHLOROPHYLL-*a*

ABSTRACT. – Cross frontal changes in chlorophyll-*a* (chl-*a*) concentration and diatom (> 20 µm) community species composition between South Africa and the Prince Edward Islands and in the mid-Indian Ocean were investigated during four cruises of the Marion Island Oceanographic Survey (MIOS I-IV) conducted in April/May between 1996 and 1999. Enhanced chl-*a* concentrations were recorded at stations occupied in the vicinity of the Subtropical Convergence (STC) south of Africa and in the vicinity of the Subantarctic Front (SAF) in 1998 and 1999. At these stations microphytoplankton (> 20 µm) comprised a substantial contribution (up to 15 %) of total chl-*a*. Outside these regions, however, total chl-*a* was almost entirely dominated by nano- and picophytoplankton. In the mid-Indian ocean no biological enhancement was associated with the STC. Species richness was highest in the region south of Africa (up to 44 species), particularly in the waters north of the STC. The high number of species recorded here can be related to the complex oceanographic regime. In the mid-Indian Ocean, species richness was consistently low, < 8 species. Numerical analyses indicated that south of Africa distinct diatom assemblages, separated by the major frontal systems, were associated with different water masses. South of Africa, the STC represented a strong biogeographic boundary to the distribution of diatom species. Within this region, a unique diatom assemblage was associated with the STC proper. In the mid-Indian Ocean, the STC did not act as a boundary to the distribution of diatoms, which is likely, the result of a reduced intensity of the front which allows for species to penetrate the front. During all four cruises, the SAF represented an important biogeographic boundary to the distribution of diatoms.

DIATOMÉES
BIOGÉOGRAPHIE
SUBTROPICAL
CONVERGENCE
CHLOROPHYLLE-*a*

RÉSUMÉ. – La comparaison des variations au niveau des fronts de la concentration en chlorophylle-*a* et de la composition spécifique des communautés de Diatomées (>20 µm) de l'Afrique du Sud aux Iles Prince Edwards d'une part, avec l'Océan Indien moyen d'autre part, a été étudiée au cours de quatre campagnes du Marion Island Oceanographic Survey (MIOS I-IV) conduites en avril-mai de 1996 à 1999. Des concentrations en chl-*a* élevées ont été relevées dans les sites situés à proximité de la Convergence Subtropicale (STC) au Sud de l'Afrique, ainsi que dans le voisinage du Front Subantarctique (SAF) en 1998 et 1999. Dans ces stations, le microphytoplancton (> 20 µm) représente une contribution importante (jusqu'à 15 %) à l'ensemble de la chlorophylle-*a* totale. Hors de ces régions, cependant, le nano- et le picoplancton dominant entièrement la chlorophylle-*a* totale. Dans l'Océan Indien moyen, aucune augmentation significative n'est associée à la STC. La richesse spécifique est la plus élevée dans la zone au sud de l'Afrique (jusqu'à 44 espèces), surtout dans les eaux au nord de la STC. Le nombre élevé d'espèces recensé dans cette région peut être lié au régime océanographique complexe. Dans l'Océan Indien moyen, la richesse spécifique est notablement basse, inférieure à 8 espèces. Les analyses numériques montrant que les communautés de Diatomées du Sud de l'Afrique, séparées par les systèmes frontaux majeurs, sont associées aux différentes masses d'eau. Au sud de l'Afrique, la STC représente une importante barrière biogéographique à la distribution des espèces de Diatomées. Dans ces régions une seule communauté est associée à la STC. Dans l'Océan Indien moyen, la STC n'intervient pas comme barrière à la répartition des Diatomées qui est probablement le résultat d'une activité moindre du front qui permet aux espèces de le traverser. Pendant les quatre campagnes, le Front Subantarctique représente une barrière biogéographique importante à la distribution des Diatomées.

INTRODUCTION

The major oceanic frontal systems south of Africa are well defined for a number reasons. Firstly, they form part of the Antarctic Circumpolar Current that is not constricted such as in the region of New Zealand, thus allowing for their full development (Duncombe Rae 1989, Lutjeharms & Vallentine 1984, Belkin & Gordon 1996, Lutjeharms *et al.* 1993, in review). Secondly, the northern boundary of the Southern Ocean, the Subtropical Convergence (STC) is enhanced by the juxtaposition of the Agulhas Current (AC) and the Agulhas Return Current (ARC) (Lutjeharms & Vallentine 1984, Weeks & Shillington 1994, 1996). As a consequence the frontal systems in this region have been the subject of extensive investigation (Lutjeharms & Emery 1983, Lutjeharms & McQuaid 1986, Lutjeharms *et al.* 1993). Results of these investigations have shown considerable variability in the position and intensity of the fronts (Lutjeharms & McQuaid 1986, Lutjeharms *et al.* 1993; Anson *et al.* 1999, Froneman *et al.* 1999, Pakhomov *et al.* 2000a). For example, the ARC that carries warm Subtropical surface waters may coalesce with the STC resulting in a frontal feature with a sharp transition in temperature and salinity (Pakhomov *et al.* 2000a). Similarly, the position of the Subantarctic Front (SAF) may vary as much as 100 km over a period of less than a month (Anson *et al.* 1999, Froneman *et al.* 1999, Lutjeharms *et al.*, in review). In contrast to the STC south of Africa, field data and Multi-channell Sea Surface Temperature charts collected in the mid-Atlantic Ocean showed that STC was ephemeral and weak and was characterised by a poorly defined horizontal gradient in physico-chemical parameters (Lutjeharms *et al.* 1993, Barange *et al.* 1998). There is evidence in the literature to suggest that the intensity of the STC in the mid-Indian Ocean also decreases (Belkin 1989).

Spatial distribution of diatoms ($> 20 \mu\text{m}$) south of Africa in austral summer has been the subject of extensive investigation on several occasions (Boden *et al.* 1988, Boden & Reid 1989, Froneman *et al.* 1995a, 1995b). Nutrient availability, light environment (Laubscher *et al.* 1993, Froneman *et al.* 1999) and biological factors such as grazing by zooplankton are implicated in determining the distribution of diatoms in the region (Froneman & Perissinotto 1996, Pakhomov & Perissinotto 1997). Boden *et al.* (1988) and others (see for example Froneman *et al.* 1995a, 1999) showed that distinct diatom assemblages were associated with different water masses or with hydrological features such as the Agulhas Return Current (ARC) and the STC south of Africa. The studies further showed that the major frontal systems south of Africa represented

strong biogeographic boundaries to the distribution of diatoms. For example Boden *et al.* (1989) showed that the STC represented the southern boundary for the distribution of several subtropical zone diatom species including *Cerataulina pelagica* and *Hemialus hauckii*. More recently, Froneman *et al.* (1995) demonstrated that the SAF represented the southern boundary for the distribution of sub-antarctic diatom species such as *Pseudoeunotia doliolus* and *Thalassionema frauenfeldii*. The importance of the fronts as boundaries appeared to be the result of the sharp horizontal gradients in temperature associated with these features (Deacon 1982, Boden *et al.* 1988, Froneman *et al.* 1995a, 1995b). Subsequent studies conducted in the region have shown that the major frontal systems also represent important biogeographic barriers to the distribution of zooplankton (Pakhomov & McQuaid 1986, Pakhomov & Perissinotto 1997, Barange *et al.* 1998). A recent study showed a high degree of spatial variability of the STC as a biogeographic boundary, with the mid-Atlantic Ocean front representing a weak biogeographic boundary (Barange *et al.* 1998). The variability appeared to reflect changes in the intensity of the front in the open waters which allowed for species to be transported across the frontal system. It should be noted that although the STC represents a strong biogeographic boundary to the distribution of plankton south of Africa, warm core eddies shed from the Agulhas Return Current may at times transport plankton across the front (Froneman *et al.* 1997, Pakhomov & Perissinotto 1997).

The importance of the SAF as a barrier to the distribution of both phytoplankton and zooplankton in the Atlantic sector of the Southern Ocean in austral summer has been documented on several occasions (Deacon 1982, Froneman *et al.* 1995b; Pakhomov *et al.* 2000b). A recent study conducted in the Indian sector of the Southern Ocean in austral summer 1996 indicated that the SAF did not represent an important biogeographic boundary to the distribution of plankton (Froneman & Pakhomov 1998). The absence of this feature as a biogeographic boundary appeared to be related to cross frontal mixing which transported species across the front. These facts suggest strong spatial variability in the importance of the SAF as a biogeographic boundary.

During this study inter-annual variability of the importance of the major frontal systems south of Africa as biogeographic barriers to the distribution of microphytoplankton is investigated. These data are then compared with results obtained along a transect occupied in the mid-Indian Ocean to investigate spatial variability in biogeography of microphytoplankton.

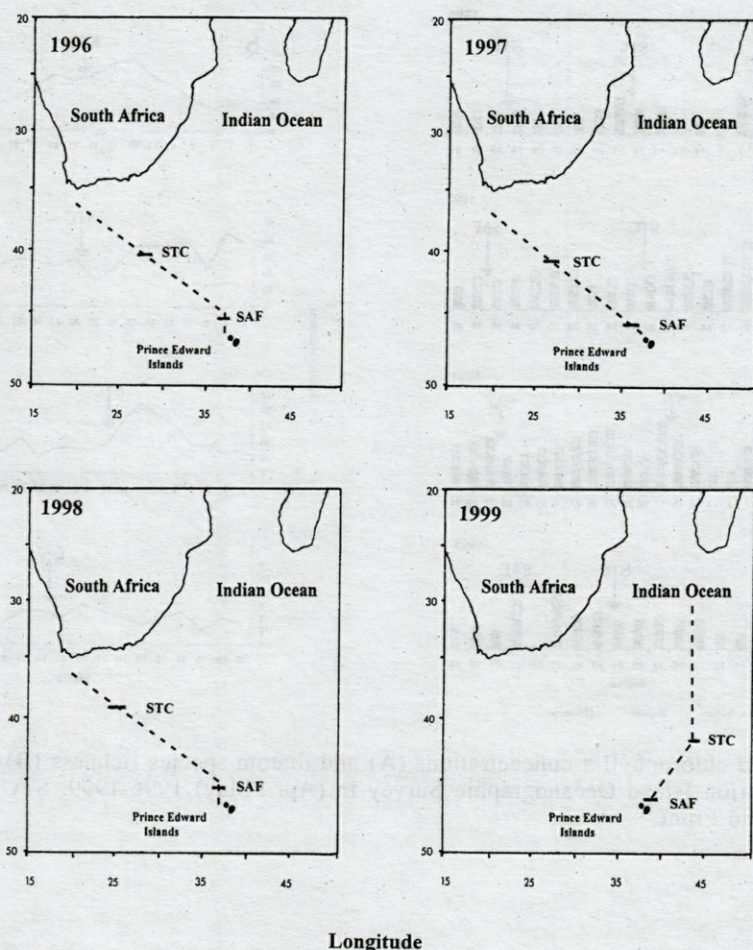


Fig. 1. – Cruise tracks during the four cruises of the Marion Island Oceanographic Survey conducted in April/May 1996-1999. STC = Subtropical Convergence; SAF = Subantarctic Front.

