Universitat de Girona

ECOLOGICAL ANALYSIS OF PERIPHYTIC DIATOMS IN MEDITERRANEAN COASTAL WETLANDS (EMPORDÀ WETLANDS, NE SPAIN)

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ECOLOGICAL ANALYSIS OF PERIPHYTIC DIATOMS IN MEDITERRANEAN COASTAL WETLANDS

(Empordà wetlands, NE Spain)

by

Rosa Trobajo Pujadas

2005

Als meus pares

"Few objects are more beautiful than the minute siliceous cases of the diatomaceae: were these created that they might be examined and admired under the higher powers of the microscope?"

C. Darwin
(The Origin of Species, 1872)

"Els aiguamolls són encara,
a pesar de l'home,
una meravella de la naturalesa"

J. Sargatal & J. Fèlix
(Els Aiguamolls de l'Empordà, 1989)

CONTENTS

1. GENERAL INTRODUCTION

1.1 Periphyton and diatom community

Many terms are used to distinguish groups of benthic organisms that live in different aquatic habitats. Although new definitions are required when new information is developed and new ideas about how systems are organised, there is a need to standardise the use of terms since consistency facilitates communication (Stevenson 1996a). The term *benthos* has a broad meaning, since it includes the entire assemblage of organisms associated with the solid-liquid interface in aquatic systems (Margalef 1983, Wetzel 2001). Recently, Wetzel (2001) proposed a narrower concept referring to *benthos* as animals associated with substrata. *Aufwuchs* is a German word that means "to grow upon" and is not often used in the modern literature. *Periphyton* is a commonly used term that usually refers to the microflora on substrata, but includes the microscopic algae, bacteria and fungi. *Biofilm* is essentially synonymous to periphyton (Wetzel 2001) and *microphytobenthos* can also be considered synonymous to periphyton according to MacIntyre *et al*. (1996). The definition of microphytobenthos is unicellular eukaryotic algae and cyanobacteria that grow within the upper several millimeters of illuminated sediments (MacIntyre *et al*. 1996). Taking into account these definitions, periphyton is considered an important base of the food chain, and in some aquatic systems can comprise the most abundant producers (Wetzel 1964, Goldsborough & Robinson 1996). Nevertheless the role of periphyton has been little studied in comparison with phytoplankton (McQueen *et al.* 1989, Lowe 1996, Wetzel 2001). The data presented by Lowe (1996) are significant since over the past 10 years, there has

been only one periphyton-based research paper per every 20 phytoplankton-based research papers.

Diatoms are an important and often dominant component of periphyton, and their contribution to primary production in aquatic systems has largely been underestimated (Sullivan 1999). Apart from the qualitative and quantitative importance of diatoms in the periphyton, the study of diatoms has the added value that they are excellent environmental indicators, since they are present in almost all aquatic habitats and react with speed and sensitivity to environmental changes (Margalef 1955, Patrick 1973, Coste 1976, Lange-Bertalot 1979, Kobayasi & Mayama 1982, Fabri & Leclerq 1986, Sabater *et al.* 1988, Rott 1991, Stevenson & Pan 1999, Sullivan & Currin 2000). Specifically, they have been shown to be effective indicators of pH, salinity and nutrients and they have become one of the most widely used environmental indicators in relation to water quality problems such as water acidification (Charles *et al*. 1990, Battarbee *et al*. 1990, Battarbee *et al*. 1999), salinification (Fritz 1990, Juggins 1992, Cumming & Smol 1993), eutrophication (Smol *et al*. 1983, Engstrom *et al*. 1985, Whitmore 1989, Anderson 1990, Bennion *et al*. 2000) and climate change (Smol & Cumming 2000). Their bioindicative value is used in current water assessments as well as in paleoecology.

Taxa with wide ecological amplitudes are usually considered poor indicators (Descy 1984), but the importance of elucidating whether a taxon is eurytopic, or comprises several ecologically discrete taxa has also been recognised (Cox 1995). Even if the former case applies, ecomorphs can be used as environmental indicators provided all the factors affecting valve morphology are known. In fact, part of the taxonomic confusion in some diatom species can

be attributed to the lack of studies on the causes of morphological variation in diatoms (Cox 1997).

1.2 The ecological importance of studying transitional and fluctuating ecosystems

Shallow coastal wetlands can be considered as transitional gradients between terrestrial and aquatic systems, be they continental fresh-water or marine (Casado & Montes 1995, Sullivan 1999). One important characteristic of these environments is that they are highly dynamic, basically because they change configuration relatively frequently due to the wind and marine or river currents. This dynamism determines one of the principal ecological characteristics of the coastal wetlands, which is the fluctuation and interaction of many of the parameters used to define them (such as salinity, relationship between nutrients, water turnover, production). They are also in general very open systems, actively exchanging materials and energy with adjacent systems (Comín 1989, Tiner 1995, Wetzel 2001). Because the functioning of these systems is complex, with continual changes and interaction between factors, they are difficult to study and to model conceptually (Sullivan 1999). But it is precisely this difficulty in determining which factors govern fluctuating and transitional systems that makes them interesting, since they demand a more dynamic and functional approach. Another part of their intrinsic interest lies in the fact that they represent an ideal place to study species' responses to environmental gradients, which may help to explain the relative importance of the biotic and abiotic factors which structure a community (Gido *et al.* 2002).

Most coastal wetlands in the Mediterranean area are clear examples of fluctuating systems and are recognised for their ecological and economic value, but still remain poorly studied (Britton & Crivelli 1993). The aquatic systems in the Empordà wetlands (NE Spain) are typically Mediterranean, with enormously variable hydrology, determined primarily by floods, caused by sea storms and/or heavy rains and subsequent summer desiccation (Quintana *et al*. 1998a, b and Chapter 3). This zone offers an interesting mosaic of environmental conditions which change greatly over time, but also spatially.

1.3 The study of periphyton in shallow coastal wetlands

Although studies highlighting the importance of periphyton in standing waters are increasing, the knowledge of lentic periphyton communities lags far behind the knowledge of lotic periphyton and even further behind the knowledge of phytoplankton biology (Lowe 1996, Goldsborough & Robinson 1996). In spite of the fact that the shallowness of many coastal wetlands provides favourable conditions for the development of periphyton, there is very little information about the factors determining its dominance in these environments (MacIntyre *et al*. 1996, Miller *et. al* 1996). In the particular case of the Empordà wetlands, the studies conducted into the aquatic community, have been focussed on animal communities (Quintana 1995, Quintana *et al*. 1998b, Moreno-Amich *et al*. 1999, Gifre *et al*. 2002, Quintana 2002, Quintana *et al*. 2002) or on phytoplankton (Quintana & Moreno-Amich 2002), hence there is a gap of knowledge concerning periphyton.

Despite the fact that diatoms are a very important component of the periphyton in estuarine and shallow coastal waters, there still is not a consensus on the

main factors that determine diatom species composition and distribution in these systems, and results from different studies may prove contradictory (MacIntyre *et al*. 1996, Sullivan 1999, Sullivan & Currin 2000, Underwood and Provot 2000). In particular, few studies on Mediterranean coastal wetlands include diatoms (Danielidis 1980, Noel 1984a and b, Delgado 1986, Tomàs 1988, Sabater *et al*. 1990, Tolomio *et al*. 2002), hence the autecology of diatom species inhabiting Mediterranean wetlands is poorly understood. The most ubiquitous and common component of the benthic diatoms in salt marshes are the motile species, particularly those belonging to the genera *Navicula*, *Nitzschia* and *Amphora* (Williams 1962, Drum & Webber 1966, Sullivan 1975, 1977, 1978), all of which are represented by numerous taxa showing considerably morphological variability.

1.4 Study approach

The study of environmental conditions affecting periphyton in the Empordà wetlands was approached at three different levels of organisation: ecosystem level, considering the role of periphyton among the primary producers; community level, analysing periphytic diatom species composition; and population level, studying phenotypic plasticity of selected diatom species.

At the ecosystem level, the aim was to determine under which environmental conditions periphyton becomes the predominant primary producer above phytoplankton and macrophytes in the waterbodies of the Empordà wetlands. The idea was to study the ecosystem as a whole, taking advantage of the great variety of lentic environments present in the Empordà wetlands (temporary or permanent brackish lagoons, small bodies of flooded marsh, freshwater springs

and oxbows, creeks of trapped seawater or agricultural run-off) and of the wide range of environmental conditions which occur there. A multifactor approach to physical and chemical water characteristics makes it possible to classify the main waterbodies, an essential prerequisite to understanding the functioning of a wetland (Finlayson & Van der Valk 1995).

At the community level it is necessary to define the factors that determine the species composition and the distribution patterns of diatom assemblages. This ecological study of the periphyton diatom community has been designed with the dynamics of the system in mind. For that reason the zone selected was the one where variations in environmental conditions were the highest, that zone is the salt marshes of the Empordà Wetlands National Park. The study of any community presupposes knowledge of the taxonomy of the individuals that live there. Although this study was not planned as a taxonomic one, the lack of a comprehensive flora for these fluctuating and transitional environments, and the fact that many diatom taxa present exhibited great morphological variability (Sullivan & Currin 2000) meant that considerable attention had to be given to taxonomy. In the absence of consistency in taxonomic determination, any further deduction based on that must be subject to doubt.

At the population level it is interesting to determine whether fluctuations in environmental factors result in morphological changes in periphytic diatom species. Such a relationship would indicate the physiological response of the particular species to environmental factors. This research had to be focussed on a taxon showing phenotypic plasticity, which, as well as being typical of the environments under study, is present and abundant in other environments as well. All these criteria were amply fulfilled by *Nitzschia frustulum* (Kützing) Grunow, since it is one of the most abundant taxon in the Empordà wetlands,

and is widely distributed (Krammer & Lange-Bertalot 1997b, Witkowski *et al*. 2000) and common in many aquatic environments (Hendey 1964, Aleem 1973, Main & McIntire 1974, Archibald 1983, Wilderman 1986, Gasse 1986, Tomàs 1988, Wendker 1990a, Fritz *et al.* 1993, Krammer & Lange-Bertalot 1997b). The morphological variability of the valves have made it one of the most easily confused taxa, as evidenced by the number of synonyms which exist for *N. frustulum*.

1.5 Objectives

General objective:

To analyse the effects of environmental factors on the periphyton in fluctuating systems (Empordà wetlands) at three levels of organisation: effects favouring the predominance of different primary producers, phytoplankton, periphyton or macrophytes (the ecosystem level), effects on the species composition of diatom assemblages, (the community level), and effects on morphological variation within diatom species (the population level).

Specific objectives:

- To differentiate and classify the fluctuating and lentic waterbodies in the Empordà wetlands by studying the physical and chemical composition of the water

- To study which factors favour the dominance of periphyton, and to establish a predominance model of the different aquatic primary producers

(phytoplankton-periphyton-macrophytes) in the waterbodies of the Empordà wetlands

- To describe the species composition of periphytic diatoms in the salt marshes of the Empordà wetlands

- To establish what factors determine the species composition and their relative abundance in the periphytic diatom community

- To determine the effects of the fluctuation of abiotic factors (such as salinity, nutrient content and water movement) on the valve morphology of *Nitzschia frustulum*.

2. STUDY AREA

2.1 Empordà wetlands

Twenty two waterbodies representative of the Empordà wetlands were chosen to study the factors favouring the predominance of different types of aquatic primary producers (periphyton, phytoplankton and macrophytes). The Empordà wetlands (NE Spain) are a set of shallow lentic waters free from tidal influence (Figure 2.1). They lie on a plain formed by sedimentary materials from three rivers: Muga, Fluvià and Ter, with highly variable and irregular flow rates (Julià *et al*. 1994). In general terms, and from a geographical and limnological point of view, the waterbodies (=basins) studied included coastal lagoons, small bodies of flooded marsh, creeks of trapped seawater or agricultural run-off, freshwater ponds and oxbows located further inland. They provide a good sample of waterbody diversity in the area, a common feature in Mediterranean wetlands.

The zone nearest the coast is characterised by occasional influxes of seawater. During the dry seasons (winter and summer), the water level gradually decreases, mainly due to evaporation and infiltration, and the salinity increases. Levels are usually very low, especially during the summer when a large number of depressions dry out completely. During the wet seasons there are frequent changes in water level and water chemistry. Sea storms, rain and the entry of fresh water from rivers often coincide.

The hydrology of the more inland zone is related to both surface water and fresh groundwater circulation (Bach 1990), following the pluvial and fluvial

regime, whereas marine influence is occasional or non-existent. This is the area most transformed by human activities.

In all the area, the chemical characteristics of water are influenced by agricultural activity. The circulating freshwater contains a significant concentration of nitrogenous fertilisers.

The inventory of the waterbodies studied is shown in Table 2.1.

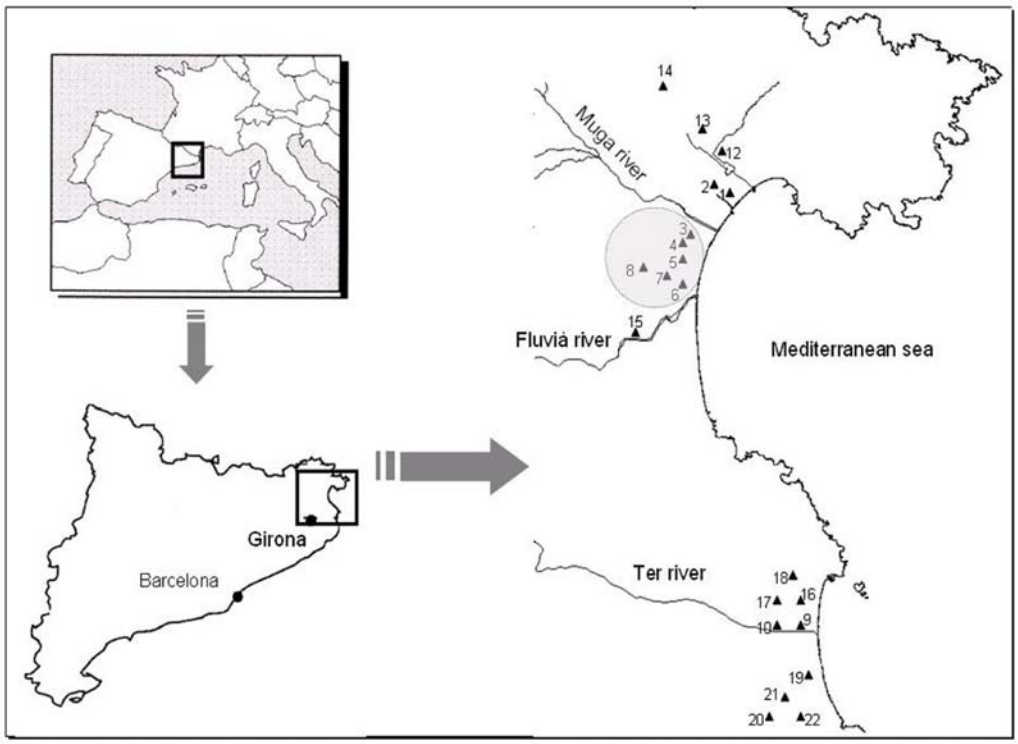


Fig 2.1 Sketch map of the Emporda Wetlands and the waterbodies studied. The grey circle corresponds to salt marshes of the Empordà Wetlands Natural Park (more detailed in Fig.2.2) where the study of the periphytic diatom community was conducted

Table 2.1. List of waterbodies (chosen as representatives of the area) and their main biological communities. Semi permanent waters get dry only in very dry years. Temporary waters get dry at least once a year. Chuster correspond to waterbodies classification found in Chapter 4.Vegetal communities following Gesti (2000)

Cluster	Waterbody Identification	Name	UTM square 1 km^2	Depth (cm) maximum	mean	Water permanence	Vegetal communities hydrophytic	helophytic/halophytic	Main heleoplankton species
1	1	clot Llúdriga	EG 1178	91.6	73	Permanent	*Chaetomorpho-Ruppietum*	*Puccinellio-Arthrocnemetum fruticosi typicum*	*Eurytemora velox, Mesochra rapines, Harpacticus littoralis*
	2	bassa Angula	EG 1178	56	34.4	Semipermanent	*Chaetomorpho-Ruppietum*	*Puccinellio-Arthrocnemetum fruticosi typicum*	*Eurytemora velox, Mesochra rapiens, Canuella perplexa*
	9	Pletera-fra Ramon	EG 1453	135	101.1	Permanent	*Chaetomorpho-Ruppietum*	*Puccinellio-Arthrocnemetum fruticosi typicum*	*Calanipeda aquae-dulcis, Eurytemora velox, Diacyclops bicuspidatus odessanus, Halicyclops rotundipes, Mesochra rapiens*
	10	Pletera-bassa petita	EG 1453	150	57.1	Semipermanent	—	*Puccinellio-Arthrocnemetum fruticosi typicum Suaedo maritimae-Salicornietum patulae*	*Calanipeda aquae-dulcis, Eurytemora velox, Diacyclops bicuspidatus odessanus*
2	3	Estany d'en Túries	EG 0975	100	63.9	Semipermanent	*Chaetomorpho-Ruppietum*	*Puccinellio-Arthrocnemetum fruticosi typicum*	*Calanipeda aquae-dulcis, Eurytemora velox, Diacyclops bicuspidatus odessanus, Cyprideis torosa, Loxoconcha elliptica*
	4	bassa Connectada	EG 0975	95	61	Temporary	*Chaetomorpho-Ruppietum*	*Puccinellio-Arthrocnemetum fruticosi typicum*	*Calanipeda aquae-dulcis, Eurytemora velox, Diacyclops bicuspidatus odessanus*
	5	bassa Tamariu	EG 0975	97	76.1	Temporary	—	*Puccinellio-Arthrocnemetum fruticosi typicum Scirpetum compacto-littoralis*	*Calanipeda aquae-dulcis, Eurytemora velox, Diacyclops bicuspidatus odessanus*
	6	La Rogera	EG 0974	100	55	Permanent	*Chaetomorpho-Ruppietum*	*Puccinellio-Arthrocnemetum fruticosi typicum Puccinellio-Arthrocnemetum fruticosi aeluropetosum*	*Calanipeda aquae-dulcis, Diacyclops bicuspidatus odessanus*
	7	La Riereta	EG 0874	111.3	80	Temporary	*Chaetomorpho-Ruppietum*	*Puccinellio-Arthrocnemetum fruticosi typicum Puccinellio-Arthrocnemetum fruticosi aeluropetosum*	*Calanipeda aquae-dulcis, Diacyclops bicuspidatus odessanus, Acanthocyclops robustus, Cyclops sp*
	8	rec Muntanyeta	EG 0874	79.1	70	Temporary	—	*Spartino versicolori-Juncetum maritimi juncetosum maritimi Scirpetum compacto littoralis Suaedo maritimae-Salicornietum patulae*	*Daphnia pulicaria Diacyclops bicuspidatus odessanus, Acanthocyclops robustus, Cyclops sp Eucypris virens, Cypridopsis vidua*
3	17	Ter Vell (pont)	EG 1555	105	40.4	Permanent	—	*Typho-Schoenoplectetum tabernaemontani*	—
4	11	Caseta de l'Estany	EG 1080	122	43.1	Permanent	—	*Typho-Schoenoplectetum tabernaemontani*	*Eucypris virens Eucyclops serrulatus, Diacyclops bicuspidatus odessanus*
	12	rec Madral	EG 0981	128	36.7	Permanent	—	*Typho-Schoenoplectetum tabernaemontani*	*Eucyclops serrulatus, Acanthocyclops robustus, Diacyclops bicuspidatus odessanus, Eucypris virens Chydorus sphaericus*
	13	rec de Palau	EG 0981	119	40	Permanent	*Al. Potamion*	*Typho-Schoenoplectetum tabernaemontani*	*Acanthocyclops robustus, Megafenestra aurita, Simocephalus vetulus, Alona rectangula, Bosmina longirostris Eucypris virens, Cypridopsis vidua*
	14	Vilaüt	EG 0982	92	40.5	Permanent	*Lemno-Azolletum*	*Typho-Schoenoplectetum tabernaemontani*	*Acanthocyclops robustus Daphnia magna, Simocephalus vetulus*
	15	meandre Armentera	EG 0669	96	40	Permanent	*Myriophyllum-Nuphaetum*	*Typho-Schoenoplectetum tabernaemontani Cirsio-Holoschoenetum*	*Acanthocyclops robustus, Cyclops sp Cypridopsis vidua*
	16	Ter Vell (platja)	EG 1655	110	61.4	Permanent	—	*Typho-Schoenoplectetum tabernaemontani*	*Acanthocyclops robustus, Calanipeda aquae-dulcis Chydorus sphaericus, Moina brachiata*
	18	Ter Vell (bomba)	EG 1655	78	45.4	Permanent	—	*Typho-Schoenoplectetum tabernaemontani*	*Acanthocyclops robustus,Calanipeda aquae-dulcis Chydorus sphaericus, Daphnia pulcaria, Moina brachiata, Pleuroxus aduncus, Simocephalus vetulus*
	19	Basses d'en Coll	EG 1650	160	40.2	Permanent	*Al. Potamion*	*Typho-Schoenoplectetum tabernaemontani*	*Moina brachiata, Daphnia magna, Chydorus sphaericus, Simocephalus vetulus, Pleuroxus aduncus Acanthocyclops robustus, Eucyclops serrulatus*
5	20	ullal 1	EG 1348	97	54.53	Permanent	—	*Typho-Schoenoplectetum tabernaemontani*	*Chydorus sphaericus, Pleuroxus aduncus Eucyclops serrulatus, Macrocyclops albidus*
	21	ullal 2	EG 1348	132	91.9	Permanent	*Al. Potamion*	*Typho-Schoenoplectetum tabernaemontani Cirsio-Holoschoenetum*	*Pleuroxus aduncus, Ceriodaphnia laticaudata, Chydorus sphaericus, Eucyclops serrulatus, Megacyclops viridis Cypridopsis vidua*
	22	ullal 3	EG 1348	90	82.9	Permanent	*Al. Potamion*	*Typho-Schoenoplectetum tabernaemontani*	*Chydorus sphaericus, Pleuroxus laevis*

2.2 The salt marshes of the Empordà Wetlands Natural Park

Six waterbodies in the reserve integral of the salt marshes of the Empordà Wetlands Natural Park were chosen for the study of periphytic diatom communities. The hydrology of this area depends mainly on sudden and irregular intrusions during sea storms and intense rainfall. Subterranean circulation of both fresh and salt water is active due to the abundance of sand deposits in the surface aquifer (Bach 1990, Quintana 2002). After sea storms, rainfall or entry of fresh water from rivers, the marshes remain confined (lack of water supply) for a long time and tend towards desiccation. During confinement the water level of the ponds and lagoons gradually falls, and the salinity increases. One surface freshwater channel (located at the south of the area) from the cultivated plain supplies the zone studied. Thus, two sectors can be differentiated (Fig. 2.2): the 'south sector' with a larger fresh water supply influenced from this channel (and consequently with a greater nutrient supply) and a further area, the 'north sector', with much less influenced fresh water supply, that is with longer periods of confinement (Bach 1990, Quintana *et al*. 1998a, 1999 and 2002).

Estany d'en Túries (E.Túries), bassa Connectada (b.Connectada) and bassa Tamariu (b.Tamariu) were the three shallow waterbodies selected from the north sector and La Rogera, La Riereta and rec Muntanyeta (r.Muntanyeta) are those of the south sector. Due to the proximity of r.Muntayeta to the freshwater channel, this waterbody is the one showing the most artificially altered hydrology, continually receiving nutrient-rich freshwater inputs.

The identification numbers corresponding to the waterbodies studied are 3-8 (see Fig. 2.1 and Table 2.1).

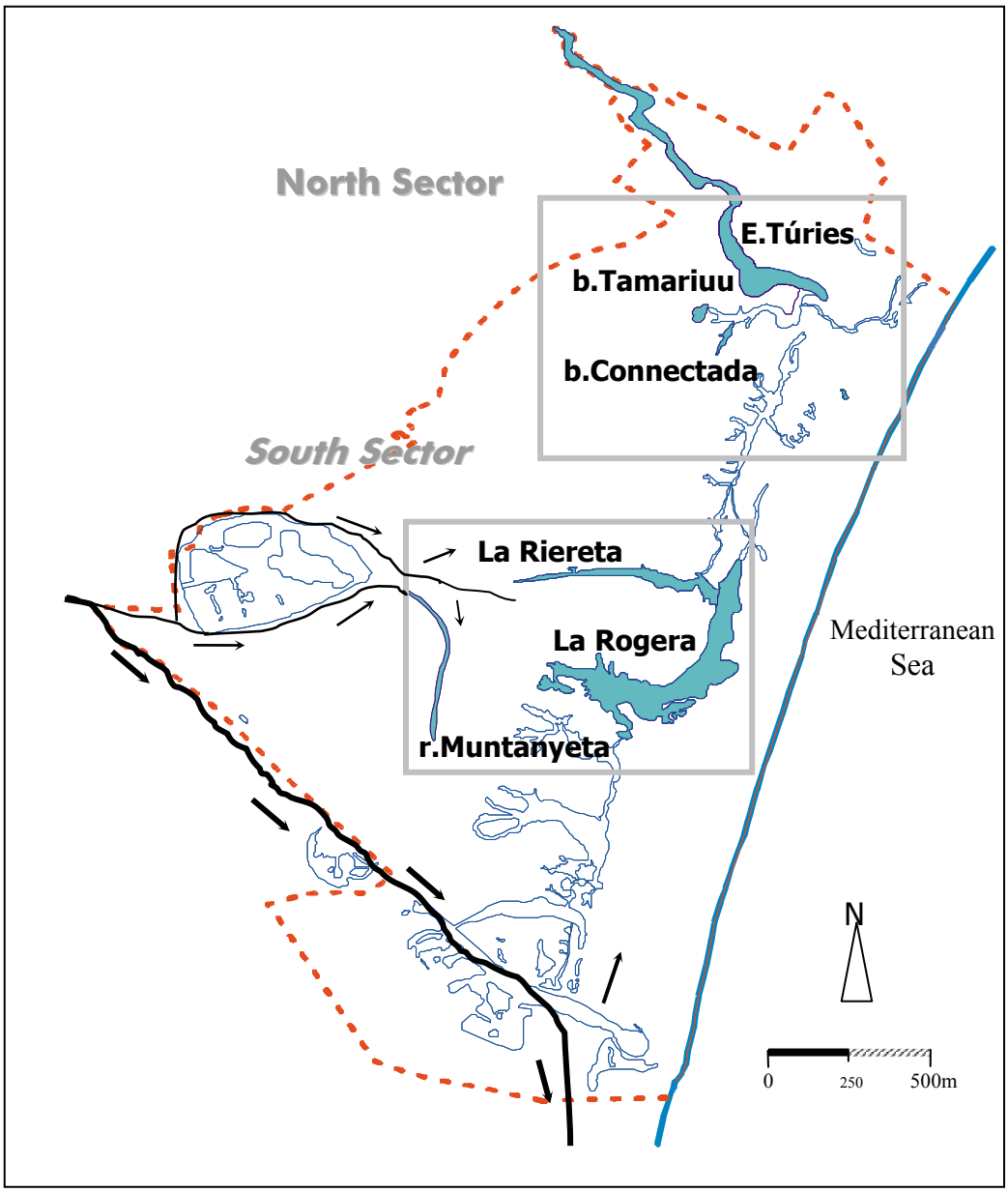


Fig. 2.2. Detailed map of the salt marshes of the Empordà Wetlands Natural Park. Note that north and south sectors are distinguished. Arrows show draining area of the surface freshwater channel in the south sector. The arrow thickness is related to the magnitude of water inputs.

3. MATERIAL AND METHODS

3.1 Sampling design

Every waterbody was sampled monthly from March 1997 to March 1998. For each, water level, temperature, electrical conductivity (EC_{25}) and pH were measured *in situ*. Although conductivity is the direct measure and salinity depends on the nature of the salt content, in order to facilitate comparisons with other works, salinity (expressed as grams per litre) was calculated by applying a correction factor to conductivity. Surface macrophyte coverage was estimated visually and recorded as greater or lower than 50%. A water sample was taken in order to determine the concentration of nutrients and phytoplankton chlorophyll *a*. To avoid the variability due to substratum and depth, samples of periphyton were taken from an artificial substratum (glass rod of 4 mm diameter and 55 mm length; 220 cm^2 surface). A mobile float (Fig 3.1) was used to maintain the substratum always at the same depth (7cm). Measures of periphyton biomass are given in $\mu g\ cm^{-2}$ of artificial substratum.

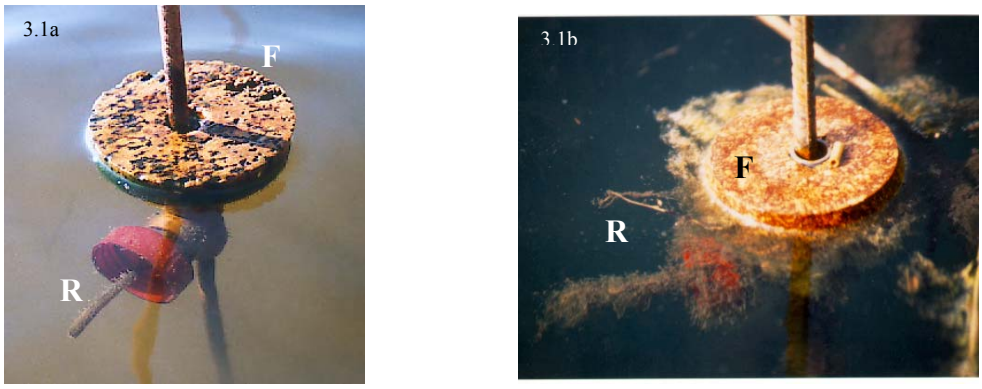


Fig. 3.1a-b Artificial substrata (after one month of exposure) used for sampling periphytic diatoms. **R**: glass rod used as artificial substratum. **F**: mobile float.

3.2 Analysis of nutrients and chlorophyll concentration

Analysis of inorganic nutrients, ammonium (NH_4^+), nitrite (NO_2^-), nitrate (NO_3^-), soluble reactive orthophosphate (SRP) and dissolved inorganic silicate (Si) were measured from filtered samples following Grasshoff *et al.* (1983). For computing DIN / SRP ratios, undetectable concentrations are considered equal to the minimum detection level of the analysis methods (SRP: 0.03μM, NO_3^-: 0.05μM, NO_2^- and NH_4^+: 0.001μM). Analysis of total nitrogen (total-N) and total phosphorus (total-P) were done using unfiltered samples following Grasshoff *et al.* (1983). Total organic carbon (TOC) was measured using a TOC analyser. For the latter, the samples homogenisation previous to acidification (pH value lower to 2) was done with a blender and then purged with air-sparging. Between 2-4 oxidations per sample were carried out following EPA 9060A.TOC.

Periphyton chlorophyll *a* was extracted using 90% acetone and measured using Jeffrey & Humphrey's expressions (Rowan 1989). Phytoplankton chlorophyll *a* was extracted using 80% methanol after filtering the water sample (filters Whatman GF/C), and measured using Talling & Drivers's expressions (Talling & Drivers 1963).

3.3 Defining aquatic primary producers predominance

Chapter 4 includes situations of macrophyte, phytoplankton and periphyton dominance, but does not include metaphyton dominance situations, because they chiefly occur under stable water conditions (Goldsborough & Robinson

1996), and their occurrence in the Empordà wetlands is rare.

The predominance of phytoplankton and periphyton was established on the basis of the relative importance of the respective biomass production across samples. The concentration of chlorophyll *a* is expressed in different units: μg l^{-1} for phytoplankton chlorophyll, and μg cm^{-2} of artificial substratum for periphyton chlorophyll, which are not directly comparable. In order to compare phytoplankton and periphyton biomass units, both variables were rescaled to a range of zero to one, after dividing by the respective maximum values across samples. Surface macrophyte coverage was also recorded to establish the relationship between proliferation of macrophytes and the predominance of periphyton or phytoplankton. Since two stable states (vegetation dominated state and turbid state) can be expected from the vegetation-turbidity interaction model (Scheffer 1998), 50% vegetation coverage was used as a reasonable breakpoint to classify samples into one or another tendency.

3.4 Diatom identification and valve counting

The diatoms studied (Chapter 5 and 6) were collected from the artificial substrata (two replicates of artificial substratum were collected each time). They were cleaned of organic material using H_2SO_4 and KNO_3 (Hustedt 1930). Clean valves were mounted in Naphrax. The permanent slides were examined by phase contrast light microscopy. For scanning electron microscopical observations, the cleaned material was gold coated. The relative abundance of diatom species was determined by counting a minimum of 500 valves in each substratum replicate (the results given for a month are the mean of the two artificial substrata replicates for that month). The floras by Hustedt (1930),

Krammer & Lange-Bertalot (1991a, 1991b 1997a and 1997b) and the monograph by Witkowski *et al.* (2000) were mainly used, although many other taxonomic and floristic works were also used (Hustedt 1955, Reimann *et al*. 1963, Voigt 1963, Patrick & Reimer 1966 & 1975, Hargraves & Levandowski 1971, Lange-Bertalot & Bonik 1978, Lange-Bertalot & Simonsen 1978, Sullivan 1979, Coste & Ricard 1980, Germain 1981, Takano 1983, Tomàs 1982, Archibald 1983, Bérard-Therriault & Cardinal 1986, Cardinal *et al*. 1986, Gasse 1986, Williams & Round 1986, Aboal 1987, Bérard-Therriault *et al*. 1987, Cox 1987, Karayeva 1987, Sabater 1987, Tomàs 1988, Kuylenstierna 1990, Osada & Kobayasi 1990, Round *et al*. 1990, Sabater *et al.* 1990, Lange-Bertalot 1993, Snoeijs 1992, Sánchez-Castillo 1993, Snoeijs 1993, Snoeijs & Vilbaste 1994, Witkowski 1994, Sabbe & Vyverman 1995, Snoeijs & Potapova 1995, Snoeijs & Kasperoviciene 1996, Tomas 1997, Snoeijs & Balashova 1998, Witkowski *et al.* 1998, Lange-Bertalot & Genkal 1999, Clavero *et al.* 2000, Rumrich *et al*. 2000, Lange-Bertalot 2001, Bussse & Snoeijs 2002, Trigueros *et al.* 2002)

3.5 Multivariate analysis

3.5.1 Ordination analysis

Principal Components Analysis (PCA)

Water physico-chemical data variability was analysed through the principal components analysis using previously standardized variables (Chapter 4). The data set contained 421 samples and 10 variables: pH, temperature, EC_{25}, NH_4^+, NO_2^-, NO_3^-, SRP, total-P, phytoplankton chlorophyll *a* and periphyton

chlorophyll *a*. Unfortunately, total nitrogen and TOC values were not available for all samples. They have been excluded from the PCA analysis and used only for pairwise Pearson correlations. All variables that expressed concentration were transformed to natural logarithms. Ecological interpretation of the principal components was done on the basis of the factor scores of the original variables (listed above), and the correlation coefficient between factors and additional variables or between factors and combined variable ratios (Water level, TOC, total-N / total-P, DIN / SRP, Phytoplankton chlorophyll-*a* / TOC).

Correspondence Analysis (CA)

Variability of diatom species abundance was analysed with Correspondence Analysis (Chapter 6). Since our primary goal was to study the patterns of variations of diatom assemblage composition rather than the patterns of variations of diatom density, we used the relative abundance data. Pearson correlation coefficients were used to study the relationships between CA dimension and environmental variables. Because rare species can have a strong effect on the position of samples in multivariate space (ter Braak 1995), from the total diatom taxa encountered (=165) only those with a relative abundance $\geq 0.5\%$ and that occurred in a minimum of 12% of the sites were included in the CA.

3.5.2 Clustering analysis

Hierarchical cluster analysis was utilised for the physico-chemical classification of the waterbodies (Chapter 4). Only the most explicative variables from the first two PCA resultant axes were used (variables with PCA factor value above 0.4). The cluster method chosen was complete linkage, since this is recommended in community ecology (Gauch 1980, Gauch 1982);

distance was Manhattan, which, although not as commonly used as Euclidean or squared Euclidean (Milligan & Cooper 1988), has been recommended (Gauch 1980, Gauch 1982, Legendre & Legendre 1998) if values are small. Additionally, Manhattan distances, unlike Euclidean methods, do not employ squared differences to determine proximity matrices, and therefore do not underestimate small differences.

Hierarchical cluster analysis was also used to establish similarity between diatom species (Chapter 6). The data used in this case were the coordinates obtained for each species with the CA using the relative abundances of species. Since we were mainly interested in species dominance, we used Euclidian distance because it underlines differences between high values. The cluster method chosen was average linkage.

3.5.3 Analysis of variance and covariance

In the experimental study of the environmental variables affecting *Nitzschia frustulum* valve morphology (Chapter 6), multivariate analysis of variance (MANOVA) was used to test for significant differences in cell morphology between treatments (using salinity, N / P ratio and water movement as interacting factors). The analysis of covariance (ANCOVA) was used to test the possible effect of any covariant on the variation of the different characters (variables). The level of statistical significance used was $P < 0.05$.

All calculations and statistical analyses done in this study were carried out using the statistical package SPSS 10.1 for Windows.

4. FACTORS FAVOURING THE PREDOMINANCE OF DIFFERENT TYPES OF AQUATIC PRIMARY PRODUCERS (PHYTOPLANKTON-PERIPHYTON-MACROPHYTES) IN LENTIC WATERS OF THE EMPORDÀ WETLANDS

4.1 Introduction

Macrophytes and algae represent the first level in the structure of the aquatic community, by means of which energy and matter are incorporated into the biological community. Despite the global abundance of wetland habitats, phycological research has mainly focused on rivers, lakes, and oceans. Consequently, information on the algal assemblages of wetlands remains fragmentary (Goldsborough & Robinson 1996) and represents a major void in our understanding of wetland ecology (Klarer & Millie 1992). Nevertheless, four quasi-stable states may be recognised in wetlands dominated alternatively by epipelon, periphyton, metaphyton, or phytoplankton (Robinson *et al.* 1996), whose proportional abundances vary spatially and temporally (Goldsborough & Robinson 1996).

The factors that regulate aquatic macrophyte abundance in shallow waters are still not well known. However, the role of some dominant driving forces has been demonstrated. Light limitation, mainly depending on turbidity (which in most cases is due to phytoplankton abundance), is generally considered the main factor affecting submerged macrophytes, more than other factors such as nutrient availability, temperature, substratum, grazing and bioturbation. The relationship between turbidity and aquatic macrophyte dominance has been well stated (see e.g. Scheffer 1998 and Scheffer *et al.* 1993a and b) and, according to the model of vegetation-turbidity interactions, two stable states

(vegetation dominated state and turbid state) can be expected. Thus, the hypothesis that dominance by vegetation and/or phytoplankton are states that represent alternative equilibrium has been discussed extensively over the past decade (for a review Scheffer 1998).

Ecosystem states in lakes and shallow waters have been studied extensively in NW Europe (Forsberg & Ryding 1980, Samuels & Manson 1997, Scheffer 1990, Verdonschot 1992a, 1992b, 1992c and Wheeler & Proctor 2000) but much less in Mediterranean wetlands.