MATERIALS AND METHODS

Data for the study were collected during four cruises of the Marion Island Oceanographic Survey (MIOS I-IV) conducted in April/May over the period 1996 to 1999. Three transects were occupied in the region between South Africa and the Prince Edward Islands over the period 1996 to 1998 (Fig. 1). A single transect was also occupied in the south Indian Ocean between the Madagascar Ridge and the Prince Edward Islands in 1999 (Fig. 1)

To determine the position of the major frontal systems along each transect occupied, Sippican T7-XBT's (Expendable Bathythermograph) were deployed at 30 nautical mile intervals to a maximum depth of 760 m. Prior to the deployment, the XBT's were placed in a water bath for 5 minutes in order to minimise the difference between the probes storage temperature (25°C) and that of the sea surface temperature. The position of the major oceanic fronts were defined by their subsurface temperature range and their subsurface axila temperature according to Park *et al.* (1993). These were as follows : Subtropical Convergence (STC) 8-12°C, 10°C; Subantarctic Front (SAF) 4-8°C, 6°C. Detailed discussion of

the results are presented elsewhere (Ansoerge *et al.* 1999, Pakhomov *et al.* 2000a, Lutjeharms *et al.* in review). The geographic position of the major frontal system during the four cruises is presented in Table I.

Water samples for the identification and enumeration of diatoms were collected at 30 nautical mile (± 55 km) intervals using a shipboard pump (Iwaki Magnetic

Table I. – Geographic position of the major oceanic fronts south of Africa and in the mid Indian Ocean in April/May 1996-1999.

Year	Subtropical Convergence (STC)	Sub-antarctic Front (SAF)
1996	42° 35'	45° 30'
1997	42° 50'	45° 45'
1998	42° 15'	45° 45'
1999	43° 30'	45° 20'

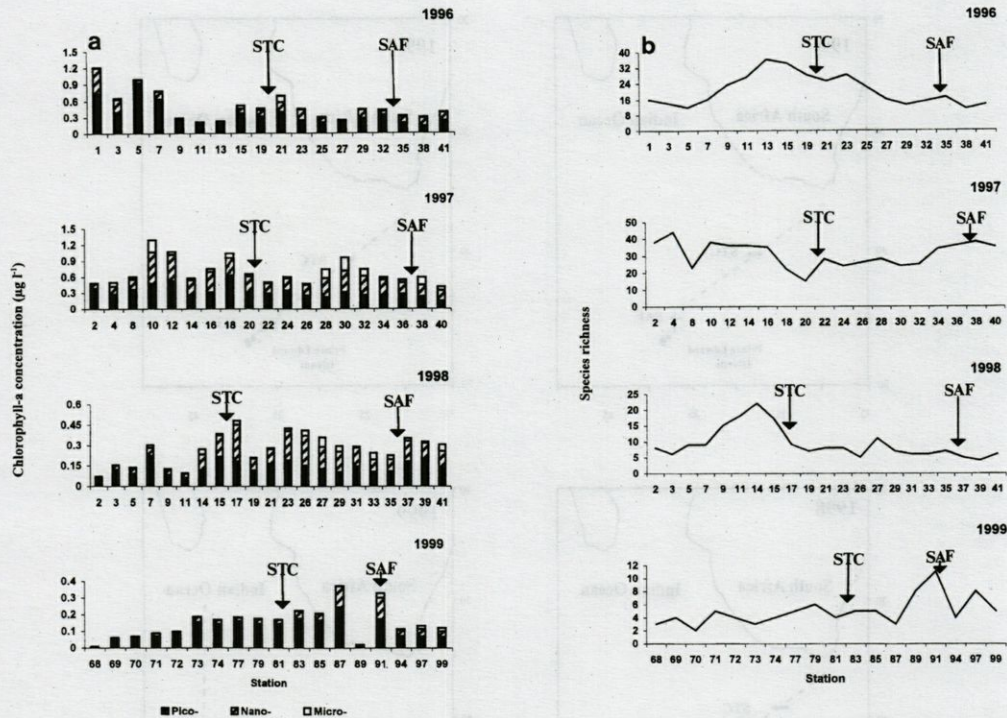


Fig. 2. – Size fractionated chlorophyll-a concentrations (A) and diatom species richness (B) during the four cruises conducted during the Marion Island Oceanographic Survey in (April/May) 1996-1999. STC = Subtropical Convergence; SAF = Subantarctic Front.

pump) made from polyvinylidene fluoride and ceramic materials, and operated at a flow rate of 4 litres per minute. The pump outlet was \pm 5 m below the sea surface and the seawater was supplied to the laboratory through PVC piping. Previous studies have shown that the collection of seawater samples using the shipboard pump does not significantly alter the diatoms community structure as a result of cell rupture or breakage (Froneman *et al.* 1995a). For the taxonomic analysis of the diatom standing stock, a 20 µm mesh filtration unit was connected to the pump outlet and a constant volume of 20 litres of seawater was filtered at each station (Berman & Kimor 1983). The diatoms retained by the filter were preserved in 2% buffered (hexamine) formalin and enumerated and identified in the laboratory using a Nikon TMS inverted microscope operated at X400 magnification. A minimum of 500 cells or the entire sample was counted from each station. Densities were then expressed as cells per litre. The diatoms were identified using the works of Tomas (1996) and Boden & Reid (1989).

To compare diatom communities during the different cruises, non-metric cluster analysis were used in conjunction with the Bray-Curtis similarity index after log transforming [$\log_{10}(x+1)$] species data. Significance levels and sources of difference between the diatom assemblages associated with the different groups of stations were tested using the similarity analysis programs SIMPER and ANOSIM of the Plymouth Routines in Multivariate Research (Primer, Clarke & Warwick 1994) computer package according to the procedure described by Field *et al.* (1982).

In addition to the diatom samples, size fractionated chlorophyll-a concentrations were determined at each station. A 250 ml aliquot seawater sample obtained from the shipboard pump was gently filtered (< 5 cm Hg) through serial filtration into pico- (< 2 µm), nano- (2-20 µm) and microphytoplankton (>20 µm) size fractions. Chlorophyll-a concentrations were then determined fluorometrically (Turner 10AU fluorometer) after extraction in 90% acetone for 24 hours in the dark (Holm-Hansen & Riemann 1978).

RESULTS

Chlorophyll-a

During 1996, total surface chlorophyll-a (chl-a) concentrations ranged from 0.28 to 1.2 µg l⁻¹ (Fig. 2a). Elevated chl-a biomass was recorded at stations occupied in the continental shelf waters south of Africa and in the vicinity of the STC. Here chl-a concentrations exceeded 0.7 µg l⁻¹. Outside these regions total chl-a concentrations were always < 0.5 µg l⁻¹. Picophytoplankton (< 2.0 µm) followed by nanophytoplankton (2-20 µm) were identified as the first and second largest contributors to total chl-a comprising between 58 and 85% and between 13 and 42% of the total pigment, respectively. Microphytoplankton generally comprised <

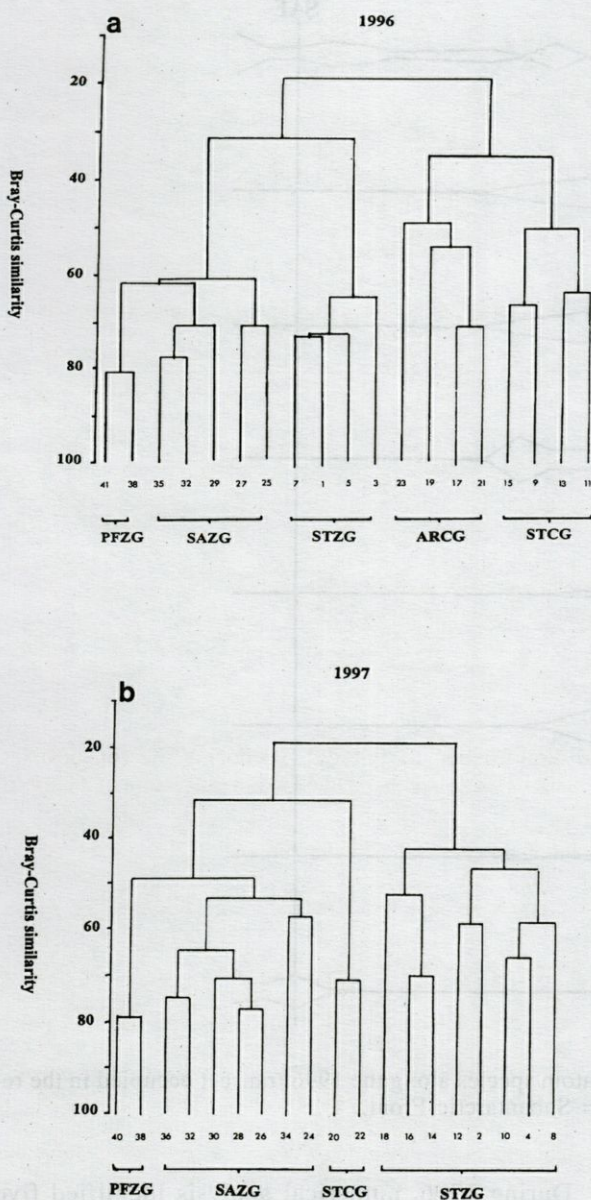


Fig. 3. – Dendrogram showing the classification of stations based on diatom abundance and species composition during the 1996 (a) and 1997 (b) cruises conducted in the region south of Africa in austral autumn. STZG = Subtropical Zone Group; SAZG = Subantarctic Zone Group; STCG = Subtropical Convergence Group; ARC = Agulhas Return Group; PFZG = Polar Frontal Zone Group.

5 % of total pigment. An exception was recorded at the station occupied in the vicinity of the STC (station 21) where microphytoplankton comprised 15 % of the total chl-*a* (Fig. 2a).

Along the 1997 transect total chl-*a* concentration ranged from 0.46 to 1.29 $\mu\text{g l}^{-1}$ (Fig. 2a). Chlorophyll-*a* concentrations were again highest at stations occupied in the continental shelf waters of Africa and in the region of the STC. In addition

to these stations, a minor peak in chl-*a* concentration was also recorded at station 30 located in the Subantarctic Waters (Fig. 2a). Picophytoplankton generally dominated total chl-*a* during the cruise. Exceptions were recorded at stations occupied in the vicinity of the STC and at stations located at the southern boundary of the front where nanophytoplankton were identified as the largest contributor to total chl-*a* concentration. Generally, however, the contribution of nanophytoplankton total pigment was < 35 %. Microphytoplankton comprised < 10 % of the total pigment. Exceptions were recorded at stations 28 and 30 located in the waters north of the SAF and at station 10 located immediately north of the STC where microphytoplankton comprised > 15 % of the total pigment (Fig. 2a).

In 1998, total surface chl-*a* concentrations ranged from 0.09 to 0.47 $\mu\text{g l}^{-1}$ (Fig. 2a). Elevated chl-*a* concentrations were again recorded at stations occupied in the region of the STC. In addition peaks in chl-*a* were also identified at stations located in the Subantarctic waters (stations 23 and 26) and at stations south of the SAF. At these stations nanophytoplankton were identified as the largest contributor to total chl-*a* concentration. Outside this region, however, picophytoplankton dominated total chl-*a* biomass. The contribution of microphytoplankton total pigment concentration was generally < 5 %. Exceptions were recorded at station 26 and 27 located at the southern boundary of the STC and at station 41 located in the waters surrounding the Prince Edward Islands where microphytoplankton comprised up to 10 % of the total pigment (Fig. 2a).

Total chlorophyll-*a* concentrations during the 1999 cruise ranged from 0.05 to 0.38 $\mu\text{g l}^{-1}$ (Fig. 2a). No enhancement in chl-*a* concentration was observed at stations occupied in the vicinity of the STC (Fig. 2a). Highest chl-*a* concentration was recorded at station 87 located in the Subantarctic Zone Waters and at station 91 in the region of the SAF (Fig. 2). Throughout the cruise, picophytoplankton were identified as the largest contributor to total pigment comprising between 65 and 93 % of the total. Nanophytoplankton contribution ranged between 2 and 36 % of the total pigment. Microphytoplankton contribution to total pigment was always < 2 % of the total (Fig. 2a).

Species richness

Total number of diatom species identified during the four cruises was highly variable. Generally, the highest number of diatom species (up to 44 species) was recorded in the waters north of the STC, south of Africa (Fig. 2b). The lowest number of species, generally < 8, was consistently recorded along the transect occupied in the mid-Indian

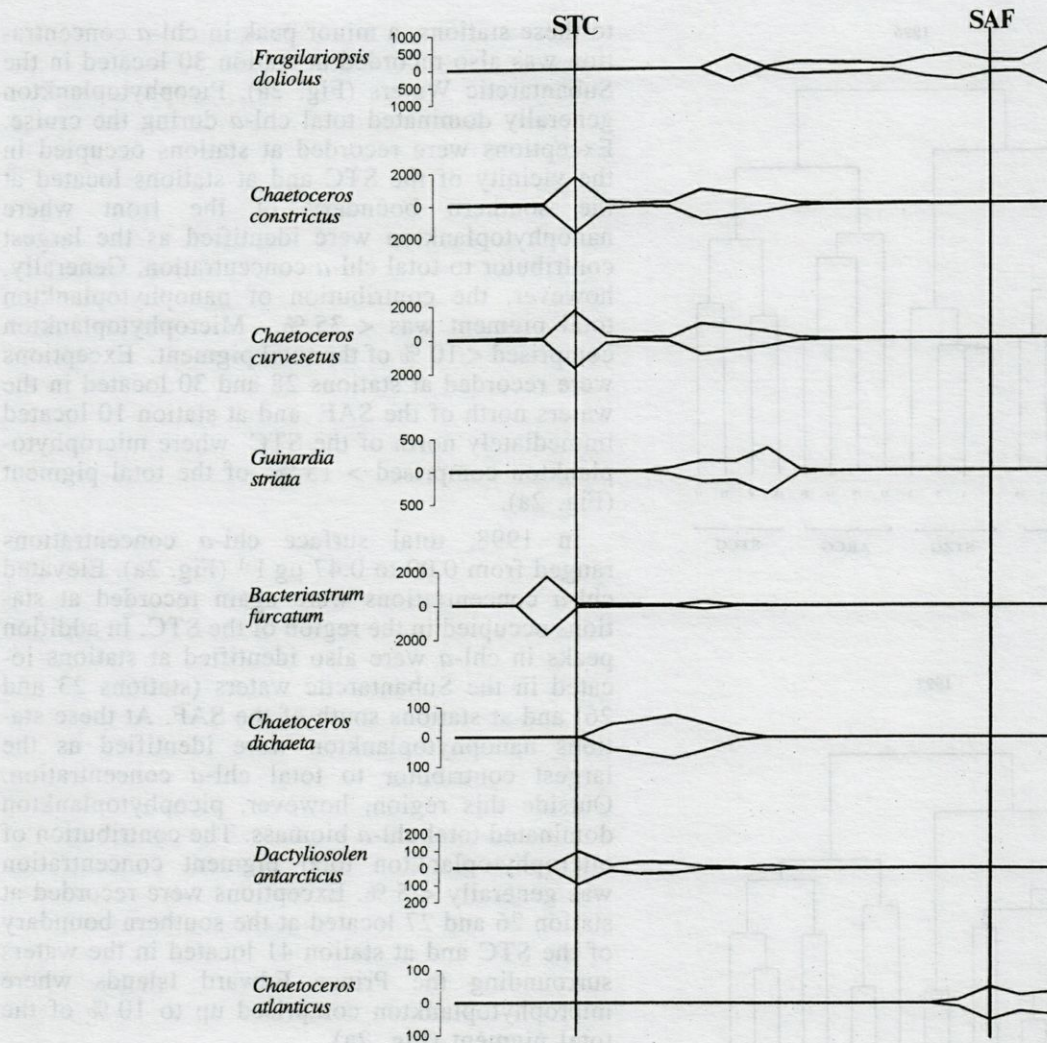


Fig. 4. – Distribution of the eight most numerically abundant diatom species along the 1996 transect occupied in the region south of Africa. STC = Subtropical Convergence; SAF = Subantarctic Front.

Ocean (Fig. 2b). Minor peaks in diatom species identified were associated with the SAF during all four cruises. Diatom species recorded during the four cruises are listed in Appendix 1.

Numerical analyses

Results of the numerical analyses conducted on the diatom data collected during the four cruises is shown in Fig. 3 and 6. Since the majority of the diatom groups were identified with a specific water mass or feature, the groups are designated by the name of the water mass or feature with which they are associated [water masses are identified after Hoffmann (1985) and Boden *et al.* (1988)]. Where groupings did not correspond to a specific oceanographic feature, the groupings are designated numerical values.

During 1996, numerical analysis identified five diatom groupings (Fig. 3a). One way ANOVA similarity test showed that the groups were significantly different from one another ($P < 0.05$). The correlation between the geographic position of the stations along the transect and groupings identified was perfect. The five groupings identified were: The Subtropical Zone Waters Group (STZG), the Agulhas Return Current Group (ARCG), the Subantarctic Zone Group (SAZG) and the Polar Front Zone Group (PFZG). In addition, a diatom grouping was associated with the STC proper and is as a consequence, designated the Subtropical Convergence Group (STCG). The distribution patterns of the eight most numerically abundant diatom species (average abundances within each grouping are indicated in brackets) is shown in Fig. 4. SIMPER analysis showed that these species accounted for up to 53 % of the dissimilarity between the groupings identified with the numerical analysis.

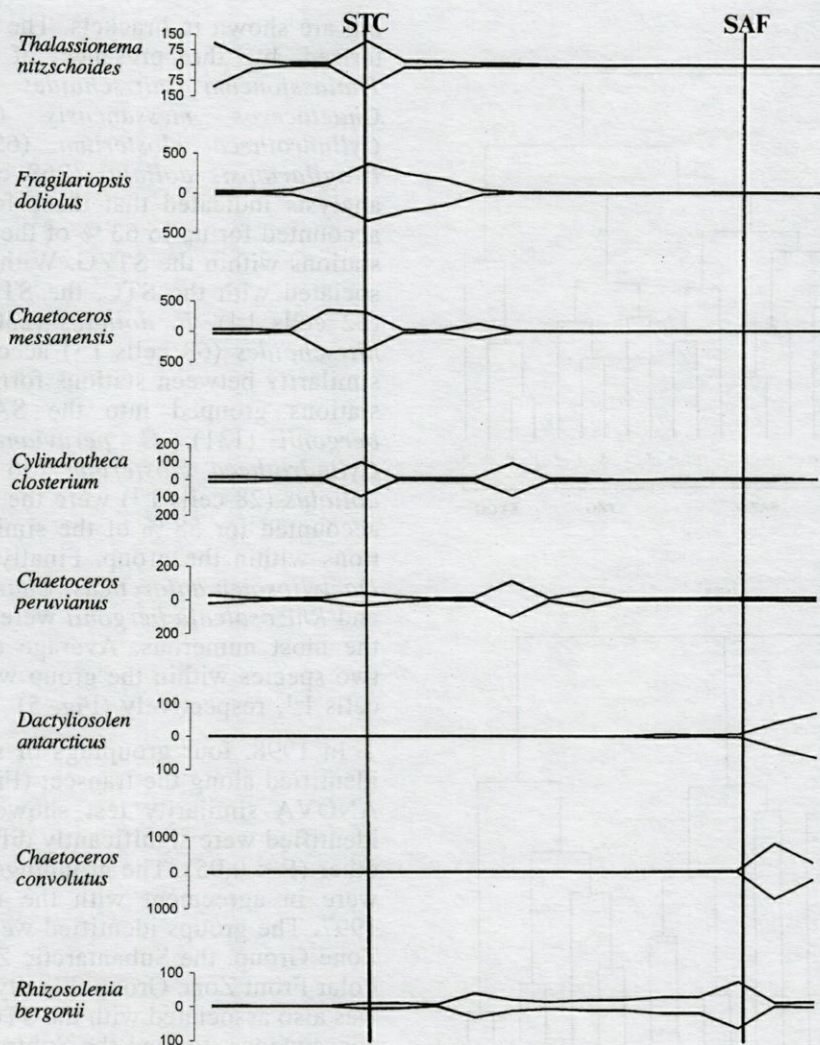


Fig. 5. – Distribution of the eight most numerically abundant diatom species along the 1997 transect occupied in the region south of Africa. STC = Subtropical Convergence; SAF = Subantarctic Front.

The STZG group was characterised by the predominance of three diatom species, *Bacteriastrum furcatum*, *Chaetoceros curvestus* and *Chaetoceros constrictus*. Average abundances of these three species within the group were 103, 198 and 90 cells l^{-1} , respectively. SIMPER analysis indicated that these three diatom species accounted for up to 43 % of the similarity between stations in the group. Within the grouping associated with the Agulhas Return Current (ARCG), diatom cells counts were almost entirely dominated by *B. furcatum*, *C. constrictus* and *C. curvestus*. The SAZG was dominated by four diatom species, *Guinardia striata* (238 cells l^{-1}), *Chaetoceros dictyota* (68 cells l^{-1}) and *C. curvestus* (367 cells l^{-1}), which accounted for up to 56 % of the similarity between stations within the group. The grouping of stations associated with the STC, the STCG, comprised three main species, *C. constrictus* (1350 cells l^{-1}), *C. curvestus* (1650 cells l^{-1}) and

Dactyliosolen antarcticus (189 cells l^{-1}) (Fig. 4). Finally within the PFZG, two species predominated, *C. atlanticus* and *Fragilariopsis doliolus*. Average abundances of these two diatom species within the grouping were 90 and 286 cells l^{-1} , respectively. SIMPER analysis showed that these two diatom species accounted for up to 48 % of the similarity between stations within the grouping.