In this part of the study a model of the predominance of the different types of aquatic primary producers (phytoplankton, periphyton and macrophytes) within a group of representative Mediterranean wetlands (22 waterbodies of the Empordà wetlands) has been established (for further details of the study area as well as the waterbodies see Chapter 2, Section 2.1, Fig. 2.1 and Table 2.1). In order to find a suitable approach for fluctuating systems with rapid changes in nutrient supply the model is mainly based on those variables which affect the productive processes of primary producers (such as nutrient concentration or water turnover rate) and less based on site characteristics (such as geographical location, morphometric parameters or substratum).

A classification of waterbodies is prerequisite to understand the functioning of the wetland area as a whole (Finlayson & van der Valk 1995) and such classifications are mainly based on a few abiotic factors, or on phytosociological associations (Robledano *et al*. 1991, Cowardin & Golet 1995, Pressey & Adam 1995, Zalidis *et al*. 1997). Although several authors have used a multifactor approach to account for fine-scale variation among ecosystems (Perez-Ruzafa & Marcos Diego 1993, Zogg & Barnes 1995, Zoltai & Vitt 1995, Robledano *et al.* 1987) very few of them (Brinson 1993, Zoltai & Vitt 1995)

are based on a functional perspective of the systems. Since none of these classifications gives sufficient resolution to discriminate between the waterbodies of the Empordà wetlands, we carried out our own multifactor classification.

4.2 Results

4.2.1 Interpretation of the main PCA axes

For sample variability analysis the first two axes obtained by PCA (52.74% of total variance) were considered. For variables used in the PCA see Section 3.5.1 in Chapter 3. The first axis (34.59% of variance) can be related to the water turnover rate or to a flooding/confinement gradient because it correlates positively with oxidised forms of nitrogen and water level and negatively with conductivity, pH and organic matter (Tables 4.1 and 4.2). This axis should not be related to salinity because conductivity variations do not correlate with it when each waterbody is analysed separately. On the other hand, the axis variations can be easily explained by variations in water circulation. For example, the entry of seawater into brackish waterbodies, although causing an increase in conductivity, gives positive displacement along this axis because of the increase in water turnover rate due to the water input. The correlation with conductivity is high because the waterbodies with highest water turnover rate are fresh, due to freshwater flooding, and the more confined are brackish, due to evaporative concentration of salts. The correlation with nitrate is explained because increases in NO_3^- are always related to water inputs, whilst long retention time due to water confinement leads to drastic reduction of NO_3^- through denitrification (Quintana *et al.* 1998a). The second axis (18.15% of

variance) can be related to a gradient of eutrophy because it shows strong correlation with both forms of phosphorus (SRP and total-P) and related ratios (Tables 4.1 and 4.2). If we consider eutrophy as the capacity to produce and accumulate organic matter, it is mainly related to the concentration of the limiting nutrient. In most cases phosphorus acts as a limiting factor, but in some cases there is a limitation by nitrogen, especially in confined waters, where denitrification is relevant.

Table 4.1 Percentage of explained variance and factor scores (after Varimax rotation) of the standardized environmental variables used in PCA. Values below 0.4 are excluded. All variables that express concentration have been log transformed.

Variable	Factor 1	Factor 2
% explained variance	34.591	18.148
NO_3^-	0.862	-
EC_{25}	0.769	-
NO_2^-	0.762	-
pH	-0.726	-
Periphyton chlorophyll *a*	0.561	-
Temperature	0.447	-
Total-P	-	0.840
SRP	-	0.848

Table 4.2 Pearson correlation coefficients between the two main axes and environmental variables ($P < 0.01$). All variables that express concentration have been log transformed.

Variable	Factor 1	Factor 2
Water level	0.569	-
TOC	-0.701	0.455
Total-N / Total-P	0.371	-0.691
DIN / SRP	0.660	-0.595
Phytoplankton chlorophyll *a* / TOC	0.540	-

4.2.2 Typification of the waterbodies

The cluster analysis (Section 3.5.2 in Chapter 3) produced five groups (Figure 4.1, see also Table 2.1 in Chapter 2), each one typifying a hydrological dynamic. Table 4.3 shows the mean and range of variation of some physical/chemical variables for each cluster. For waterbody location, see Figure 2.1 in Chapter 2.

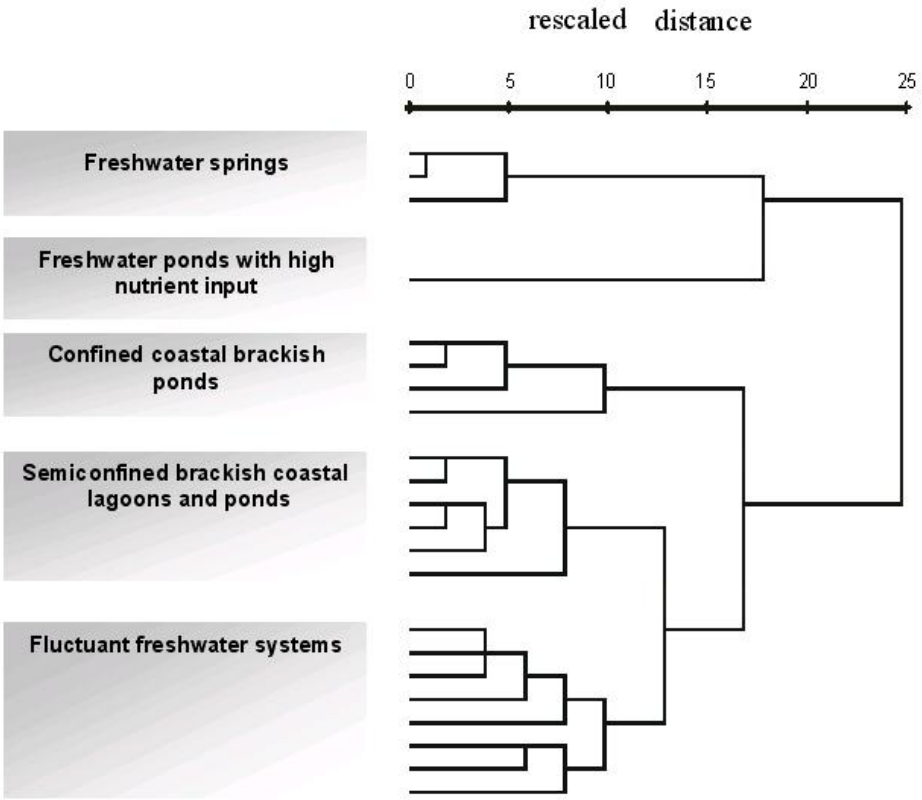


Fig.4.1 Dendrogram showing the hierarchical classification of 22 waterbodies studied

Cluster 1: Confined coastal brackish or hyperhaline ponds.

Made up of highly confined, marine-influenced salt marsh ponds. Conductivity is high and variable, with a mean value in excess of that of sea-water due to confinement (Table 4.3). During confinement low DIN / SRP ratios are found, very probably caused by intense denitrification. The macrophytes *Ruppia cirrhosa* and *Ruppia maritima* dominate.

Cluster 2: Semiconfined brackish coastal lagoons and ponds.

As with cluster 1, very close to the sea but situated over a more active aquifer (Bach 1990, Quintana 1995), and so less confined and always less saline than the sea. Surrounding vegetation is also halophyte (*Arthrocnemum fruticosum*, *Scirpus maritimus*, *Juncus acutus*), although submerged macrophytes are generally absent.

Cluster 3: Freshwater pond with high nutrient inputs

This group contains only one permanent freshwater coastal lagoon. Water circulation is very active and subject to a great deal of anthropogenic pressure. Water input is mainly from field run-off, with high levels of dissolved nutrients, organic matter and suspended solids. Mean nutrient values are therefore high (Table 4.3). Its surrounding vegetation is primarily *Phragmites australis*.

Cluster 4: Fluctuating freshwater systems

Made up of freshwater lagoons and channels (with occasional marine intrusions). Surrounding vegetation is mainly helophytic (*Phragmites australis* and *Typha angustifolia*). The waterbodies in this group vary greatly in water origin and circulation; the common factor is the high DIN / SRP ratio.

Cluster 5: Freshwater springs

These are freshwater springs surrounded by cultivation, giving a major water input which is almost entirely subterranean. This is the most oligotrophic group, with a mean phosphorus concentration close to 1μM (Table 4.3) and rich in macrophytes (*Myriophyllum verticillatum* and *Ceratophyllum demersum*). Nitrogen content, mainly as nitrate, is high. The high DIN / SRP ratio is typical of underground waters which have absorbed fertilisers from surrounding fields (Soria 1993).

Table 4.3 Mean and range of variation (in parentheses) of some environmental variables studied by cluster. EC_{25} is in $mScm^{-1}$; NH_4^+, NO_2^-,NO_3^-, Total-N, SRP and Total-P are in μM; TOC is in mg l^{-1}; Phytoplankton chorophyll *a* is in μg l^{-1} and Periphyton chorophyll -*a* is in μg cm^{-2}.

	Cluster									
	1		2		3		4		5	
EC_{25}	**49.30**	(8.80;149)	**18.85**	(0.74;51.4)	**2.00**	(0.60;7.60)	**3.90**	(0.12;41.3)	**1.14**	(0.11;9.00)
pH	**8.06**	(7.29;8.87)	**8.20**	(7.08;9.83)	**7.80**	(7.23;8.62)	**7.65**	(6.45;8.78)	**7.10**	(6.43;8.11)
NH_4^+	**7.00**	(0.03;117)	**2.80**	(0.01;50.0)	**26.02**	(0.10;118)	**6.44**	(0.01;231)	**2.63**	(0.09;60.8)
NO_2^-	**0.82**	(0.00;35.7)	**0.72**	(0.01;11.2)	**4.85**	(0.10;16.4)	**2.38**	(0.20;61.4)	**5.53**	(0.10;51.7)
NO_3^-	**1.83**	(0.03;33.4)	**6.85**	(0.02;86.9)	**104.75**	(16.8;277)	**38.71**	(0.04;327)	**705.80**	(357;1084)
Total-N	**238.50**	(5.98;2263)	**125.90**	(2.00;615)	**219.45**	(39.3;533)	**117.96**	(9.57;631)	**851.90**	(410;1440)
SRP	**4.82**	(0.02;92.4)	**1.21**	(0.04;10.3)	**2.65**	(0.05;9.77)	**3.14**	(0.01;44.68)	**0.94**	(0.01;17.8)
Total-P	**11.65**	(0.58;181)	**5.07**	(0.65;41.5)	**14.45**	(2.00;37.3)	**6.33**	(0.06;48.4)	**1.95**	(0.28;17.8)
DIN/SRP	**77.80**	(0.01;1912)	**46.05**	(0.12;1696)	**470.00**	(4.90;3974)	**242.95**	(0.01;3731)	**11877.3**	(33.6;1375.)
TOC	**30.16**	(2.42;466)	**12.05**	(3.87;31.4)	**4.80**	(3.23;9.10)	**7.00**	(1.17;32.6)	**2.33**	(0.71;10.9)
Phytoplankton chl *a*	**22.24**	(0.28;327)	**15.94**	(1.11;68.2)	**7.69**	(0.28;16.5)	**16.14**	(0.00;243)	**18.11**	(1.25;116)
Periphyton chl *a*	**1.30**	(0.00;6.61)	**1.84**	(0.00;13.2)	**9.28**	(4.68;16.3)	**4.54**	(0.31;19.0)	**1.63**	(0.03;9.46)

4.2.3 Ordination of the clusters in the PCA factor space

Analysis of sample distribution in the PCA factor space (Fig. 4.2), shows clusters ordered along the first axis, from positive to negative coordinate: 3 and 5, 4, 2, 1; indicating that the main differences between clusters are related to confinement. Clusters 3 and 5 are well differentiated by the second axis, which mean that they differ from their level of eutrophy.

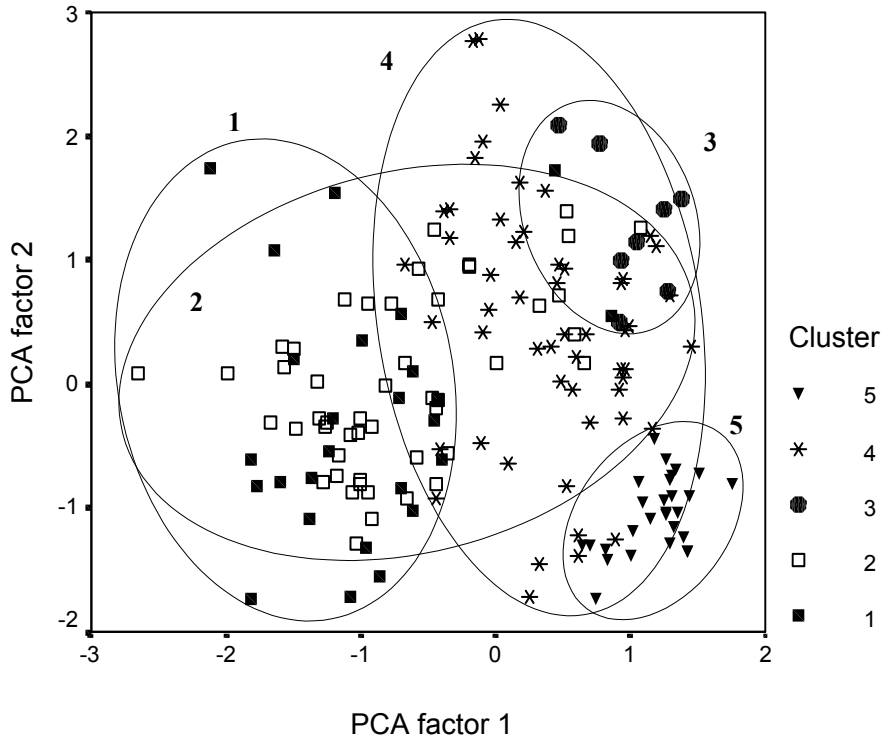


Fig. 4.2 Representation of samples in the PCA factor space [1,2]. Circles correspond with the cluster derived from the hierarchical classification of waterbodies

4.2.4 Checking the alternative predominance hypothesis

Figure 4.3 shows that high relative concentrations of phytoplankton chlorophyll *a* correspond with low relative concentrations of periphyton chlorophyll *a* and vice versa, producing a hyperbola-like pattern. In addition, 97% of samples with >50% macrophyte coverage gave standardized concentration values of periphyton and phytoplankton chlorophyll *a* of less than 0.3. This supports the idea that these 3 types of aquatic primary producers exclude each other, consequently appearing as three classes of predominance: phytoplankton, periphyton or macrophytes. That is what we call the alternative predominance hypothesis.

For sample classification, 'predominance of periphyton' was defined when the ratio of standardized chlorophyll concentration [periphyton chlorophyll *a*] / [phytoplankton chlorophyll *a*] was higher than 1, and 'predominance of phytoplankton' when lower, whereas 'predominance of macrophytes' was defined as >50% macrophyte coverage.

Complementary details of the definition of aquatic primary producer predominance are given in Section 3.3, Chapter 3.

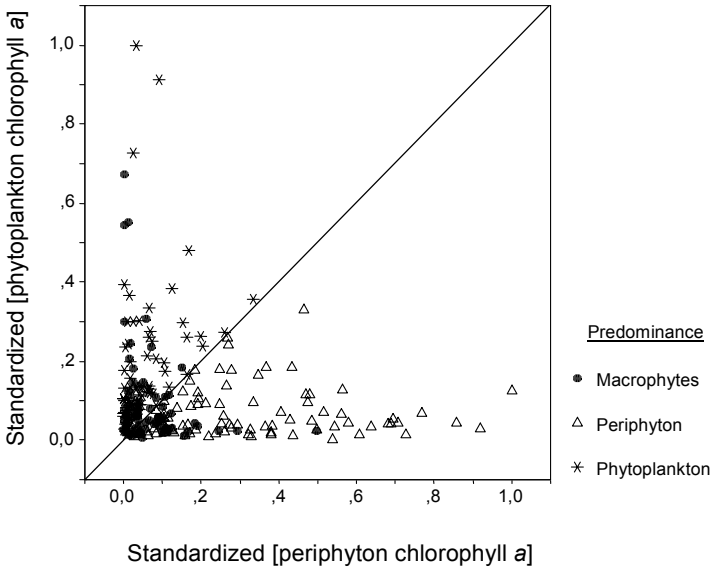


Figure 4.3 Biplot of the standardized concentration of periphyton and phytoplankton cholorophyll *a*. Crossing line corresponds to X/Y ratio = 1. Marks identify the predominance of periphyton (X/Y ratio > 1), predominance of phytoplankton (X/Y ratio < 1) and the observed dominance of macrophytes (covering > 50%).

4.2.5 Ordination of phytoplankton, periphyton and macrophyte assemblages in PCA factor space

The distribution of samples in the factor space [1,2] of the PCA (Fig. 4.4), indicated by the predominance of phytoplankton, periphyton or macrophytes, shows a relatively aggregated distribution depending on the predominant assemblage. Thus, samples with predominance of macrophytes appear with a negative coordinate of factor 2, predominance of periphyton is more represented with a positive coordinate of factor 1, and predominance of phytoplankton, with the negative coordinate of factor 1 (Fig. 4.4).

A more accurate analysis can be made by cross-classifying the samples by predominant type and cluster. The distribution of the centroids of the clouds of

points corresponding to these groups (Fig. 4.5) indicates that brackish-water clusters (1 and 2) show a similar, but opposite functioning from freshwater clusters (3, 4 and 5). Although clusters 1 and 2 appear separated due to different levels of eutrophy, there is a sequence of the predominance of macrophytes-phytoplankton-periphyton parallel to the increase of water turnover rate and the related increase of eutrophy. On the other hand, the relationship between eutrophy and water turnover rate is opposite in the fresh water- bodies studied: a decrease in water turnover rate leads to an increase in eutrophy, changing predominance from macrophytes to periphyton, which dominates in combinations of intermediate eutrophy and high water turnover rate. Excessive eutrophication, shown at low values of turnover rate, causes the predominance of phytoplankton. Phytoplankton dominating under conditions of high eutrophy is mainly composed of green algae, while in conditions of intermediate eutrophy with low water turnover rate it is mainly made up of cyanobacteria.

It is noteworthy that, unlike to the waterbodies of cluster 1, the predominance of macrophytes in cluster 2 occurs under conditions of lower water turnover rate combined with relative higher eutrophy. Two comments should be made: first, cluster 2 waterbodies reach this situation during the summer desiccation process, when confinement is at a maximum, and the apparent eutrophy is due to concentration of organic matter but not to nutrient input. Second, in these cases the predominance of macrophytes may be related more to previous periods of production (normally in spring) than to the prevaling conditions.

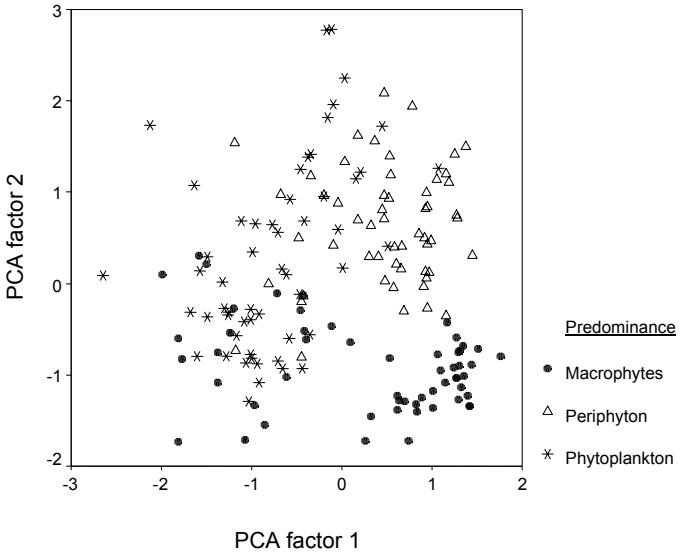


Fig. 4.4 Representation of simples in the PCA factor space [1,2]. Marks identify the predominant typology of primary producers

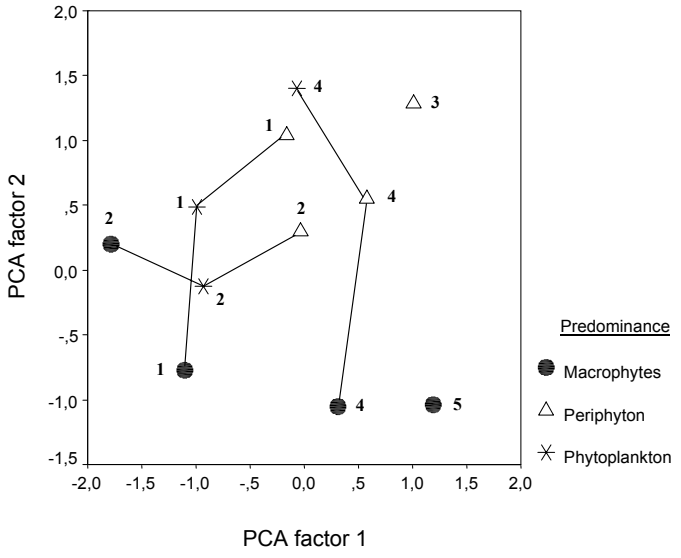


Fig. 4.5 Ordination of the predominant typologies of primary producers by cluster. Points represent the centroids of the clouds of points corresponding to the cross-classification of the samples by predominant typology and cluster

4.3. Discussion

4.3.1 Model of alternative dominance of phytoplankton-periphyton-macrophytes

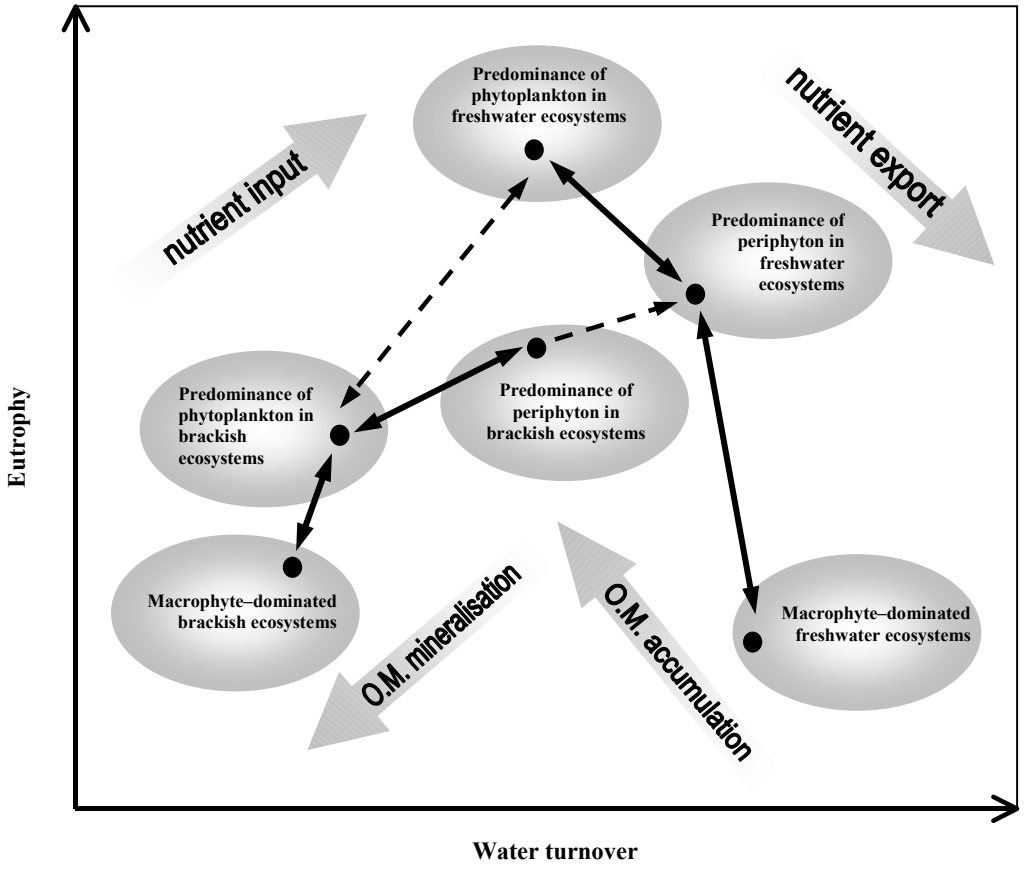


Fig. 4.6 Model of predominante of primary producers explained by two main gradients: water turnover and eutrophy. Solid arrows correspond to the observed dynamics and dashed arrows are hypothetical pathways consistent with limnological processes.

Our model of alternative predominance (Figure 4.6) derives from the combination of the cross-classification of samples by cluster and by predominant primary producers on the PCA factor space. This model is explained by two main gradients: water turnover rate and eutrophy (according to the respective interpretation of the two principal components). Macrophytes always dominate waterbodies with relative oligotrophy, in situations of both high and low water turnover rate, favoured by their capacity to capture nutrients from the sediment (McRoy & McMillan 1977, Thursby & Harlin 1982, Short & McRoy 1984, Brix & Lyngby 1985). In situations of high water turnover rate the relative oligotrophy is due to low nutrient concentration in the circulating water or to rapid washing-out of the scarce elements. In situations of confinement (low waterturnover rate), without nutrient input, nutrients become exhausted and primary production depends on nutrient recycling by mineralisation of organic matter. Positive feed-backs, such as the shading effect of macrophytes (less light available for algae) or their capacity as alternative nutrient sinks, which means that fewer nutrients are available for algal growth (Howard-Williams, 1981) and, in some cases, the existence of allopathic effects (Weaks 1988,Wim-Andersen *et al.* 1982), may favour the maintenance of macrophyte dominance. In any case, these effects can only appear after establishment of macrophyte dominance which, according to our model, depends on oligotrophic conditions.

A predominance of periphyton is found in situations of intermediate nutrient concentrations and intermediate to high water turnover rates, but periphyton does not predominate under intermediate nutrient concentrations in more confined ponds. Two different factors may explain this. According to Stevenson (1996b) the absence of water circulation in confined eutrophic

ponds favours high spatial and temporal variability in the chemistry of the periphyton mat, and the existence of unmixed layers around cells, where nutrient concentration and oxygen depletion occur. Additionally, in these systems nitrogen acts a limiting factor (Quintana *et al*. 1998b) for those organisms which can not obtain atmospheric nitrogen. The fact that cyanobacteriae phytoplankters, which can fix atmospheric nitrogen (Wehr 1989 and 1991, Stockner 1991), dominate in these conditions, supports this explanation.

Phytoplankton predominates under the most eutrophic conditions, which are found at intermediate water turnover rates. Under confined conditions, eutrophy increases with water turnover rate due to the fact that water inputs also represent nutrient inputs. On the other hand, under water motion conditions the degree of eutrophy decreases with water turnover rate, because this increases nutrient export and may also favour washing out of the phytoplankton.

Phytoplankton predominance in highly eutrophic situations agrees with the model of Phillips *et al*. (1978), which explains the shift from periphyton to phytoplankton predominance with eutrophication. The shading effects of phytoplankton favours its maintenance (Hill 1996), but always after its establishment, which is promoted by the high eutrophy and intermediate water turnover rate.

We hypothesize (one directional dashed arrow in Fig. 4.6) that if a periphyton-dominated brackish pond changed to a freshwater situation, due to increased circulation of fresh water, periphyton would continue to predominate. In contrast, if a reduction of water turnover rate in a phytoplankton-dominated freshwater system makes it as confined as a brackish one, phytoplankton

predominance would be expected instead of periphyton due to the existence of unmixed layers over the substratum, cited above. The opposite route is also possible via a water supply with high nutrient concentrations (bi-directional dashed arrow in Fig. 4.6).

Note that it is impossible to pass directly from one macrophyte-dominated situation to another. Starting from the macrophyte-dominated freshwater ecosystems, in the hypothetical case of water turnover gradually slowing to a stop, washing out of recycled nutrients would decrease and organic matter accumulation would rise, increasing eutrophy. The plant community would then shift gradually to periphyton and phytoplankton predominance. On the other hand, in macrophyte-dominated brackish ecosystems, the increase of water turnover rate causes nutrient input, which leads to the dominance of phytoplankton or periphyton. Thus, the whole model has a horseshoe structure, where the two extremes are dominated by macrophytes and where the higher levels of eutrophy are found at intermediate turnover rates.

4.3.2 Waterbody typification and confinement

An ecological, multifactor approach is useful to account for fine-scale variation among ecosystems often neglected by single-factor classifications (Perez-Ruzafa & Marcos Diego 1993, Zogg & Barnes 1995). Multifactor approaches have been applied by means of tabular comparison of the ranges of variation of some water chemistry parameters (Zoltai & Vitt 1995), by means of statistical multivariate analysis (Robledano *et al*. 1987) or on the basis of a single sample data set per pond (Zogg & Barnes 1995). These types of classification provide only a coarse typification of the ponds in the Empordà wetlands, where a functional approach, which analyses similarity between ponds according to the

dynamics of the systems after identification of the main ecological factors, is more desirable. A similar approach has been applied by López (1983) to classify Spanish Mediterranean saline coastal ecosystems by their physico-chemical characteristics only, sampling on a quarterly basis.

The typification we have obtained apparently suggests that the main factor is salinity, as López (1983) also concluded, and the correlation observed between the first principal component and conductivity seems to support this idea. Nevertheless, within the clusters and when analysing each waterbody separately there is a poor correlation between PCA factor 1 and conductivity. Furthermore, the marine intrusions do not cause displacements to a more negative coordinate, which would have expected from the entry of more saline water, but to a more positive one, due to the entry of water and nutrients. Thus, the concur of high conductivity with negative values of PCA factor 1 are mainly due to the evaporative concentration of salts during confinement.

This agrees with the theory of confinement (Guerlorget & Perthuisot 1983) that rejects salinity as an essential parameter to explain the composition and productivity of the communities occupying the paralic domain (Guerlorget & Perthuisot 1983), and proposes confinement as the main factor, related to water turnover rate. In this way the same level of production can be reached both with an excess of concentration, with exhaustion of particular elements below the concentrations required, and with excess dilution, and rapid leaching of these scarce elements. The importance of confinement in these and similar environments has also been discussed by Pérez-Ruzafa & Marcos Diego (1993) and by Quintana et al. (1998a).

5. DIATOM TAXA OF THE SALT MARSHES OF THE EMPORDÀ WETLANDS

5.1 Diatom check-list

Achnanthes brevipes var. *intermedia* (Kützing) Cleve
A. exigua Grunow
Achnanthidium minutissimum (Kützing) Czarnecki
Amphora acutiuscula Kützing
A. coffeaeformis (Agardh) Kützing
A. holsatica Hustedt
A. hybrida Grunow
A. libyca Ehrenberg
A. cf. *luciae* Cholnoky *sensu* Archibald
A. margalefii Tomas
A. micrometra Giffen
A. pediculus (Kützing) Grunow
A. staurophora Juhlin-Dannfelt
A. subholsatica Krammer
A. veneta Kützing
Amphora sp.1
Anomoeoneis sphaerophora (Ehrenberg) Pfitzer
Ardissonia crystallina (Agardh) Grunow
Astartiella bahusiensis (Grunow) Witkowski, Lange-Bertalot & Metzeltin
Bacillaria paradoxa Gmelin
Berkeleya antarctica (Harvey) Grunow
B. fennica Juhlin-Dannfelt
B. rutilans (Trentepohl) Grunow
Caloneis amphisbaena f. *subsalina* (Donkin) Van der Werff & Huls
Chaetoceros salsuguineus Takano
Cocconeis placentula Ehrenberg
C. scutellum Ehrenberg
Craticula halophila (Grunow) D.G.Mann
Cyclotella atomus Hustedt
C. meneghiniana Kützing
Cylindrotheca gracilis (Brébisson) Grunow
Cymbella pusilla Grunow

C. tumidula Grunow
Diploneis bombus Ehrenberg
D. decipiens var. *parallela* Cleve
D. didyma (Ehrenberg) Cleve
Encyonema minutum (Hilse in Rabenhorst) D.G.Mann
Entomoneis alata (Ehrenberg) Ehrenberg
E. paludosa (W. Smith) Reimer
E. pseudoduplex Osada & Kobayasi
E. puctulata (Grunow) Osada & Kobayasi
Fallacia pygmaea (Kützing) Stickle & D.G.Mann
F. tenera (Hustedt) D.G. Mann
Fistulifera cf. *saprophila* (Lange-Bertalot & Bonik) Lange-Bertalot
Fragilaria capucina Desmazières
F. sopotensis Witkowski & Lange-Bertalot
Gomphonema gracile Ehrenberg
G. parvulum Kützing
G. truncatum Ehrenberg
Gomphonemopsis obscurum (Krasske) Lange-Bertalot
Gyrosigma acuminatum (Kützing) Rabenhorst
G. eximium (Thwaites) Boyer
G. nodiferum (Grunow) Reimer
Haslea spicula (Hickie) Lange-Bertalot
Hippodonta hungarica (Grunow) Lange-Bertalot, Metzeltin & Witkowski
Kolbesia ploenensis (Hustedt) Round & Bukhtiyarova
Luticola mutica var. *mutica* (Kützing) D.G.Mann
Mastogloia pumila (Grunow) Cleve
M. pusilla (Grunow) Cleve
Melosira moniliformis var. *octogona* (Grunow) Hustedt
M. nummuloides (Dillwyn) Agardh
Navicula arenaria Donkin
N. cancellata Donkin
N. cincta (Ehrenberg) Ralfs
N. cryptocephala Kützing
N. cryptotenella Lange-Bertalot
N. duerrenbergiana Hustedt
N. erifuga Lange-Bertalot
N. gemmifera Simonsen
N. gregaria Donkin
N. cf. *indifferens* Hustedt
N. korzeniewskii Witkowski, Lange-Bertalot & Metzeltin

N. lanceolata (Agardh) Ehrenberg
N. margalithii Lange-Bertalot
N. menisculus Schumann
N. microcari Lange-Bertalot
N. microdigitoradiata Lange-Bertalot
N. normaloides Cholnoky
N. paul-schulzii Witkowski & Lange-Bertalot
N. cf. *paul-schulzii* Witkowski & Lange-Bertalot
N. perminuta Grunow
N. phyllepta Kützing
N. radiosa Kützing
N. recens (Lange-Bertalot) Lange-Bertalot
N. salinarum Grunow
N. salinicola Hustedt
N. stachurae Witkowski, Lange-Bertalot & Metzeltin
N. tripunctata (O. F. Müller) Bory
N. trivialis Lange-Bertalot
N. veneta Kützing
Navicula sp.1
Navicula sp. 2
Navicula sp. 3
Nitzschia acicularis (Kützing) W.Smith
N. cf. *acicularis* 1 (Kützing) W.Smith
N. cf. *acicularis* 2 (Kützing) W.Smith
N. agnewii Cholnoky
N. amphibia Grunow
N. archibaldii Lange-Bertalot
N. aremonica Archibald
N. aurariae Cholnoky
N. calcicola Aleem & Hustedt
N. calida Grunow
N. capitellata Hustedt
N. clausii Hantzsch
N. closterium (Ehrenberg) W. Smith
N. coarctata Grunow
N. communis Rabenhorst
N. cf. *commutata* Grunow
N. constricta (Kützing) Ralfs
N. debilis (Arnott) Grunow
N. dissipata (Kützing) Grunow

N. dissipata var. *media* (Hantzsch) Grunow
N. draveillensis Coste & Ricard
N. cf. *draveillensis* Coste & Ricard
N. elegantula Grunow
N. filiformis (W.Smith) Van Heurck
N. fontifuga Cholnoky
N. frequens Hustedt
N. frustulum (Kützing) Grunow
N. graciliformis Lange-Bertalot & Simonsen
N. gracilis Hantzsch
N. gracilis Hantzsch f. *acicularoides* Coste & Ricard
N. cf. *gracilis* Hantzsch
N. granulata Grunow
N. hungarica Grunow
N. intermedia Hantzsch ex Cleve & Grunow
N. littoralis Grunow
N. microcephala Grunow
N. nana Grunow
N. navicularis (Brébisson) Grunow
N. ovalis Arnott ex Grunow in Cleve & Grunow
N. palea (Kützing) W.Smith
N. paleacea Grunow
N. pararostrata (Lange-Bertalot) Lange-Bertalot
N. pellucida Grunow
N. perpsicua Cholnoky *sensu* Archibald
N. cf. *pumila* Hustedt
N. pusilla Grunow
N. cf. *pusilla* Grunow
N. reversa W.Smith
N. rosenstockii Lange-Bertalot
N. scalpelliformis (Grunow) Grunow
N. sinuata var. *delongei* (Grunow) Lange-Bertalot
N. supralitorea Lange-Bertalot
N. thermaloides Hustedt
N. vitrea Norman var. *vitrea*
N. vitrea var. *salinarum* (Grunow)
Nitzschia sp. 1
Opephora guenter-grassii (Witkowski & Lange-Bertalot) Sabbe & Vyverman
O. horstiana Witkowski
Planothidium delicatulum (Kützing) Round & Bukhtiyarova

P. jan-marcinii Witkowski, Metzeltin & Lange-Bertalot
P. lanceolatum (Brébisson) Round & Bukhtiyarova
Pleurosigma cf. *elongatum* W.Smith
P. salinarum Grunow
Rhoicosphenia abbreviata (Agardh) Lange-Bertalot
Rhopalodia acuminata Krammer
R. constricta (W. Smith) Krammer
Sellaphora pupula (Kützing) Mereschkowsky
Staurophora amphioxys (Gregory) D.G.Mann
Surirella cf. *brebissonii* Krammer & Lange-Bertalot
Tabularia fasciculata (Agardh) Williams & Round
Thalassiosira pseudonana Hasle & Heimdal
T. wiessflogii (Grunow) Fryxell & Hasle

5.2 Diatom taxa with difficult taxonomy

Amphora libyca Ehrenberg [AMLIB]
Plate 6: Fig. 44

The measurements of our specimens conform to the size range of *A. libyca*, which according to Krammer & Lange-Bertalot (1997a) is characterised by frustules that are 20-80 μm in length, 14-35μm in width and have 11-15 dorsal striae in 10μm at the middle of the valve. However, it cannot be excluded that some of the specimens studied would correspond to small frustules of *A. marina* W. Smith. The frustule size of the latter is 24-46.5 μm in length, 14.5-23 μm in width with 15-20 dorsal striae in 10 μm at the middle of the valve (Schoeman & Archibald 1986). This is due to the fact that frustule length and width of both taxa overlap to a certain extent, and precise counting of the dorsal striae density is often difficult under LM.