Hierarchical cluster analysis identified four groupings of stations along the 1997 transect (Fig. 3b). One way ANOVA showed that all four groups identified were significantly different from one another ($P < 0.05$). The correlation between the geographic position and groupings identified was again, perfect. The first group contained all those stations found north of the STC and is, therefore, designated the Subtropical Zone Group. The second groupings comprised those stations which were in the immediate proximity to the STC and is therefore, designated the Subtropical Convergence

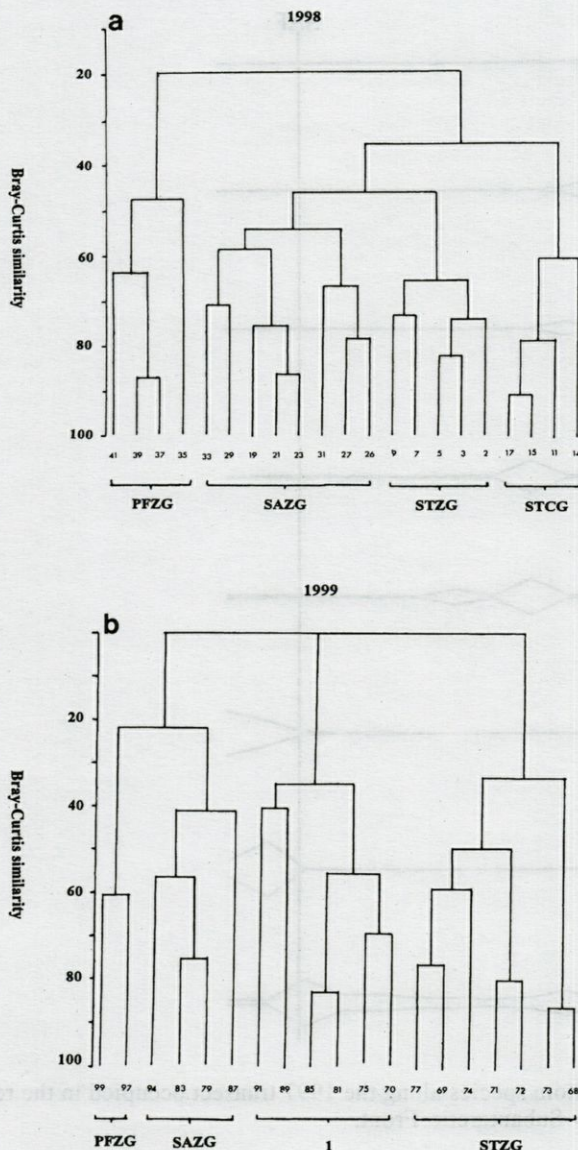


Fig. 6. – Dendrogram showing the classification of stations based on diatom abundance and species composition during the 1998 (A) and 1999 (B) cruises occupied in the region south of Africa and in the mid Indian Ocean in austral autumn. STZG = Subtropical Zone Group; SAZG = Subantarctic Zone Group; STCG = Subtropical Convergence Group; PFZG = Polar Frontal Zone Group.

Group (STCG). Finally groups three and four contained those stations located in the Subantarctic Zone and stations within the Polar Front Zone. As a consequence the two groups are designated the Subantarctic Zone and Polar Front Zone Groups (Fig. 3b).

The distribution patterns of the eight most numerically abundant diatom species accounting for up to 65 % of the dissimilarity between the diatom groupings identified is shown in Fig. 5. Average abundances of diatom species within each group-

ing are shown in brackets. The STZG was characterised by the presence of 4 main species, *Thalassionema nitzschoides* (84 cells l^{-1}), *Chaetoceros messanensis* (142 cells l^{-1}), *Cylindrotheca closterium* (65 cells l^{-1}) and *Fragilariopsis doliolus* (268 cells l^{-1}). SIMPER analysis indicated that these four diatom species accounted for up to 63 % of the similarity between stations within the STZG. Within the grouping associated with the STCG, the STZG, *C. peruvianus* (32 cells l^{-1}), *F. doliolus* (230 cells l^{-1}) and *T. nitzschoides* (68 cells l^{-1}) accounted for 34 % of similarity between stations forming the STCG. At stations grouped into the SAZG, *Rhizosolenia bergonii* (131), *C. peruvianus* (67 cells l^{-1}), *Cylindrotheca closterium* (36 cells l^{-1}) and *F. doliolus* (28 cells l^{-1}) were the most abundant and accounted for 58 % of the similarity between stations within the group. Finally within the PFZG, *Dactyliosolen antarcticus*, *Chaetoceros convolutus* and *Rhizosolenia bergonii* were identified as being the most numerous. Average cells counts of the two species within the group were 63, 328 and 32 cells l^{-1} , respectively (Fig. 5)

In 1998, four groupings of stations were again identified along the transect (Fig. 6a). A one way ANOVA similarity test showed that the groups identified were significantly different from one another ($P < 0.05$). The groupings identified in 1998 were in agreement with the results obtained in 1997. The groups identified were: the Subtropical Zone Group, the Subantarctic Zone Group and the Polar Front Zone Group. Finally a diatom grouping was also associated with the STCG proper and is as a consequence, termed the Subtropical Convergence Group (Fig. 6a).

Fig. 7 shows the distribution patterns of the eight most numerically abundant diatom species along the 1998 transect. SIMPER analysis indicated that these species were responsible for up to 53 % of the dissimilarity between groupings identified. In the STZG, three diatom species, *Dactyliosolen antarcticus* (170 cells l^{-1}), *Banquisia belagicae* (90 cells l^{-1}) and *Fragilariopsis kerguelensis* (1176 cells l^{-1}) dominated cells counts. Collectively, these species accounted for 39 % of the similarity between stations making up the STZG. Within the SAZG, *Rhizosolenia bergonii* (21 cells l^{-1}), *F. kerguelensis* (706 cells l^{-1}), *Thalassiosira antarcticus* (106 cells l^{-1}), *D. antarcticus* (131 cells l^{-1}) and *C. atlanticus* (108 cells l^{-1}) were identified as being the most numerous. These species accounted for 56 % of the similarity between stations making up the STZG. *Hemialus cuniformis* (66 cells l^{-1}), *C. atlanticus* (98 cells l^{-1}) and *F. kerguelensis* (767 cells l^{-1}) were identified as the most abundant at stations occupied within the PFZG (Fig. 7). Combined these three species accounted for up to 39 % of the similarity between stations within the group. Finally within

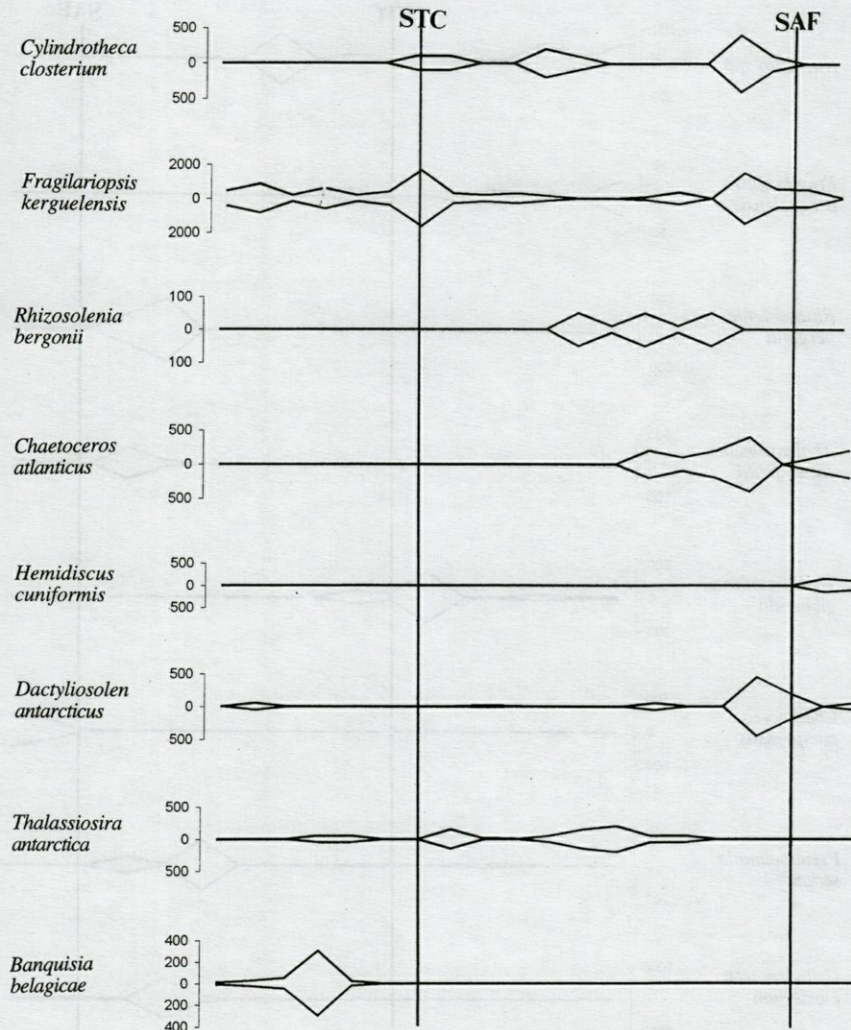


Fig. 7. – Distribution of the eight most numerically abundant diatom species along the 1998 transect occupied in the region south of Africa. STC = Subtropical Convergence; SAF = Subantarctic Front.

the grouping associated with the STC, the STZG, *F. kerguelensis* (1176 cells l^{-1}) and *C. atlanticus* (237 cells l^{-1}) dominated cells counts (Fig. 7).

During the 1999 cruise, hierarchical cluster analysis identified four groupings of stations along the transect (Fig. 6b). The first group contained those stations located at the northerly section of the transect and is designated the Subtropical Zone Group (STZG). The second grouping comprised those stations located immediately north and south of the STC including those stations in the vicinity of the front. Since the grouping was not associated with any specific feature or water mass, the grouping is designated Group 1. Group three contained stations located within the Subantarctic Zone, and group 4 stations found south of the SAF. These groupings are designated as the Subantarctic Zone Group (SAZG) and the Polar Front Zone Group (PFZG). One way ANOVA similarity test showed that only STZG and PFZG were significantly different from one another ($P < 0.05$).