Amphora margalefii Tomàs [AMMAR]
Plate 6: Fig. 45-48

Size ranges and mean values (in brackets) of the specimens studied. L= length, W= frustule width:

	L (μm)	**W** (μm)	***Dorsal striae in10μm***	***Ventral striae in 10μm***
LM n=10	14.28– 16.32 (16)	5.1 – 7.17 (6)	24– 30 (27)	
SEM n=7	10.22 – 15.25 (13)	4.51 – 4.57 (5)	30– 34 (32)	57 – 60 (54)

Size ranges of *Amphora margalefii* Tomàs and *Amphora margalefii* var. *lacustris* P. Sánchez according to Sánchez-Castillo (1993):

	L (μm)	**W** (μm)	***Dorsal striae in10μm***	***Ventral striae in 10μm***
A. margalefii	6.7 – 15.8	4.6 – 6.4	ca. 25	ca. 50
A.margalefii var. *lacustris*	18 – 27	6.5 – 10	18 – 20	30 – 39

A. margalefii was described by Tomàs in Sabater *et al*. (1990) from periphytic samples collected in a little creek in Port de la Selva (Cap de Creus, Girona, NE Spain). The variety *lacustris* of this species was described by Sánchez-Castillo (1993) from epipelon of the brackish water lagoons: Laguna Chica and Laguna Grande in Archidona (Málaga, SE Spain).

The individuals encountered in this study possessed features in common with both varieties. In terms of size and density of striae they are closer to the nominate variety, but in terms of shape (linear-elliptical, Plate 6: Figs. 45- 47) and of the ventral striation ultrastructure (rows of more than three pores, Plate 6: Fig. 48) closer to the variety *lacustris*.

According to Sánchez-Castillo (1993) the frustule shape in the nominate variety of *A. margalefii* is elliptical to linear-elliptical and the ventral striae are composed of one to three pores in row, while the variety *lacustris* has a linear-elliptical shape and the striae are composed of three to seven pores in row. The results of the present study together with the fact that frustule shape and the ultrastructure of the ventral striae are the two main features that Sánchez-Castillo (1993) used as distinctive characters between the varieties suggest that the division of *A. margalefii* into two varieties is not clear.

Distribution and ecology:

The only two citations of this species are from Tomàs (Sabater *et al.* 1990) and from Sánchez-Castillo (1993). There is no physical and chemical data for the type locality (little creek in Port de la Selva) from which Tomàs in Sabater *et al.* (1990) described *A. margalefii.* It is only known (Tomàs *et al.* 1987) that this little creek lies in a siliceous area and is characterised by very low flow rates, shallow depth, with high salinity, which is, however, subject to strong fluctuations (mean of 1147 μS /cm but can achieve up to 4000 μS / cm), with an important marine influence (occurrence of Cl^- ions) and also fluctuating pH. The lagoons of Archidona from which Sánchez-Castillo (1993) described the variety *lacustris* are oligohaline systems of moderate trophic status (meso-eutrophic) according to Sánchez-Castillo (personal communication).

This species was present in all the waterbodies studied in the Empordà salt marshes (Appendix II) in waters with low dissolved nitrogen concentration but with high organic nitrogen content.

Amphora cf. **luciae** Cholnoky *sensu* Archibald 1983 [cAMLUC]

Plate 8: Fig. 55-59

	L (μm)	**W** (μm)	***Dorsal striae in 10μm***	***Ventral striae in 10μm***
LM n=23	12.24 – 18.36 (15)	3.06 – 4.08 (4) 6.12 – 9 (7)	17– 26 (22)	–
SEM n=13	11.22 – 16 (14)	4.75 – 6.38 (6)	20 – 30 (25)	39.5 – 47 (43)

Size range of the specimens studied: Minimum-maximum and mean values (in brackets). n= number of individuals measured. L = length and W = width (under SEM only valve width is available, under LM valve and frustule width are listed).

Light microscopy:

Frustules elliptical with distinctly protacted ends. Valves with strongly convex dorsal margin and straight ventral margin. Valve poles subrostrate sometimes ventrally deflected. Intercalary bands visible, but the pores cannot be resolved with LM. Dorsal striae, 12.24-18.36 in 10μm, parallel at the centre of the valve, becoming slightly radiate at the poles, very often distinctly punctate. Ventral striation much denser and finer than the dorsal, almost invisible (Plate 8: Fig. 55).

SEM:

Intercalary bands with longitudinal rows of pores (Plate 8: Fig. 56). Usually a thin conopeum with bluntly rounded ends is present (Plate 8: Fig. 58). Central external raphe endings slightly expanded and deflected towards the dorsal side (Plate 8: Figs. 58). Terminal raphe fissures curved dorsally and terminating below the junction of the conopeum with the valve apices (Plate 8: Fig. 58). Dorsal striae formed by a row of round to rectangular pores. The ventral striae

composed of rectangular elongated pores, shorter at the centre of the valve below the central area (Plate 8: Figs. 58 and 59).

Taxonomical comments:

This taxon agrees perfectly with the description of *A. luciae* Cholnoky done by Archibald (1983). The LM images presented by Archibald (1983) conform very well to the shape of the specimens in this study. The only difference is the number of the ventral striae. *A. luciae* illustrated in Archibald (1983) had 28 to 30 ventral striae in 10 μm, while the specimens studied here possess 39 to 47 ventral striae in 10 μm. Such difference in striation and the fact that Archibald (1983) did not illustrate the ultrastructure of *A. luciae* make at difficult to accept with certainty the allocation of the Empordà wetlands specimens to this species.

The size range of *A. luciae* illustrated by Kuylenstierna (1990) coincides with that of the present study. It is worth to mentioning that Kuylenstierna (1990) did not present any information on the ventral striae. His SEM images also coincide with those from the present study. However, the LM images of *A. luciae* shown by Kuylesntierna (1990) differ from ours. One of the possible explanations for this discrepancy might be the larger size of Kuylenstierna specimens. Their length ranged from 22 to 30 μm, while the specimens from the present work did not exceed 18 μm. Unlike to the length difference, the width difference is much lower. In the present study specimens ranged from 3 to 4 μm, while the width range for Kuylenstierna was 2.8 and 3.5 μm.

Kuylenstierna (1990) also includes specimens that he calls *A. tenerrima* Aleem and Hustedt *sensu* Bérard-Therriault, Cardinal and Poulin (1986). The size ranges of his specimens perfectly match with those of *A. luciae sensu*

Archibald. The SEM image published by Kuylenstierna (1990, Fig. 488) as *A. tenerrima sensu* Bérard-Therriault, Cardinal et Poulin (1986) is very similar to the one he called as *A. luciae sensu* Archibald (Kuylenstierna 1990, Fig. 483). A recent study of the type material of *A. tenerrima* by Clavero *et al*. (2000) proves that the specimens illustrated by Bérard-Therriault, Cardinal et Poulin (1986) do not belong to the latter species. The dorsal striae of *A. tenerrima* are composed of double rows of fine pores (cf. Clavero *et al.* 2000) while the specimens that Bérard-Therriault, Cardinal et Poulin (1986) called *A. tenerrima* possessed uniseriate dorsal striae, composed of rectangular pores. These results suggest that the specimens that Kuylenstierna (1990) showed as *A. tenerrima sensu* Bérard-Therriault, Cardinal et Poulin (1986) belonged to the same species as the specimens that he considered as *A. luciae sensu* Archibald.
Most probably *A. luciae* belongs to the small group of *Amphora* species from brackish waters for whose identification light microscopial observations are insufficient. Light and electron microscope studies of the original material from the type locality of *A. luciae* (Santa Lucia Lagoon in South Africa), are required for reliable identification of such taxa.

Distribution and ecology of *A. luciae sensu* Archibald:
Archibald (1983) found this species in brackish waters of the Sundays and Great Fish Rivers in the eastern part of the Cape Province in South Africa. Kuylenstierna (1990) reported *A. luciae sensu* Archibald as common to very common in the outer part of the Nodre Älv estuary (western coast of Sweden). Witkowski *et al*. (2000) considered it a species distributed in brackish waters of the entire Baltic Sea.

This taxon occurred in all 6 basins studied in the Empordà salt marshes, but its highest abundance was recorded in the northern sector basins (b.Connectada, b.Tamariu and E.Túries). See Appendix II. The species tolerates certain concentrations of ammonium, nitrate, phosphate and total nitrogen.

Amphora sp. aff. **tenuissima** Hustedt [AMSP1]
Plate 9: Figs. 60-65

	L (μm)	**W** (μm)	***Dorsal striae in 10μm***	***Ventral striae in 10μm***
LM n=15	13 – 17 (16)	4 – 6 (5)	_	_
SEM n=7	8.4 – 14.88 (12)	1.76 –2.20 (2) 4.58 – 5.30 (5)	34 – 37 (35)	52 – 56 (53)

Size range of the specimens studied: Minimum-maximum and mean values (in brackets). n = number of individuals measured, L= length and W= width (under LM only valve width is available, under SEM valve and frustule width are listed).

Light microspopy:

Frustules linear-elliptical, linear with protacted ends. Valves with slightly convex dorsal margin and straight ventral margin. Intercalary bands very difficult to distinguish. The transapical striae on the dorsal side are very dense, barely resolvable in LM, parallel throughout the valve, sometimes becoming less dense at the centre of the valve. Ventral striation unresolvable under LM.

SEM:

Intercalary bands with longitudinal series of pores (Plate 9: Figs. 62 and 64). The conopeum shows variable development, in some cases being extremely thin and even not crossing the centre (Plate 9: Fig. 62). Proximal external raphe endings very slightly expanded and very slightly deflected to the dorsal side (Plate 9: Figs. 61 and 62). Dorsal striae formed of a row of transapically elongated rectangular pores.

Taxonomical comments:

This taxon is similar in size and shape to *Amphora tenuissima* Hustedt. The differences are seen at the ultrastructural level. A recent study by Clavero *et al*. (2000) on specimens of *A. tenuissima* from the type material from which the original description of the taxon was made (Hustedt 1955) shows that *A. tenuissima* has uniseriate dorsal striae that are composed of small round pores. In that sense, none of the SEM micrographs in the literature under the name *A. tenuissima* published prior to Clavero *et al*'s. (2000) work, e.g. Hargraves & Levandowsky (1971) and Sullivan (1979), have the same ultrastructure as the specimens found in the type material. The picture of Hargraves & Levandowsky (1971) would correspond to *A. tenerrima* Aleem & Hustedt. The specimens studied by Sullivan (1979) very closely resembled those encountered in the Empordà wetlands. These specimens mainly differ from *A. tenuissima* in the external areola openings of the dorsal striae. The areola of the Empordà wetlands specimens, as well as those in Sullivan (1979), are transapically elongated. However, as Clavero *et al*. (2000) already pointed out, none of the specimens from the type material used in their SEM study completely coincided with the specimens on the type slide of *A. tenuissima*.

Adding the lack of information on the variability of *A. tenuissima,* we can not establish a clear relationship between *A. tenuissima* and very similar taxa, such as the studied here or by Sullivan (1979).

Other species to which this taxon could be related are: *A. delicatissima* Krasske and *A. tenerrima* Aleem & Hustedt. The taxon under study differs from *A. delicatissima* by its denser striation (dorsal and ventral) and by the ultrastructure of the dorsal striae. Karayeva (1987) showed that dorsal striae of *A. delicatissima* have double rows of fine pores, becoming uniseriate towards the valve margin. It also differs from *A. tenerrima* by its denser striation (dorsal and ventral), as well as by the ultrastructure of the striae (According to Clavero *et al.* 2000, the dorsal striae of *A. tenerrima* are biseriate, formed of double rows of fine pores).

Some of the ultrastructural features of the specimens studied, such as the composition of striae, both dorsal and ventral, the development of the conopeum and the external proximal raphe endings are very similar to those of *A. hybrida* Grunow. However, the latter is much larger (length and width) and has a lower density of striae (dorsal and ventral). These features clearly differentiate *A. hybrida* from the taxon under study.

Thus, among the closely related taxa, the closest are the specimens that Sullivan (1979) illustrated under SEM as *A. tenuissima*, and the specimens of Kuylenstierna (1990) under the name of *Amphora* sp. J. Although Kuylenstierna only showed LM pictures, the shape of his specimens as well as the size range coincide completely with the individuals from the salt marshes of the Empordà wetlands.

Distribution and Ecology:

Due to uncertainties in the taxonomic position of this taxon, very little on the ecological information has been obtained from the literatue. *A. tenuissima* was described by Hustedt (1955) from Beaufort Bay, North Carolina. Sullivan (1979) obtained his specimens from samples of periphyton on three sea grasses from Horn Island in Mississippi Sound, Gulf of Mexico. Kuylenstierna (1991) reported his taxon as common to very common in association with *A. luciae* and *Nitzschia perspicua* in a sample of periphyton on *Vaucheria compacta* in the Nodre Älv estuary (western coast of Sweden).

In the present study, its maximum abundance (see Appendix II) was recorded in b.Connectada and in b.Tamariu in March and April 1997 samples. It is a taxon that lives in waters with low dissolved nitrogen concentration but with high organic nitrogen content.

Fistulifera cf. **saprophila** (Lange-Bertalot & Bonik) Lange-Bertalot [cFISAP]
Syn.: *Navicula saprophila* Lange-Bertalot & Bonik

All the small specimens (not longer than 8 μm in length), of round-oval shape, that appeared hyaline under the light microscope were considered under this name. The only feature recognisable with LM was the raphe system. The striae were completely unresolvable. The following species (all of them with ecology and distribution very similar and previously placed in the genus of *Navicula sensu lato*) can also be included in this group: *Fistulifera pelliculosa* (Brébisson *ex* Kützing) Lange-Bertalot [= *Navicula pelliculosa* Brébisson *ex* Kützing], *F. iranensis* (Hustedt) Lange-Bertalot [= *Navicula iranensis* Hustedt], *Navicula minuscula* var. *muralis* (Grunow) Lange-Bertalot,

Mayamaea atomus var. *permitis* (Hustedt) Lange-Bertalot [= *Navicula atomus* var. *permitis* Hustedt], *M. lacunolaciniata* (Lange-Bertalot & Bonik) Lange-Bertalot & Bonik [= *Navicula lacunolaciniata* Lange-Bertalot & Bonik]. These taxa can only be distinguished from each other under the SEM or TEM (cf. Archibald 1983, Krammer & Lange-Bertalot 1997a). Due to their low frequency of occurrence and especially due to their low abundance, SEM examination was not possible in the present study. Therefore they are provisionally retained under the name, *F.* cf. *saprophila,* and after further sampling their true taxonomic position will be resolved.

The size range (between 6.12 μm and 8.16 μm length and 2.55 μm and 3.06 μm valve width) of the individuals encountered in this study allowed us to use the tentative name of *F.* cf. *saprophila*. The above size ranges coincide perfectly with those of *F. saprophila* (4.5-7.6 μm of length and 2-4 μm of valve width; Krammer & Lange-Bertalot 1997a). The size range coincidence of our specimens with the other taxa is less convincing. *F. pelliculosa* (9-12.5 μm x 4-6.2μm), *Navicula minuscula* var. *muralis* (8-16μm x 3.2-5.5 μm), *Mayamaea atomus* var. *permitis* (6-9μm length), *M. lacunolaciniata* (7-8.5 μm x 3.5-4μm) according to Krammer & Lange-Bertalot (1997a) and *F. iranensis* (9-16μm x 3-4μm) *sensu* Lange-Bertalot (2001)

Kolbesia ploenensis (Hustedt) Round & Bukhtiyarova [KOPLO]
Bas.: *Achnanthes ploenensis* Hustedt
Plate 4: Figs. 28-29

The large specimens of *Achnanthes amoena* Hustedt and the small ones of *K. ploenensis* are difficult to distinguish under the light microscope. The only

difference is the striae density (16-23 in 10 μm in *K. ploenensis* and 18-22 in 10 μm in *A. amoena* according to Krammer & Lange-Bertalot 1991a). The stria density of the problematic specimens is ca. 16 in 10 μm. Due to their low abundance and, sometimes poor sample quality, the examination of these specimens under SEM was impossible. It cannot be excluded that some individuals ascribed to this taxon might actually belong in *A. amoena* Hustedt.

Luticola cf. **mutica** var. **mutica** (Kützing) D.G. Mann [cLUMU]
Bas.: *Navicula mutica* Kützing var. *mutica*

The taxonomic study of *L. mutica* and related taxa by Lange-Bertalot & Bonik (1978) identified the following features as distinctive for *L. mutica*: 1) lanceolate valves and rounded apices 2) transapical striae formed by transapically elongated pores 3) an isolated, transapically elongated stigma in the central area. It is still, however, impossible unequivocally to distinguish this taxon from small specimens of *Luticola goeppertiana* (Bleish) D.G. Mann [= *Navicula goeppertiana* Bleish] or from *Luticola saxophila* (Bock) D.G. Mann [=*Navicula saxophila* Bock] under the light microscope.

Navicula gregaria Donkin [NAGRE]
Plate 11: Fig. 77

Morphological variation of the taxon in question makes its determination difficult (e.g. Cox 1987, Lange-Bertalot 2001). Lange-Bertalot & Rumrich in Rumrich *et al*. (2000) described a new species *N. supergregaria,* giving length,

width and the lineola density as discriminating characters from *N. gregaria*. According to these authors, *N. supergregaria* is larger, broader and has lower lineola density than *N. gregaria*. There is no clear distinction in their ecology.
The size range of the specimens found in this study is 24.48-38.76 (29.14) μm in length, 6.12-8.16 (6.72) μm in width and 10-16.39 (12.78) transapical striae in 10μm (number of specimens counted = 13). These measurements let us consider the specimens studied as either *N. gregaria* or as *N. supergregaria.* Since the lineolae have not been studied under SEM, the classification of our specimens as *N. gregaria* is based on resemblance of the individuals encountered with those presented in Lange-Bertalot (2001) as *N. gregaria*. It is worth mentioning that, as already pointed out by other authors (Cox 1987, Lange-Bertalot 2001), further study of the morphological variation of different populations of these taxa under various environmental conditions is required.

Navicula cf. **indifferens** Hustedt [cNAIND]

The specimens resembling *Fistulifera* cf. *saprophila* but rhomboidal in shape were included under this name.
The individuals considered here could represent the following species: *Navicula indifferens*, *N. krasske*i Hustedt and *N. kuelbsii* Lange-Bertalot. A SEM revision of this group of small, rhomboidal naviculoid diatoms with barely resolvable transapical striae under the light microscope, will allow the specific identify of the taxon in question to be determined.

Navicula cf. **paul-schulzii** Witkowski & Lange-Bertalot [cNAPSC]

All the individuals in which we were able to measure and count the stria density without any problems were included in *N. paul-schulzii*. Whereas those individuals that due to their small size and the density of striae have been difficult to determine under the light microscope were considered as *N.* cf. *paul-schulzii*. The stria density is important in such taxa since the small forms of *N. phyllepta* (=*N.phylleptosoma* Lange-Bertalot), *N. paul-schulzii* and *N. biskanterae* Hustedt can often be confused. The only criterion that differentiates them, is stria density: 17-20 striae in 10μm in *N. phylleptosoma*, 21-24 in *N. paul-schulzii* and 24 in *N. biskanterae*, according to Witkowski *et al.* (2000).

Navicula phyllepta Kützing [NAPHY]
Plate 11: Fig. 84

Lange-Bertalot (Lange-Bertalot & Genkal 1999) described *N. phylleptosoma* as a new species. Its distinctive features with respect to *N. phyllepta* are: smaller size (length and width), denser striation, higher density of lineolae and the ultrastructure of the external central raphe endings. The size range of the individuals studied here conforms not only to *N. phylleptosoma* but also to *N. phyllepta*. Since ultrastructure was not studied in our individuals (because of the low abundance of that taxon in the samples) and because there is no distinction in the ecology of the two species in question, the individuals in this study have been considered as *N. phyllepta sensu lato.*

Navicula sp. 1 [NASP1]

	L (μm)	**W** (μm)	***Striae in 10μm***
LM n=8	12.24– 22.40 (16.05)	3.06 – 5.10 (3.74)	16.40

Valves linear-lanceolate, with slightly convex margins and undifferentiated, more or less obtusely rounded apices. Raphe filiform with external proximal endings close to each other. The axial area is very narrow, central area nearly absent. The transapical striae parallel throughout.

The individuals studied here would correspond to *Navicula* spec. cf. *salinicola* Hustedt *sensu* Witkowski *et al*. (2000, Plate 125, Figures 9-11). They are also similar in size, in striation pattern and in the proximity of the central external raphe endings to the images the above authors show as *N. syvertsenii* Witkowski, Metzeltin & Lange-Bertalot (Plate 141, Figures 7-12) and *N. wasmundii* Witkowski, Metzeltin & Lange-Bertalot (Plate 141, Figures 7-12), although these species possess conspicuous central areas. This feature is absent in ours specimens.

Navicula sp. 2 [NASP2]
Plate 11: Fig. 78

Included in this taxon are all forms of linear-lanceolate forms related to *N. salinicola* Hustedt. However, they differ from it with respect to their larger size, slightly differentiated apices and distinctly more radiate transapical striae in the middle of the valve. Numerous individuals conform to some of the

images presented as *Navicula* spec. in Witkowski *et al.* (2000, Plate 126, Figures 8-29).

Navicula sp. 3 [NASP3]

Valves linear-lanceolate with slightly convex margins and undifferentiated, obtusely rounded apices. Raphe filiform, axial area very narrow. The transapical striae in the middle of the valve are radiate, becoming parallel towards poles. The central area is conspicuous, rhomboid in shape, developed as a result of the shortening of the central transapical striae.
The characteristics of the individuals considered here coincide closely with those presented as *Navicula* spec. "Salinen Salzkotten" in Witkowski *et al.* (2000, Plate 125, Figures 33-39).

Nitzschia cf. **acicularis** 1 [cNIAC2]

The morphology of the valve of *Nitzschia acicularis* (Kützing) W. Smith and of *N. draveillensis* Coste & Ricard is identical. The only difference between the two species is the space between the two median fibulae (not equidistant in *N. draveillensis*).
Observation under the light microscope to determine whether this space is present or not is often difficult. Therefore all specimens whose morphology conforms to *N. acicularis* and *N. draveillensis,* in which we were not able to

distinguish unequivocally between presence or absence of equidistant median fibulae were included under this name.

Nitzschia cf. **acicularis** 2 [cNIAC3]

Included in this taxon are all the individuals in which we were not able to decide precisely whether they belong to *N. acicularis* or to *N. rev*ersa W. Smith. Sometimes we found individuals with sigmoid apices (characteristic for *N. reversa* but absent in *N. acicularis*) showing very subtle curvature. That raises the question whether the curvature resulted from teratology or the sample treatment. In addition the equidistant position of the middle fibulae (a feature characteristic for *N. reversa*) was not clearly distinguishable.

Nitzschia cf. **commutata** Grunow [cNICMM]

It is very difficult to distinguish *Nitzschia commutata* from *N. gisela* Lange-Bertalot under light microscope. Specimens of *N.gisela* are more slender, but this character is difficult to notice when the two species do not occur together. Krammer & Lange-Bertalot (1997b) reported *N. commutata* as a species of brackish coastal waters and also from inland waterbodies of high electrolyte content. The same authors reported *N. gisela* as the "freshwater variety" of *N. commutata* with an affinity for calcium. The definitive distinction between these two species can only be made under SEM (the areolae in the area of the raphe keel do not bifurcate in *N. commutata*).

Nitzschia cf. **draveillensis** Coste & Ricard [cNIDRA]

All species in which was not possible to distinguish unequivocally their belonging to *N. draveillensis* or to *N. rev*ersa W. Smith were included under this name. The only distinctive feature is the curvature of the valve apices (sigmoid in *N. reversa*, straight in *N. draivellensis*). The subtle deflection of the apices of the specimens observed made us doubt of their specific identify.

Nitzschia frustulum (Kützing) Grunow [NIFRU]
Plate 14: Figs. 106-107

Although several works (e.g. Lange-Bertalot & Simonsen 1978, Wendker 1990b, Lange-Bertalot 1993) advocate the conspecificity of *N. frustulum* and *N. inconspicua* Grunow, due to shared ultrastructural characteristics, differences in valve shape and ecology have often been used to separate them. Over many years the short and roundish shape from freshwater systems has been identified as *N. inconspicua* and the longer and thinner shape as *N. frustulum*. In this work, not only were the intermediate shapes of the two extremes found, but we also observed different forms in the samples (samples with different salinity conditions: *e.g.* at 1 and 13 mS / cm). In addition, in the experimental work on the morphological variation of *N. frustulum* (see chapter 7) we obtained the shorter and roundish shape in a wide range of salinities. Thus, we considered not only the long and thin specimens, but also the small roundish ones, as well as all the intermediate forms as *N. frustulum*.
For further information about *N. frustulum* see Chapter 7.

Nitzschia gracilis Hantzsch f. **acicularoides** Coste & Ricard [cNIGRA1]

N. gracilis is a conflictive species (Tomàs 1988). The concept of this species differs with respect to size range and valve shape between Krammer & Lange-Bertalot (1997b) and Germain (1981).

N. gracilis sensu Germain (1981) is broader and more distinctly fusiform than *N. gracilis sensu* Krammer & Lange-Bertalot (1997b). In addition, the stria density of *N. gracilis* according to Krammer & Lange-Bertalot (1997b) ranges between 38 and 42 in 10 μm (possible to observe under light microscopy with good optics and oblique illumination). However, the stria density of *N. gracilis* according to Germain (1981) ranges from 50 to 55 (completely unresolvable under LM).

The individuals considered in this study (narrow valves, distinctly fusiform, with strongly tapering apices and equidistant middle fibulae) coincide in shape and size range with *N. gracilis sensu* Germain (1981). They also conform to the Figure 4, Plate 85 in Krammer & Lange-Bertalot (1997b), a specimen which the authors present as *N. acicularis* with a question mark.

On the other hand, Coste & Ricard (1980) described a new form of *N. gracilis* i.e. *N. gracilis* f. *acicularoides*. The size range and shape of *N. gracilis* according to Coste & Ricard (1980) is the same as that of Krammer & Lange-Bertalot (1997b) and the distinctive characteristics of the forma *acicularoides* with respect to the nominate one are: greater valve length and width, and that the striae cannot resolved under the light microscope. These characteristics are shared by the individuals studied here and also by those that Germain (1981) presented as *N. gracilis*. Coste & Ricard (1980) pointed out the possibility that

N. gracilis f. *acicularoides* could have been confused with *N. acicularis*. This is due to its distinctly fusiform shape and tapering apices. Thus, careful revision of these taxa, as well as a study of the morphological variability of their valves, is required.

Size range (mean in brackets) of *N. gracilis* f. *acicularoides*, and *N. gracilis* according to different authors and of the specimens studied here.

Species	*N.gracilis*			*N. gracilis* f. *acicularoides*	Specimens studied in this work
	Krammer & Lange-Bertalot 1997	Coste & Ricard 1980	Germain 1981	Coste & Ricard 1980	(N= 8)
L (μm)	30-110	50-70	38-110	60-80	42.84-75.48 (65.15)
W μm)	2.5-4	2.2-2.6	2.5-4	3-3.7	3.90-4.08 (4.05)
Fibulae in 10μm	12-18	15-17		15-17	13.11-16.40 (14.55)
Striae in 10μm	38-42	39-41	50-55	Unresolvable under LM	

In this study, individuals were been classified as *N. gracilis* on the basis of Krammer & Lange-Bertalot's (1997b) concept of *N. gracilis*.

Ecology and distribution:

Germain (1981) referred *N. gracilis* as a species sometimes occurring in the plankton of the Loire river, but much more frequent in the benthos of highly polluted systems.

Although, Krammer & Lange-Bertalot (1997b) believed that it is difficult to determine the precise ecological requirements of this species, they qualified *N. gracilis* as an oligo- to β-mesosaprobic species inhabiting waters with high electrolyte content. They noted the absence of this species from highly eutrophic rivers.

Coste & Ricard (1980) did not give ecological characteristics of form *acicularoides* of *N. gracilis* in their description.

Referring to the ecology of *N. acicularis,* with which *N. gracilis* f. *acicularoides* could be confused (Coste & Ricard 1980, Krammer & Lange-Bertalot 1997b): it is regarded as a taxon of wide ecological amplitude, but preferring waters with relative eutrophy level and with a certain electrolyte content. They consider it resistant to α-mesosaprobic pollution level, but intolerant of polysaprobic conditions. These authors do not recommend its use as an indicative species due to the fact that *N. acicularis* can potentially live in plankton therefore its autochthonous occurrence in the benthos sampling site cannot be assured.

In the Empordà salt marshes most of the specimens considered as *N. gracilis* f. *acicularoides* were found exclusively in r.Muntanyeta, with a maximum of abundance reached in the March and April 1997 samples (see Appendix II).

Nitzschia cf. **gracilis** [cNIGRA2]

The species considered here is what completely conforms to Figure 10 of Plate 66 in Krammer & Lange-Bertalot (1997b), presented as *N. gracilis*. The specimen shown in this figure is very slightly fusiform (like the specimens encountered here) compared with the others figures also presented as *N. gracilis* (cf. with Figures 1-9 of the same plate). Thus, although the specimens studied here exibit a size range and stria density that completely conform with *N. gracilis sensu* Krammer & Lange-Bertalot (1997b) an accurate revision of *N. gracilis* and related taxa should be made in order to unequivocally identify this diatom.

Nitzschia cf. **pumila** Hustedt [cNIPUM]

N. pumila can be mistaken for small forms of *N. palea* var. *tenuirostris* Grunow and for *N. gracilis*. Their differentiation remains unclear. Thus, all the small specimens whose shape and size conform to the one whose three above taxa are included.

Nitzchia cf. **pusilla** (Kützing) Grunow *emend*. Lange-Bertalot [cNIPUS]
Plate 13: Fig. 101

This includes the large specimens (ca. 20µm of length) of forms similar to *N. pusilla*. These individuals resemble closely the large individuals presented as "*N. pusilla* änhliche Sippen aus Brackwasser" by Krammer & Lange-Bertalot (1997, Plate 79; Figures 20-21).

Nitzschia sp. aff**.** "Falsche *Nitzschia sigma*-Sippen" [NISP1]
Plate 16: Figs. 116-123

	L (µm)	**W** (µm)	***Fibulae in 10µm***	***Striae in 10µm***
LM n=23	42.84 – 90.78 (60.7)	2.55 – 4.59 (3.56)	7.84 – 12.11 (10.8)	–
SEM n=13	54.267– 71.9 (63.82)	3.65 –4.39 (4.12)	–	49.26 – 54.97 (50.76)

Size range of specimens studied: Minimum-maximum and mean in brackets. n= number of individuals measure, L= length and W= valve width.

Light microspopy:

Frustules linear sigmoid in girdle view (Plate 16: Figs. 166 and 118). Valves narrowly lanceolate to linear-lanceolate, various sigmoid, with slightly convex margins, gradually tapering towards the apices. Valve length and width varie considerably: 42.8-90.8 μm of long, 2.55-4.6 μm of broad. The apices are acutely rounded, undifferentiated, to slightly capitate. The raphe is eccentric. The fibulae are short, rectangular in shape, distributed randomly (7.8-12.1 in 10 μm), the two middle ones are widely spaced (Plate 16: Figs. 117 and 118). The transapical striae are very fine and very dense, barely visible in the light microscope.

SEM:

The transapical striae are composed of fine longitudinal slits (Plate16: Figs. 121-132). The striation is extended onto the mantle. The girdle is composed of a few perforated bands (Plate 16: Fig. 122). Fibulae are thick and the middle ones distinctly further apart (Plate 16: Fig. 120). The raphe slit is straight and raised on a keel. The keel does not posseses a conopeum. The external central endings are straight and positioned close to each other (Plate16: Fig. 122). The external central endings do not show any deflection or expansion, which are characteristic for *Nitzschia* section *Obtusae*, to which this species initially might have been assigned because of the sigmoid shape of the frustule and o the distant position of the middle fibulae.

Taxonomical comments:

This species, with respect to shape and size, closely resembles *N. sigma* (Kützing) W. Smith and to *N. sigmaformis* Hustedt. However, it differs from

these taxa by having much finer striation and additionally from *N. sigma* by the distant position of the middle fibulae. As shown for some other *Nitzschia* species, the distant position of the two middle fibulae is a highly variable character (Wendker & Geissler 1988, Chapter 7 in this work). Therefore, its significance as a taxonomic criterion should be revised.
The closest taxon found in the published works is what Krammer & Lange-Bertalot (1997b) called "Falsche *Nitzschia sigma*-Sippen"

Distribution and ecology:
Because the only taxon that can be related the individuals studied is the"Falsche *Nitzschia sigma*-Sippen" of Krammer & Lange-Bertalot (1997b)it is very difficult to have accurate information about the distribution and ecology of this taxon.
It was present in all the waterbodies studied. Its maximum abundance was recorded in the July sample from La Rogera (see Appendix II). The specimens were present in waters with low dissolved nitrogen concentration but high organic nitrogen content.
This taxon was also recorded by Witkowski (personal communication) from the German North Sea tidal flat in Dangast.

Pleurosigma cf. **elongatum** W.Smith [cPLELO]

The distinction between *P. elongatum* and *P. strigosum* W. Smith var. *strigosum* is at ultrastructural level (18-20 transverse striae in 10 μm for *P. elongatum*, and 15-18 by *P. strigosum* var. *strigosum*, *sensu* Patrick & Reimer

1966). Due to its rarity (low incidence of occurrence) and low abundance in the samples studied, it could not been assigned unequivocally to one species.

Surirella cf. **brebissonii** Krammer & Lange-Bertalot [cSUBRE]

Like the previous taxon, the rarity and low abundance of this taxon have not allowed its study under SEM to determine the number of portulae between the fibulae (1 portula between two fibulae in *S. ovalis* Brébisson; more than one portula between two fibulae in *S. brebissonii*), and then not being possible to assign the specimens to one of the two species.

6. FACTORS AFFECTING THE PERIPHYTIC DIATOM COMMUNITY IN THE SALT MARSHES OF THE EMPORDÀ WETLANDS

6.1 Introduction

Several authors have pointed out the ecological importance of diatoms in the periphyton in estuarine and shallow coastal environments (Goldsborough & Robinson 1996, Sullivan 1999, Sullivan & Currin 2000, Underwood & Kromkamp 1999). However, the studies on diatom communities of these fluctuating systems are few, especially when compared with the situation in freshwater systems (Sullivan 1999, Underwood & Provot 2000). Difficulties in the identification of the resident species may be one of the factors accounting for the lack of information, since the majority of salt marsh diatom species are small forms mostly belonging to some of the most taxonomically complex genera (*Nitzschia*, *Navicula* and *Amphora*) and most of the individual taxa show considerable morphological variability (Sullivan & Currin 2000, Chapters 5 and 6 in this work). Furthermore, the study of fluctuating systems (such as coastal wetlands and estuaries) is complex, especially because of the continuous fluctuations and interactions between physico-chemical factors. Nevertheless, the fluctuating conditions and the high number of environmental factors involved make the study of these transitional environments (neither fully marine nor fully freshwater but sharing hydrological characteristics of both) very useful for elucidating the factors affecting diatom distribution and to refine on knowledge of diatom ecology.

The Empordà wetlands fulfil the above mentioned conditions, showing great variation in environmental parameters over small scales of time and space (see

Chapter 4) and being a suitable place for investigations into the ecological properties of diatom assemblages characteristic of these systems. From the whole area of the Empordà wetlands, the waterbodies selected for the ecological study of periphytic diatoms were those situated in the salt marshes of the Empordà Wetlands Natural Park (Chapter 2, Fig. 2.1), since it is the area in which the environmental parameters fluctuate most. The waterbodies studied are those classified as semi-confined brackish coastal wetlands, lagoons and ponds in Chapter 4 (see this Chapter for further limnological details of the waterbodies, and Chapter 2, Section 2.2 for the hydrology of the salt marshes of the Empordà Wetlands Natural Park).

The aim of the present chapter is to determine the ecological preferences of periphytic diatoms in the lentic systems of the Empordà salt marshes. The ecological preferences of the most characteristic diatom assemblages are highlighted by using multivariate analysis of direct ordination, which allows diatom distribution to be compared with the main, potentially influential, physical and chemical variables.

6.2 Results

6.2.1 Variation ranges of physical and chemical parameters

Table 6.1 shows the mean values, coefficients of variation and variation ranges for the physical and chemical parameters where the investigated species were found. The species listed in Table 6.1 are those whose distribution is well explained by the CA dimensions (the species with a value ≥ 0.1 for the contribution of CA dimensions to their inertia) and that we consider to be the most representative taxa. The variation ranges of all parameters were very high

for most of the species. This was especially true for salinity, nutrient and TOC concentrations. Interestingly, dissolved nutrient concentrations showed the highest coefficients of variation, but with low means, especially for the dissolved forms of inorganic nitrogen. Although total nitrogen and organic matter concentrations can also show high coefficient of variations, their mean values were also high.

According to OECD guidelines (OECD 1982) all the waterbodies included in this study are eutrophic. With respect to salt content and depending on time, the shallow waters studied can be considered as ranging from freshwater to polyhaline systems, according to the Anonymous (1959) saline classification. Therefore, the investigated diatoms may be considered euryhaline and eutrophic-water species. The species showed a minimum coefficient of variation for pH, with a mean always over 7.5. However, it cannot be determmined whether the species are pH indifferent or alkalibiontic, since the waters always had pH values higher than 7.

Acronym	Diatom taxa	Ass.	Dim	N	Temperature (ºC)	Salinity (‰)	pH	TOC (mg/l)	Si (µM)	NH_4^+ (µM)	NO_2^- (µM)	NO_3^- (µM)	PO_4^{-2} (µM)	Total-N (µM)	Total-P (µM)
NAERI	*Navicula eitfuga*	1	1	9	12.2 (10.2); 4.7-21.8	2.4 (20.8); 0.3-16.1	8.1 (1.9); 7.4-8.5	11.4 (11.8); 5.8-18.0	135 (13.8); 131-217	4.7 (183); 0-40.7	0.8 (26); 0-1.5	22.7 (172); 0-197	7.9 (103); 0.1-44.5	146 (48); 53.6-455	11.8 (56.9); 1.7-41.5
NAGRE	*Navicula gregaria*	1	1	49	17.5 (53.7); 4.7-33.5	5.2 (61.5); 0.2-25.4	8.0 (4.7); 7.1-9.2	12.9 (32.4); 3.9-26.1	173 (20.7); 9.3-258	8.8 (149); 0-49.2	0.6 (215); 0-9.9	21(230); 0-203	6.4 (161); 0.1-46.1	122 (80); 52.7-616	8.7 (102); 1.4-41.5
ADMIN	*Achnantidium minutissimum*	2	1	13	24.6 (13); 10.4-26.5	1.4 (221); 0.2-18.4	8.0 (3.7); 7.7-9.1	8.7 (24); 3.9-17.6	170 (21.2); 85.2-253	4.2 (109); 0-43.1	0.1 (161); 0-1.5	3.1 (690); 0-203	1.6 (303); 0.1-46.1	126 (57.3); 50.7-616	5.3 (73); 1.5-38.8
AMVEN	*Amphora veneta*	2	1	18	17.8 (39.3); 4.7-31.0	4.3 (158); 0.2-25.4	8.1 (6.7); 7.1-9.3	9.2 (31); 5.0-23.6	128 (54.9); 9.3-257	3.4 (216); 0-40.7	0.2 (216); 0-1.5	11.5 (335); 0-197	2.9 (256); 0.1-44.5	98.7 (69.4); 53.6-455	5.3 (124); 1.5-41.5
CRHAL	*Craticula halophila*	2	1	16	9.3 (45.1); 4.7-25.9	4.7 (106); 0.2-14.6	8.0 (6.6); 7.4-9.2	9.4 (31.7); 3.9-18.0	102 (56.6); 9.3-246	7.7 (134); 0-43.1	0.3 (136); 0-1.5	10.0 (212); 0-203	4.0 (133); 0.1-46.1	88.2 (61.6); 50.7-616	6.3 (84.1); 1.5-38.8
FAPYG	*Fallacia pygmea*	2	1	13	21.2 (34.7); 4.7-25.9	4.9 (53); 0.2-16	8.3 (3.8); 7.4-8.9	12.9 (22.69); 7-18	196 (12.6); 85.2-257	1.8 (267); 0-22.3	0.2 (93.2); 0-1.4	2.0 (305); 0-29.3	1.4 (133); 0.1-8.7	96 (19.8); 50.7-200	4.1 (58.5); 1.5-13.3
CFISAP	*Fistulifera cf. saprophila*	2	1	20	24.3 (279); 4.7-30.6	6.6 (127.3); 0.2-25.4	8.1 (4); 7.6-9.2	14.0 (43); 7.0-25.2	187 (22.8); 85.2-258	3.1 (166); 0-22.3	0.2 (136); 0-0.9	2.0 (277); 0-26.0	1.8 (105); 0.1-8.7	122 (34.2); 51-207	5.1 (39.6); 1.5-647
GOPAR	*Gomphonema parvulum*	2	1	15	17.6 (36.4); 4.7-27.7	1.7 (141.2); 0.2-18.8	8.2 (5.2); 7.4-9.1	10.4 (25.5); 7.0-27.2	136 (26.4); 85.2-258	2.6 (69.5); 0-5	0.3 (97.8); 0-1.4	6.3 (105); 0-29.3	3.0 (84); 0.1-6.2	115 (26); 50.7-209	6.6 (49); 1.2-13.3
HIHUN	*Hippodonta hungarica*	2	1	17	19.6 (36.7); 4.7-25.9	2.2 (1847); 0.17-17.1	8 (4.3); 7.5-8.9	9.4 (25.3); 7-21	177 (31.4) 85.2-253	4.8 (113); 0-22.3	0.3 (103); 0-1.45	3.6 (186); 0-29.3	2.2 (111); 0.1-8.7	116 (2356); 50.7-201	6 (46); 1.3-13.3
NASPC	*Navicula paul-schulzii*	2	1	15	14.5 (48) 4.7-29.8	9.3 (65.2) 0.34-19.4	8 (5.9) 7.08-9.14	8.9 (56) 3.9-25.2	182 (842) 9.3-258	15.4 (122) 0-43.1	0.6 (114) 0-1.51	60.8 (150) 0-203	14.9 (133) 0.28-46.1	243 (98) 53-616	15 (101) 1.33 -39
NAVEN	*Navicula veneta*	2	1	20	18.3 (38.4); 4.7-33.5	1.8 (128); 0.2-20.8	8.2 (5.2); 7.4-9.1	10.1 (25.9); 7.0-26.1	138 (27.4); 85.2-219	4.1 (136); 0-22.3	0.3 (109); 0-1.4	6.2 (678); 0-110	2.7 (102); 0.1-8.7	107 (27.8); 51-201	6.1 (56.8); 1.3-13.3
NIACI	*Nitzschia acicularis*	2	1	20	12.3 (59.8); 4.7-33.5	6.8 (103); 0.2-25.4	8.1 (7.1); 7.1-9.3	11.0 (54); 5.0-30.1	143 (27.4); 85.2-258	10.2 (101); 0-30.8	0.6 (89); 0-1.4	27.7 (148); 0-149	5.8 (109); 0.1-34.6	112 (60); 50.7-416	8.5 (70.3); 1.4-32.4
NIAUR	*Nitzschia auariae*	2	1	26	12.3 (40.3); 4.7-29.8	5 (84); 0.2-18.8	8 (5.1); 7.5-9.1	9.5 (31.4); 3.9-25.2	177 (35.1); 9.3-258	14.7 (117); 0-47	1.3 (179); 0-9	37.7 (174); 0-203	9.8 (149); 0.1-46.1	165 (107); 50.7-616	10.8 (106); 1.2-38.8
NICAP	*Nitzschia capitellata*	2	1	13	8.9 (51.5); 4.7-24.6	9.2 (67.4); 0.4-16.3	8.1 (4.3); 7.6-9.1	9 (26.5); 5.4-14.7	144 (20.3); 101-247	8.5 (105); 0-30.8	0.9 (60); 0-1.7	17.5 (81); 0-149	5.5 (69.7); 0.2-34.6	87.7 (42.2); 50.7-416	6 (80.7); 1.1-32.4
NIFRU	*Nitzschia frustulum*	2	1	58	22.5 (32.8); 4.7-33.5	9.6 (83.3); 0.2-30.4	8.2 (4.6); 7.4-9.8	14.1 (42); 3.9-31.4	187 (19.1); 9.3-452	5.8 (223); 0-49.2	2.2 (305); 0-10	8.5 (342); 0-203	2.9 (221); 0.1-46.1	124 (54.3); 51-616	5.4 (97.2); 1.1-41.5
CNIGRA1	*Nitzschia cf. gracilis f. acicularoides*	2	1	9	14.1 (20.2); 7.7-14.1	0.5 (142); 0.2-11	8.7 (3.8); 7.8-9.1	7.8 (20); 7-16	100 (9.45); 85-131	0.6 (174); 0-5	0.05 (29); 0-.77	1.1 (265); 0-14	0.6 (216); 0.11-6.2	61.8 (37.7); 51-133	2.1 (99.5); 1.15-10.4
NIHUN	*Nitzschia hungarica*	2	1	21	23.9 (18.4) 4.7-28.2	5.2 (27.3) 0.17-18.8	8.5 (2.35) 7.4-9.1	14.3 (17.6) 7-33.6	191 (15.6) 85.2-258	1.3 (553) 0-47	0.36 (363) 0-9	1.3 (565) 0-47	1.2 (129) 0.1-9.8	93.6 (12) 50.6-277	3.5 (52.3) 1.33-20
NIMIC	*Nitzschia microcephala*	2	1	40	14.9 (52.8); 4.7-30.6	4.3 (79); 0.2-25.4	8.1 (5.6); 7.1-9.2	11.2 (30.7); 3.9-30.1	161 (30.9); 9.3-258	9.4 (144); 0-47	0.6 (206); 0-9	20 (227) 0-203	6.2 (164); 0.1-46.1	125 (95.5); 50.7-616	8.4 (98); 1.4-38.8
NINAN	*Nitzschia nana*	2	1	11	12.6 (5); 6.7-25.9	5.7 (68.4); 0.2-19.4	7.9 (5.2); 7.1-8.9	7.2 (25.6); 5-18	193 (23.2); 101.1-217	18.9 (102); 0-41	0.7 (104); 0-1.5	87.2 (112); 0-198	19.9 (110); 0.1-44.5	240 (81); 5.7-456	19.9 (96.8); 1.5-41.5
NIPAL	*Nitzschia palea*	2	1	42	15.5 (53.6). 4.7-33.5	7.6 (98.5); 0.2-30.4	8 (5.2); 7.1-9.8	8.5 (35); 3.9-31.4	141 (62); 9.3-452	7.1 (161); 0-49.2	0.4 (236); 0-9.9	17.8 (289); 0-203	4.8 (239); 0.1-46.1	125 (92.5); 50.7-616	6.2 (146); 1.1-41.5
CNIPUS	*Nitzschia cf. pusilla*	2	1	17	14.2 (55.3); 4.7-24.4	8.9 (65); 0.3-19.4	8.1 (6.2); 7.1-8.7	10.4 (35.4); 3.9-17.6	145 (47); 9.3-258	10.2 (143); 0-43.1	0.4 (116); 0-1.5	28.7 (216); 0-203	8.4 (162); 0.1-46.1	152 (108); 53.6-616	10.9 (94.4); 1.5-38.8
BAPAR	*Bacillaria paradoxa*	A	2 CA2	18	27.5 (4.8); 7.7-28.2	5.5 (18.2); 0.2-15.2	8.3 (1.7); 7.8-9.1	17.2 (12.9); 7.7-18.2	201 (4.34); 106-258	0.2 (55.8); 0-13.4	0.1 (29.3); 0-0.5	0.03 (56.6); 0-6.8	2.1 (31.6); 0.1-3.3	101.0 (6); 67.4-141	4.3 (14); 1.5-6.8
BEFEN	*Berkeleya fennica*	B	2 CA2	19	20.6 (40); 5.5-28.2	7.5 (57.3); 0.4-16.3	8.4 (1.9); 7.5-8.9	13.1 (28.1); 6.1-18.2	202 (12.7); 94.3-258	0.9 (652); 0-49.2	0.3 (346); 0-9.9	0.8 (813); 0-59.7	1.2 (106); 0.1-9.8	89.1 (17.6); 50.7-120	3.0 (38); 1.1-9.6
ENPUC	*Entomoneis punctulata*	B	2 CA2	12	25.8 (9.1); 11.7-30.6	6 (51.7); 2.5-25.4	8.4 (2); 7.7-8.7	15.5 (14.8); 3.9-23.6	202 (2.1); 202-258	1 (671); 0-47	0.3 (366); 0-9	1.5 (897); 0-203	1.5 (199); 0.2-46.1	101 (35.4); 84.5-616	3.7 (60.8); 1.2-38.8
NICLA	*Nitzschia clausii*	B	2 CA2	8	26.3 (13.5); 5.5-28.2	5.8 (24); 5.0-16.3	8.4 (1.8); 7.8-8.7	16.3 (14.1); 7-18.2	202 (0.43); 202-219	0.021 (908); 0-2.9	0.1 (29.8) 0-0.2		1.7 (43.8); 0.3-2.5	97.7 (7.2); 52.7-124	3.9 (20.4); 1.1-5.8
NIDIS2	*Nitzschia dissipata var. intermedia*	B	2 CA2	8	24.0 (33.1); 5.5-28.2	7.1 (49.3); 4.8-16.3	8.3 (1.5); 7.8-8.5	15.7 (25.7); 7-18.2	202 (2.1); 181-258	0.1 (426); 0-1.5	0.1 (31); 0.002-0.2		2 (40.8); 0.2-2.5	93.2 (16.5); 52.7-111	3.8 (32); 1.1-5.8
NISP1	*Nitzschia sp. 1*	B	2 CA2	32	25.2 (26); 4.7-29.8	6.6 (43.9); 0.2-21	8.2 (2.4); 7.1-9.2	16.2 (25); 3.9-27.2	162 (49); 9.3-258	1.1 (5.9); 0-43.1	0.2 (0.3); 0-1.5	5.5 (30.4); 0-203	3 (200); 0.1-46.1	109 (64); 52.7-616	5 (96); 1.2-38.8
NANOR	*Navicula normaloides*	B	2 CA2	27	26.7 (18.7); 5.5-33.5	6.2 (30.6); 0.8-20.8	8.3 (1.1); 7.6-8.8	17.3 (15.8); 3.9-26.1	191 (20.6); 9.3-254	0.1 (1600); 0-43.1	0.1 (58.9); 0-1.5	0.3 (2633); 0-201	2.4 (74.1); 0.1-46.1	99.1 (21.4); 52.7-616	4.4 (34.7); 1.1-38.8
AMHYB	*Amphora hybrida*	C	1 CA2	16	8.8 (33.1); 6.7-21.8	11.3 (47.8); 2.5-21	7.6 (1.7); 7.1-8.4	5.4 (22.4); 3.9-17.6	85.6 (1119); 9.3-247	14 (129); 0.1-49.2	0.6 (162); 0-9.9	60.8 (148); 0-203	14.5 (135); 0.1-46.1	228 (93); 63.9-616	14.3 (112); 1.7-41.5
AMMIC	*Amphora micrometra*	C	1 CA2	35	11 (45.3); 4.7-30.6	9.6 (66.7); 2.1-30.4	7.9 (3.7); 7.1-9.8	6.7 (55.6); 3.9-31.4	185 (49.4); 9.3-452	24.8 (81.7); 0-49.2	1.3 (154); 0-9.9	104 (93.7); 0-203	23.7 (91.6); 0.1-46.1	292 (86.7); 52.7-616	17.4 (100); 1.1-41.5
NAPER	*Navicula perminuta*	C	1 CA2	48	9.9 (33.7); 5.5-30.6	15.1 (26.5); 0.3-25.4	7.7 (4.1); 7.1-9.2	7.7 (22.5); 3.9-33.6	120 (41.8); 9.3-258	10.8 (120); 0-49.2	1.7 (145); 0-9.9	27.7 (141); 0-203	4.6 (165); 0.1-46.1	85.6 (79.5); 52.7-616	5.7 (112); 1.1-41.5
NASAM	*Navicula salinarum*	C	1 CA2	31	8.2 (37.6); 4.7-25.9	10.8 (54); 0.2-19.4	7.6 (2.3); 7.1-9.1	6.7 (35.6); 3.9-27.2	88.4 (98.9); 9.3-258	12.6 (115); 0-49.2	0.6 (171); 0-9.9	38 (180); 0-203	9.5 (152); 0.1-46.1	158 (105); 50.7-616	10.7 (111); 1.4-41.5
BERUT	*Berkeleya rutilans*	C	2 CA2	18	9 (25.6); 5.5-27.7	16.1 (18.6); 2.5-21	7.7 (4.8); 7.1-8.7	7.8 (8.6); 3.9-21	154 (44.2); 104.1-258	7.4 (104); 0-47	1 (145); 0-9	13 (121); 0-203	2.4 (145); 0.1-46.1	69.1 (50.9); 52.7-616	3.6 (74.6); 1.1-38.8
HASPI	*Haslea spicula*	C	2 CA2	10	7.6 (36.6); 5.5-20.1	15.4 (18.2); 2.5-17.8	8.0 (4.3); 7.5-8.8	7.4 (9.5); 7-14.7		12.8 (127); 0.2-47	2.1 (152); 0-0.9	15.9 (100); 0-47.6	3.1 (106); 0.3-9.8	64.7 (14.5); 52.7-110	2.5 (73.5); 1.1-6.8
THPSE	*Thalassiosira pseudonana*	C	2 CA2	11	13.2 (17.4); 4.7-16.3	7.6 (44.7); 2.1-14.6	7.7 (2.6); 7.5-8.4	7.4 (20.3); 5.4-14.7	156.3 (53); 9.3-247	38.2 (41.6); 0.2-49.2	5.3 (4.0); 0-9.9	88.4 (75.8); 0-196	19.4 (88.7); 0.1-44.5	207 (81.6); 73.4-456	17.2 (96); 2.1-41.5
NIARC	*Nitzschia archibaldii*	D	2 & 1CA2	22	23.9 (13.5); 13-33.5	7.5 (69.3); 0.3-25.4	8.6 (3); 8-9.3	13.8 (34.3); 7-30.1	211 (23.9); 85.2-258	0.005 (56.8); 0-0.5	0.2 (126); 0-0.9	1.2 (214); 0-6.5	0.9 (64); 0.1-2.5	101 (29); 50.7-209	3.9 (32.8); 1.2-6.8
OPHOR	*Opephora horstiana*	D	2 CA2	9	23.4 (17.52); 15.6-31.0	7.5 (42.6); 4.6-25.4	8.5 (2.35); 8.4-9.3	12.9 (16.3); 7.7-18.4	201 (15.5); 181-254	0.7 (71.43); 0-1.8	0.2 (100); 0-0.9	0.1 (1000); 0-6.5	0.4 (75); 0.2-1.7	111 (9.3); 71.5-156	1.8 (38.9); 1.2-3.1
COPLA	*Cocconeis placentula*	E	1 & 1CA2	54	22.6 (32.5); 4.7-33.5	13.4 (59.7); 0.2-30.4	8.4 (6.8); 7.1-9.8	15.3 (46); 3.9-33.6	209 (40); 9.3-452	7.3 (209); 0-49.2	0.7 (274); 0-9.9	28.2 (228); 0-203	6.7 (207); 0.1-46.1	173.9 (75); 52.7-615	8.6 (135); 1.1-41.5
AMSTA	*Amphora staurophora*	E	1 CA2	37	9 (44.4); 5.5-27.7	13.7 (29.2); 2.5-21	8 (3.7); 7.1-8.8	8 (28.7); 3.9-27.2	155 (51); 9.3-258	7.6 (171); 0-49.2	0.9 (233); 0-9.9	18.8 (239); 0-203	3.9 (249); 0.1-46.1	85.7 (106); 52.7-616	4 (173); 1,1-41,5

Table 6.1: Mean, coefficient of variation (in brackets) and minimum and maximum values of the environmental parameters of the water where the 39 species considered (the ones well explained by the dimensions of CA's) were found. Values are weighted by diatom abundance. **Ass**.= diatom assemblages to which the species belong. **Dim** = the dimensions by which the species are well explained [CA: Correspondence Analysis including all the waterbodies; CA2: Correspondence Analysis excluding r.Muntanyeta data]. **N** is the number of samples in which each species was found.

6.2.2 Multivariate ordination

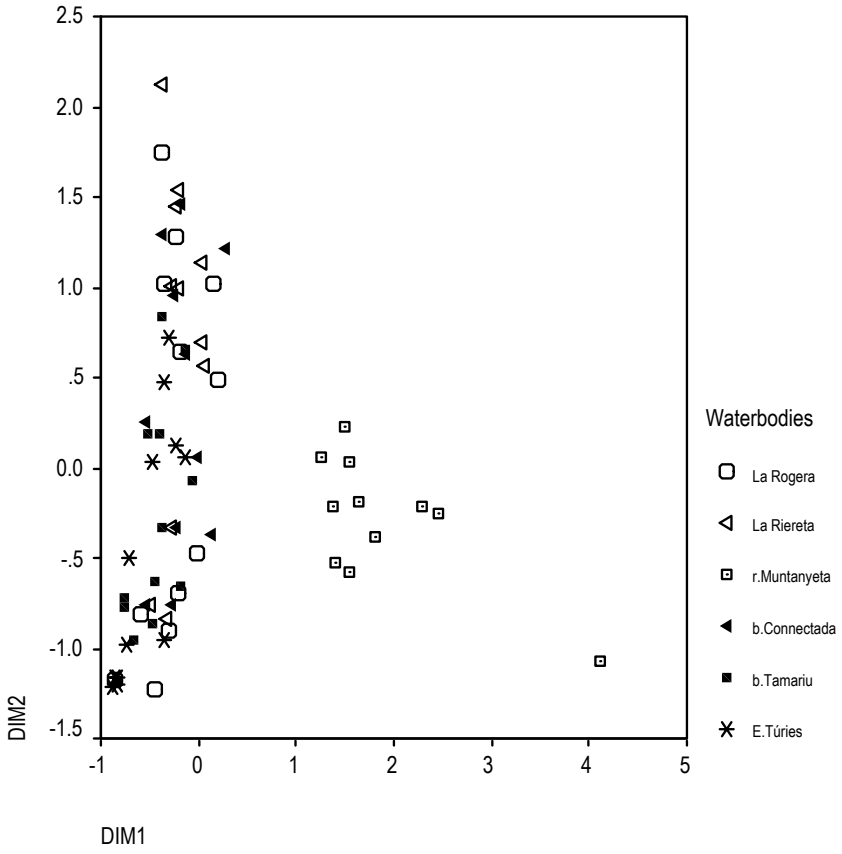


Figure 6.1: Representation of the samples in the plane defined by the two first CA dimensions.

CA	Dimension 1	Dimension 2
% explained variance	9.4	8
Conductivity	-0.799	n.s.
Water depth	n.s.	0.595
Temperature	n.s.	-0.580
TOC	n.s.	-0.577
pH	n.s.	-0.521
Diatom abundance	n.s.	0.447

Table 6.2: Pearson correlation coefficients between the two main CA dimensions and some environmental parameters. Only significant correlations ($P<0.01$) and values >0.4 are listed. All variables that express concentrations have been log transformed.

A Correspondence Analysis (CA) using diatom relative abundances was performed (see Section 3.5.1 in Chapter 3 for further details).

The first dimension of the CA, explains 9.4 % of total variation. This dimension clearly differentiated one waterbody (r. Muntanyeta) from the rest (Fig. 6.1) and showed a distributional discontinuity in the periphytic diatom composition studied (Fig. 6.2). In spite of the strong and negative correlation of this dimension with water conductivity (Table 6.2) and despite the fact that r.Muntanyeta was the most freshwater studied site (Fig. 6.3), (due to the continuous freshwater supply, see Section 2.2 in Chapter 2), several arguments do not allow this axis to be defined as a salinity gradient. Conductivity variations do not correlate with it when r.Muntanyeta only was analysed. The sample with the highest factor score for this dimension did not have the lowest conductivity. Other waterbodies in situations of similar conductivity to r.Muntanyeta (e.g. b.Connectada in November, see Fig. 6.3) did not have a positive factor score for this dimension as r.Muntanyeta did. Although many of the species with positive coordinates for this axis showed a lower mean

salinity than those of the species with negative coordinates, there was no clear pattern of the distribution of diatom taxa according to salinity. It is true that all of the species considered were found living over a wide range of salinities and some of mean salinity values for the species characteristic of r.Muntanyeta were higher than the others (e.g. *Navicula paul-schulzii, Nitzschia capitellata, Nitzschia frustulum*) and viceversa (*Bacillaria paradoxa*, *Navicula normaloides* or *Nitzschia* sp. 1) (Fig. 6.2 and Table 6.1).

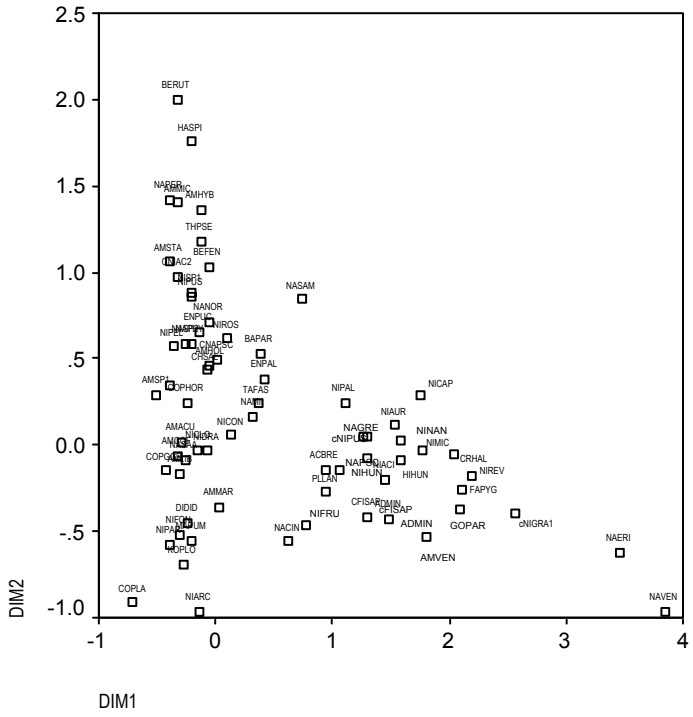


Fig. 6.2. Ordination of species in the CA dimension space. For species names corresponding to acronyms see Appendix I. Note that the highest abundance of species with a positive coordinate for dimension 1 was recorded in r.Muntayeta samples (see Appendix II)

Fig. 6.3a

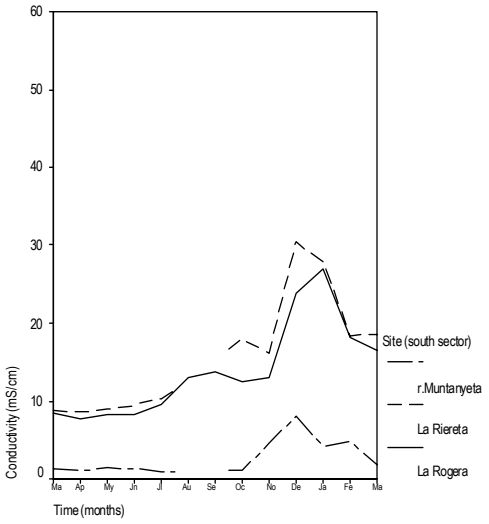


Fig. 6.3b

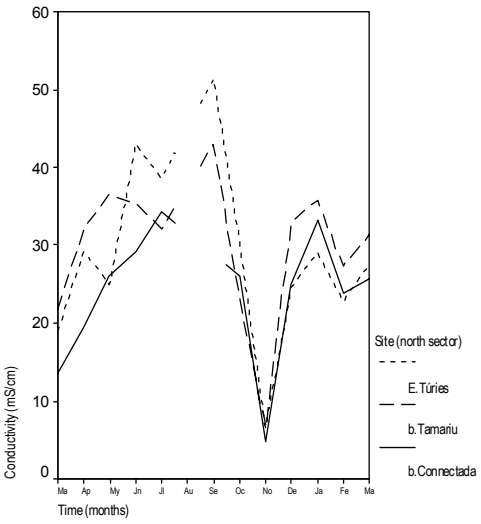


Figure 6.3: Monthly conductivity values for the 6 waterbodies studied. Fig. 6.3a: Waterbodies placed in the south sector (with a higher fresh water supply influence). Fig. 6.3b: Waterbodies placed in the north sector. Notice that highest water conductivity is reached in the north sector during periods of confinement (no water entry). Maximum confinement: period between May and October, except the unusual rainy episode that occurred

To elucidate the variability of the other five basins and to reduce the discriminating effect of r.Muntanyeta, another CA (CA2), excluding r.Muntanyeta data, was conducted. The two first dimensions from CA2 accounted for 19.7 % of total variation and were able to discriminate between conditions in the different waterbodies. The first axis (10.7 % of the variation), was positively correlated with water level and negatively with pH, organic matter and temperature (Table 6.3) indicating that it could be related to a confinement/flooding gradient. The significant water inputs were caused by sea storms or intense rainfall, mainly in autumn-winter. Samples taken after sea storms showed positive coordinates for this axis. During the periods of

confinement (lack of water entry and absence of water turnover), usually in spring and summer, increases of pH, temperature and TOC accumulation were observed.

CA2 (without r.Muntanyeta data)	Dimension 1	Dimension2
% explained variance	10.7	9
pH	-0.608	n.s.
Water depth	0.603	n.s.
TOC	-0.599	n.s.
Temperature	-0.594	n.s.
Diatom abundance	0.509	0.589

Table 6.3: Pearson correlation coefficients between the two main CA2 dimensions and some environmental parameters. Only significant correlations (P<0.01) and values >0.4 are listed. All variables that express

The second dimension (9% of total variation) was positively correlated with diatom abundance (density of diatom per cm^2 of glass rod) and hence with diatom growth rate. This axis has been related to system productivity based on the following arguments: 1) The only correlation of this dimension with diatom abundance (Table 6.3) suggest a relationship with periphytic diatom growth or production (since artificial substrata were replaced monthly); 2) The highest positive coordinates corresponded to spring-summer samples from the south sector where water and nutrient inputs were the highest (Quintana *et al.* 1999); 3) It cannot be strictly related to seasonality, because it was not correlated with temperature and because some spring-summer samples had negative

coordinates (it is worth noting that these samples belong to the most confined situations of the most confined basins, where there was no dissolved nutrient availability, i.e spring-summer samples from north sector in Fig. 6.4); 4) When only spring-summer samples are taken into account, dimension 2 is significantly and positively correlated with the Chlorophyll-*a* / TOC ratio ($P < 0.01$, r = 0.775). This ratio could be related with the ratio production / biomass.

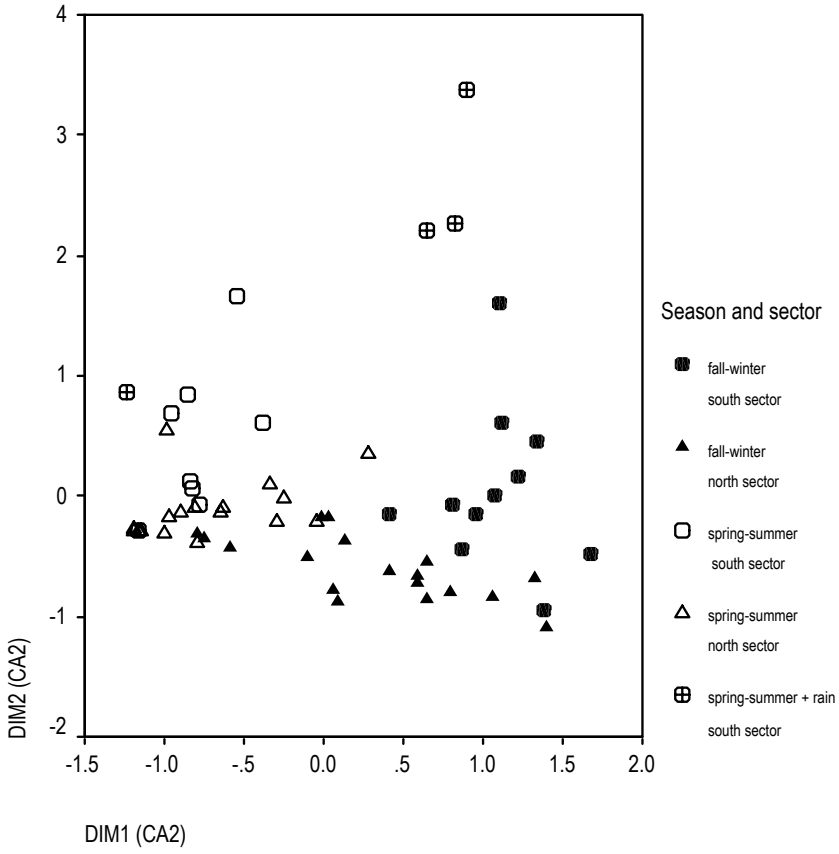


Figure 6.4: Ordination of the samples in the plane defined by the two first CA2 (excluding r. Muntanyeta data) dimensions. Samples are represented (symbols) according to season and sector, since both dimensions arrange situations rather than waterbodies. Spring-summer+rain: unusual rainy espisode (more than 70 l/m^2 accumulated in 15 days) occurred between June and July.

6.2.3 Diatom assemblages

Using the coordinates obtained for each species' CA dimensions, clustering was carried out with the aim of grouping the species according to their ecological preferences (Fig. 6.5). Diatom assemblages have been determined using those species that were well explained by tha CA's dimension of each cluster. For further details of cluster analysis see Section 3.5.2 in Chapter 3.

From the whole data set, three groups of species were distinguished (Fig. 6.5a). The first two clusters corresponded to diatom assemblages characteristic of the freshwater basin r.Muntanyeta (Fig. 6.6). The group comprised *Navicula veneta* and *Navicula erifuga* (assemblage 1) and corresponds to only one sample from r.Muntanyeta (October 1997) and showed relatively high DIN and TOC concentrations. Assemblage 2 includeded all the other species (*Achnanthidium minutissimum, Amphora veneta, Craticula halophila, Fallacia pygmaea, Fistulifera* cf. *saprophila, Gomphonema parvulum, Hippodonta hungarica, Navicula gregaria, Nitzschia acicularis, N. aurariae*, *N. capitellata*, *N. frustulum*, *N. gracilis* f. *acicularoides*, *N. hungarica*, *N. microcephala*, *N. nana*, *N. palea* and *N.* cf *pusilla*) and were not restricted to r.Muntanyeta, but showed their highest relative abundance in that waterbody (see Appendix II).

The third group obtained was refined using a hierarchical cluster excluding r.Muntayeta data (Fig. 6.5b). From this analysis 5 diatom assemblages with distinct ecological patterns could be distinguished (Fig. 6.7). Assemblages A, B and C, which had positive coordinates on the CA2 dimension 1, were characteristic of low water confinement. Assemblages D and E which had more negative coordinates along this axis could be considered typical assemblages from waters with a certain degree of confinement to highly confined waters.

Among the diatom assemblages typical of low water confinement, assemblage C (composed of *Amphora hybrida*, *Amphora micrometra*, *Berkeleya rutilans, Haslea spicula, Navicula perminuta*, *Navicula salinarum* and *Thalassiosira pseudonana*) appeared in the wake of typical autumn-winter disturbances (sea storms, intense rainfalls). Assemblages A (*Bacillaria paradoxa*) and B (*Berkeleya fennica, Entomoneis punctulata*, *Navicula normaloides*, *Nitzschia clausii*, *Nitzschia dissipata* var. *media* and *Nitzschia* sp. 1) occurred after a summer rain episode, which would involve the highest system productivity according to the above interpretation of CA2 dimensions. Also according to this interpretation, assemblage D (characterised by *Nitzschia archibaldii* and *Opephora horstiana*), would differ ecologically from assemblage E (characterised by *Cocconeis placentula* and *Amphora staurophora*) by its appearance under higher productivity conditions (predominantly during confinement in south sector waterbodies).

Fig. 6.5a

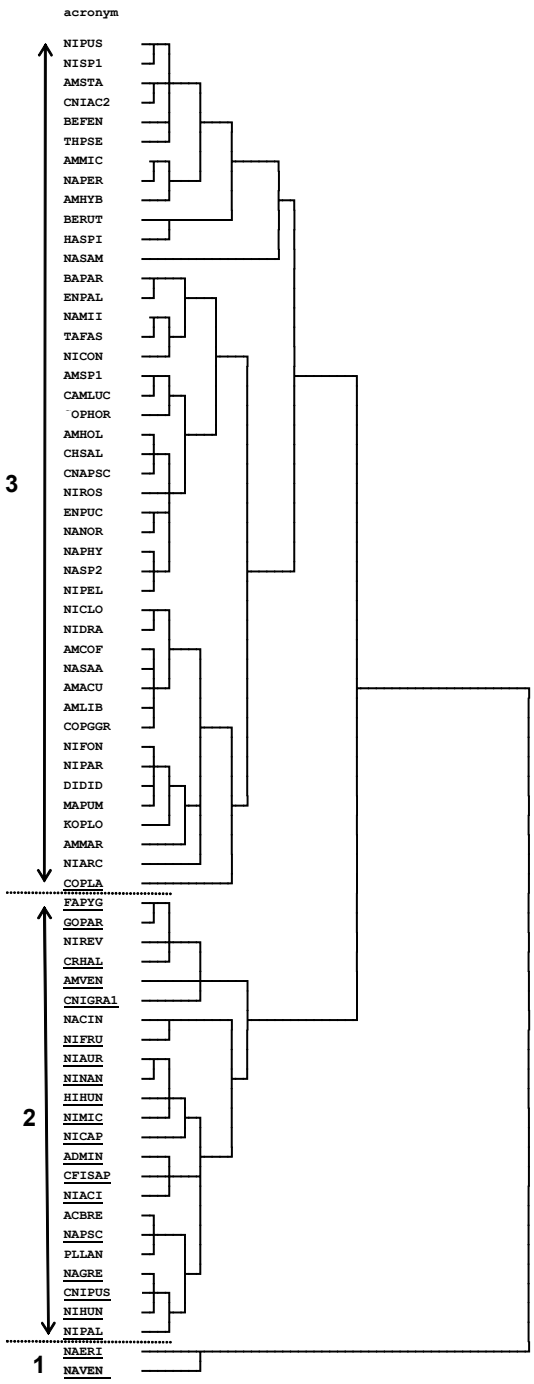


Fig. 6.5a and b: Clusters of diatom species organised by coordinates of CA dimensions. The species that are well explained by CA's dimensions are underlined (that is species showing a value ≥ 0.1 for the contribution of CA dimensions to their inertia).

Figure 6.5a: Dendrogram showing the hierarchical classification of the 72 species treated on the CA whole data. Numbers correspond to diatom assemblages clusters considered.

Fig. 6.5b

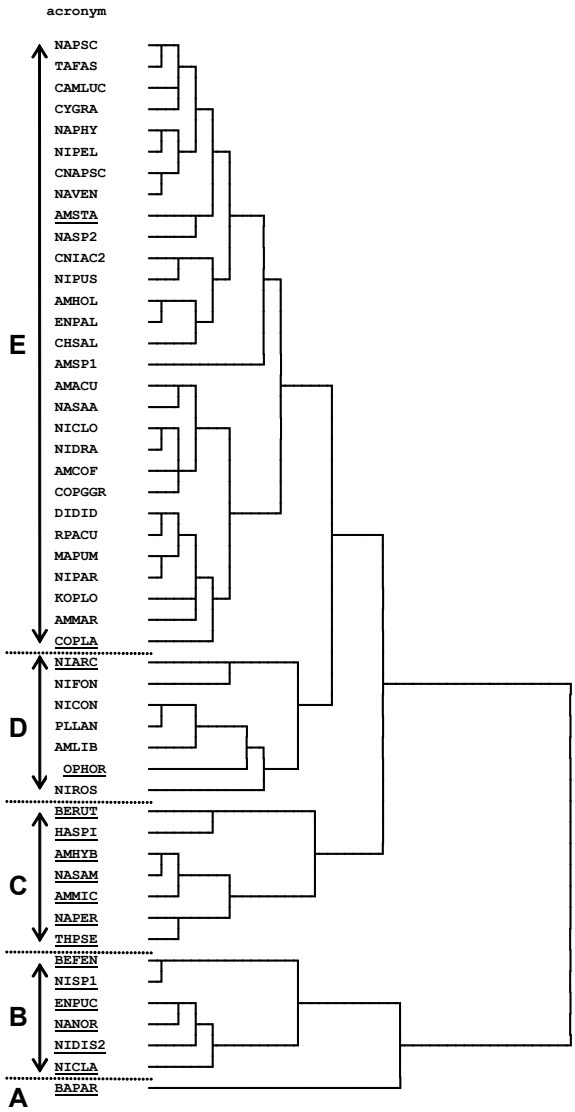


Figure 6.5b: Dendrogram showing the hierarchical classification of the 50 species considered on CA2 (without r.Muntanyeta data). Single capital letters correspond to the diatom assemblages considered. For species names corresponding to acronyms see Appendix I

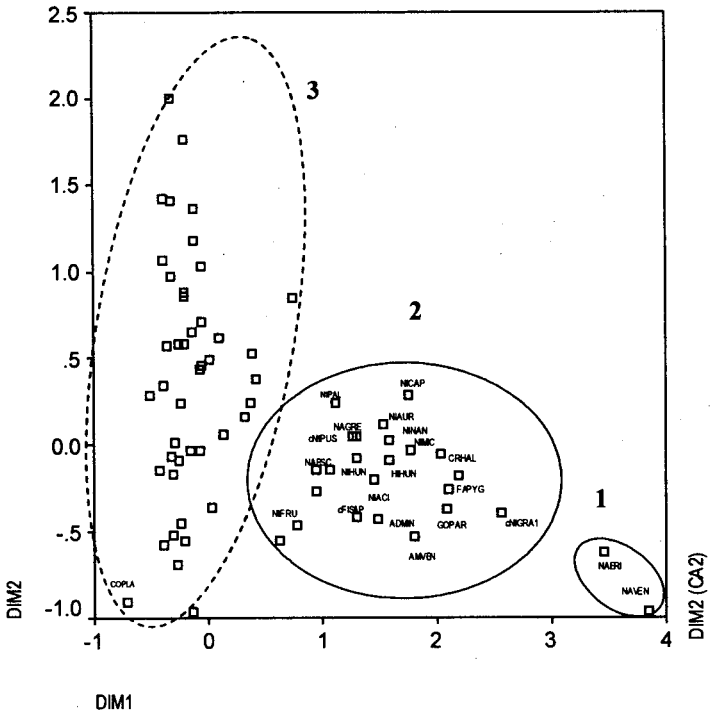


Figure 6.6: Ordination of the species in the plane defined by the two first CA dimensions. Circles correspond with the cluster derived from the hierarchical classification of species (see Fig.6.5a).Acronyms for only taxa well explained by dimension 1 are shown. For species name corresponding to acronyms see Appendix I.