The distribution patterns (average abundances within the grouping indicated in brackets) of the 8 most numerically abundant species along the transect occupied in 1999 is shown in Fig. 8. SIMPER analysis indicated that these species were responsible for up to 38 % of the dissimilarity between the grouping identified. Within the STZG, *Fragilariopsis kerguelensis* (7 cells l^{-1}), *Thalassiosira gibberula* (31 cells l^{-1}) and *Nitzschia* spp. (33 cells l^{-1}) were identified as being the most abundant (Fig. 8). Combined these species accounted for 95 % of the similarity between stations making up the STZG. Within the grouping comprising stations located to the north and south of the STC, *T. gibberula*, *Rhizosolenia bergonii*, *Nitzschia* spp, *Thalassionema frauenfeldii* and *Pseudoeunotia seriata*. Average cells counts of these four species were 11, 135, 926, 86 and 926 cells l^{-1} , respectively. At stations comprising the SAZG, *Pseudoeunotia seriata*, *Cylindrotheca closterium*, *R. bergonii* and *Thalassionema frauenfeldii* dominated. Finally

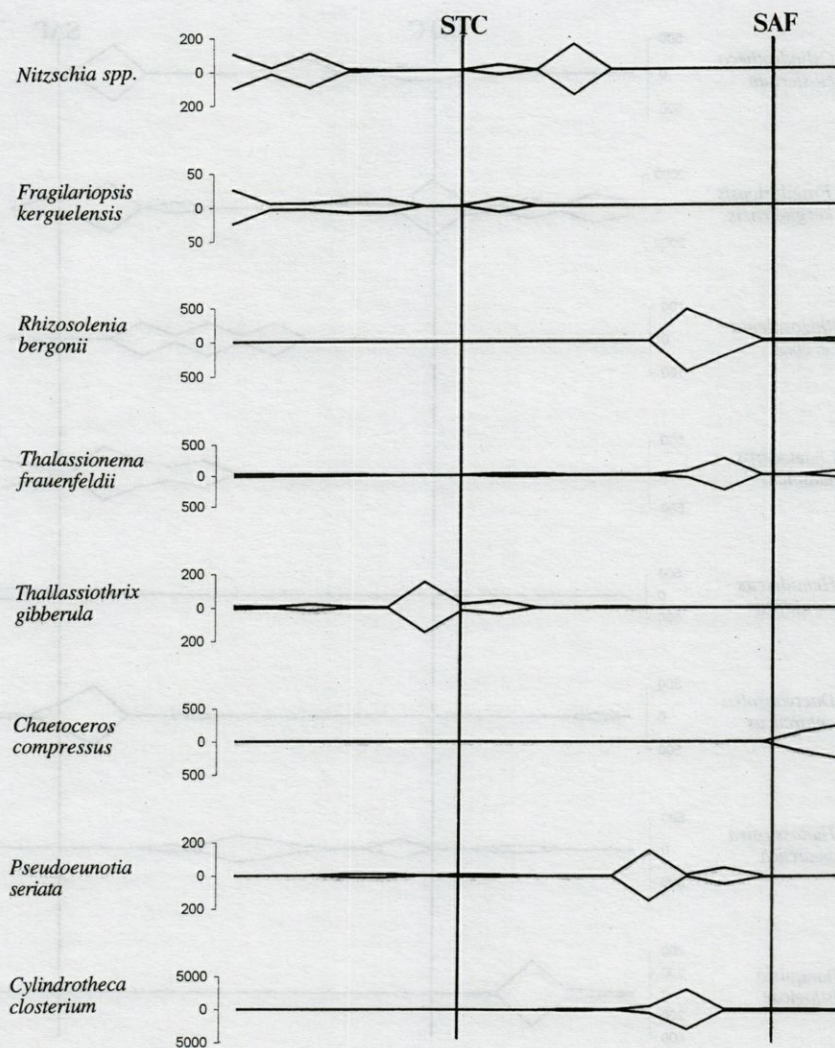


Fig. 8. – Distribution of the eight most numerically abundant diatom species along the 1999 transect conducted in the mid-Indian Ocean in autumn. STC = Subtropical Convergence; SAF = Subantarctic Front.

within the PFZG, *Chaetoceros compressus* (250 cells l^{-1}) and *Cylindrotheca closterium* (50 cells l^{-1}) were identified as being the most abundant. Combined SIMPER analysis showed that these two species accounted for 63 % of the similarity between stations within the group (Fig. 8).

DISCUSSION

Pigment concentrations

During the three transects occupied in the region south of Africa in autumn, enhanced chlorophyll-*a* (chl-*a*) concentrations were recorded in the vicinity of the Subtropical Convergence (STC) (Fig. 2a). Elevated biological activity in the vicinity of the STC in different sectors of the Southern Ocean is

well documented (Laubscher *et al.* 1993, Sullivan *et al.* 1993, Froneman *et al.* 1995a, 1999, Bradford-Grieve *et al.* 1997). Chlorophyll-*a* concentrations recorded in the vicinity of the STC during this investigation, are in the same range as values reported in summer (Laubscher *et al.* 1993; Froneman *et al.* 1995a, 1995b) suggesting little seasonality in phytoplankton biomass. This result is in agreement with studies conducted in the vicinity of the STC in the region near New Zealand (Bradford-Grieve *et al.* 1997, Chang & Gall 1998). No biological enhancement was recorded in the vicinity of the STC in the mid-Indian Ocean. There is evidence to suggest that the elevated chl-*a* concentration recorded in the vicinity of the STC is the result of increase *in situ* phytoplankton production resulting from increased water column stability, macronutrient concentrations and iron availability (Laubscher *et al.* 1993, Comiso *et al.* 1993, Bradford-Grieve *et al.* 1997, Froneman *et al.* 1999).

While the absence of chl-*a* signal within the mid-Indian Ocean may reflect biological interactions such as grazing by zooplankton, preliminary data collected during the 1999 cruise suggested that zooplankton biomass in the region of the front was in the same order of magnitude as values reported in the region south of Africa (Pakhomov *et al.* 2000a). We can only speculate on the potential causes for the low chl-*a* concentrations recorded in vicinity of the STC in the mid-Indian Ocean. Weeks and Shillington (1994) proposed that the elevated chl-*a* concentrations recorded in the vicinity of the STC were the result of the mixing of warm-nutrient poor Subtropical waters with the colder Subantarctic waters which results in density stratification thus creating conditions favourable for phytoplankton growth. Indeed, chl-*a* concentrations in the region of the front have been shown to be strongly correlated to frontal intensity (Weeks & Shillington 1996). Belkin (1989) showed that the temperature gradient across the STC in the mid-Indian Ocean decreases. Under these conditions, density stratification would also be reduced resulting in less favourable conditions for phytoplankton growth. Alternatively, it is possible that the absence of a chl-*a* signal in the vicinity of the STC in the mid-Indian Ocean may reflect increased wind stress that would reduce phytoplankton growth (Weeks & Shillington, 1994, Froneman *et al.* 1999).

Finally the elevated chl-*a* concentrations recorded in the continental shelf waters south of Africa in 1996 is in agreement with previous studies conducted in the region (Laubscher *et al.* 1993; Froneman *et al.* 1999). According to Boden *et al.* (1988), the elevated chl-*a* concentrations recorded in continental shelf waters of southern Africa is the result of the transportation of phytoplankton cells in the Agulhas Current to the region. Alternatively, it is possible that the elevated chl-*a* concentrations recorded in the shallow continental shelf waters are the result of increased *in situ* phytoplankton production resulting from increased nutrient availability (Laubscher *et al.* 1993).

Species richness

Species richness during the four surveys was highest in the waters immediately north of the STC south of Africa (Fig. 2b). The increase in the number of diatom species in this region reflects the complex oceanographic regime. South of Africa, two oceanographic features are encountered, the Agulhas Current (which later retroflects to form the Agulhas Return Current (ARC)) and the Subtropical Convergence (Lutjeharms & Vallentine 1984, Duncombe Rae 1989, Lutjeharms *et al.* 1993). Boden *et al.* (1988) showed that warm subtropical diatom species (for example *Ceratulina pelagica*) may be transported in the Agulhas Cur-

rent to the region south of Africa. It is worth noting that in 1996, a distinct diatom grouping was associated with the Agulhas Return Current (Fig. 3a). The low number of diatom species recorded in the mid-Indian Ocean suggests that water mass modification may have occurred as no indicator species of Agulhas Current waters were recorded (Appendix 1). Following this, the low number of species recorded along the transect in mid-Indian Ocean likely reflects the low nutrient availability of Subtropical waters which limits the growth of large phytoplankton cells (Laubscher *et al.* 1993; Froneman *et al.* 1999).

The diatom species recorded during this investigation are similar to studies conducted in the region during summer (Boden *et al.* 1988; Froneman *et al.* 1995a, 1995b). It should be noted, however, that while similar species were recorded during the four cruises, there was considerable inter-annual variability in the dominants. In the absence of ecophysiological data, we cannot determine the cause of the variability in the dominants. However, the variability likely reflects the complex hydrological processes in the region that favour the growth of individual species.

Numerical analyses

Results of the numerical analysis indicate that distinct diatom groupings were associated with the different water masses in the south-east Indian Ocean. This result is in agreement with previous studies conducted in different sectors of the Southern Ocean during both summer and winter (Froneman *et al.* 1995a, 1995b, Fiala *et al.* 1998). Differences in the species composition within the different water masses reflect the spatial and temporal variations in the Southern Ocean pelagic ecosystem (Boden *et al.* 1988, Fiala *et al.* 1998).

In contrast to the region south of Africa, the STC did not appear to represent a biogeographic barrier to the distribution of diatoms in the mid-Indian Ocean. This result is in agreement with a similar study conducted in the mid-Atlantic Ocean (Barange *et al.* 1998). South of Africa, the STC is characterised by a sharp horizontal gradient in temperature which at times may be as high as 3°C per 10 km (Lutjeharms & Emery 1983). Given the extreme temperature gradient across the front, it is not surprising that it represents a strong biogeographic boundary to the distribution of plankton. In contrast in the mid-Indian Ocean, the temperature gradient across the STC decreases (Belkin 1989). Due to this decrease plankton species are able to penetrate the front. Alternatively, it is possible that the surface expression of the STC in the mid-Indian Ocean is intermittent rather than weak as demonstrated in the mid-Atlantic Ocean (Lutjeharms *et al.* 1993, Barange *et al.* 1998). Weeks and Shillington (1996) showed that pigment

levels in the region of the STC were largely a function of the frontal intensity. The variability in intensity of the front may partially explain the inter-annual variability in pigment concentrations in the region of the STC as demonstrated by the Coastal Zone Color Scanner (CZCS) measurements (Weeks & Shillington 1994). It should be noted, however, that south of Africa diatoms may on occasions be transported across the STC by warm-core eddies shed from the Agulhas Return Current (Froneman *et al.* 1997).

Distinct diatom assemblages were associated with the STC proper during the three transects conducted south of Africa. This result is in agreement with a previous study conducted in the mid-Atlantic Ocean (Barange *et al.* 1998). Barange *et al.* (1998) suggested that the presence of a unique plankton community associated with the STC was the result of specific hydrological features of the frontal zone which allowed the presence of species from different water masses to occur in the immediate proximity of the front. During a study conducted in the Atlantic sector of the Southern Ocean, Froneman *et al.* (1995b) identified a distinct phytoplankton community associated with the Antarctic Polar Front (APF). The community associated with the front comprised species from the water masses to the north and south of the front. During the present study, the microphytoplankton groupings associated with the STC contained indicator species of both Subtropical Zone (*Hemialus hauckii*) and Subantarctic Zone waters (*Rhizosolenia bergonii*) (Boden *et al.* 1988). These data are consistent with the findings of Frontier (1977) who suggested that interaction of different water masses in the region of frontal systems may result in a unique and specific fauna.

The importance of the Subantarctic Front (SAF) as a barrier to the distribution of plankton in the Southern Ocean is not well documented. Although the front appears to represent an important barrier to the distribution of plankton in the Atlantic and Pacific sectors of the Southern Ocean (Froneman *et al.* 1995b, Pakhomov & McQuaid 1996, Pakhomov *et al.* 2000b), recent studies conducted in the region of the Prince Edward Islands in the Indian sector of the ocean failed to identify the front as a biogeographic boundary (Froneman & Pakhomov 1998). The absence of the front as a biogeographic boundary to the distribution of plankton appeared to be related to both cross frontal mixing and variability in the surface expression of the front, which transferred plankton across the front. Possibly, eddies generated by instabilities in the flow of the Antarctic Circumpolar Current may also have contributed to the transfer of species across the SAF (Ansorge *et al.* 1999, Froneman *et al.* 1999). During the present study the SAF always represented a strong biogeographic boundary to the distribution of diatoms. Oceanographic studies conducted in

the vicinity of the Prince Edward Islands have demonstrated that the flow pattern of the ACC in the region of the islands comprises two distinct components. Upstream of the islands (west), the flow pattern of the ACC appears to be substantially affected by bathymetry (Froneman *et al.* 1999). This results in less disturbances in the flow pattern of the ACC (Froneman *et al.* 1999). As a consequence of the reduced disturbances, cross frontal mixing is less pronounced resulting in plankton not being transported across the SAF. In contrast, downstream (east) of the islands the flow of the ACC is highly disturbed. This disturbance generates cross frontal mixing and the formation of eddies which transfer plankton species across the SAF (Ansorge *et al.* 1999, Froneman *et al.* 1999). These facts highlight the spatio variability in the importance of fronts as barriers to the distribution of plankton.

CONCLUSION

Results of the study suggest that the major oceanic fronts south of Africa, in particular the STC, are characterised by biological enhancement and represent strong biogeographic boundaries to the distribution of diatoms. In contrast in the mid-Indian Ocean, the STC did not demonstrate increased chlorophyll-*a* concentrations and was not important in limiting the distribution of diatom species. Differences between the two regions appears to be related to the intensity of the STC. It is likely that the importance of the STC as biogeographic boundary to the distribution of diatoms in the mid-Indian Ocean will display marked spatial variability. For example in the region of the Crozet Plateau, the SAF converges with the STC resulting in a frontal feature with a sharp horizontal temperature gradient (Belkin 1989). Here, the coalescing of the two fronts would likely result in the feature representing a strong biogeographic barrier. Finally, although the data presented here represent only a small portion of the plankton community, it is worth noting that the results obtained here are in agreement with studies that have investigated the distribution of zooplankton across the major frontal regions of the Southern Ocean (Pakhomov & McQuaid 1996, Young *et al.* 1996, Barange *et al.* 1998, Pakhomov *et al.* 2000b).

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Appendix 1

1996

Actinocyclus octonarius Ehrenburg
Asteromphalus hookeri Ehrenburg
A. roperianus (Greyville) Ralfsin Prichard
Banquisia belgicae Paddock
Ceratualina pelagica Hendy
Chaetoceros affinis Lauder
C. atlanticus Cleve
C. convolutus Castracane
C. constrictus Gran
C. dictaeta Ehrenburg
C. didymus Ehrenburg
C. messanensis Castracane
C. peruvianus Brightwell
Corethron criophilum Castracane
Coscinodiscus concinniformis Simonsen
Cylindrotheca closterium Ehrenburg
Dactyliosolen antarcticus Castracane
Fragilariopsis doliolus Medlin & Sims
F. kerguelensis Hustedt
Grammatophora marina Kutzling
G. angulosa H. Pergallo
Guinardia striata Hasle
G. cylindrus Hasle
Haslea gigantea Simonsen
Hemialus hauckii Grunow
Hemidiscus cuneiformis Wallich
Melosira sol Kutzling
Nitzschia bicapitata Cleve
Planktoniella sol Schutt
Proboscia alata Brightwell
P. indica Ehrenburg
Pseudo-nitzschia spp.
Pseudoeunotia seriata H. Pergallo
Pleurosigma directum Grunow
Rhizosolenia bergonii H. Pergallo
R. hebetata f. semispina Gran
R. simplex Karsten
Thalassionema nitzschioides Grunow
T. frauenfeldii Hallegraeff
Thalassiothrix longissima Cleve & Grunow
T. antarctica Hasle

1997

Actinocyclus octonarius
Asteromphalus hookeri
A. marylandica Ehrenburg
A. roperianus
Banquisia belgicae
Ceratualina pelagica
Chaetoceros affinis
C. atlanticus
C. convolutus
C. constrictus
C. dictaeta
C. didymus
C. messanensis
C. peruvianus
Corethron criophilum
Coscinodiscus concinniformis
Cylindrotheca closterium
Ditylum sol Grunow
Dactyliosolen antarcticus
Fragilariopsis doliolus
F. kerguelensis
Grammatophora marina
G. angulosa
Guinardia striata
G. cylindrus
Hemialus hauckii
Hemidiscus cuneiformis
Melosira sol
Nitzschia bicapitata
Planktoniella sol
Proboscia alata
P. indica Hasle
Pseudoeunotia spp.
Pseudoeunotia seriata
Pleurosigma directum
Rhizosolenia bergonii
R. hebetata f. semispina
Synedra indica Taylor
Thalassionema nitzschioides
T. frauenfeldii
Thalassiothrix longissima
T. antarctica
T. heteromorpha Hallegraeff

1998

Actinocyclus octonarius
Asteromphalus marylandica
Asteromphalus hookeri
A. roperianus
Bacteriastrum furcatum Shadbolf
Ceratualina pelagica
C. atlanticus
C. compressus
C. decepiens
C. didymus
C. messanensis
C. peruvianus
C. convolutus
Ceratualina pelagica
Corethron criophilum
Cosconodiscus spp
Cylindrotheca closterium
Dactyliosolen antarcticus
Fragilariopsis spp
Fragilariopsis doliolus
F. kerguelensis
Guinardia striata
Haslea gigantea
Hemialus hauckii
Odontella longicruris Hoban
Planktoniella sol
Pleurosigma directum
Pseudoeunotia seriata
Rhizosolenia bergonii
Proboscia alata
P. indica
Skeltonema costatum Cleve
Synedra indica
Thalassionema nitzschioides
T. frauenfeldii
Thalassiothrix longissima

1999

Asteromphalus heptactis Ralfs
Chaetoceros atlanticus
C. dictaeta
C. concavicornis Mangin
C. neglectus
Corethron criophilum
Dactyliosolen antarcticus
Fragilariopsis kerguelensis
Nitzschia spp
N. bicapitata
Proboscia indica
Pseudoeunotia seriata
Rhizosolenia bergonii
Thalassionema nitzschioides
Thalassiosira giberula Hasle
Thalassiothrix antarctica
T. longissima

SPECIES BODY-SIZE DISTRIBUTION AND SPATIAL SCALE IN IBERIAN ANTS

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ANT ASSEMBLAGES
BODY SIZE
IBERIAN PENINSULA
MACROECOLOGY
SPATIAL SCALING

ABSTRACT – The specific body size distribution (BSD) for Iberian ants (workers) was compiled and compared to subsamples of that distribution at four smaller scales, from very local samples to species-lists for autonomous regions. The BSD of Iberian ants was right-skewed on a log scale and approached normality. The mean dry body mass \pm s.d. was $0,93 \pm 1,55$ mg and the median 0,31 mg. Neither local samples nor samples at intermediate scales differed from random samples from the underlying Iberian distribution in median or skewness. Limited geographical scope or a misdirected measure (single individual mass) in this study could explain why we did not find the pattern of a previously reported difference in BSD of local samples as compared to regional samples in mammals. The BSD of local samples in Iberian ants was not influenced by latitude.

COMMUNAUTÉS DE FOURMIS
TAILLE CORPORELLE
PÉNINSULE IBÉRIQUE
MACROÉCOLOGIE
ÉCHELLE SPATIALE

RÉSUMÉ. – La distribution spécifique de la masse corporelle des ouvrières de Fourmis ibériques est recensée et comparée à celle de sous-échantillons à différentes échelles spatiales allant du niveau local au niveau de listes spécifiques de communautés régionales. La distribution des masses en logarithmes est biaisée à droite mais approche d'une normale. La moyenne (\pm p.s.) des masses corporelles (matière sèche) est de $0,93 \pm 1,55$ mg et la médiane de 0,31 mg. Les échantillons à différentes échelles ne diffèrent pas d'échantillons aléatoires de la distribution ibérique, en ce qui concerne la médiane et la skewness. La restriction géographique limitée à la Péninsule Ibérique, ou bien une mesure non appropriée dans notre étude pourraient expliquer l'absence du pattern connu chez les Mammifères, dans le sens d'une différence entre les masses corporelles des échantillons locaux comparées à celles des échantillons régionaux. La masse corporelle des Fourmis ibériques ne semble pas influencée par la latitude.

INTRODUCTION

The distribution of body size of many animal species, from mammals (Brown & Nicoletto 1991, Maurer *et al.* 1992), birds (Blackburn *et al.* 1990, Maurer *et al.* 1992, Blackburn & Gaston 1994a), fish (Brown *et al.* 1993) to insects (Schoener & Janzen 1968, Morse *et al.* 1988, Basset & Kitching 1991, Blackburn *et al.* 1990, Siemann *et al.* 1996, Novotny & Kindlmann 1996) and intertidal invertebrates (Navarrete & Menge 1997) shows a distinct skewed pattern. There are relatively more small than large species. This is invariable when body size is plotted on a log scale. Furthermore, when body-size distribution (BSD) on different spatial scales are compared, differences have emerged: BSD from local communities is markedly

different from BSD on a larger or global scale. The shape of the BSD in North American mammals changes from log-skewed on a continental scale to log-uniform at smaller scales, with an intermediate pattern on a regional scale (Brown & Maurer 1989, Brown & Nicoletto 1991); this has also been indicated for Australian mammals (Blackburn & Gaston 1994b). A scale-related difference in BSD for aquatic communities has been shown by Fenchel (1993). We are not aware of other published analyses of systematic differences in BSD between local and regional assemblages. The generality of this scale-related pattern is unknown.

Here we document the interspecific body size distribution of Iberian ants and test the validity of the described pattern of change in the BSD with increasing spatial scale, from local habitats (< 1 km²) to Iberian Peninsula level (580.000 km²). Our

study aimed to determine (1) the shape of the body size distribution for the ant species of the Iberian Peninsula, (2) trends of change of that distribution according to spatial scale, (3) discover possible methodological and temporal biases in the data base used.

MATERIAL AND METHODS

Peninsular assemblage of Iberian ants: a species list of Iberian ants was compiled, using different sources. The data base for the Iberian Peninsula was based on Collingwood (1978), updated with all posterior papers concerning Iberian ants, with descriptions of new species and/or revisions of species-groups. We added 9 still undescribed species. A two-step process was followed: (1) head length (HL) of workers was directly measured under the stereoscopic microscope to the nearest 0.006 mm for the smallest ants (up to 1.3 mm HL; $n = 110$ species) or nearest 0.013 mm for bigger ants ($n = 32$ species); for 95 species HL was taken directly from published information; (2) dry body mass was then obtained by applying the transformation from Kaspari & Weiser (1999): dry body mass in g (M) = $(4.7297 \times 10^{-4}) \text{HL}^{3.179}$. Data are presented in mg instead of g.