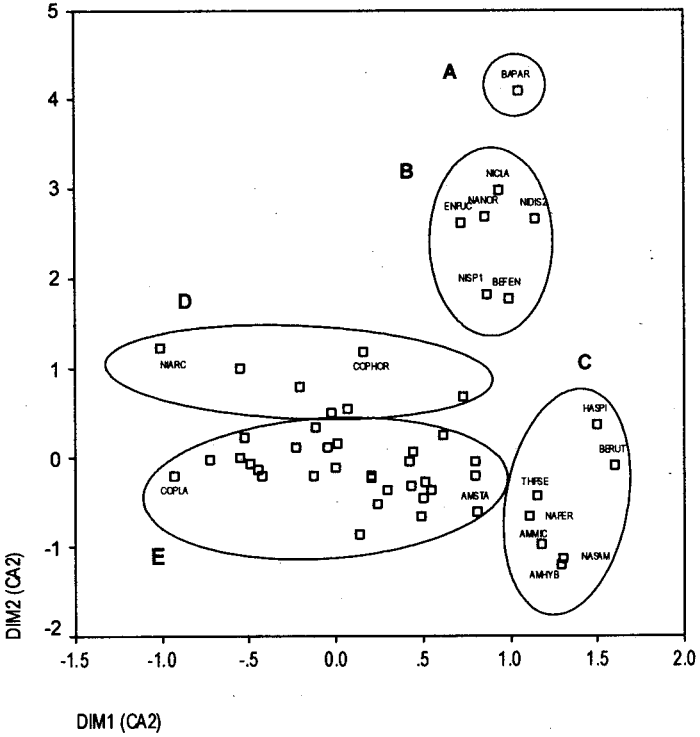


Figure 6.7: Ordination of species in the CA2 (excluding r.Muntanyeta data) dimension space. Circles correspond to diatom assemblages derived from the hierarchical classification of waterbodies (see Fig. 6.5b). Acronyms for only taxa well explained by dimensions are shown. For species name corresponding to acronyms see Appendix I.

6.3 Discussion

6.3.1 Diatoms in Mediterranean coastal wetlands

The Mediterranean coastal systems studied are mainly characterised by the irregularity (in time and in intensity) of water inputs and by low inorganic dissolved nutrients and salinity fluctuations (Quintana *et al.* 1998a). The highly dynamic nature of the system results in great variability of the physical and chemical composition of the water. Consequently, the diatom species inhabiting the salt marshes of the Empordà wetlands are change-tolerant to most of the environmental variables studied. The extracellular polymeric substances (EPS) of the diatom cells may account for this tolerance. Most of the diatoms collected in this study are reported to live in a polysaccharide matrix (Drum & Weber 1966, Cox 1977a and b, Underwood 1994) and according to Benet (1963) and Drum & Webber (1966) these extracellular layers may serve to aid diatoms in the selection and capture of both inorganic and organic nutrients, or may shield diatoms from the rigours of osmotic variation.

The limiting role of nitrogen is frequent in salt marshes (Sullivan & Daiber 1974, Valiela & Teal 1974, van Raalte *et al.* 1976). Most of the species considered are able to live under low concentrations of dissolved inorganic nitrogen but with high values of organic nitrogen suggesting a possible heterotrophy of the taxa. Remarkably, *Nitzschia* and *Amphora* which were very common in the marshes studied, are the diatom genera showing most pronounced development of heterotrophic abilities (Hellebust & Lewin 1977). Furthermore, several of the species commonly found in these wetlands have been proved (under experimental conditions) of being capable of growing on

organic substances in the dark, or assimilating organic nitrogen compounds (Hellebust & Lewin 1977, Admiraal *et al.* 1987, Chelf 1990).

6.3.2 Factors affecting diatom distribution

Confinement and productivity have appeared as principal factors affecting the distribution and composition of the periphytic diatom community in the salt marshes of the Empordà wetlands. In these systems, and from an energetic point of view, conditions of low confinement (occurrence of water supply) can be regarded as an entry of external energy. External energy moves water which transports or mobilizes nutrients and fertilizes the system (Quintana *et al*. 1998b). Confinement represents the minimum entry of external energy during which desiccation reduces the water volume of the basin and so concentrates the organic matter and salt content (Guerlorguet & Perthuissot 1983, Quintana *et al*. 1998a).

Water turnover rate, frequency and intensity of disturbances and trophic status were found to be important factors accounting for the variation of other organisms (ostracods, zooplankton communities, and typologies of primary producers such as macrophytes, phytoplankton and periphyton) in the same area (Quintana *et al*. 1998b, Moreno-Amich *et al*. 1999, Gifre *et al.* 2002, Chapter 4 in this work). Diatom studies in Mediterranean shallow coastal waters are very few in number (Danielidis 1980, Noel 1984a and b, Delgado 1986, Tomàs 1988, Sabater *et al*. 1990, Tolomino *et al.* 2002) especially compared with freshwater studies. Tomàs (1988) showed that the benthic diatom assemblages found in the epicontinental brackish waters along the Spanish Mediterranean coast were discriminated by salinity and eutrophy. That diatom distribution pattern is similar to our results with respect to salinity being

an indirect effect of confinement. Most of the 57 waterbodies studied by Tomàs (1988) have hydrological characteristics comparable to those of the salt marshes of the Empordà wetlands (shallow, with scarce, occasional water inputs).

In other fluctuating systems such as estuaries, salinity and seasonality have often been considered as important factors accounting for diatom distribution (Cox 1977a, McIntire 1978, Admiraal 1984, Underwood 1994, Wilderman 1987, Sullivan & Montcreiff 1988, Oppenheim 1991, Laird & Edgar 1992, Snoeijs 1995, Peletier 1996, Bąk *et al.* 2001). At first glance, our results also seemed to suggest salinity as a key factor influencing the distribution of diatom species. However, when data were analysed thoroughly, salinity as a single factor, cannot be considered a determinant of diatom assemblage composition in the salt marshes studied. It is true, however, that tolerance to salinity changes is a prerequisite for diatoms living in such fluctuating environments (Hoeck *et al.* 1979, Round 1960, Underwood 1994, Sullivan & Currin 2000). Nevertheless, the role of salinity in fluctuating systems could have been overestimated, since in most of these systems salinity usually co-varies with other environmental variables which also influence diatom species composition (Underwood & Kromkamp 1999, Underwood & Provot 2000, Thornton *et al.* 2002). Only further multifactorial experimental studies will allow one to distinguish the amount of variability attributable to salinity, as a single factor, from other environmental variables that co-vary with it. Similarly seasonality also co-varies with nutrient concentration, light, temperature and disturbance events (Underwood & Krompkamp 1999).

In temperate estuarine systems temperature, salinity, nutrients and organic matter vary on a seasonal basis related to rainfall patterns and hydrological

processes (Hessen 1999), and rainfall patterns and hydrological processes could be regarded as the expression of the entry of external energy into estuaries. Then, confinement and seasonality are factors affecting diatom distribution as a result of energy flux to the system. They are integrative factors involving different processes (nutrient availability, temperature, etc), where productivity can be regarded as the system response to energy flux.

6.3.3 The ecology of diatom species

Cluster analysis (Fig. 6.5) synthesizes the information from Table 6.1 and describes the ecological preferences of the most abundant diatom species present in the salt marshes of the Empordà wetlands. Ecological preferences of the species can only be discussed for those whose distribution is well explained by the CA's dimensions, since the presence of the other species could be affected by factors not related to the CA's solutions.

The diatom assemblages 1 and 2, contrary to the rest of the assemblages, are waterbody-specific, making it difficult to elucidate with certainty which factors are affecting their appearance. What is true is that assemblages 1 and 2 are typical of waterbodies with continuous, nutrient-rich, freshwater supply.

On the basis of the coordinates of the species in the plane defined by the two first CA2 dimensions, 5 more assemblages (A-E, Figs. 6.5b and 6.7) would be distinguished. According to the CA2 interpretation, assemblages A-C were typical of low confinement as a result of flooding conditions, but they also characterise different degrees of productivity. Assemblage C (*Amphora hybrida*, *Amphora micrometra*, *Berkeleya rutilans, Haslea spicula, Navicula perminuta*, *Navicula salinarum* and *Thalassiosira pseudonana*) was typical of low productivity (mainly after autumn and winter sea storms and intense

rainfalls). Assemblage B (*Berkeleya fennica, Entomoneis punctulata*, *Navicula normaloides*, *Nitzschia clausii*, *Nitzschia dissipata* var. *media* and *Nitzschia* sp. 1) is typical of high productivity (after spring and summer rainfalls). Finally, assemblage A, containing only *Bacillaria paradoxa,* appeared when the system productivity was the highest.

There is little published data on the autecology of diatom species considered with respect to variables related to productivity (such as nutrients and organic matter preferences or tolerances). Most of the trophic and saprobic classifications are mainly based on species inhabiting freshwater systems (Denys 1991, Hofmann 1994, van Dam *et al*. 1994) and when some species of estuarine and shallow coastal waters are included they are generally considered eutraphentic and tolerant to certain degree of organic pollution (β-mesosaprobous to α-mesosaprobous). This information can only be considered a rough approach to the ecology of diatom species inhabiting systems which, intrinsically, already have a certain level of nutrients or organic matter content, such is the case of the salt marshes of the Empordà wetlands.

Bacillaria paradoxa is considered as euryhaline (Kolbe 1927, Hustedt 1930, Foged 1959) and eurythermic (Baudrimont 1973). We found *Bacillaria paradoxa* in spring-summer samples, but Sabater (1987) found it very abundant in the river Ter mouth (only few kilometres from the area studied in this work) in a January sample. Therefore it could be argued that the distribution of this species does not depend on seasonality. *B. paradoxa* distribution might depend on a certain nutrient availability and high organic matter content in the water. These are the features in common between Sabater's sample (Sabater 1987) and the occasions when *B. paradoxa* was abundant in the salt marshes of the Empordà wetlands. Assemblage C forms

after an intense input of external energy (mainly sea storms). *Navicula salinarum* (a representative species of assemblage C) is one of the most common and very abundant taxa in estuaries and Mediterranean salt marshes (Tomàs 1988, Kuylenstierna 1991, Underwood & Provot 2000, Busse 2002). *Navicula salinarum* has been suggested as a potential pollution tolerant species for this type of environment (Sullivan 1999). The presence of *Navicula salinarum* in the systems studied appears to be more related to organic matter inputs rather to organic matter accumulation due to water evaporation.

Assemblages D and E were typical of confined situations where there is depletion of dissolved nutrients but organic matter accumulation. In situations of maximum confinement and low productivity *Cocconeis placentula* dominates the diatom community. When maximum confinement is reached in basins with higher productivity, this dominance is shared by *Nitzschia archibaldii*.

There is some controversy about the ecology of *Cocconeis placentula*. While Pipp & Rott (1993) considered that its occurrence and abundance can be favoured by NO_3^- increases, Eulin (1997) considered that the species was not affected by the water nutrient content. While Luttenton & Rada (1986) found that *C. placentula* thrived well in high currents, we found it clearly dominating in maximum confinement situations. This suggests that *C. placentula* can be considered an opportunistic species with high capacity for adaptation that proliferates well in the absence of resource competitors in a variety of situations, ranging from maximum confinement conditions, low light intensity (Hickman 1982), high current velocities (Luttenton & Rada 1986), grazing pressure (Kesler 1981) or herbicide exposure (Goldsborough & Robinson 1986).

7. MORPHOLOGICAL VARIATION OF *Nitzschia frustulum* AS A RESPONSE TO CHANGES IN SOME ENVIRONMENTAL VARIABLES

7.1 Introduction

Nitzschia frustulum (Kützing) Grunow is a widely distributed diatom species (Krammer & Lange-Bertalot 1997b, Witkowski *et al*. 2000) which is often very common (or the most abundant taxon) in different types of inland, coastal and marine waters (Hendey 1964, Aleem 1973, Main & McIntire 1974, Archibald 1983, Wilderman 1986, Gasse 1986, Tomàs 1988, Wendker 1990a, Fritz *et al*. 1993, Krammer & Lange-Bertalot 1997b). However, little is known about its ecology apart from the fact that it is markedly euryhaline (Wendker 1990a, Denys 1991). *N. frustulum* is an extremely variable taxon, in size, shape, stria and fibula density. The variability of these characters as well as the small size of some of its representatives make this taxon one of the most problematic diatom species, reflected in the large number of synonyms for this species (Table 7.1).

Table 7.1. List of *N. frustulum* synonyms according to Krammer & Lange-Bertalot 1997b and Tomàs 1988.

Synonyms of *Nitzschia frustulum*
Synedra frustulum Kützing 1844 [Basionym]
Synedra minutissima Kützing 1844
Synedra perpusilla Kützing 1844
Synedra quadrangula Kützing 1844
Synedra minutissima β pelliculosa Kützing 1849
Nitzschia minutissima W. Smith 1853
Nitzschia inconspicua Grunow 1862
Nitzschia inconspicua Rabenhorst 1864
Nitzschia var. *perminuta* Grunow in Van Heurck (1880-85)
Nitzschia var. *perminuta* fo. *curta* Grunow in Van Heurck (1880-85)
Nitzschia frustulum var. *subsalina* Husted 1925
Nitzschia invisitata Husted 1942

Ideally, a good indicator species has a wide geographical distribution, well-defined ecological range and is easily and reliably identified (Geissler 1982). However, not only can different species with different ecological requirements be used as bioindicators, but the morphological variability within a taxon can also be used, provided that the variability is a clear response to environmental conditions (Cox 1995). Experimental works have shown how changes in environmental factors can modify the valve morphology of a number of diatoms (Geissler 1970a, 1970b, 1982, 1986, Schultz 1971, Schmid 1976, Jahn 1986, Wendker & Geissler 1988, Cox 1995). In the case of *N. frustulum*, however, there is only one published field study (Wendker 1990b), although several authors have noted its morphological variability (Lange-Bertalot & Simonsen 1978, Archibald 1983, Gasse 1986, Tomàs 1988).

N. frustulum was the second most abundant diatom taxon in the salt marshes of the Empordà wetlands (Appendix I), was present in all the waterbodies studied and its morphological variability has been evident not only between individuals of different samples but also between individuals of the same sample.

The aim of this chapter is to determine the effects of particular environmental conditions (salinity, N : P ratio, water movement) on the growth of *N. frustulum*, testing whether its morphological variability is a response to changes in these environmental conditions. Because the above environmental variables often co-vary in the field their effects can only be separated under controlled experimental conditions (Lowe *et al*. 1986, Cox 1995, Underwood *et al*. 1998).

7.2 Culture conditions

In March 2002 benthic diatoms were collected from the Empordà wetlands. Rough cultures were established at different salinities, from which individual cells were selected by micropipetting and grown on in small plastic petri dishes. Once a clone of *N. frustulum* had been isolated, cells were cultured under different conditions of salinity, N : P ratio and water movement using a factorial design (Table 7.2).

Table 7.2. Factorial design used in the experiment, giving 18 different combinations of three factors, with salinity values in parts per thousand (‰) listed in the table.

	N:P (‰)			
	6.5:1	16:1	32:1	
Water movement	0.5	0.5	0.5	↓ decreasing salinity
	7	7	7	
	17.5	17.5	17.5	
No water movement	0.5	0.5	0.5	↓ decreasing salinity
	7	7	7	
	17.5	17.5	17.5	

Salinities of 7 and 17.5 ‰ were prepared by adding 20 ml and 50 ml of f/2 medium (McLachlan 1973) to 80 ml and 50 ml Woods Hole MBL medium (Nichols 1973) respectively. All media were sterilised by autoclaving. The various N : P ratios were achieved by keeping the phosphorus concentration identical in all treatments (0.2 mM) and varying the nitrogen concentration (1.30, 3.2 and 6.4 mM) by adding $NaNO_3$. Placing petri dishes on a shaker generated water movement. All cultures were grown at 25 $^{\circ}$C under a light intensity of 45 µmol / m^2 /sec. and a light : dark cycle of 16 : 8 h. Depending on the medium, pH ranged from 8.5 to 8.7. Approximately 10 individuals from the stock clone were initially inoculated into each treatment.

After 10 days of culture, the cells were cleaned by heating with nitric acid. They were mounted in Naphrax or coated with gold-palladium for frustule examination using light microscopy or scanning electron microscope

respectively. Because of the small size of the specimens all the cell measurements were made under a high-resolution field emission scanning electron microscopy (Philips XL 30). However, individuals from each treatment were also examined with light microscopy (Zeiss Universal). The variables measured from at least 10 valves in each treatment were: length (µm), width (µm), number of fibulae / 10 µm [sd], number of striae / 10 µm, distance between the two median fibulae [dMF], and distance between two adjacent, non-median fibulae, taken randomly [dNMF]. This allowed calculation of the relative difference between dMF and dNMF [dFr = (dMF – dNMF) / dMF].
For statistical analysis see Section 3.5.3 in Chapter 3.

7.3 Results

There were significant differences in valve length, width, and number of fibulae / 10 µm at different salinities, in the number of fibulae with different N : P ratios, and in valve width with water movement (Tables 7.3 and 7.4). The statistical assumption of MANOVA (normality of variables and homogenity of variances) were met by these data.
Valve length increased with higher salinity (Fig. 7.1), while contrastingly, valve width decreased with raised salinity (Fig. 7.2). The number of fibulae in 10 µm also decreased with increased water salinity, but in this case only the highest salinity showed a significant change in the number of fibulae (Fig. 7.3). Under different N : P ratios, the number of fibulae / 10 µm was significantly lower in the intermediate N : P ratio (16 : 1) than at the other N : P ratios (Fig. 7.4). Water movement had a significant effect on valve width (Table 7.3), with

valve width being greater in the presence of water movement (Fig. 7.5). There were no significant interactions between the studied variables (Table 7.4).

Bivariate Pearson correlations between variables only show significant negative correlations between the pairs, length - width, and length - number of fibulae in 10 μm (r = -0.315, $P < 0.001$ and r = - 0.249, $P = 0.001$, respectively). In spite of the low correlations, using length as a covariate and width and number of fibulae as dependent variables, two single ANCOVA tests were performed. ANCOVA showed that there is no significant relationship between these variables (Table 7.5). That is, there is no significant variation of width or number of fibulae due to variation in length, since the pooled regression coefficient between groups is not significantly different from zero.

Fig. 7.6 shows the frequencies obtained for the variable dFr, which compares the distance of the two median fibulae (dMF) with the distance of two non median fibulae (dNMF) of the same valve. Thus a dFr value of zero means that dMF is the same as dNMF (Fig. 7.8). dFr values are significantly and positively different from zero (t = 26.18, $P< 0.001$) proving that, on average, the distance between the two median fibulae is larger than between the non-median fibulae (Fig. 7.7 and 7.10). However, the frequency distribution (Fig. 7.6) indicates variability in this character. In 12.5 % of cases dNMF is equal or greater than dMF (Figs. 7.8 and 7.12). It has also been observed than in some valves, the average dNMF is greater than the dMF.

Table 7. 3. Minimum, maximum, mean (x), standard deviation (s) and coefficient of variation (CV) of valve length and width, fibula and stria densities and distance between the median fibulae under different salinity, N : P and water movement regimes. All the units are µm. (NB. Distances between the median fibulae were measured in nm under SEM.)

0.5 ppt Salinity	Length (µm)	Width (µm)	# fib / 10 µm	# str / 10 µm	dMF (nm)
min-max	6.1-9.5	2.3-3.4	13.2-18.9	26.2-31.3	397-1060
x	7.55	2.81	15.52	27.98	612.94
s	0.63	0.23	1.32	0.96	139.78
CV (%)	8.29	8.23	8.48	3.44	22.81
n = 50					

N : P = 6.5	Length (µm)	Width (µm)	# fib / 10 µm	# str / 10 µm	dMF (nm)
min-max	6.2-9.5	2.1-3.3	12.7-18.8	25.2-30.0	397-915
x	7.73	2.65	15.51	27.91	616.84
s	0.55	0.21	1.36	0.96	133.07
CV (%)	7.11	8.00	8.78	3.42	21.57
n = 51					

7 ppt Salinity	Length (µm)	Width (µm)	# fib / 10 µm	# str / 10 µm	dMF (nm)
min-max	6.4-8.9	2.1-3.1	13.1-18.4	25.2-29.6	389-120
x	7.72	2.66	15.44	27.74	613.95
s	0.51	0.18	1.21	0.90	122.14
CV (%)	6.57	6.78	7.81	3.25	19.89
n = 51					

N : P = 16	Length (µm)	Width (µm)	# fib / 10 µm	# str / 10 µm	dMF (nm)
min-max	6.1-9.5	2.2-3.4	13.0-17.5	26.5-31.3	389-1020
x	7.81	2.67	14.94	27.89	630.93
s	0.71	0.24	1.12	0.98	131.72
CV (%)	9.04	9.16	7.52	3.53	20.88
n = 52					

17.5 ppt Salinity	Length (µm)	Width (µm)	# fib / 10 µm	# str / 10 µm	dMF (nm)
min-max	6.6-9.2	2.1-2.9	12.7-17.5	26.3-30.4	442-1500
x	8.12	2.53	14.96	27.94	653.75
s	0.54	0.17	1.24	1.00	166.71
CV (%)	6.64	6.83	8.28	3.58	25.50
n = 55					

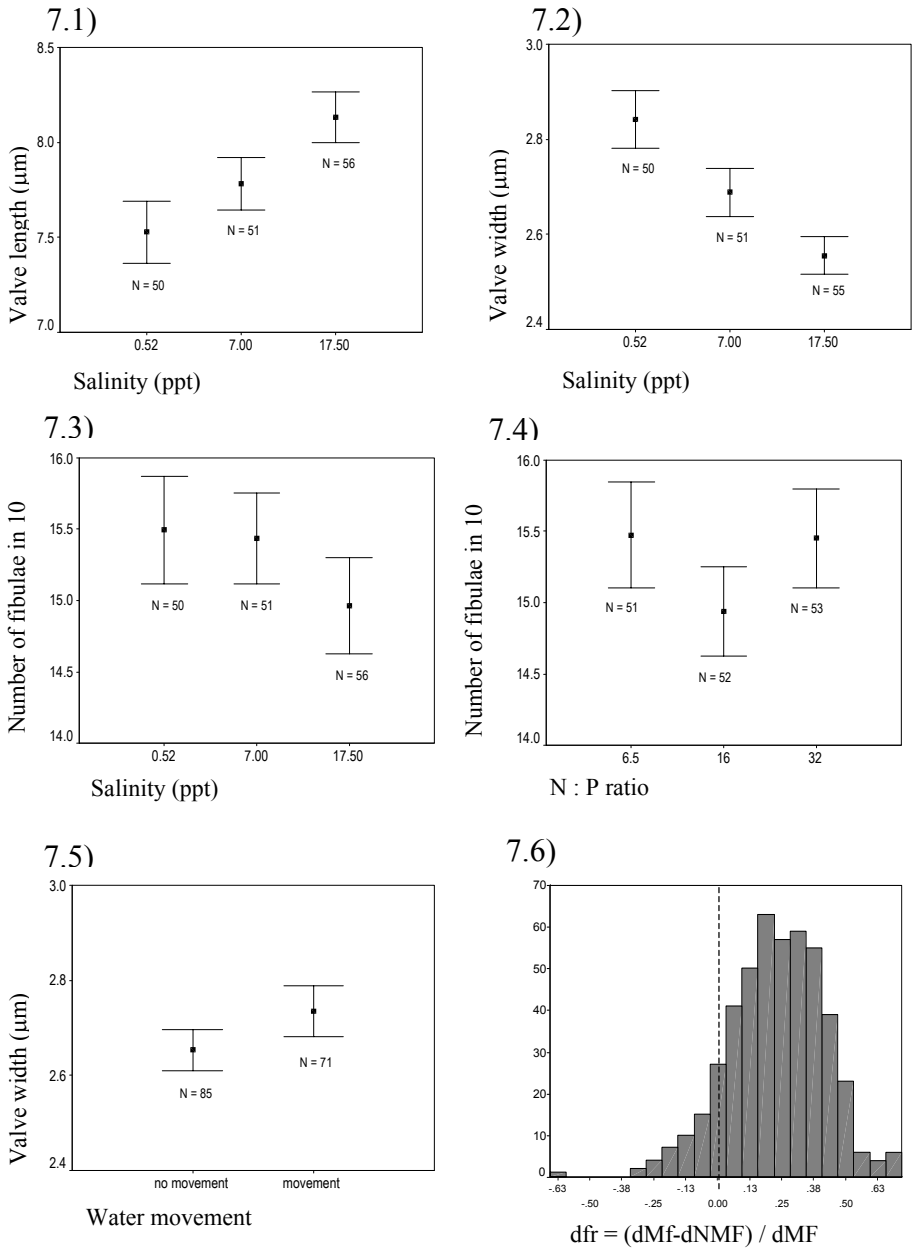
N : P = 32	Length (µm)	Width (µm)	# fib / 10 µm	# str / 10 µm	dMF (nm)
min-max	6.3-9.1	2.1-3.3	12.7-18.9	26.3-31.3	412-1500
x	7.84	2.68	15.44	27.85	633.96
s	0.55	0.23	1.25	0.94	168.53
CV (%)	7.05	8.45	8.11	3.38	26.58
n = 53					

Water movement	Length (µm)	Width (µm)	# fib / 10 µm	# str / 10 µm	dMF (nm)
min-max	6.2-9.5	2.1-3.4	12.7-18.9	25.2-31.3	389-1500
x	7.79	2.62	15.21	27.73	623.40
s	0.63	0.22	1.29	0.93	147.16
CV (%)	8.05	8.25	8.47	3.34	23.61
n = 71					

No water movement	Length (µm)	Width (µm)	# fib / 10 µm	# str / 10 µm	dMF (nm)
min-max	6.1-9.1	2.3-3.4	12.9-18.8	26.3-31.3	397-1060
x	7.79	2.72	15.40	28.06	631.93
s	0.58	0.23	1.25	0.96	141.92
CV (%)	7.48	8.38	8.11	3.44	22.46
n = 85					

Table 7.4. Results of multivariate analysis of variance (MANOVA) of characters against environmental variables. Degrees of freedom (df), *F*-statistics and *P* values. Shading indicates significant difference with variable.
Characters investigated: valve length and width, number of fibulae in10 µm, number of striae in 10 µm, distance between the two median fibulae (dMF) and relative difference (dFr) in the distance between the two median and two non-median fibulae, i.e. (dMF – dNMF) / dMF.

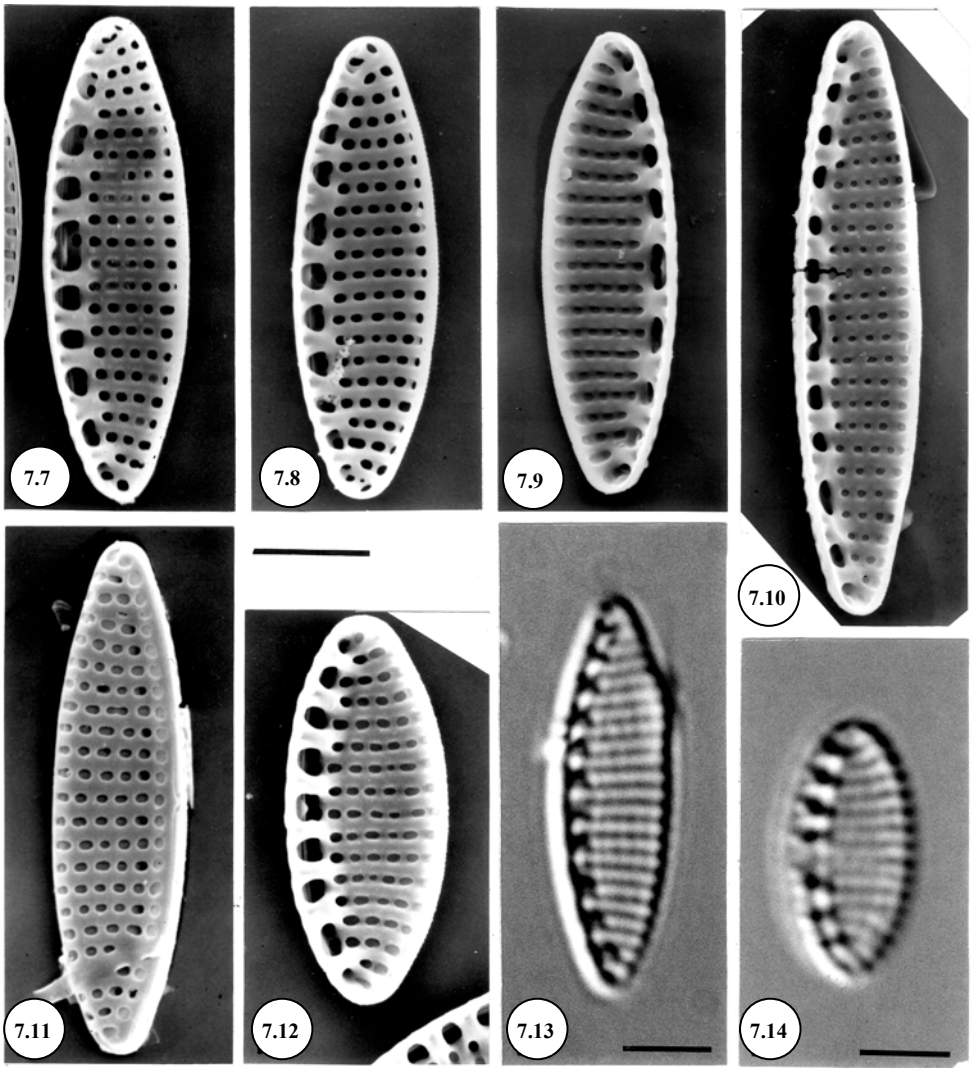
Source of variation	Variable	df	*F*	*P*
Salinity	**Length**	2, 142	16.37	**< 0.001**
	Width	2, 142	37.57	**< 0.001**
	# fib / 10mm	2, 142	3.60	**0.03**
	# str / 10µm	2, 142	1.88	0.156
	dMF	2, 142	0.90	0.411
	dFr	2, 142	1.86	0.160
N : P ratio	Length	2, 142	1.81	0.167
	Width	2, 142	0.55	0.577
	# fib / 10µm	2, 142	3.34	**0.038**
	# str / 10µm	2, 142	0.22	0.806
	dMF	2, 142	0.13	0.882
	dFr	2, 142	0.96	0.384
Water movement	Length	1, 142	0.44	0.507
	Width	1, 142	13.12	**< 0.001**
	# fib / 10µm	1, 142	1.10	0.296
	# str / 10µm	1, 142	3.24	0.074
	dMF	1, 142	0.03	0.865
	dFr	1, 142	< 0.001	0.987
Salinity x N : P ratio	Length	4, 142	0.62	0.650
	Width	4, 142	0.88	0.479
	# fib / 10µm	4, 142	2.24	0.068
	# str / 10µm	4, 142	1.40	0.236
	dMF	4, 142	0.11	0.980
	dFr	4, 142	1.96	0.105
Salinity x water movement	Length	2, 142	0.87	0.423
	Width	2, 142	2.14	0.122
	# fib / 10µm	2, 142	0.25	0.776
	# str / 10µm	2, 142	1.10	0.336
	dMF	2, 142	0.01	0.994
	dFr	2, 142	0.34	0.713
N : P ratio x water movement	Length	2, 142	0.56	0.572
	Width	2, 142	1.35	0.263
	# fib / 10µm	2, 142	1.38	0.254
	# str / 10µm	2, 142	1.03	0.360
	dMF	2, 142	0.05	0.956
	dFr	2, 142	0.06	0.945



Figs. 7.1-7.6 Fig.7.1: Graph showing variation in valve length with salinity regime. **Fig.7.2**: Graph showing variation in valve width with salinity regime, **Fig. 7.3**: Graph showing variation in number of fibulae in 10µm with salinity regime, **Fig. 7.4**: Graph showing variation in number of fibulae in 10µm with N : P ratio. **Fig. 7.5**: Graph showing variation in valve width with water movement. **Fig. 7.6**: Histogram showing variation in dFr (the distance between two adjacent non-median fibulae taken at random (dNMF) compared with the distance between the two median fibulae (dMF) of the same valve). When dFr is zero, dMF is the same as dNMF. Most dFr values are significantly greater than zero ($t = 26.18$ $P < 0.001$), i.e. the distance between the two median fibulae is larger than between the non-median fibulae.

Table 7.5. Results of analysis of covariance (ANCOVA), using length as a covariable, width and number of fibulae in 10 μm as dependent variables. The parallelism hypothesis (i.e., homogeneity of slopes) was not rejected. Degrees of freedom, *F*-statistics and *P* values are shown.

	dependent variable: **Width**			dependent variable: **# fib / 10 μm**		
Source of variation	df	*F*	*P*	df	*F*	*P*
Length (covariable)	1, 156	1.25	0.27	1	3.81	0.053
Salinity	2, 156	27.09	< 0.001	2	1.40	0.251
N : P ratio	2, 156	0.72	0.487	2	3.11	0.048
Water movement	1, 156	13.56	< 0.001	1	1.36	0.246
Salinity X N : P ratio	4, 156	0.78	0.542	4	2.18	0.074
Salinity X water movement	2, 156	2.11	0.125	2	0.43	0.651
N : P ratio X water movement	2, 156	1.50	0.228	2	1.18	0.31



Figures 7.7-7.14. Figs. 7.7-7.12: SEM's showing valve shape variation and the variability on the distance between the two median fibulae (Scale bar = 2 μm). Notice in Figs. 7.7 and 7.10 the distance between the two median fibulae (dMF) is clearly larger than the distance of two non median fibulae (dNMF). In Figs. 7.8 and 7.12 the dMF is equal or shorter than the dNMF.
Figs. 7.13 & 7.14: LM's showing valve shape variation (Scale bar = 2 μm).

7.4 Discussion

7.4.1 Effects of growth conditions on valve morphology

Although they are subtle, significant differences in the valve morphology of *N. frustulum* can be detected within 2 weeks of growth under the experimental regimes tested. Salinity has the greatest effect, modifying the length and width of valves, as well as the number of fibulae in 10 μm, but not showing any effect on stria density. Other culture work on other diatoms (Schmid 1976, Cox 1995) has shown that valve width increases with increasing salinity, and that valve pattern also varies with salinity (Schultz 1971). Thus, there is no consistent pattern of salinity effects on valve morphology, but the responses are taxon specific. Interestingly, while stria density remained more or less constant in the raphid diatoms (Schmid 1976, Cox 1995, this study), a centric diatom (*Cyclotella cryptica* Reimann, Lewin & Guillard) showed greater variability in stria pattern under different salinity regimes (Schultz 1971). In a longer term study monitoring stria density as cells decreased in length (Cox 1983), showed that stria densities fluctuated about a mean. If one assumes that fibula spacing is controlled in a similar manner, fibula spacing might be expected to fluctuate slightly with decreasing valve length. This was not evident in *N. frustulum*. However, our experiments were conducted over a shorter period, and fibula densities were much lower than the stria densities in *Donkinia* Ralfs (Cox 1983). Subtle shifts in density would therefore be harder to detect. In addition to salinity, other factors such as N : P ratio and water movement can affect the valve morphology of *N. frustulum*. Valve width is slightly greater under moving water than in still conditions. This might be explained as an adaptation to provide a wider surface for attachment under

turbulent conditions than still ones, but further evidence is required. It is intriguing, but currently inexplicable, that fibula density is lower at the intermediate N : P ratio (i.e. 16) but higher when one of the nutrients is relatively low.

Environmental factors, such as water movement, nutrient availability and concentration, frequently co-vary with salinity, especially in estuarine systems (Nedwell & Trimmer 1996; Ogilvie *et al*. 1997, Chapters 4 and 6 of this study), and it is not possible to separate their effects based on field observations only (Lowe *et al*. 1986, Cox 1993, Underwood *et al.*1998). This is the case for Wendker's work (1990b) on the Schlei estuary in which she found that valve length, width and fibula density of natural populations of *N. frustulum* increased with salinity towards the mouth of the estuary. However, although she stressed that other factors must be involved, she concluded that valve width increased with salinity (correlation with proximity to the estuary mouth), whereas salinity did not have this effect under our experimental conditions, although water movement did. It is possible that the correlation between increased valve width and increased salinity (Wendker 1990b) could reflect more dynamic conditions (= water movement) at the estuary mouth, but the increase in fibula density downstream also coincides with a decrease in [P]. Unfortunately, in the absence of data about [N] in the Schlei estuary, it is impossible to know at what N : P ratio the increase in fibula density occurred.

7.4.2 Taxonomic aspects

The number of striae in 10µm is the most stable character for *N. frustulum*. Of all the variables measured, it had the lowest coefficient of variation (3.25-3.58%) and was not affected by any of the environmental conditions studied.

Geissler (1970a, b) and Wendker & Geissler (1988) similarly obtained a low coefficient of variation for stria density in *Nitzschia linearis* (Agardh) W. Smith, *Nitzschia palea* (Kützing) W. Smith and *Nitzschia gandersheimiensis* Krasske. Thus, stria density is probably a taxonomically stable character for these species. On the other hand, length and width show higher coefficients of variation (6.57-9.04% and 6.78-9.16% respectively) and are not allometrically related. This suggests that, valve length, width and length / width ration can be affected by environmental conditions whereas stria density is much more constant and thus taxonomically more informative for *N. frustulum.*

The greater distance between the two median fibulae has been correlated with the presence of a central nodule, which is often used to define some of the groups in the Nitzschia Lanceolatae, (Krammer & Lange-Bertalot 1997b, Lange-Bertalot 1980, Lange-Bertalot & Simonsen 1978). In most of the valves measured, the distance between the two median fibulae was greater than the other distances and was unaffected by the environmental conditions. However, the variable itself has a wide range of variation (19.87-26.66%), which includes equidistant median fibulae. Similar results were found for *N. palea* and *N. gandersheimiensis* (Wendker & Geissler 1988). Thus, the distance between the median fibulae should be used with caution as a taxonomic character since it is only detectable at the population level.