When analysing body size distributions authors use an average adult body mass, sometimes for a specific sex (females in birds, Blackburn & Gaston 1994). Roughly a third of Iberian species show a marked variation in size, originating from true polymorphism (*sensu* Wilson 1953) (38 species, from *Camponotus*, *Messor*, *Proformica*, *Cataglyphis*, *Pheidole*) or due to highly variable monomorphism (some *Tapinoma*, *Formica*, *Lasius*, *Aphaenogaster*). In polymorphic species, the minimum and maximum were taken and the mean used. It should be noted that in so doing three non-existent body sizes, from the purely dimorphic species of *Pheidole* were used; we assume that three in 237 is too small a proportion to change the shape of the BSD. Log-transformed body masses are used throughout the paper unless otherwise stated.

Local and other spatial scale assemblages of Iberian ants: Several distinct spatial scales were compared. The smallest scale (scale 1) studied was the range 1-10 km². 17 species lists were compiled from published information for local (=homogeneous habitat) samples and data restricted to those papers where an exhaustive effort had been made to detect the maximum number of species; usually covering at least one or more sampling years. A second scale (scale 2; $n = 9$) was from 100 to 1000 km², scale 3 ($n = 6$) from 1000 to 10000 km² and scale 4 ($n = 4$) from 10000 to 100000 km². Scale 5 comprised the entire Iberian Peninsula (581.600 km²). A BSD for every sample at each different scale was generated, including the Iberian Peninsula data base.

Latitudinal trend: Geography may influence insect size patterns. Schoener & Janzen (1968) found temperate ants to be smaller than tropical ants. In Europe, Cushman *et al.* (1993) found that body size in European ants shows a latitudinal trend: body size increases significantly with increasing latitude. To determine whether this trend could interact with BSD we regressed mean

body size against latitude. Only the very local samples (scale 1), assumed to be a single point (=without range) in space, were used.

Statistical analysis: A formal test of normality for the whole log-transformed BSD for Iberian ants was done with a Lilliefors test, an equivalent of the widely used Kolmogorov-Smirnov test, but preferable when the mean and s.d. of the normal distribution to which the data are compared are unknown and are estimated from the data (Sokal & Rohlf 1981: 711) with a Shapiro-Wilk W test. As shown by Loder *et al.* (1997) the slope of the frequency distribution for species in body size classes above the modal size class changes from -2.05 when 80 classes are used, to -2.4 for 40 classes and to -3.36 when just 5 size classes are used. In the absence of external justification, the number of classes used in the Lilliefors test is an arbitrary component and the Lilliefors test is sensitive to the number of classes used, but only for very big changes. Results of the Lilliefors test on Iberian ant BSD did not change for a range of 5 to 40 size classes. For visual presentations, inter-scale comparisons were done using the same number of size classes, that was set at 12.

There are several approaches to comparing BSD at different scales. Both central and dispersion parameters can be used. We have followed the same protocol as Brown & Nicoletto (1991): the BSD among species for local samples were compared with null models assuming that species were random samples from a larger-scale species pool. For each of the 17 local samples, 1000 bootstraps were done on the Iberian Peninsula BSD, with the number of species for that local sample and the distribution of medians and skewness of the simulated BSDs used to evaluate the null hypothesis of no difference of BSD for each local sample with the BSD for the Iberian Peninsula. The proportion of the 1000 simulations less than the observed value is the probability of failing to reject the null hypothesis. This procedure was repeated for the other scales, with the number of species per sample adjusted as needed. Analyses were done with Statistica 5.01 (Statsoft, Inc; Tulsa, OK) and Simstat for Windows 1.01 (Provalis Research, Montreal, QC).

RESULTS

Peninsular body-size distribution

There are currently 237 described Iberian ant species with workers. The BSD (Fig. 1) shows that most species are of intermediate size, with smaller numbers of both larger and smaller species. The very smallest species show the generally observed decline in frequency. The mean dry body mass \pm s.d. was 0.93 ± 1.55 mg and the median 0.31 mg. The modal class was composed mainly of *Leptothorax* species. The largest size (9.76 mg; big workers of *Camponotus ligniperdus* (Latreille) was 2570 times the smallest one (0.0038 mg; *Leptanilla zaballosi* López, Martínez & Barandica). Though approaching normality, both the Lilliefors test (max $D = 0.076$; $P < 0.01$) and the Shapiro-Wilk

Table I. – Body mass of Iberian ants according to subfamily. Mean \pm s.d. in mg. n: number of species. ANOVA, $F_{4,231} = 51.0$; $p < 0.001$. Different superscripts indicate statistical differences by a post-hoc Tukey's test.

Subfamily	Mean \pm s.d.	n
Ponerinae ^a	0.28 \pm 0.32	9
Myrmicinae ^a	0.41 \pm 0.65	131
Dolichoderinae ^a	0.18 \pm 0.11	10
Formicinae ^b	1.99 \pm 2.15	81
Leptanillinae ^c	0.008 \pm 0.003	5

test ($W = 0.98$; $P = 0.024$) on log-transformed body mass showed that the BSD departed statistically from a normal distribution. There was a strong taxonomical component of variation in body size. When broken down by subfamily, body mass of Iberian ants were strongly divergent (Table I).

Local and other spatial scale assemblages of Iberian ants

A visual inspection of BSD for scale 1 samples (not presented) appears to show an almost uniform distribution but local samples did not differ—either in median or skewness—from a random sample of the whole assemblage of Iberian ants (Table II). Two cases of local samples nested in levels 3 and 4 are presented in Fig. 2. The same results apply for scales 2 to 4 (Table III). The coefficients of variation (Table II, III) did not differ among scales (ANOVA $F_{3,32} = 0.58$; $P = 0.63$).

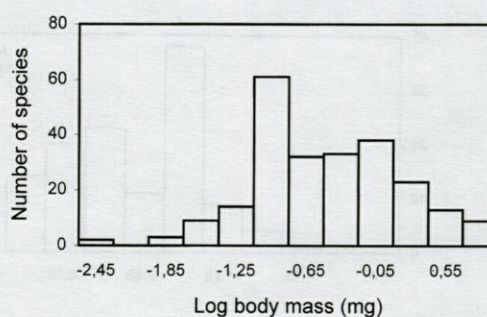


Fig. 1. – Frequency distribution (BSD) of log dry body mass of workers of Iberian ant species ($n = 237$). Mean dry body mass \pm s.d. was 0.93 ± 1.55 mg and the median 0.31 mg. The modal class was composed mainly of *Leptothorax* species. Numbers indicate the lower limit for each class, that is 0.3 wide.

Latitudinal trend

The BSD of local samples was not influenced by latitude. Mean body mass showed no significant increase with latitude (mean dry body mass = $-0.02 + 0.01$ latitude; $r^2 = 0.02$; $F = 0.35$; $P = 0.56$) suggesting that ant communities from more northern latitudes in the Iberian Peninsula do not have greater mean mass than those from southern latitudes.

DISCUSSION

The Iberian Peninsula ant fauna showed a greater number of small species and fewer larger

Table II. – Summary statistics for frequency distribution of Log_{10} of body mass (in mg) for Iberian ants in 17 local samples of homogeneous habitat (scale 1; surface 1-10 km^2). Median simulated: mean of the median for 1000 bootstraps of the Peninsular BSD with the number of species as needed for each locality. Skewness simulated: mean of the skewness for 1000 bootstraps of the Peninsular BSD with the number of species as needed for each locality. P is the proportion out of 1000 simulated bootstraps less than the observed value. C.V.: coefficient of variation (s.d.x 100/mean).

Locality	N	Median observed	Median simulated	P	Skewness observed	Skewness simulated	P	C.V.	Ref.
Güejar Sierra	11	-0.37	-0.49	0.53	-0.59	0.04	0.15	117	1
S ^a Loja QL	14	-0.76	-0.46	0.26	0.77	0.07	0.89	99	2
Cenes de la Vega	15	-0.37	-0.54	0.57	0.17	0.07	0.54	207	3
Sabiote	15	-0.21	-0.51	0.65	-0.54	0.07	0.15	295	4
S ^a Alfaguara QA	16	-0.55	-0.47	0.42	0.37	0.05	0.72	115	2
Arganda	16	-0.27	-0.49	0.67	-0.19	0.05	0.30	233	4
S ^a Nevada EN	17	-0.27	-0.51	0.59	0.06	0.01	0.51	275	2
S ^a Alfaguara RA	17	-0.16	-0.48	0.73	-0.27	0.03	0.27	355	2
Punta Entinas	19	-0.64	-0.47	0.41	0.11	0.05	0.51	118	9
S ^a Nevada RN	21	-0.47	-0.50	0.53	0.30	-0.01	0.77	139	2
Valdelaguna	22	-0.38	-0.47	0.58	0.09	0.04	0.37	180	4
San Juan de la Peña	25	-0.37	-0.49	0.55	0.65	0.03	0.70	359	5
S ^a de l'Obac	27	-0.31	-0.51	0.60	0.25	-0.00	0.70	162	6
Sant Cugat	27	-0.66	-0.42	0.39	0.31	0.00	0.73	120	8
Sariñena	30	-0.47	-0.49	0.50	0.42	-0.01	0.83	136	7
S ^a Loja EL	30	-0.63	-0.45	0.44	0.37	0.01	0.81	108	2
S ^a Nevada EA	35	-0.39	-0.48	0.55	0.15	0.05	0.55	157	2

Ref: 1: González *et al.* 1988; 2: Tinaut *et al.* 1994; 3: Tinaut 1982; 4: Serrano 1982; 5: Franch & Espadaler 1988; 6: Cerdá *et al.* 1989; 7: Espadaler 1986a; 8: Espadaler & López-Soria 1991; 9: Tinaut *et al.* 1995.