Although some authors (Lange-Bertalot 1993, Lange-Bertalot & Simonsen 1978) have argued that the shared ultrastructural features of *N. frustulum* and *N. inconspicua* indicate that they are conspecific, differences in valve shape and ecology have often been used to separate them. Thus, for many years the "shorter, fatter" morph found in freshwater has been identified as *N. inconspicua,* and the "longer, thinner" morph from more brackish waters as *N.*

frustulum (cf. Wendker 1990b). Since we obtained the "shorter, fatter" shapes in all treatments (freshwater to brackish) (Figs 11-15) the use of valve shape and conductivity regime as diagnostic criteria by which to distinguish *N. inconspicua* from *N. frustulum* cannot be supported. Lange-Bertalot (1993) argued that *N. frustulum* and *N. inconspicua* are conspecific, but also suggested that another taxon with blunt apices, very similar to *N. inconspicua*, can be found in fresh or slightly brackish water. This, he suggested, should be called either *Nitzschia abbreviata* Hustedt, *N. invisitata* Hustedt or *Nitzschia epiphytica* O. Müller, although he failed to provide a final decision on this issue. Further work on the specific boundaries and nomenclature of *N. frustulum* is in progress.

7.4.3 Bioindicator value of *N. frustulum*

Small "fat" diatoms, very similar to *N. frustulum*, have been reported from many freshwater habitats, especially eutrophic rivers (Sabater *et al*. 1987, Aboal *et al*. 1996, Leclercq 1995, Merino *et al.* 1995, O'Connell *et al*. 1997, Winter & Duthie 2000). We hypothesise that the "shorter, fatter" shapes tend to occur in eutrophic waters whatever the salinity regime (In this work variation in the "shorter, fatter" shape over a wide range of salinities have been found, but all the assays were carried out under high nutrient regimes). This supports with classification of *N. inconspicua* as α-mesosaprobic and of *N. frusutulum* as β-mesosaprobic (van Dam *et al.* 1994). Additionally, based on our findings, water movement and the fresher water of rivers could encourage this shorter, fatter shape, if valve width increases with water movement, and low salinity reduces cell length. There was no net decrease in cell length across all treatments due to size reduction of the cultures.

Taxa with wide ecological amplitudes are usually considered poor indicators (Descy 1984), but the importance of elucidating whether a taxon is eurytopic, or comprises several ecologically or physiologically discrete taxa has also been recognised (Cox 1995). If the latter case applies, ecotypes can be used as environmental indicators provided all the factors affecting valve morphology are known. To refine the bioindicator potential of *N. frustulum*, it will be important to study the range of variation over longer incubation periods, as well as to investigate the response under similar N : P ratios, but at lower absolute nutrient concentrations.

8. GENERAL DISCUSSION

8.1 Importance of confinement and eutrophy

Confinement and eutrophy play an important role in the functioning of the aquatic ecosystem studied. Their importance is shown at the three levels of organisation: at ecosystem level, since confinement and eutrophy are the decisive factors in the alternative predominance of phytoplankton, periphyton or macrophytes; at community level, because they are also relevant factors affecting diatom species composition as well as the diatom assemblages; at population level, since valve morphology of some species such as *Nitzschia frustulum* is affected by single environmental variables which, in the Empordà wetlands depend on confinement and eutrophy.

Confinement is related (inversely) to water turnover and to water disturbance (Quintana 1998a). The degree of eutrophy is considered as the capacity of production and thus synonymous with productivity (Margalef 1989). Both factors have also been described as essential to explain the composition and production of other aquatic communities in these and similar environments (Guerloget & Perthuisot 1983, Comín 1984, Pérez-Ruzafa & Marcos Diego 1993, Quintana *et al.* 1998a, Moreno-Amich *et al*. 1999, Gifre *et al*. 2002). Therefore, it is reasonable to conclude that confinement and eutrophy are relevant environmental factors affecting aquatic communities and the functioning of the Mediterranean coastal wetlands.

In other, non-Mediterranean, fluctuating systems such as estuaries and temperate shallow coastal wetlands, other environmental factors such as salinity, light or seasonality have been considered to be important for diatom species distribution and ecosystem functioning. However, taking into account a generalizable model based on external energy inputs to explain the ecosystem processes (Quintana *et al.* 1998b), some analogies can be found between Mediterranean and temperate wetlands. In temperate estuarine and shallow coastal waters, salinity, nutrients and organic matter vary on a seasonal basis related to rainfall patterns and hydrological processes (Hessen 1999) and rainfall patterns and hydrological processes could then be regarded as the expression of the entry of external energy into estuaries. Then, confinement and seasonality are a result of the energy entry into the system.

In fluctuating environments, where many environmental factors co-vary or interact, it would be more meaningful to examine combinations of ecological conditions acting in synergy, rather than to consider the effects of single environmental variables in isolation, in order to understand the functioning of the system as well as the community and population variation patterns (MacIntyre *et al*. 1996). In that sense, the confinement gradient (in Mediterranean wetlands) and seasonality (in temperate estuaries and shallow coastal waters) are integrative factors involving different processes (nutrient availability, salinity, temperature, etc…) and eutrophy can be regarded as the response of the system to the energy flux.

8.2 Difficulties in the assessment of trophic state in shallow coastal wetlands

In fluctuating systems the results of the assessment of waterbody trophic state, using chemical and biological data (e.g. total nutrients or chlorophyll a content of the water), have been proved considerably differ to those using zooplanktonic organisms (Badosa 2002). The nutrient-related trophic state indices were developed in temperate lakes where phosphorus is the chief factor limiting primary production (Margalef 1983, Wetzel 2001). Its application in fluctuating environments where the limiting factor is often nitrogen (Sullivan & Daiber 1974, Valiela & Teal 1974, Quintana *et al*. 1998a, Nedwell *et al*. 1999) can lead to erroneous conclusions. Additionally, the nutrient-related indices are based on total nutrients and do not take into account which are the nutrient forms available to the primary producers. In the Empordà wetlands, the low values of DIN found in many of the waterbodies studied can be explained by the lack of DIN inputs but also because of the rapid removal of inorganic dissolved forms of nitrogen (Wear *et al*. 1999). Although algal chlorophyll is a better indicator of trophic state than nutrient concentrations (Valiela *et al*. 1990), there are other factors that can also falsify the results, such as zooplankton grazing, or the presence of mixotrophic phytoplankton, commonly reported in shallow coastal systems with significant organic matter inputs (Isaksonn 1998, Jones 2000, Quintana & Moreno Amich 2002).

Thus, it seems that an assessment of the degree of eutrophy based on species composition should be the most suitable approach for the shallow coastal wetlands. Diatoms are good candidates due to their reliable bioindicative value that has been demostrated (Margalef 1955, Patrick 1973, Coste 1976, Lange-Bertalot 1979, Kobayasi & Mayama 1982, Fabri & Leclerq 1986, Sabater *et al*.

1988, Rott 1991, Stevenson & Pan 1999, Sullivan & Currin 2000). Nevertheless, there is still work to be done in order to overcome the paucity of information on the autoecology of benthic diatoms inhabiting coastal waters that intrinsically have a certain level of nutrients or organic matter, as is the case in many estuaries and salt marshes.

Most of the diatom species found in this study are reported as β to α-mesosaprobous or as pollution tolerant taxa (Lange-Bertalot 1979, Denys 1991, Hofmann 1994, van Dam *et al*. 1994). Interestingly, many of them are also referred to as facultative heterotrophic species (Cholnoky 1968, Hellebust & Lewin 1977, Admiraal *et al*. 1987, Chelf 1990). Although experimental work (Pipp & Robinson 1982) suggests that heterotrophy is not the primary method of nutrition for diatoms, the ability of some benthic diatoms to be facultatively heterotrophic may play an important role for the survival of photosynthetic diatoms in such environments, with a high proportion of organic matter or of organic nutrients with respect to inorganic nutrients. Amino acids have been described as important for diatom growth in waters where inorganic nitrogen is extremely low (Wright & Hobbie 1965, Williams 1970). In that context, studies of the range of heterotrophic diatom capabilities and their regulation in response to environmental factors would be of great relevance to the understanding of the ecology of diatom species and assemblages in these systems, which is a pre-requisite for using them as bioindicators.

8.3 Ecosystem, community and population responses to confinement

Although confinement is an important factor for the three levels of organisation, its effect on each of the considered levels is different. At the ecosystem level what is important is the balance, the net result of inputs and outputs, which is reflected in primary producers' response to confinement, where macrophytes dominate in oligotrophic conditions with both high and low water turnover. That agrees with the model of confinement proposed by Guerlorget & Perthuisot (1983) according to which the same level of production can be reached both with an excess of concentration, with exhaustion of particular elements below the concentration required, and with excess dilution, and rapid leaching of these scarce elements.

At the community level not is only the balance important, but also how the balance is achieved. In that respect, diatom species composition is completely different under maximum confinement situations than under flooding situations, although the balance of nutrients would be the same.

The population response to confinement results in changes in valve morphology. At this level, what is important are the single effects on the morphology of diatom taxa of each of parameters that co-vary with confinement and eutrophy (e.g. salinity, nutrients or water movement). Our results show that salinity, as a single environmental factor, has an effect at the *N. frustulum* population level, resulting in phenotypic plasticity, while there is no effect of salinity at the diatom community level, since in such environments with fluctuating salinity all the species present are euryhaline.

9. CONCLUSIONS

1. The 22 waterbodies of the Empordà wetlands studied are classified into 5 groups (confined coastal brackish and hyperhaline ponds; semi-confined brackish coastal lagoons and ponds; freshwater ponds with high nutrient inputs; fluctuating freshwater systems and freshwater springs) according to their hydrological dynamic and to the physical and chemical composition of their water**.**

2. In the Empordà wetlands macrophytes always dominate in waterbodies with relative oligotrophy, in situations of both high and low water turnover rate, favoured by their capacity to capture nutrients from the sediment.

3. The predominance of periphyton is limited to situations of intermediate nutrient concentration and intermediate to high water turnover rates, while phytoplankton predominates under the most eutrophic conditions, which occur at intermediate water turnover rates.

4. A total of 165 taxa have been identified from the community of periphytic diatoms of the Empordà salt marshes. 84.69% of the individuals counted belong to the genera of *Cocconeis* (*Cocconeis placentula*), *Nitzschia*, *Navicula* and *Amphora*. Among them, *Nitzschia* is the genus represented by the highest number of taxa.

5. The periphytic diatom species occurring in the salt marshes of the Empordà wetlands are tolerant of changes in many environmental variables such as salinity, temperature and nutrients.

6. In environments with fluctuating salinity regimes, the salinity fluctuations determine that all diatom species present are euryhaline, but the species distribution and assemblages are determined by factors directly involved in the flux of system energy. In the case of the salt marshes of the Empordà wetlands, these factors are confinement and productivity.

7. *Achnanthidium minutissimum*, *Amphora veneta*, *Craticula halophila*, *Fallacia pygmaea*, *Fistulifera* cf. *saprophila*, *Gomphonema parvulum*, *Hippodonta hungarica*, *Navicula erifuga*, *N. gregaria*, *N. paul-schulzii*, *N. veneta*, *Nitzschia. acicularis, N. aurariae*, *N. capitellata*, *N. frustulum*, *N. gracilis* f. *acicularoides*, *N. hungarica*, *N. microcephala*, *N. nana*, *N. palea*, and *N.* cf. *pusilla* are species typical of waterbodies characterised by continuous water inputs of freshwater with nutrient contents.

8. Based on confinement and productivity 5 diatom assemblages are distinguished.
Assemblage A: Composed only of *Bacillaria paradoxa*
Assemblage B: Composed of *Berkeleya fennica*, *Entomoneis puctulata*, *Navicula normaloides*, *Nitzschia clausii*, *N. dissipata* var. *media* and *Nitzschia* sp. 1

Assemblage C: Composed of *Amphora hybrida*, *A. micrometra*, *Berkeleya rutilans*, *Haslea spicula*, *Navicula perminuta*, *N. salinarum* and *Thalassiosira pseudonana*

Assemblage D: Composed of *Opephora horstiana* and *Nitzschia archibaldii*

Assemblage E*:* Composed of *Amphora staurophora* and *Cocconeis placentula*

9. Assemblages A, B and C are typical of low confinement resulting from flooding conditions. Assemblages A and B are also characterized by situations of high productivity. Assemblages D and E typify high confinement conditions, within which D occurs under higher productivity situations.

10. The morphology of *N. frustulum* is affected by environmental variables. Salinity modifies the length and width of the valves as well as the number of fibulae in 10μm. The valve width is also modified by water movement. The N / P ratio affects the fibula density.

11. The greater distance between the two median fibulae, a character often used for species differentiation within *Nitzschia*, shows a wide range of variation including equidistant median fibulae. Therefore its use as a taxonomic character should be treated with caution.

12. For *N. frustulum* the most stable character with respect to changes in salinity, N/P ratio and water movement is the stria density, suggesting it is appropriate to use it as a taxonomic character.

13. Length and width show higher coefficients of variation and are not allometrically related, suggesting that neither valve length, width, nor shape (in terms of length / width ratio) are taxonomically reliable for *N. frustulum.*

14. The use of valve shape and conductivity regime as diagnostic criteria by which to distinguish *N. inconspicua* from *N. frustulum* cannot be supported, since we obtained variations around the "shorter, fatter" shapes in all salinity treatments (freshwater to brackish).

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Appendix I

List of the 165 diatom taxa (ranged alphabetically) found in the salt marshes of the Empordà Wetlands Natural Park with the corresponding acronym and the relative abundance considering all the samples. Some of the most recent synonymous of some of the taxa are also given

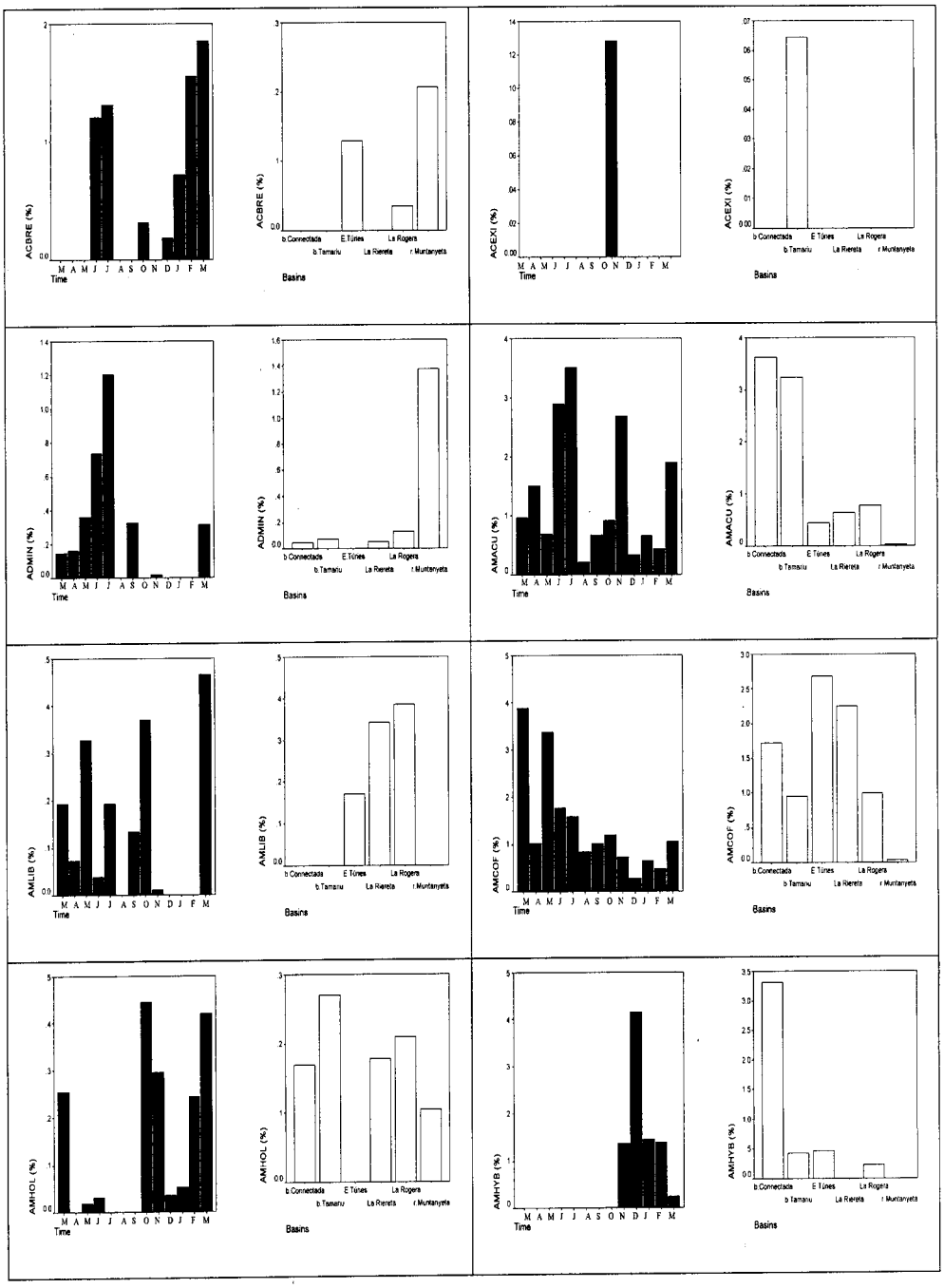
Diatom Taxa	Acronym	% relative abundance	Recent synonymous
Achnanthes brevipes Agardh	**ACBRE**	**0.07**	
Achnanthes exigua Grunow	**ACEXI**	**0.01**	
Achnanthidium minutissimum (Kützing) Czarmecki	**ADMIN**	**0.33**	*Achnanthes minutissima* Kützing
Amphora acutiuscula Kützing	**AMACU**	**1.40**	
Amphora coffeaeformis (Agardh) Kützing	**AMCOF**	**1.42**	
Amphora holsatica Hustedt	**AMHOL**	**0.17**	
Amphora hybrida Grunow	**AMHYB**	**0.79**	
Amphora libyca Ehrenberg	**AMLIB**	**0.13**	
Amphora cf. *luciae* Cholnoky *sensu* Archibald	**cAMLUC**	**3.36**	
Amphora margalefii Tomas	**AMMAR**	**0.18**	
Amphora micrometra Giffen	**AMMIC**	**2.35**	
Amphora pediculus (Kützing) Grunow	**AMPED**	**0.01**	
Amphora staurophora Juhlin-Dannfelt	**AMSTA**	**1.30**	
Amphora subholsatica Krammer	**AMSUB**	**0.10**	
Amphora veneta Kützing	**AMVEN**	**0.91**	
Amphora sp. aff. *tenuissima*	**AMSP1**	**2.40**	
Anomoeoneis sphaerophora (Ehrenberg) Pfitzer	**ANSPH**	**0.01**	
Ardissonia crystallina (Agardh) Grunow	**ARCRY**	**<0.005**	*Synedra cristallina* (Agardh) Kützing
Astartiella bahusiensis (Grunow) Witkowski, Lange-Bertalot & Metzeltin	**ASBAH**	**0.10**	*Navicula bahusiensis* Grunow
Bacillaria paradoxa Gmelin	**BAPAR**	**0.51**	
Berkeleya antartica (Harvey) Grunow	**BEANT**	**0.01**	
Berkeleya fennica Juhlin-Dannfelt	**BEFEN**	**2.00**	
Berkeleya rutilans (Trentepohl) Grunow	**BERUT**	**1.91**	
Caloneis amphisbaena f. *subsalina* (Donkin) Van der Werff & Huls	**CAAMP**	**0.02**	
Chaetoceros salsuguineus Takano	**CHSAL**	**0.43**	
Cocconeis placentula Ehrenberg	**COPLA**	**27.66**	
Cocconeis scutellum Ehrenberg	**COSCU**	**<0.005**	
Craticula halophila (Grunow) D.G.Mann	**CRHAL**	**0.86**	*Navicula halophila* Grunow
Cyclotella atomus Husted	**CYATO**	**0.01**	
Cyclotella meneghiniana Kützing	**CYMEN**	**0.17**	
Cylindrotheca gracilis (Brébisson) Grunow	**CYGRA**	**0.09**	
Cymbella pusilla Grunow	**CYPUS**	**0.01**	
Cymbella tumidula Grunow	**CYTUM**	**0.01**	
Diploneis bombus Ehrenberg	**DIBOM**	**0.04**	
Diploneis decipiens var. *parallela* Cleve	**DIDEC**	**0.01**	
Diploneis didyma (Ehrenberg) Cleve	**DIDID**	**0.15**	
Encyonema minutum (Hilse in Rabenhorst) D.G.Mann	**ENMIN**	**0.02**	*Cymbella minuta* Hilse
Entomoneis alata (Ehrenberg) Ehrenberg	**ENALA**	**0.05**	
Entomoneis paludosa (W. Smith) Reimer	**ENPAL**	**0.10**	
Entomoneis pseudoduplex Osada & Kobayasi	**ENPSE**	**0.01**	
Entomoneis puctulata (Grunow) Osada & Kobayasi	**ENPUC**	**0.18**	
Fallacia pygmaea (Kützing) Stickle & D.G.Mann	**FAPYG**	**0.06**	*Navicula pygmea* Kützing
Fallacia tenera (Husted) D.G. Mann	**FATEN**	**<0.005**	*Navicula tenera* Hustedt
Fistulifera cf. *saprophila* (Lange-Bertalot & Bonik) Lange-Bertalot	**cFISAP**	**0.23**	*Navicula saprophila* Lange-Bertalot & Bonik
Fragilaria capucina Desmazières	**FRCAP**	**0.13**	
Fragilaria sopotensis Witkowski & Lange-Bertalot	**FRSOP**	**0.04**	
Gomphonema gracile Ehrenberg	**GOGRA**	**0.02**	
Gomphonema parvulum Kützing	**GOPAR**	**0.35**	
Gomphonema truncatum Ehrenberg	**GOTRU**	**<0.005**	
Gomphonemopsis obscurum (Krasske) Lange-Bertalot	**GPOBS**	**0.07**	*Gomphonema obscurum* Krasske
Gyrosigma acuminatum (Kützing) Rabenhorst	**GYACU**	**0.15**	
Gyrosigma eximium (Thwaites) Boyer	**GYEXI**	**0.02**	
Gyrosigma nodiferum (Grunow) Reimer	**GYNOD**	**0.04**	
Haslea spicula (Hickie) Lange-Bertalot	**HASPI**	**0.05**	*Navicula spicula* (Hickie) Cleve
Hippodonta hungarica (Grunow) Lange-Bertalot, Metzeltin & Witkowski	**HIHUN**	**0.14**	*Navicula hungarica* Grunow
Kolbesia ploenensis (Husted) Round & Bukhtiyarova	**KOPLO**	**0.36**	*Achnanthes ploenensis* Hustedt
Luticola mutica var. *mutica* (Kützing) D.G.Mann	**cLUMUT**	**0.04**	*Navicula mutica* var. *mutica* Kützing
Mastogloia pumila (Grunow) Cleve	**MAPUM**	**0.76**	
Mastogloia pusilla (Grunow) Cleve	**MAPUS**	**0.02**	
Melosira moniliformis var. *octogona* (Grunow) Husted	**MEMON**	**0.19**	
Melosira nummuloides (Dillwyn) Agardh	**MENUM**	**0.13**	
Navicula arenaria Donkin	**NAARE**	**0.02**	
Navicula cancellata Donkin	**NACAN**	**0.03**	
Navicula cincta (Ehrenberg) Ralfs	**NACIN**	**0.27**	

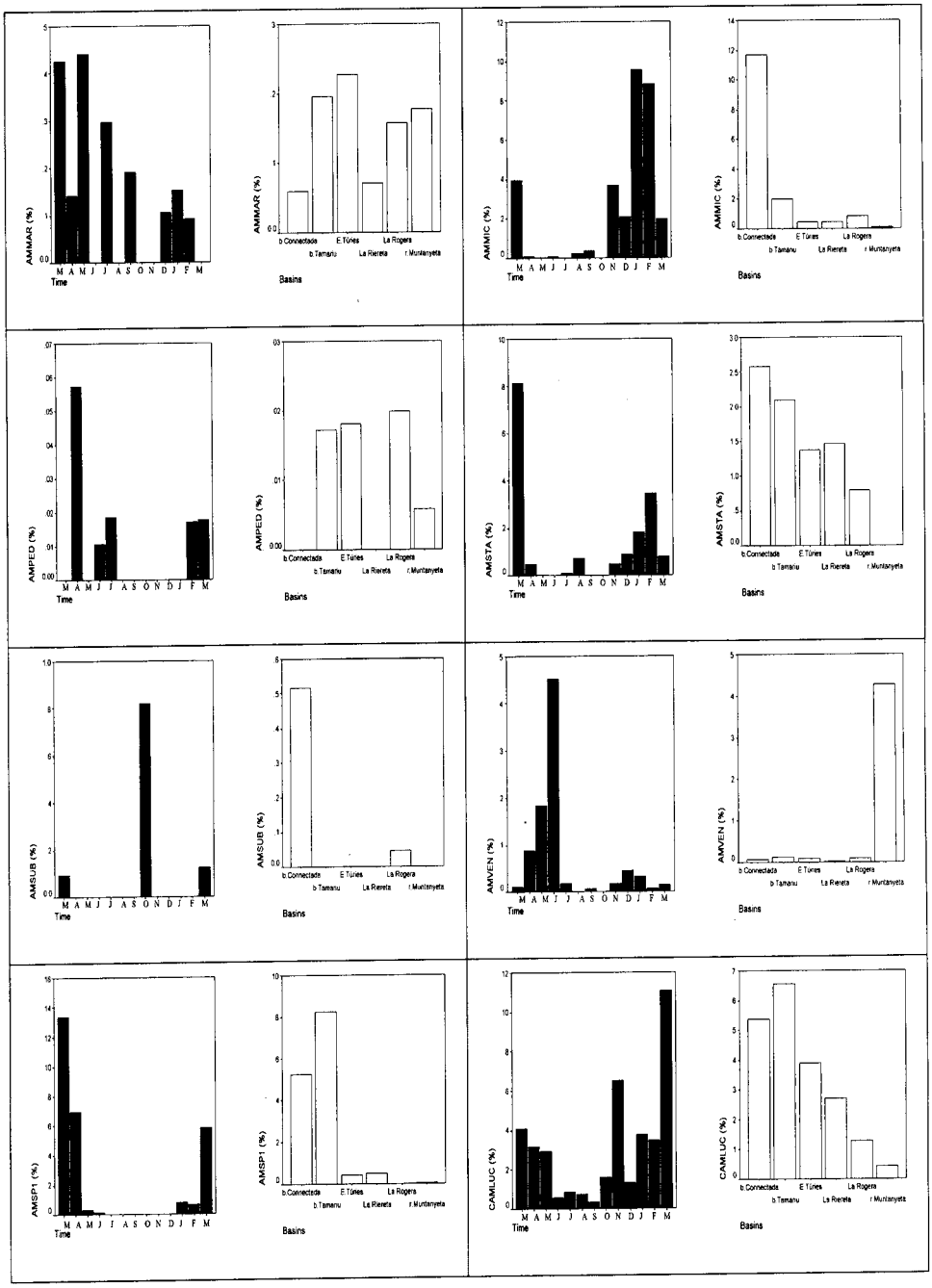
Diatom Taxa	Acronym	% relative abundance	Recent synonymous
Navicula cryptotenella Lange-Bertalot	**NACRT**	**0.01**	
Navicula duerrenbergiana Hustedt	**NADUE**	**0.01**	
Navicula erifuga Lange-Bertalot	**NAERI**	**0.42**	
Navicula gemmifera Simmonsen	**NAGEM**	**0.01**	
Navicula gregaria Donkin	**NAGRE**	**1.72**	
Navicula cf. *indifferens* Hustedt	**cNAIND**	**0.05**	
Navicula korzeniewskii Witkowski, Lange-Bertalot & Metzeltin	**NAKOR**	**0.03**	
Navicula lanceolata (Agardh) Ehrenberg	**NALAN**	**<0.005**	
Navicula margalithii Lange-Bertalot	**NAMAR**	**0.02**	
Navicula menisculus Schumann	**NAMEN**	**0.01**	
Navicula microcari Lange-Bertalot	**NAMII**	**0.07**	
Navicula microdigitoradiata Lange-Bertalot	**NAMIA**	**0.18**	
Navicula normaloides Cholnoky	**NANOR**	**0.54**	
Navicula paul-schulzii Witkowski & Lange-Bertalot	**NAPSC**	**0.22**	
Navicula cf. *paul-schulzii Witkowski & Lange-Bertalot*	**cNAPSC**	**0.20**	
Navicula perminuta Grunow	**NAPER**	**4.57**	
Navicula phyllepta Kützing	**NAPHY**	**4.05**	
Navicula radiosa Kützing	**NARAD**	**<0.005**	
Navicula recens (Lange-Bertalot) Lange-Bertalot	**NAREC**	**<0.005**	
Navicula salinarum Grunow	**NASAM**	**1.62**	
Navicula salinicola Husted	**NASAA**	**0.53**	
Navicula stachurae Witkowski, Lange-Bertalot & Metzeltin	**NASTA**	**0.01**	
Navicula tripunctata (O. F. Müller) Bory	**NATRP**	**<0.005**	
Navicula trivialis Lange-Bertalot	**NATRV**	**0.01**	
Navicula veneta Kützing	**NAVE**	**1.42**	
Navicula sp. 1	**NASP1**	**0.07**	
Navicula sp. 2	**NASP2**	**0.18**	
Navicula sp. 3	**NASP3**	**0.05**	
Nitzschia acicularis (Kützing) W.Smith	**NIACI**	**0.27**	
Nitzschia cf. *acicularis* 1 (Kützing) W.Smith	**cNIAC1**	**0.08**	
Nitzschia cf. *acicularis* 2 (Kützing) W.Smith	**cNIAC2**	**0.02**	
Nitzschia agnewii Cholnoky	**NIAGW**	**0.07**	
Nitzschia amphibia Grunow	**NIAMP**	**0.02**	
Nitzschia archibaldii Lange-Bertalot	**NIARC**	**4.15**	
Nitzschia aremonica Archibald	**NIARE**	**0.05**	
Nitzschia aurariae Cholnoky	**NIAUR**	**0.79**	
Nitzschia calcicola Aleem & Husted	**NICAL**	**0.02**	
Nitzschia calida Grunow	**NICAI**	**<0.005**	*Tryblionella calida* (Grunow) D.G. Mann
Nitzschia capitellata Husted	**NICAP**	**0.19**	
Nitzschia clausii Hantzsch	**NICLA**	**0.13**	
Nitzschia closterium (Ehrenberg) W. Smith	**NICLO**	**0.70**	
Nitzschia coarctata Grunow	**NICOA**	**<0.005**	*Tryblionella coarctata* (Grunow) D.G. Mann
Nitzschia communis Rabenhorst	**NICOM**	**0.01**	
Nitzschia cf. *commutata* Grunow	**cNICMM**	**0.02**	
Nitzschia constricta (Kützing) Ralfs	**NICON**	**0.95**	*Tryblionella apiculata* Gregory
Nitzschia debilis (Arnott) Grunow	**NIDEB**	**0.01**	*Tryblionella debilis* Arnott
Nitzschia dissipata (Kützing) Grunow	**NIDIS1**	**0.01**	
Nitzschia dissipata var. *media* (Hantzsch) Grunow	**NIDIS2**	**0.09**	
Nitzschia draveillensis Coste & Ricard	**NIDRA**	**0.10**	
Nitzschia cf. *draveillensis* Coste & Ricard	**cNIDRA**	**0.01**	
Nitzschia elegantula Grunow	**NIELE**	**0.01**	
Nitzschia filiformis (W.Smith) Van Heurck	**NIFIL**	**0.15**	
Nitzschia fontifuga Cholnoky	**NIFON**	**0.86**	
Nitzschia frequens Husted	**NIFRE**	**0.01**	
Nitzschia frustulum (Kützing) Grunow	**NIFRU**	**5.64**	
Nitzschia graciliformis Lange-Bertalot & Simonsen	**NIGRF**	**<0.005**	
Nitzschia gracilis Hantzsch	**NIGRA**	**0.03**	
Nitzschia gracilis Hantzsch f. *acicularoides* Coste & Ricard	**cNIGRA1**	**0.49**	
Nitzschia cf. *gracilis* Hantzsch	**cNIGRA2**	**0.02**	
Nitzschia granulata Grunow	**NIGRN**	**0.03**	*Tryblionella granulata* (Grunow) D.G.Mann
Nitzschia hungarica Grunow	**NIHUN**	**0.32**	*Tryblionella hungarica* (Grunow) D.G.Mann
Nitzschia intermedia Hantzsch ex Cleve & Grunow	**NIINT**	**0.02**	
Nitzschia littoralis Grunow	**NILIT**	**0.01**	*Tryblionella littoralis* (Grunow) D.G.Mann
Nitzschia microcephala Grunow	**NIMIC**	**2.11**	
Nitzschia nana Grunow	**NINAN**	**0.09**	
Nitzschia navicularis (Brébisson) Grunow	**NINAV**	**<0.005**	*Tryblionella navicularis* (Brébisson ex. Kützing) Grunow
Nitzschia ovalis Arnott ex Grunow in Cleve & Grunow	**NIOVA**	**<0.005**	

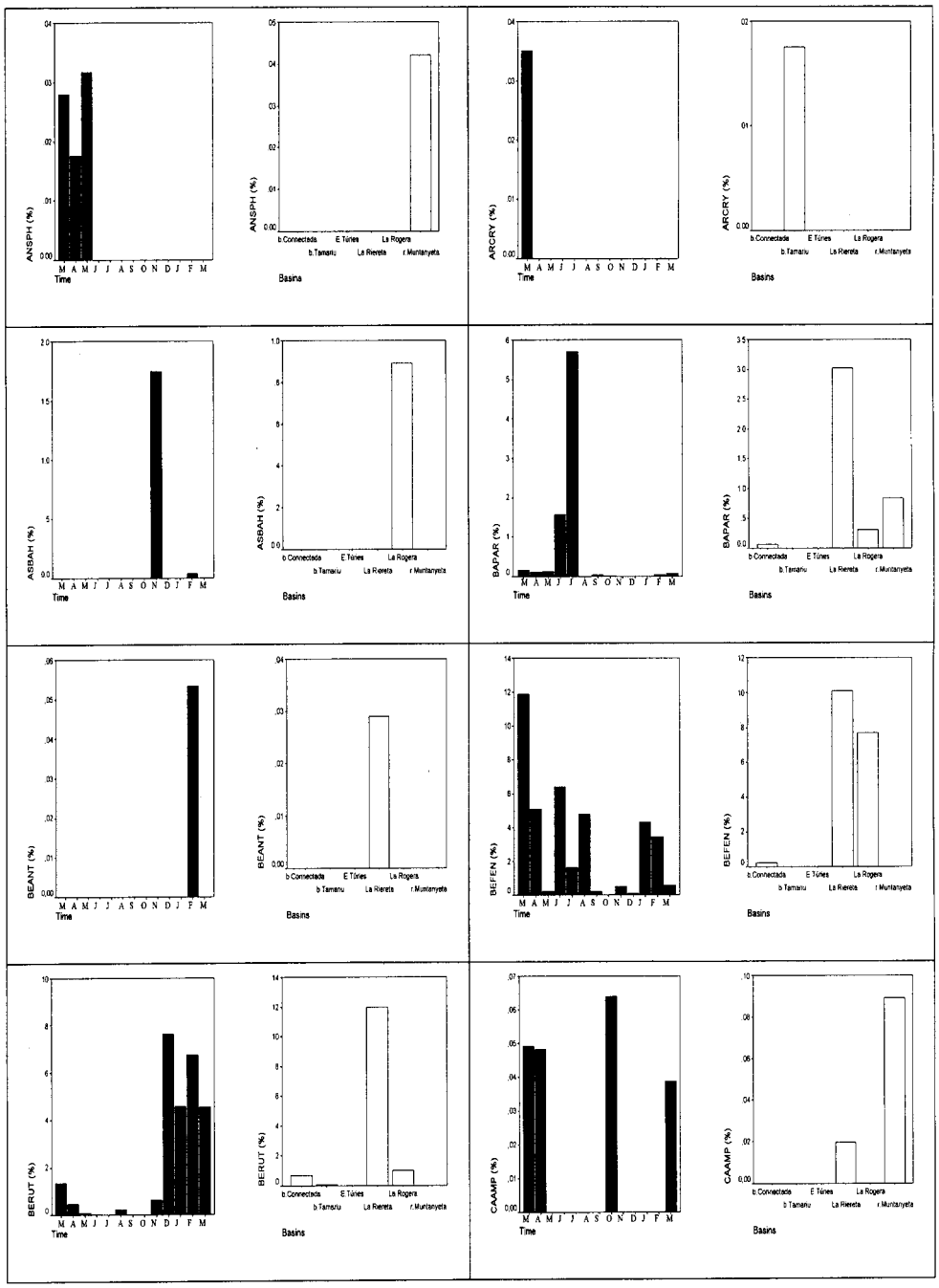
Diatom Taxa	Acronym	% relative abundance	Recent synonymous
Nitzschia paleacea Grunow	**NIPAE**	**0.23**	
Nitzschia pararostrata (Lange-Bertalot) Lange-Bertalot	**NIPAR**	**1.68**	*Nitzschia compressa* var. *pararostrata* Lange-Bertalot
Nitzschia pellucida Grunow	**NIPEL**	**0.48**	
Nitzschia perpiscua Cholnoky *sensu* Archibald	**NIPER**	**0.06**	
Nitzschia cf. *pumila* Husted	**cNIPUM**	**0.01**	
Nitzschia pusilla Grunow	**NIPUS**	**1.92**	
Nitzschia cf. *pusilla* Grunow	**cNIPUS**	**0.31**	
Nitzschia reversa W.Smith	**NIREV**	**0.23**	
Nitzschia rosenstockii Lange-Bertalot	**NIROS**	**0.61**	
Nitzschia scalpelliformis (Grunow) Grunow	**NISCA**	**<0.005**	
Nitzschia sinuata var. *delongei* (Grunow) Lange-Bertalot	**NISIN**	**0.03**	
Nitzschia supralitorea Lange-Bertalot	**NISUP**	**0.04**	
Nitzschia thermaloides Hustedt	**NITHE**	**0.17**	
Nitzschia vitrea Norman var. *vitrea*	**NIVI1**	**0.02**	
Nitzschia vitrea var. *salinarum* (Grunow)	**NIVI2**	**0.02**	
Nitzschia sp. aff. "Falsche *Nitzschia sigma*-Sippen"	**NISP1**	**1.06**	
Opephora günter-grassii (Witkowski&Lange-Bertalot) Sabbe & Vyverman	**OPGGR**	**0.24**	*Fragilaria guenter-grassi* Witkowski & Lange-Bertalot
Opephora horstiana Witkowski	**OPHOR**	**0.11**	
Planothidium delicatulumm (Kützing) Round & Buktiyorava	**PLDEL**	**0.22**	*Achnanthes delicatula* (Kützing) Grunow
Planothidium jan-marcinii Witkowski, Metzeltin&Lange-Bertalot	**PLJMA**	**0.01**	*Achnanthes jan-marcinii* Witkowski, Metzeltin & Lange-Bertalot
Planothidium lanceolatum (Brébisson) Round & Bukhtiyarova	**PLLAN**	**0.26**	*Achnanthes lanceolata* Brébisson
Pleurosigma cf. *elongatum* W.Smith	**cPLELO**	**0.01**	
Pleurosigma salinarum Grunow	**PLSAL**	**0.01**	
Rhoicosphenia abbreviata (Agardh) Lange-Bertalot	**RHABB**	**0.08**	
Rhopalodia acuminata Krammer	**RPACU**	**0.09**	
Rhopalodia constricta (W. Smith) Krammer	**RPCON**	**0.24**	
Sellaphora pupula (Kützing) Mereschkowsky	**SEPUP**	**0.01**	*Navicula pupula* Kützing
Staurophora amphioxys (Gregory) D.G.Mann	**STAMP**	**0.08**	*Stauroneis amphioxys* Gregory
Surirella cf. *brebissonii* Krammer & Lange-Bertalot	**cSUBRE**	**0.02**	
Tabularia fasciculata (Agardh) Williams & Round	**TAFAS**	**2.61**	*Synedra fasciculata* (Agardh) Kützing
Thalassiosira pseudonana Hasle & Heimdal	**THPSE**	**1.25**	*Cyclotella nana* Hustedt
Thalassiosira wiessflogii (Grunow) Fryxell&Hasle	**THWEIS**	**0.13**	

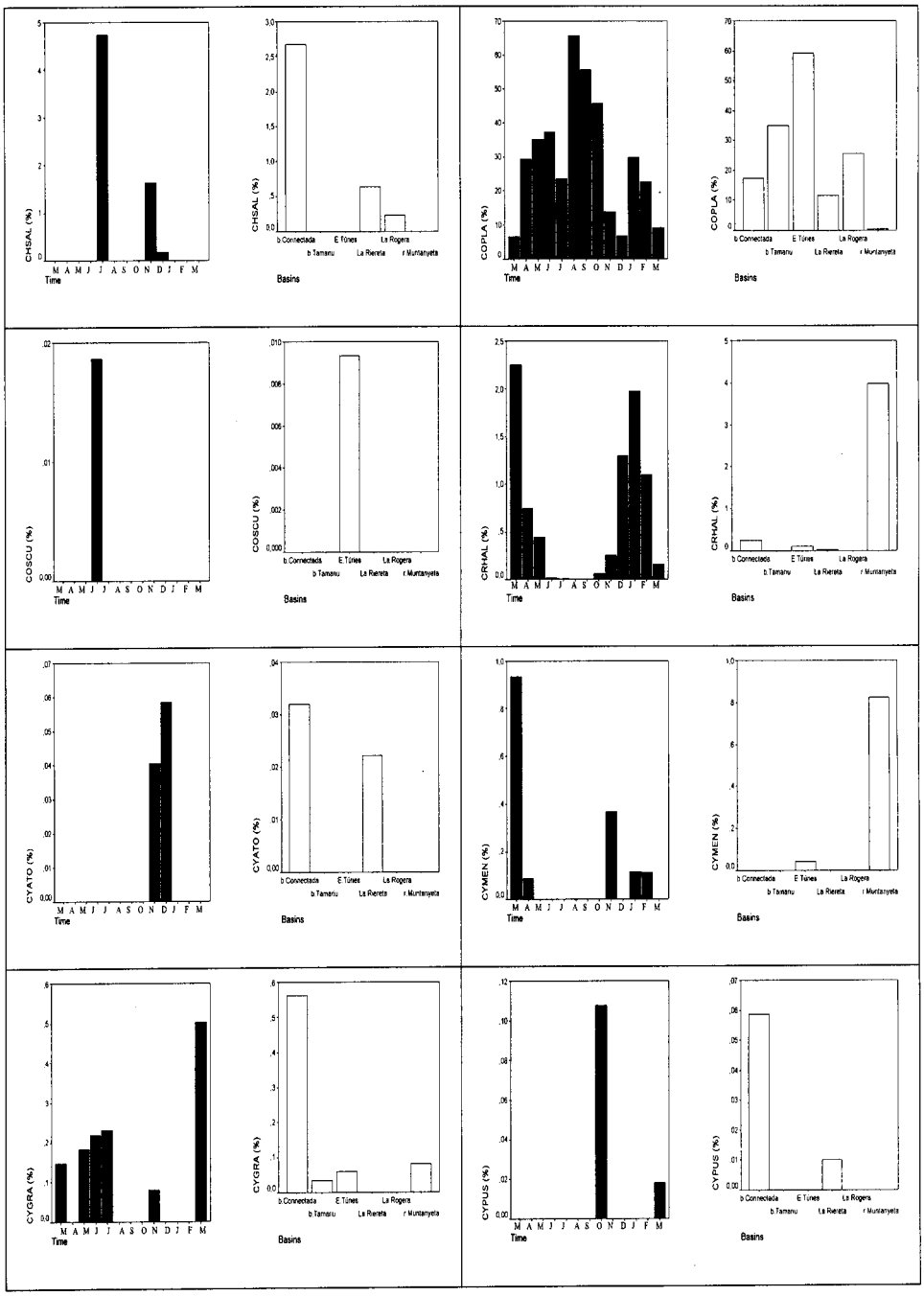
Appendix II

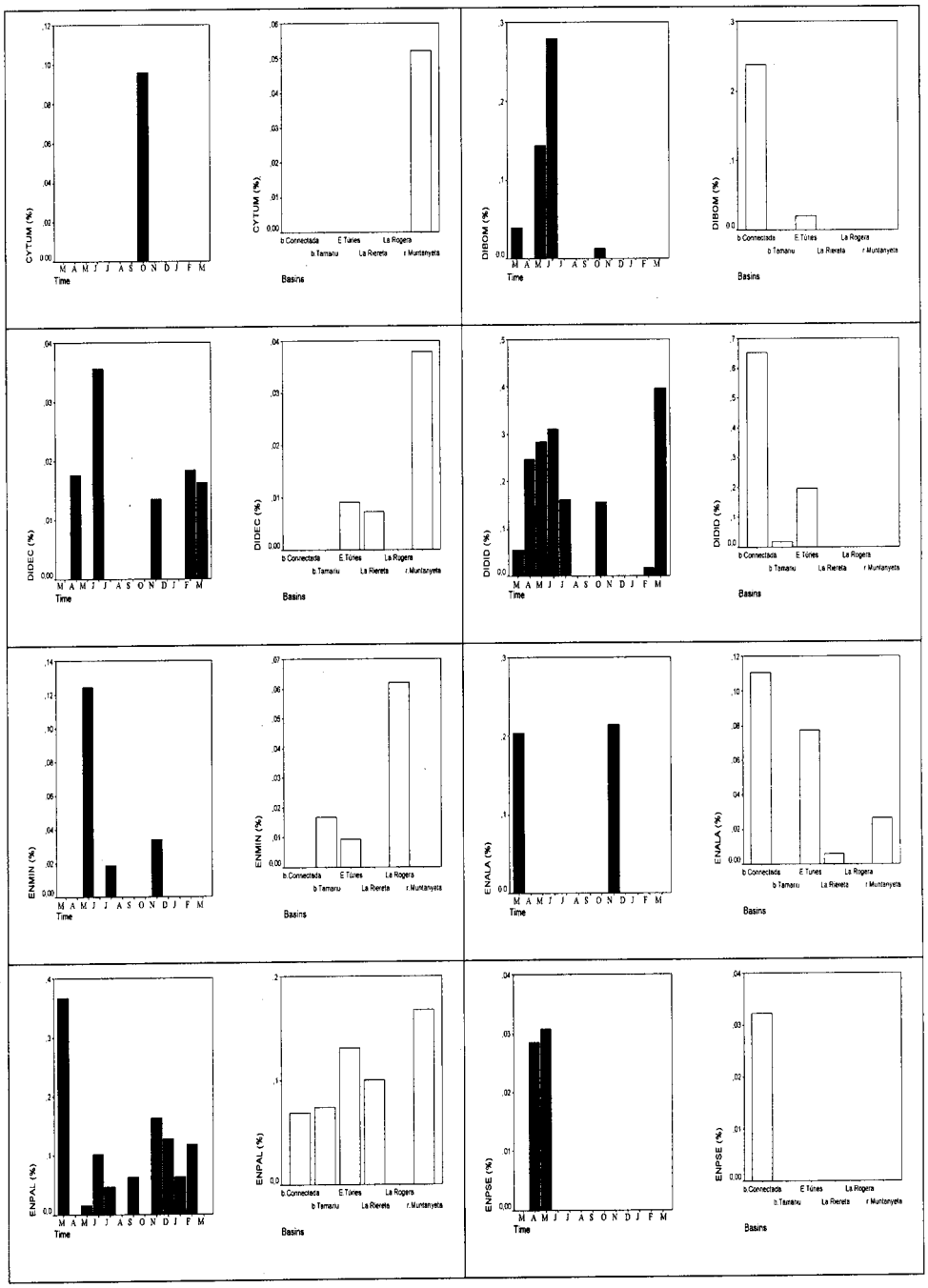
Average relative abundance of the 165 diatom taxa by month (black columns) and by waterbody (white column)

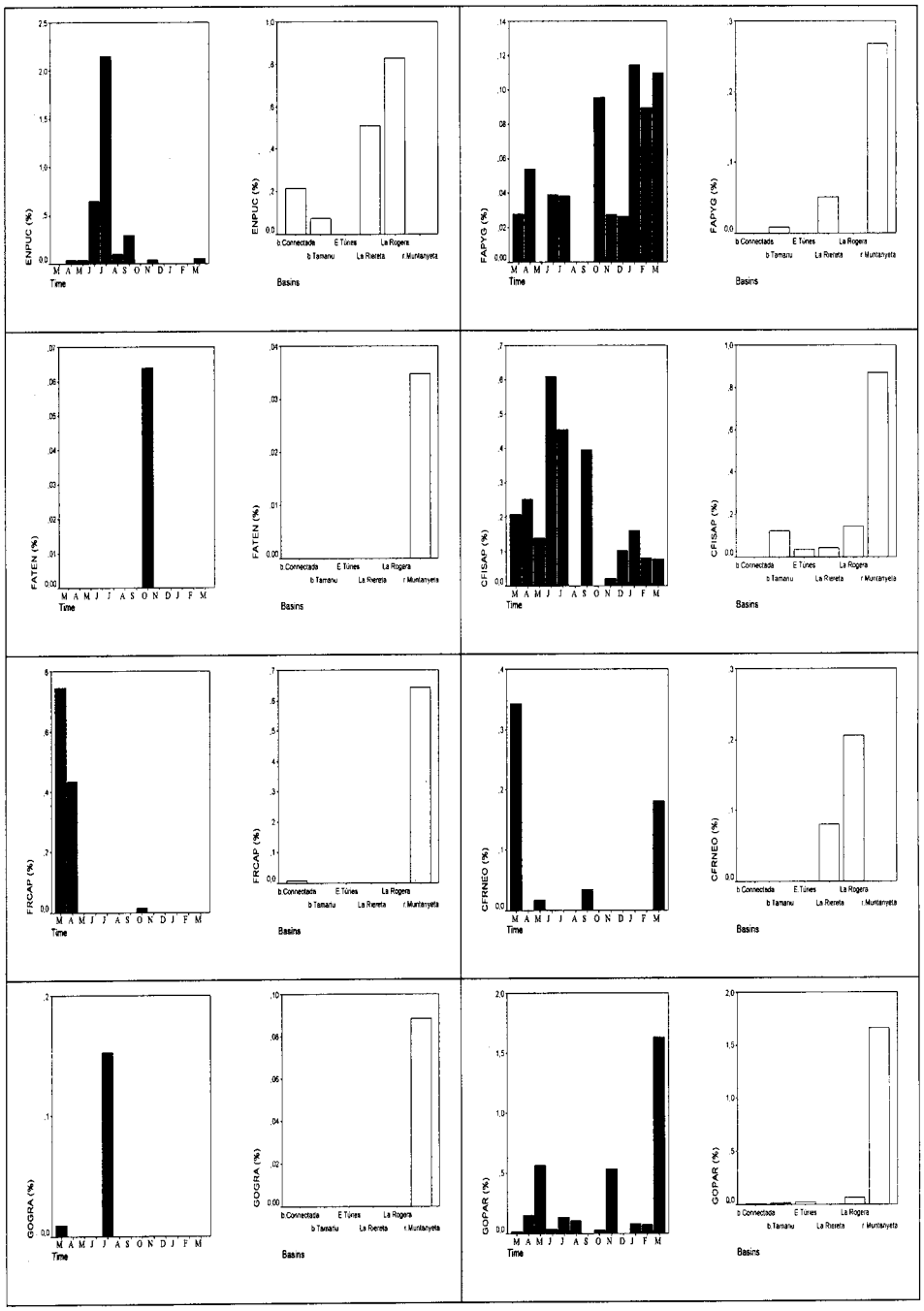

ACBRE (%)
Time
M A M J J A S O N D J F M
ACBRE (%)
b.Connectada
E.Túnes
La Rogera
b.Tamariu
La Rierota
r.Muntanyeta
Basins
ACEXI (%)
ACEXI (%)
ADMIN (%)
ADMIN (%)
AMACU (%)
AMACU (%)
AMLIB (%)
AMLIB (%)
AMCOF (%)
AMCOF (%)
AMHOL (%)
AMHOL (%)
AMHYB (%)
AMHYB (%)

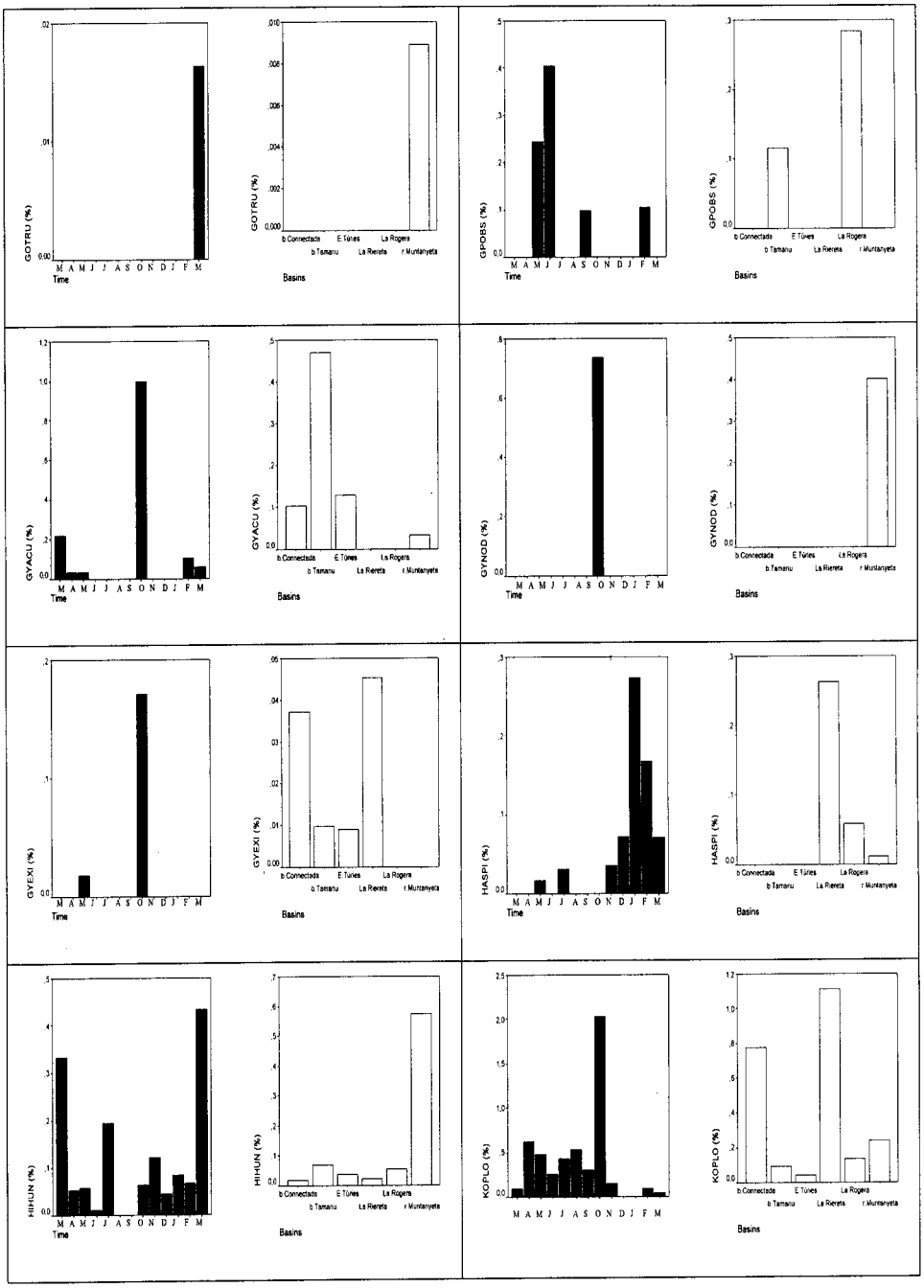

AMMAR (%)
Time
M A M J J A S O N D J F M
AMMAR (%)
b.Connectada
E.Túnes
La Rogera
b.Tamariu
La Rierela
r.Muntanyeta
Basins
AMMIC (%)
Time
AMMIC (%)
Basins
AMPED (%)
Time
AMPED (%)
Basins
AMSTA (%)
Time
AMSTA (%)
Basins
AMSUB (%)
Time
AMSUB (%)
Basins
AMVEN (%)
Time
AMVEN (%)
Basins
AMSP1 (%)
Time
AMSP1 (%)
Basins
CAMLUC (%)
Time
CAMLUC (%)
Basins

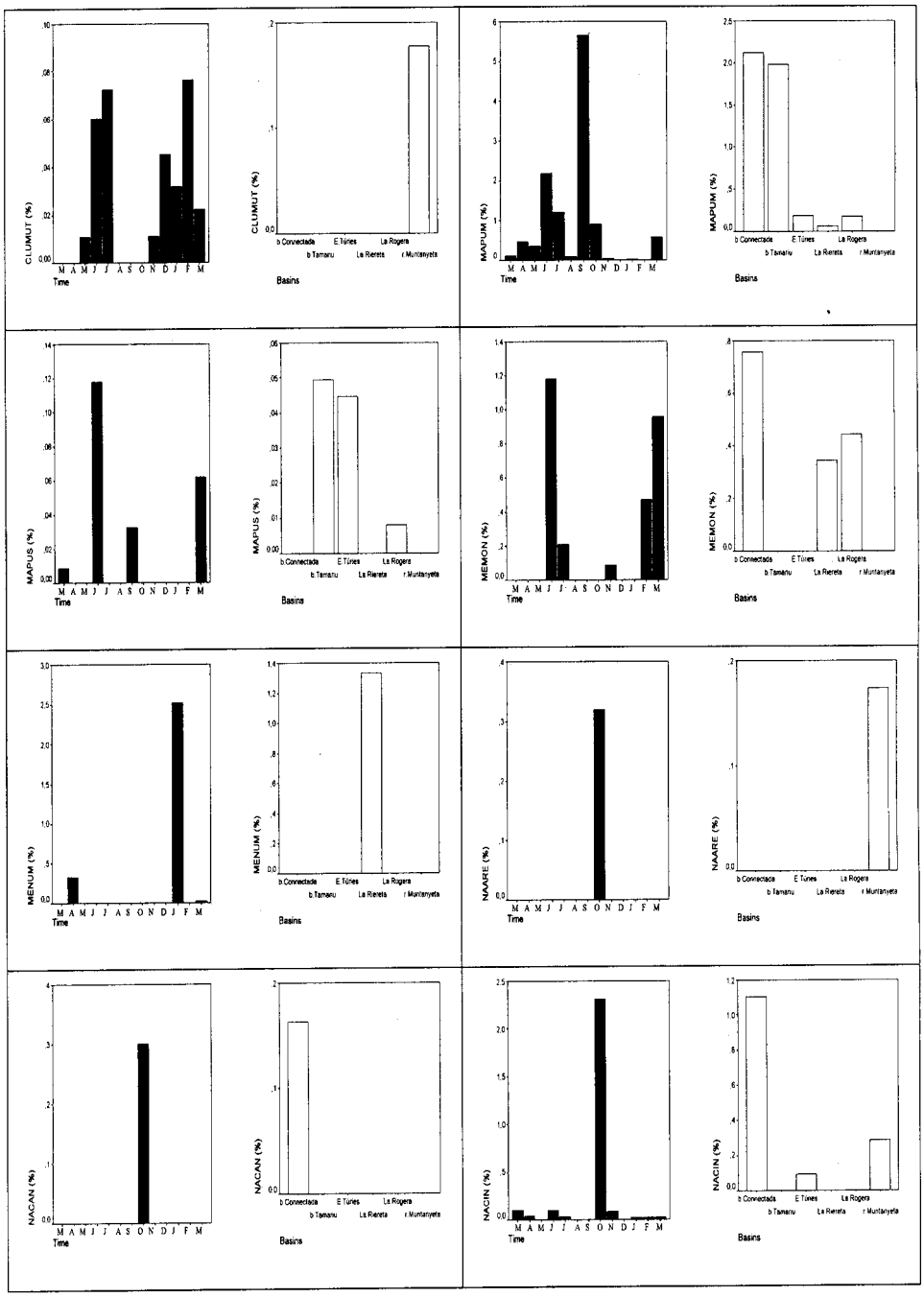

ANSPH (%)
Time
M A M J J A S O N D J F M
Basins
b.Connectada
E.Túnes
La Rogera
b.Tamariu
La Rierata
r.Muntanyeta
ARCRY (%)
BAPAR (%)
ASBAH (%)
BEANT (%)
BEFEN (%)
BERUT (%)
CAAMP (%)

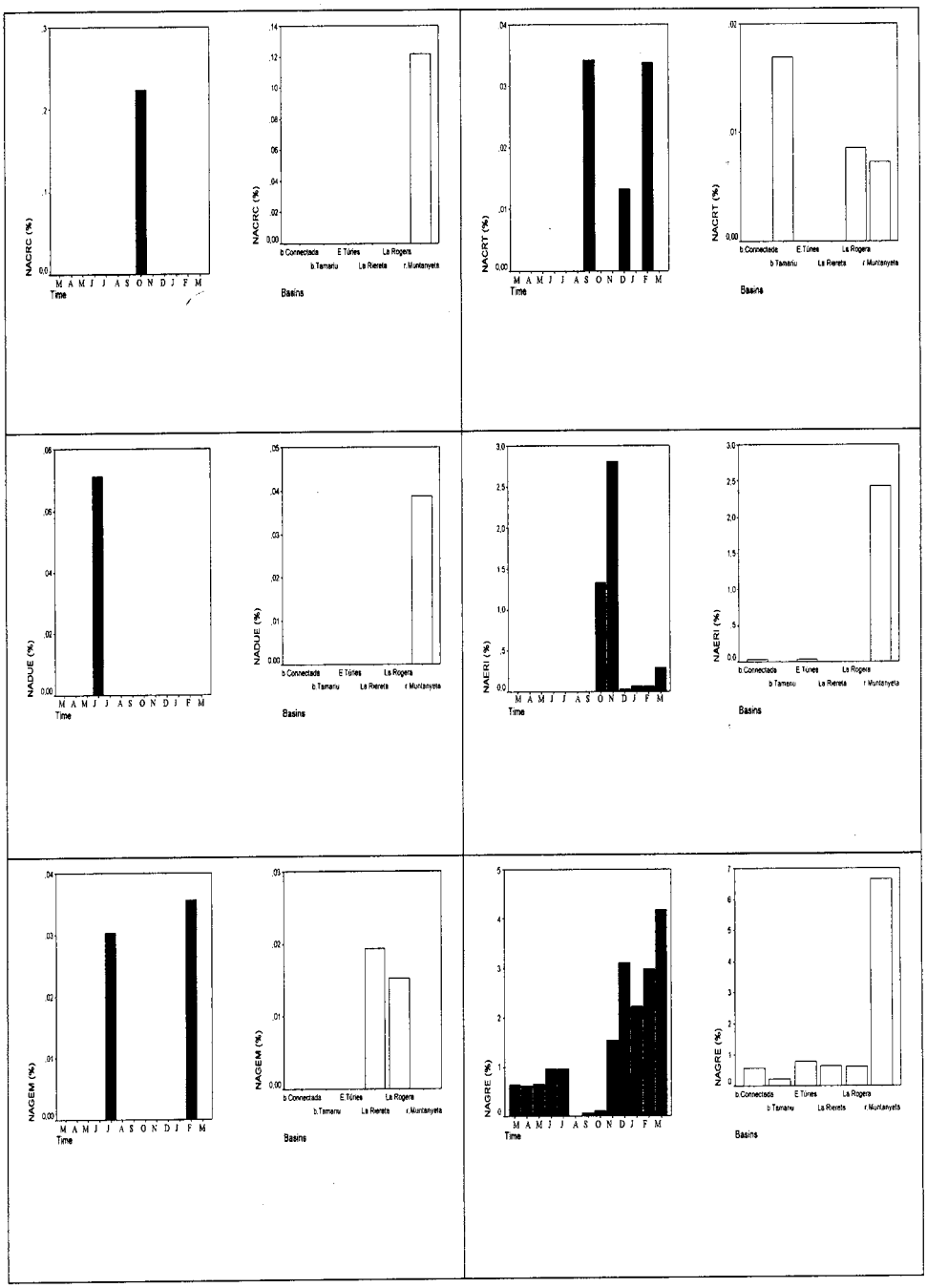

CHSAL (%)
Time
M A M J J A S O N D J F M
Basins
b.Connectada
E.Tûnes
La Rogera
b.Tamaru
La Rereta
r.Muntanyeta
COPLA (%)
COSCU (%)
CRHAL (%)
CYATO (%)
CYMEN (%)
CYGRA (%)
CYPUS (%)

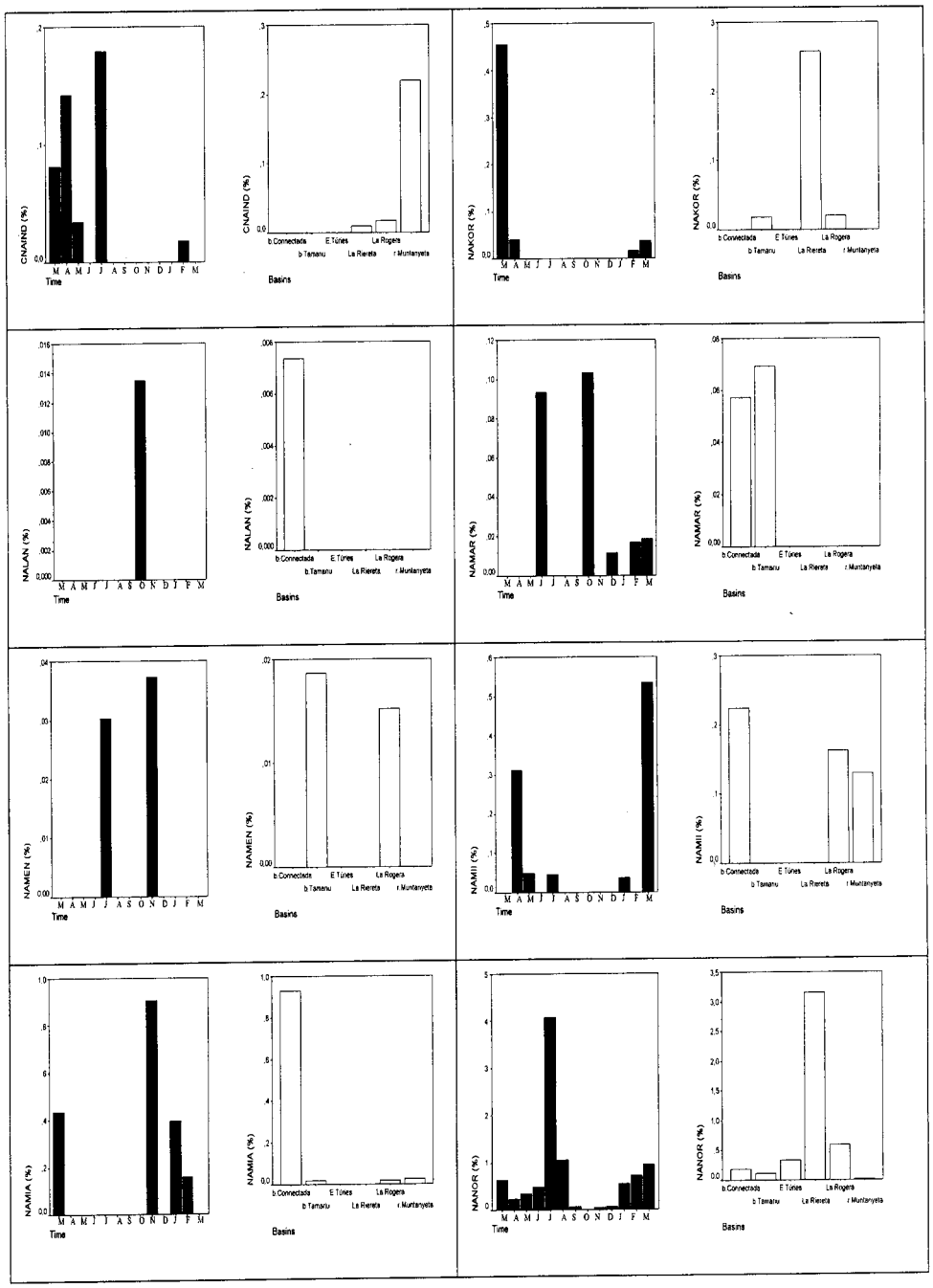

CYTUM (%)
Time
M A M J J A S O N D J F M
CYTUM (%)
b Connectada
E Túnes
La Rogera
b Tamariu
La Rierota
r Muntanyeta
Basins
DIBOM (%)
Time
DIBOM (%)
Basins
DIDEC (%)
Time
DIDEC (%)
Basins
DIDID (%)
Time
DIDID (%)
Basins
ENMIN (%)
Time
ENMIN (%)
Basins
ENALA (%)
Time
ENALA (%)
Basins
ENPAL (%)
Time
ENPAL (%)
Basins
ENPSE (%)
Time
ENPSE (%)
Basins

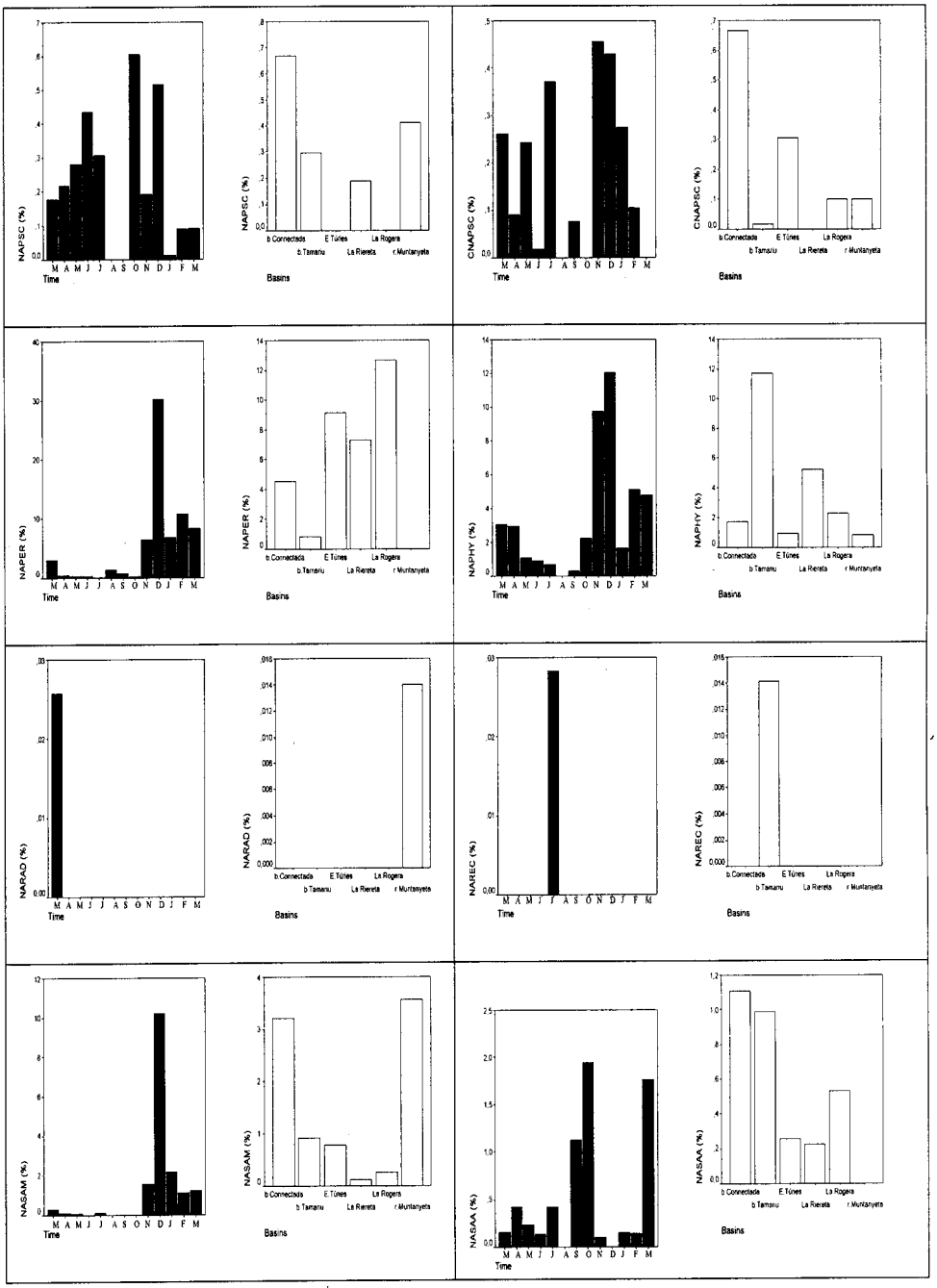

ENPUC (%)
Time
M A M J J A S O N D J F M
ENPUC (%)
b Connectada
E Túnes
La Rogera
b Tamaniu
La Rierata
r Muntanyeta
Basins
FAPYG (%)
Time
FAPYG (%)
Basins
FATEN (%)
Time
FATEN (%)
Basins
CFISAP (%)
Time
CFISAP (%)
Basins
FRCAP (%)
Time
FRCAP (%)
Basins
CFRNEO (%)
Time
CFRNEO (%)
Basins
GOGRA (%)
Time
GOGRA (%)
Basins
GOPAR (%)
Time
GOPAR (%)
Basins

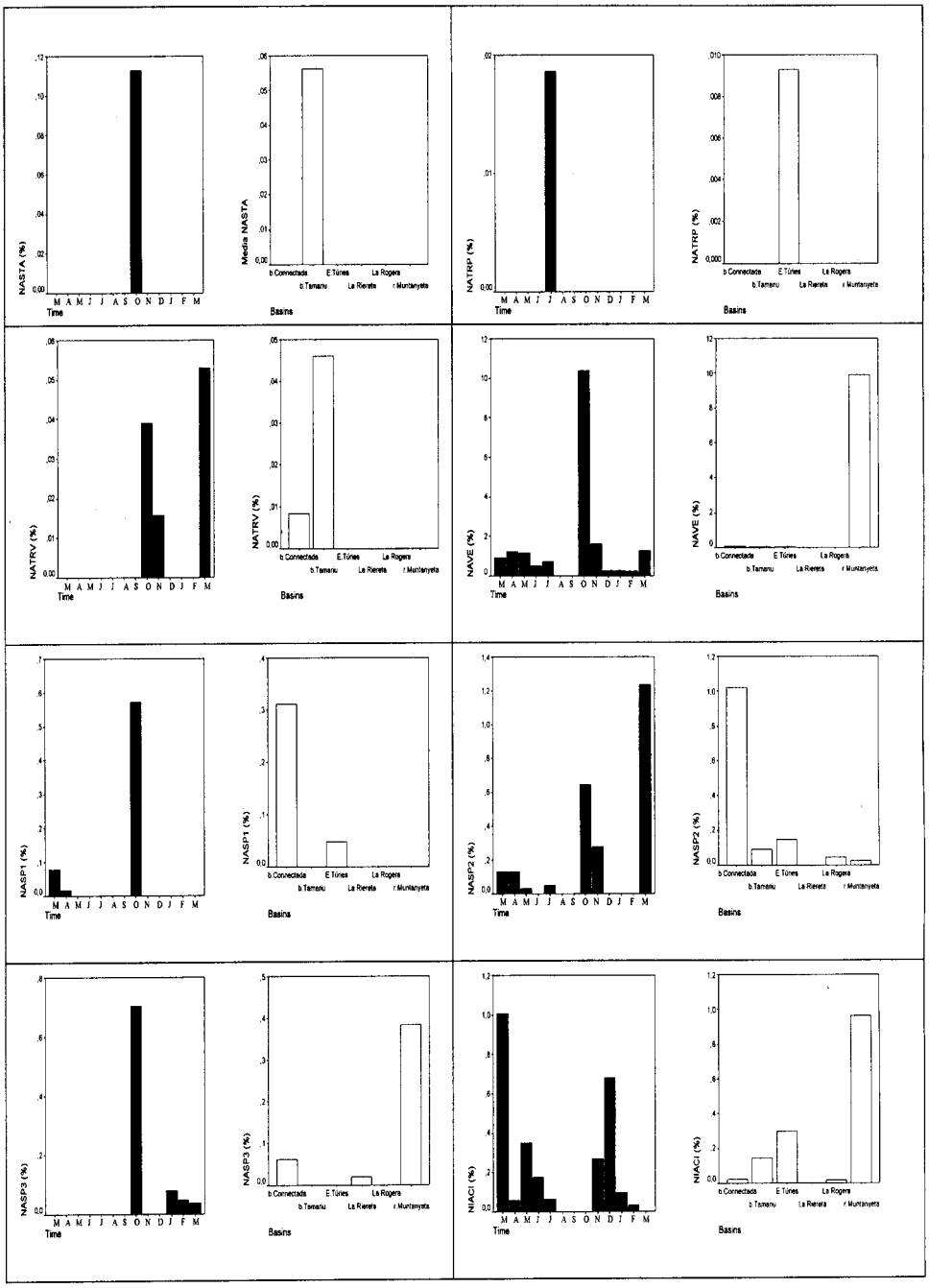

GOTRU (%)
Time
M A M J J A S O N D J F M
GOTRU (%)
Basins
b Connectada
E. Túnies
La Rogera
b Tamanu
La Rierota
r Muntanyeta
GPOBS (%)
Time
GPOBS (%)
Basins
GYACU (%)
Time
GYACU (%)
Basins
GYNOD (%)
Time
GYNOD (%)
Basins
GYEXI (%)
Time
GYEXI (%)
Basins
HASPI (%)
Time
HASPI (%)
Basins
HIHUN (%)
Time
HIHUN (%)
Basins
KOPLO (%)
Time
KOPLO (%)
Basins