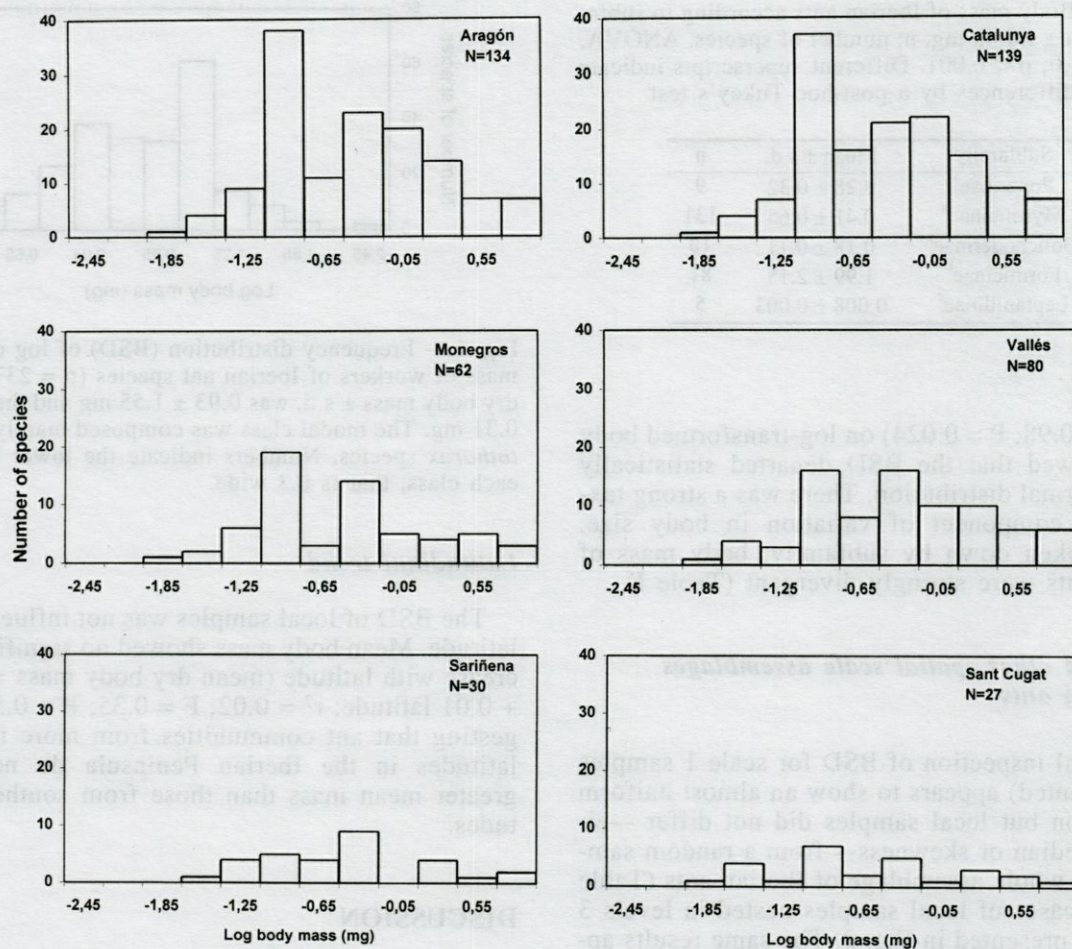


Fig. 2. – Frequency distribution (BSD) of log dry body mass of workers for two local samples (Scale 1: Sarinena and Sant Cugat) nested in their correspondingly higher level scale 3 (Monegros and Vallès) and 4 (Aragón and Catalunya). As scale gets smaller the BSD appears similar to a log uniform distribution but the median and skewness of scale 1 do not differ from random samples of its higher level BSD. N: number of species.

ant species, a pattern already detected for various assemblages by Hutchinson & MacArthur (1959). These authors also found few very small species, a rapid increase in number of species up to a modal size and a slow decline thereafter. Furthermore, bodysize distribution approached log-normal. In this way, our data do not depart from that described for a variety of taxa, from mammals to insects.

The relationships between species numbers, species abundance and body size are generally assumed to be strongly affected by the spatial scale at which studies are done (Blackburn & Gaston 1997, Brown & Maurer 1989). We studied the body-size distribution of Iberian ants, at a specific level. The range of variation of body size was virtually uniform at all scales and we could not detect any spatial effect on median body mass or skewness of the BSD. It follows, therefore, that there was no significant correlation ($\log \text{ s.d.} = 0.705 - 0.042 \log_{10} n^{\circ} \text{ species}$; $r^2 = 0.07$; $p = 0.11$) between body size

standard deviation and the logarithm of the number of species, as also found by Novotny & Kindlmann (1996) for a diverse group of taxocoenoses. The BSD of ant communities at varying nested scales seems to be no different from random samples from the underlying distribution at the largest studied scale (580.000 km²). Neither could a significant increase in the mean size of ants from local samples with an increase in latitude be detected, an effect demonstrated by Cushman *et al.* (1993) for European ants. However, these authors considered a 20° latitude range, while the Iberian Peninsula range covers only 7°. This smaller geographical range may make it difficult to uncover a trend statistically. On a subfamily level, Formicines were also found to be bigger than Myrmicines, as these authors found for northern European ants. The principles that give rise to those distributions seem to act qualitatively the same on Iberian ant communities at disparate spatial scales. We feel it prema-

Table III. – Summary statistics for frequency distribution of Log_{10} of body mass (in mg) for Iberian ants in diverse assemblages (scale 2: surface 100-1000 km^2 ; scale 3: surface 1000-10000 km^2 ; scale 4: 10000-100000 km^2 ; scale 5: Iberian Peninsula, 581.000 km^2). C.V.: coefficient of variation (s.d.x 100/mean).

Locality	N	Median observed	Median simulated	P	Skewness observed	Skewness simulated	P	C.V.	Ref.
Scale 2									
S ^a Morena	35	-0.16	-0.49	0.67	-0.45	0.00	0.14	314	1
Garraf	39	-0.27	-0.46	0.58	0.13	-0.03	0.66	237	2
Montnegre	40	-0.30	-0.44	0.62	-0.03	0.00	0.45	255	3
Collserola	42	-0.37	-0.49	0.60	0.39	0.00	0.87	167	4
Montseny	47	-0.21	-0.48	0.64	0.21	-0.02	0.75	275	5
Granada litoral	47	-0.47	-0.47	0.50	0.31	0.00	0.81	158	6
Gibraltar	54	-0.49	-0.47	0.47	0.29	-0.02	0.84	138	7
S ^a Alfacar & others	59	-0.37	-0.44	0.52	0.10	-0.02	0.66	197	8
S ^a Cazorla & others	71	-0.27	-0.48	0.59	0.21	-0.03	0.80	220	9
Scale 3									
Monegros	62	-0.48	-0.47	0.47	0.27	-0.02	0.84	145	10
Pyrenees (>1000 m)	68	-0.24	-0.51	0.70	0.03	-0.00	0.55	227	11
S ^a Nevada	72	-0.31	-0.48	0.61	0.08	-0.03	0.65	187	12
Gavarres & others	80	-0.25	-0.46	0.68	0.18	-0.03	0.80	239	13
Vallès	80	-0.31	-0.48	0.62	-0.00	-0.02	0.56	194	14
S ^a Guadarrama	100	-0.35	-0.45	0.60	-0.03	-0.02	0.49	171	15
Scale 4									
Valencia	82	-0.45	-0.48	0.51	0.19	-0.02	0.77	163	16
Portugal	98	-0.32	-0.51	0.65	0.07	-0.04	0.65	195	17
Aragón	134	-0.44	-0.44	0.48	0.19	-0.01	0.86	148	18
Catalonia	139	-0.40	-0.47	0.54	0.15	-0.04	0.84	157	16
Scale 5									
Iberian peninsula	237	-0.51			-0.04			138	see text

P is the proportion out of 1000 simulated bootstrappings that are less than the observed value. Ref: 1: Rodríguez 1981; 2: Espadaler 1992; 3: unpublished observations; 4: Lombarte *et al.* 1989, updated; 5: Espadaler 1986b, Espadaler & Ascaso 1990; 6: Ortiz 1985; 7: Tinaut 1989; 8: Pascual 1986; 9: Espadaler 1997a; 10: Espadaler 1997c; 11: Espadaler 1979, updated; 12: Tinaut 1981; 13: Suñer 1991; 14: Espadaler 1990; 15: Martínez 1987; 16: Espadaler 1997b; 17: Collingwood & Prince 1998; 18: Espadaler 1997c;

ture to propose mechanisms structuring the BSD, if there are any (Novotny & Kindlmann, 1996) until more comprehensive data bases are compiled.

Possible biases in the BSD

— Measurement errors. The BSD of Iberian ants covers three orders of magnitude, so it is assumed that measurement errors are likely to be very small in relation to interspecific body size variation. The variable size in polymorphic and monomorphic – but variable – ant species however, is undoubtedly of greater importance. The correct parameter to use for species in which size is variable remains unresolved and largely unexplored (Blackburn & Gaston 1994b). How the frequency distribution of ant assemblages and their usually associated statistical parameters may vary according to which measure of body size is used (mean, median, maximum or the full range) is currently under scrutiny.

— The number of species known to be missing is not applicable here because data for the 237 described species from the Iberian Peninsula was available. Migrant species in local samples were

probably absent or highly unlikely (nests are usually long lived in a given habitat).

— The number of undescribed species missing from the BSD is unlikely to alter the shape shown in Fig. 1. As a test for this possibility we compared the mean mass of recently (< 20 years) described species ($n = 30$ formally described + 9 still undescribed; head length \pm s.d.: 0.91 ± 0.44 mm; dry body mass \pm s.d.: 0.69 ± 1.1 mg) with the mean mass of previously known species (head length \pm s.d.: 1.02 ± 0.48 mm; dry body mass \pm s.d.: 0.98 ± 1.62 mg). Body mass for both groups was not different (ANOVA on logmass; $F_{2,232} = 2.16$; $p = 0.11$). Thus, we are confident that no systematic biases have been introduced in the data base.

Ours is a restricted database of global ant body masses. In particular, large ants are lacking since these sizes come from tropical areas (viz. 115.4 mg for *Dinoponera gigantea* (Perty) or 94.5 mg for *Camponotus (Dinomyrmex) gigas* (Latreille)); Leptanillinae are amongst the smallest ants in the world and are included in our data. So the veil line, if this concept were to apply here, belongs on the right part of the distribution. The global ant BSD is probably skewed further to the right than that of Iberian ants.

Concluding remarks

As to why there seems to be no change in the BDS of Iberian ants at different spatial scales we envisage three possibilities: 1) the peninsular scale is not as big as it should be. Ours is a "partial" study (sensu Gaston & Blackburn 1996) since it concerns an area that embraces the entire geographical range of only a limited proportion of the species considered (30 %, Iberian endemics). If this was true, our analysis would effectively be limited to small and medium scales. This could explain the absence of a different pattern for local species assemblages which may appear if compared to more "comprehensive" studies (viz. whole European ants) that are at present lacking. 2) it could be that the smaller scales analysed are not sufficiently small, at the level of the world as perceived by ants. It has recently been proposed that ants perceive their habitat differently according to their size (size-grain hypothesis; Kaspari & Weiser 1999) and that patchiness at the 1-m² scale is a property of some ant communities (Kaspari 1996). We may not have reached the scale (grain level) appropriate to analyse ant body size distribution and uncover any flattening of BSD in local samples. This could be difficult to test since the number of species at very small habitat scales in the Iberian Peninsula would be so low that statistical problems (type II error) would be too important. Loder *et al.* (1997) recognised that "systematic differences between local and regional assemblages will be difficult to identify", particularly if differences appear to be non-existent, as is the case in Iberian ants. 3) a further hypothesis, considering that ants are social animals, is that worker size is not the appropriate variable to measure. Perhaps the colony, as an integrated operating unit within its natural environment (Hölldobler & Wilson 1990) would yield a distinct pattern when analysed. If this were so, the summed size distribution of the colony members would be the functionally appropriate "size" to measure. Unfortunately, reliable data on colony size are extremely difficult to obtain (but see Kaspari & Vargo, 1995, for a mainly tropical ants data base on colony size) and data for Iberian ants are lacking.

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