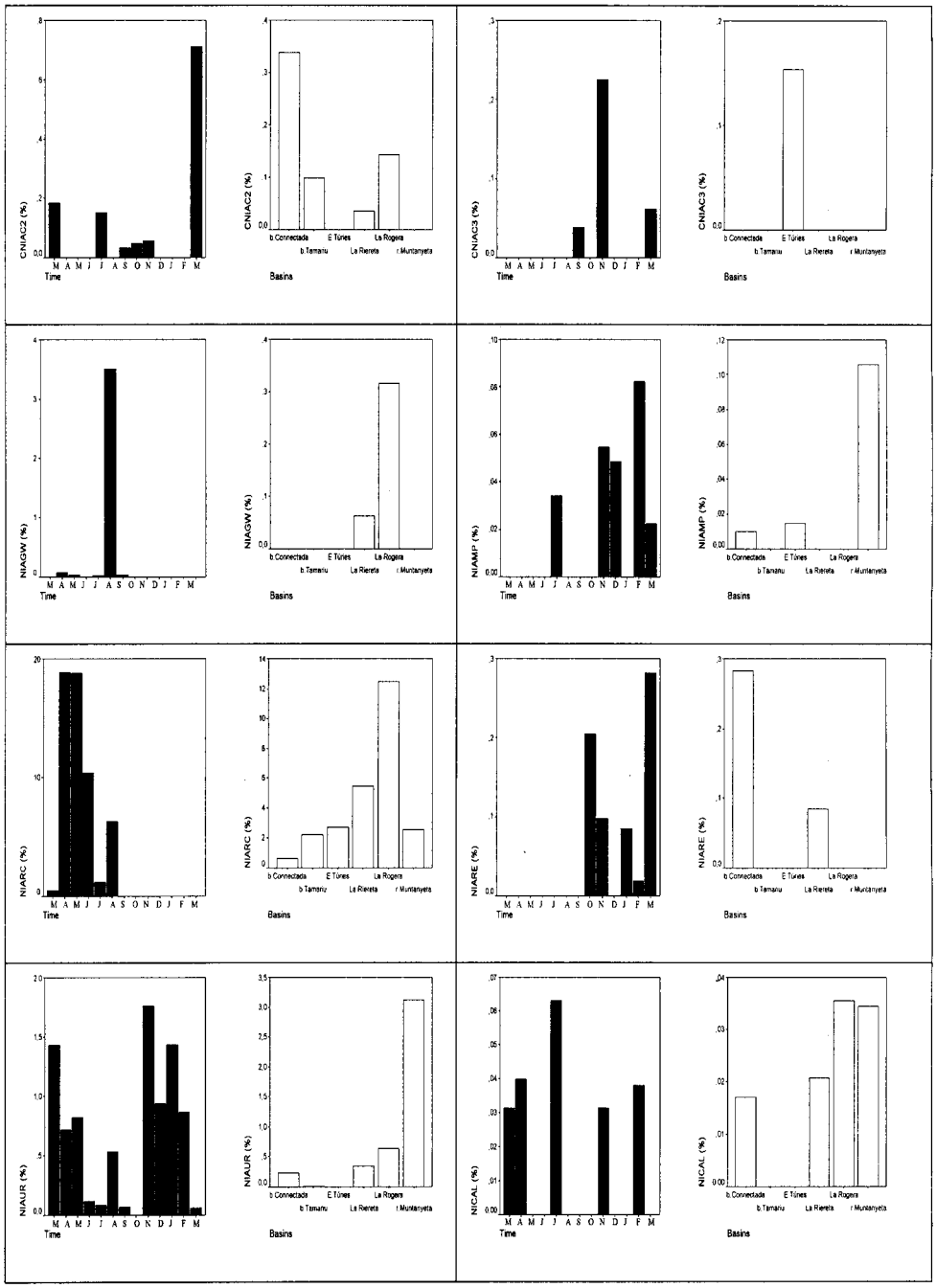

CLUMUT (%)
Time
Basins
MAPUM (%)
MAPUS (%)
MEMON (%)
MENUM (%)
NAARE (%)
NACAN (%)
NACIN (%)
M A M J J A S O N D J F M
b Connectada
E Tunes
La Rogera
b Tamariu
La Rereta
r Muntanyeta

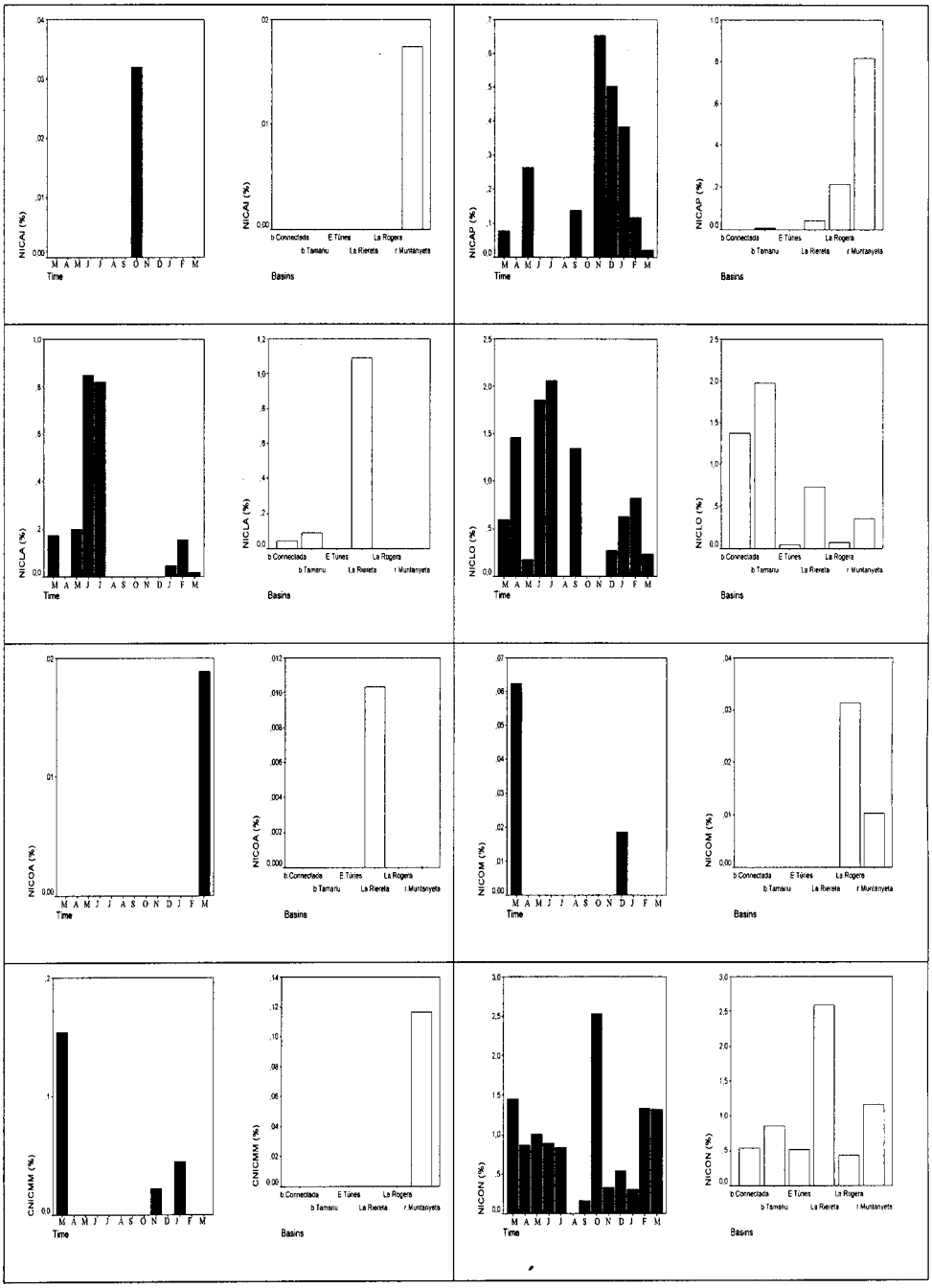

NACRC (%)
Time
M A M J J A S O N D J F M
NACRC (%)
b.Connectada
E.Túnes
La Rogera
b.Tamariu
La Reneta
r.Muntanyeta
Basins
NACRT (%)
Time
NACRT (%)
Basins
NADUE (%)
Time
NADUE (%)
Basins
NAERI (%)
Time
NAERI (%)
Basins
NAGEM (%)
Time
NAGEM (%)
Basins
NAGRE (%)
Time
NAGRE (%)
Basins

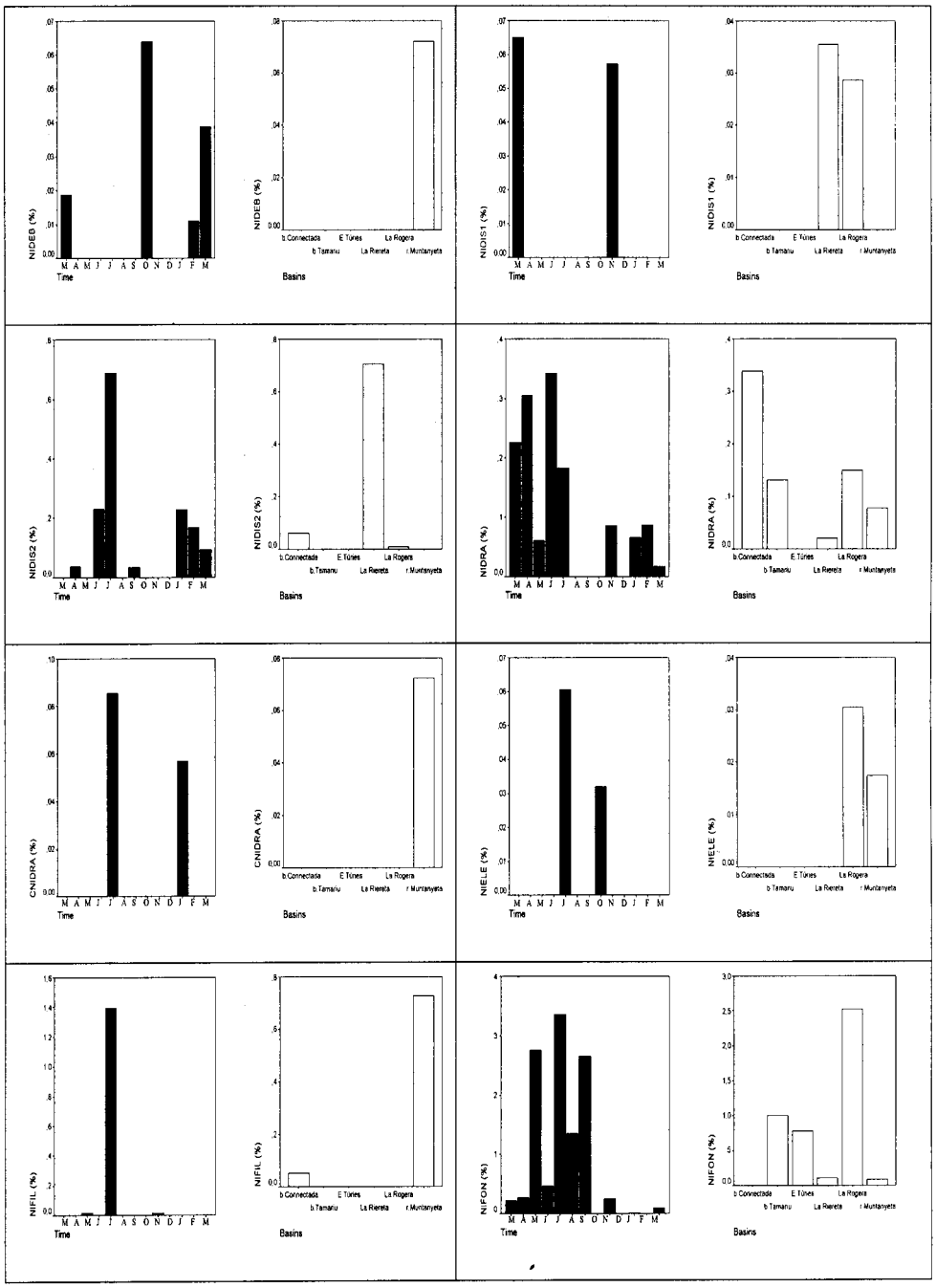

CNAIND (%)
Time
M A M J J A S O N D J F M
Basins
b.Connectada E.Túnes La Rogera
b.Tamaru La Rierata r.Muntanyeta
NAKOR (%)
NALAN (%)
NAMAR (%)
NAMEN (%)
NAMII (%)
NAMIA (%)
NANOR (%)

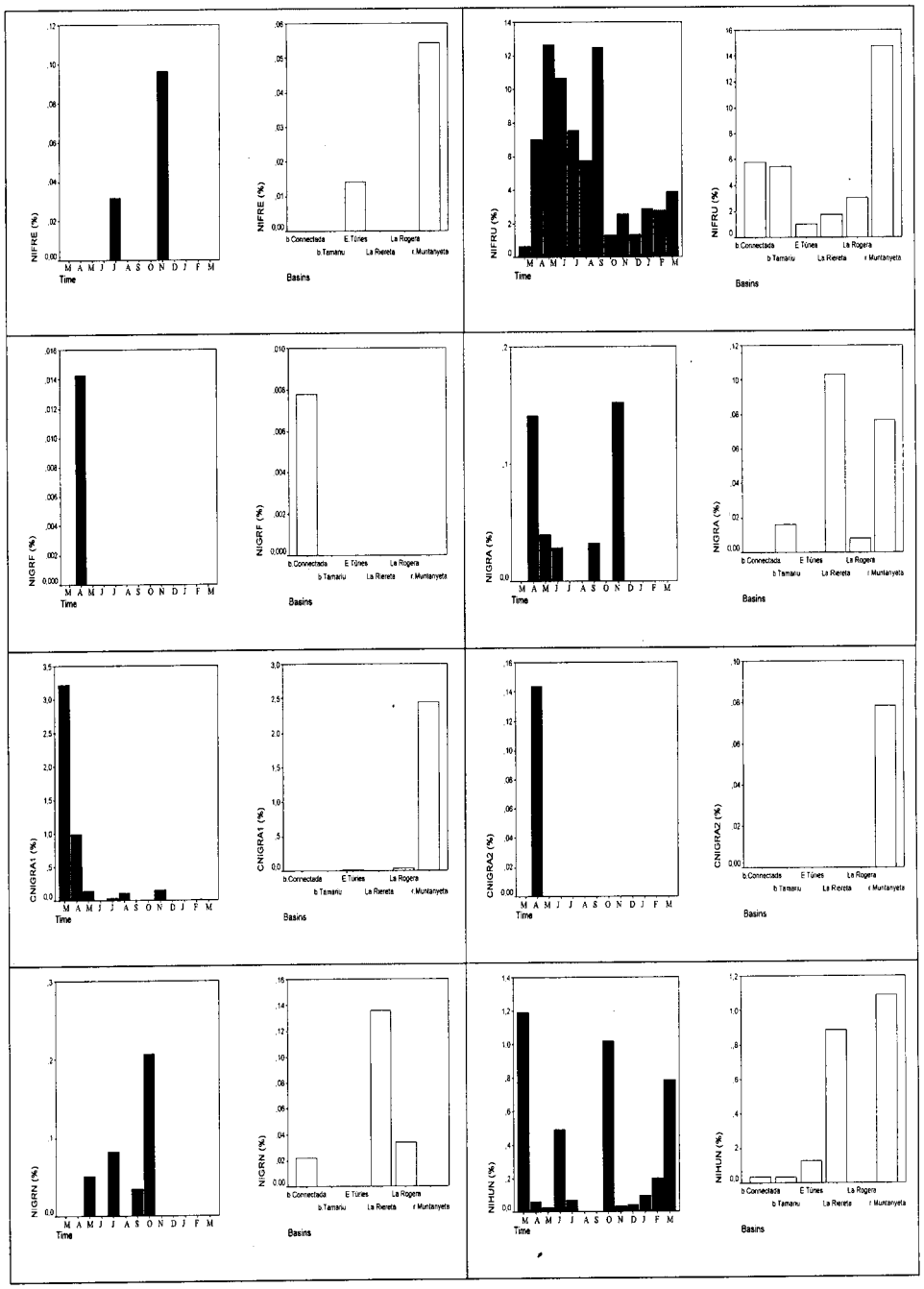

NAPSC (%)
Time
M A M J J A S O N D J F M
NAPSC (%)
b.Connectada
E.Túnes
La Rogera
b.Tamaru
La Rereta
r.Muntanyeta
Basins
CNAPSC (%)
Time
CNAPSC (%)
Basins
NAPER (%)
Time
NAPER (%)
Basins
NAPHY (%)
Time
NAPHY (%)
Basins
NARAD (%)
Time
NARAD (%)
Basins
NAREC (%)
Time
NAREC (%)
Basins
NASAM (%)
Time
NASAM (%)
Basins
NASAA (%)
Time
NASAA (%)
Basins

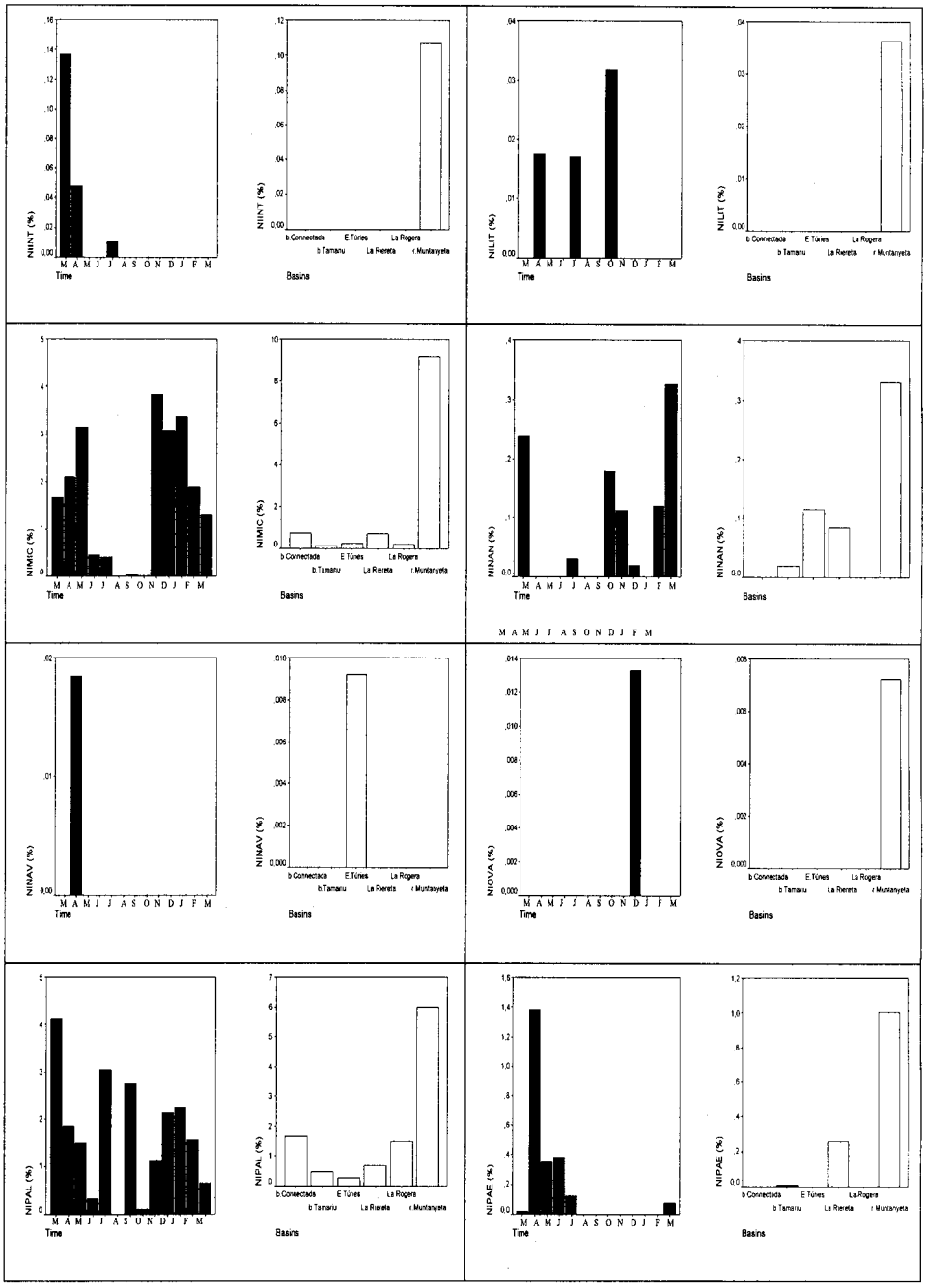

NASTA (%)
Time
M A M J J A S O N D J F M
Media NASTA
Basins
b.Connectada
E.Túnes
La Rogera
b.Tamariu
La Rierata
r.Muntanyeta
NATRP (%)
NATRV (%)
NAVE (%)
NASP1 (%)
NASP2 (%)
NASP3 (%)
NIACI (%)

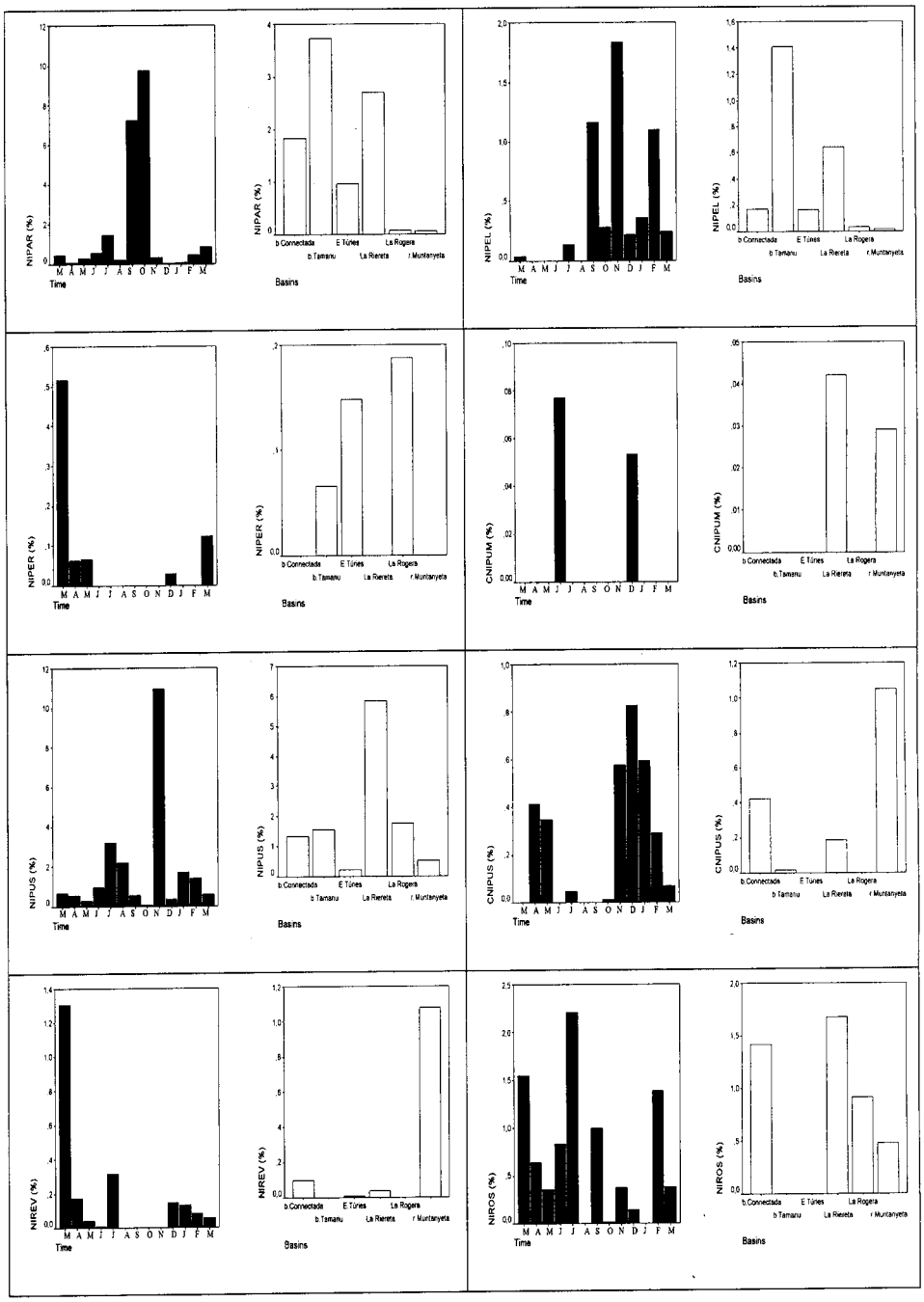

CNIAC2 (%)
Time
M A M J J A S O N D J F M
CNIAC2 (%)
b Connectada
E Túnes
La Rogera
b Tamariu
La Rierota
r Muntanyeta
Basins
CNIAC3 (%)
Time
CNIAC3 (%)
Basins
NIAGW (%)
Time
NIAGW (%)
Basins
NIAMP (%)
Time
NIAMP (%)
Basins
NIARC (%)
Time
NIARC (%)
Basins
NIARE (%)
Time
NIARE (%)
Basins
NIAUR (%)
Time
NIAUR (%)
Basins
NICAL (%)
Time
NICAL (%)
Basins

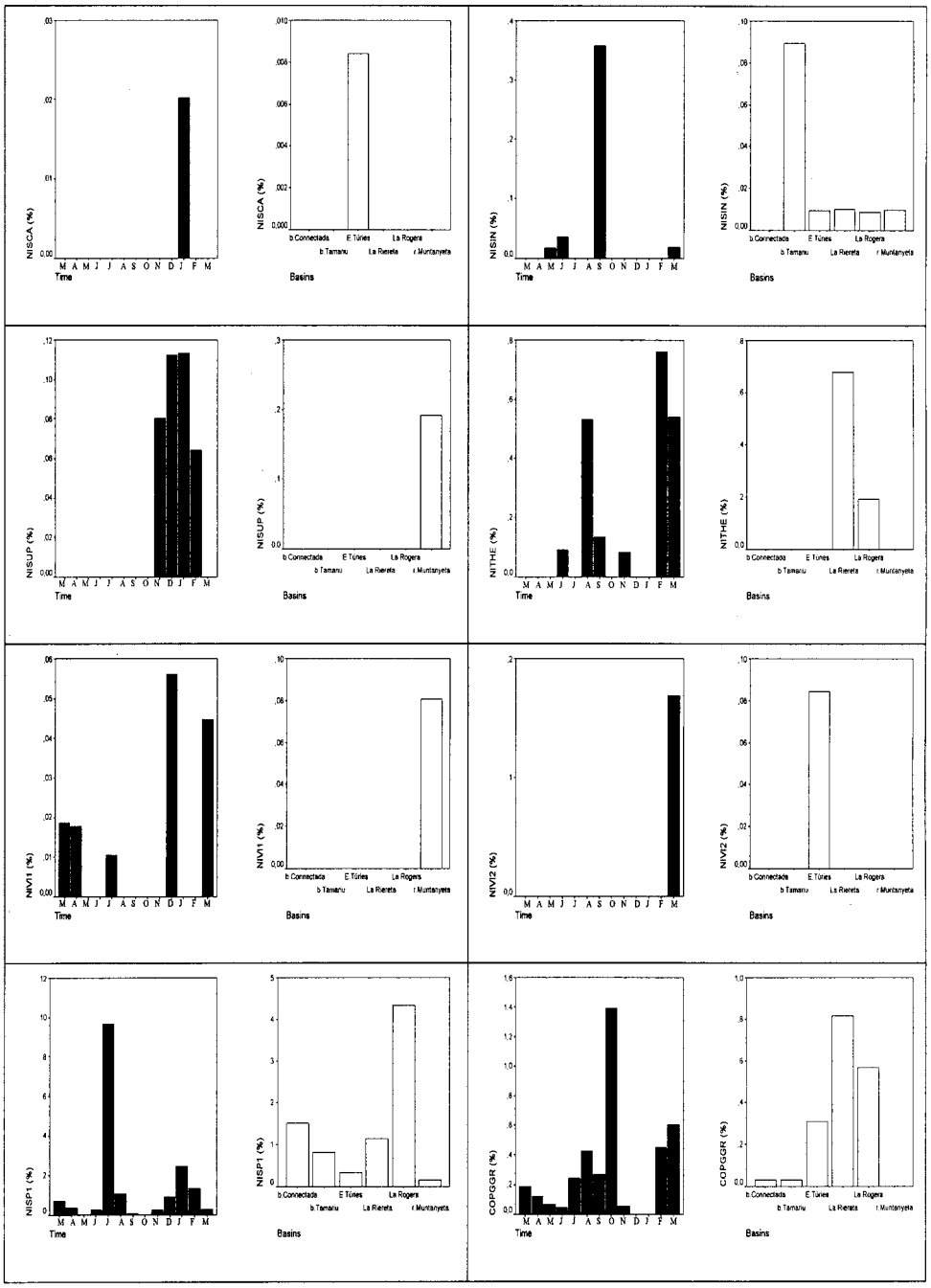

NICAI (%)
Time
M A M J J A S O N D J F M
NICAI (%)
b Connectada
E Túnes
La Rogera
b Tamaru
La Rierela
r Muntanyeta
Basins
NICAP (%)
Time
NICAP (%)
Basins
NICLA (%)
Time
NICLA (%)
Basins
NICLO (%)
Time
NICLO (%)
Basins
NICOA (%)
Time
NICOA (%)
Basins
NICOM (%)
Time
NICOM (%)
Basins
CNICMM (%)
Time
CNICMM (%)
Basins
NICON (%)
Time
NICON (%)
Basins

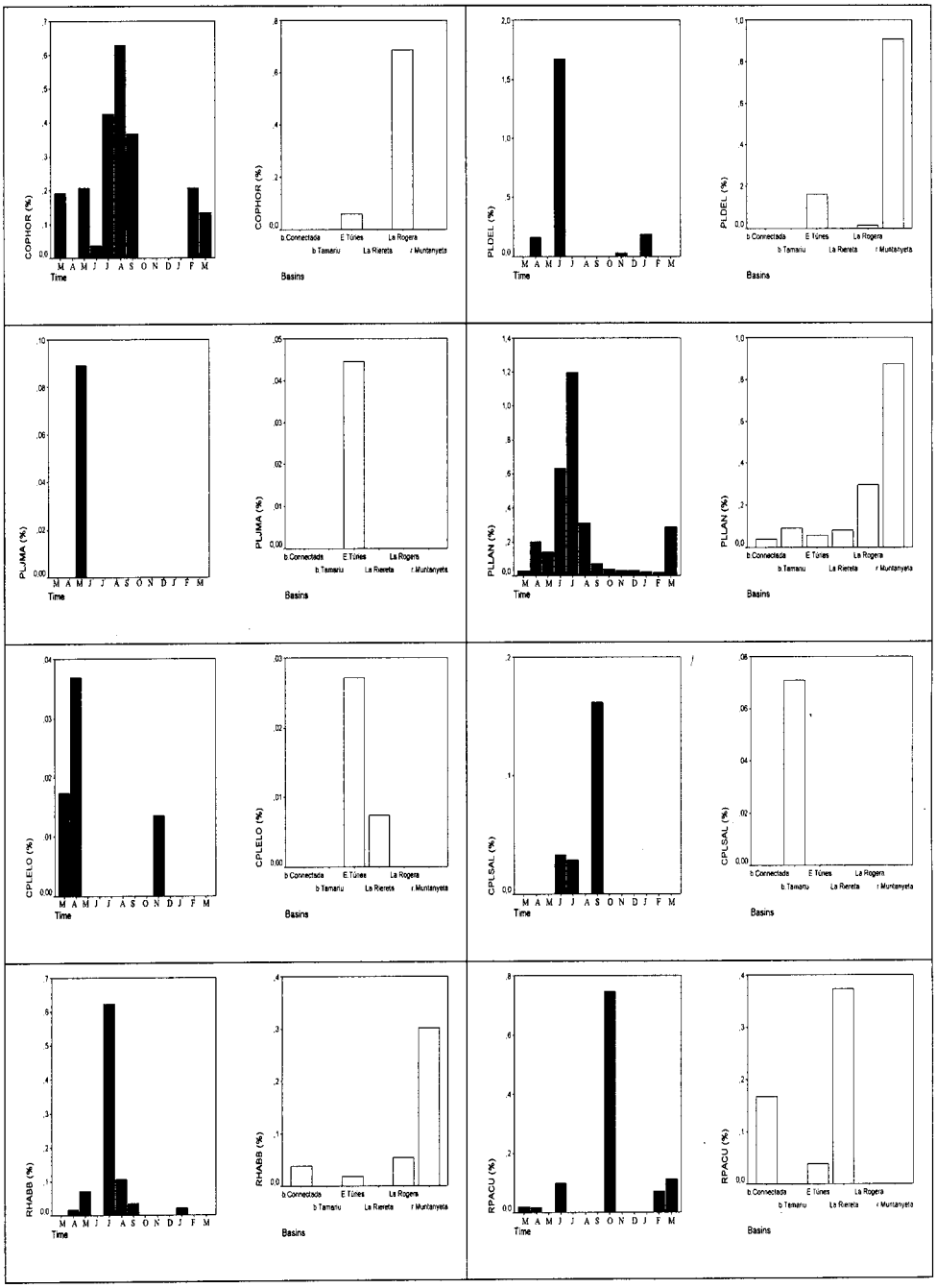

NIDEB (%)
Time
M A M J J A S O N D J F M
NIDEB (%)
b.Connectada E.Túnes La Rogera
b.Tamariu La Riereta r.Muntanyeta
Basins
NIDIS1 (%)
NIDIS2 (%)
NIDRA (%)
CNIDRA (%)
NIELE (%)
NIFIL (%)
NIFON (%)

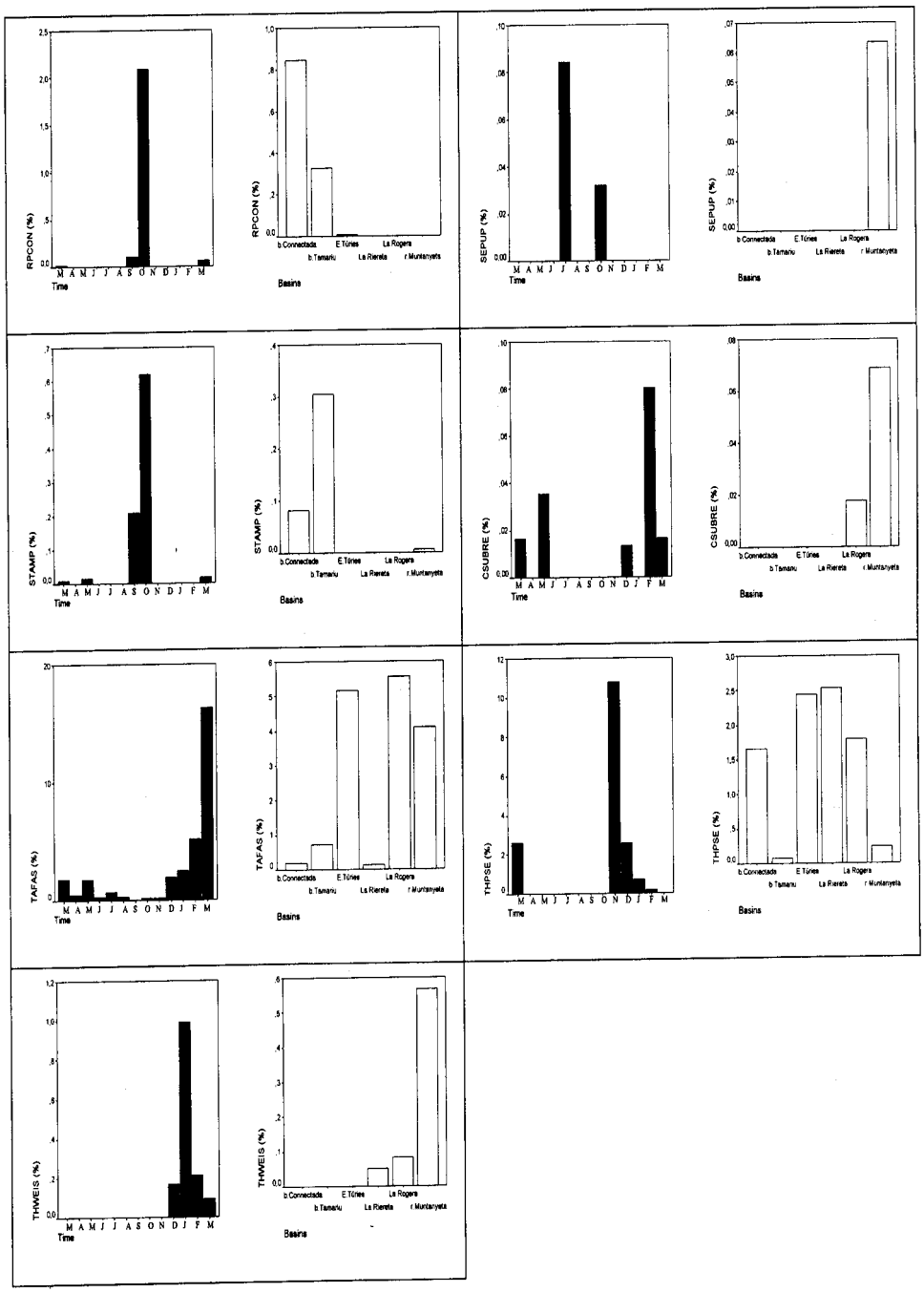

NIFRE (%)
Time
M A M J J A S O N D J F M
NIFRE (%)
Basins
b.Connectada
E.Túnes
La Rogera
b.Tamariu
La Riereta
r.Muntanyeta
NIFRU (%)
Time
NIFRU (%)
Basins
NIGRF (%)
Time
NIGRF (%)
Basins
NIGRA (%)
Time
NIGRA (%)
Basins
CNIGRA1 (%)
Time
CNIGRA1 (%)
Basins
CNIGRA2 (%)
Time
CNIGRA2 (%)
Basins
NIGRN (%)
Time
NIGRN (%)
Basins
NIHUN (%)
Time
NIHUN (%)
Basins


NIINT (%)
Time
M A M J J A S O N D J F M
NIINT (%)
Basins
b Connectada
E Túnes
La Rogera
b Tamariu
La Rierota
r Muntanyeta
NILIT (%)
Time
NILIT (%)
Basins
NIMIC (%)
Time
NIMIC (%)
Basins
NINAN (%)
Time
NINAN (%)
Basins
NINAV (%)
Time
NINAV (%)
Basins
NIOVA (%)
Time
NIOVA (%)
Basins
NIPAL (%)
Time
NIPAL (%)
Basins
NIPAE (%)
Time
NIPAE (%)
Basins


NIPAR (%)
Time
M A M J J A S O N D J F M
NIPAR (%)
Basins
b.Connectada
E.Túnes
La Rogera
b.Tamanu
La Rierata
r.Muntanyeta
NIPEL (%)
Time
NIPEL (%)
Basins
NIPER (%)
Time
NIPER (%)
Basins
CNIPUM (%)
Time
CNIPUM (%)
Basins
NIPUS (%)
Time
NIPUS (%)
Basins
CNIPUS (%)
Time
CNIPUS (%)
Basins
NIREV (%)
Time
NIREV (%)
Basins
NIROS (%)
Time
NIROS (%)
Basins


NISCA (%)
Time
M A M J J A S O N D J F M
NISCA (%)
Basins
b.Connectada
E.Túnes
La Rogera
b.Tamariu
La Rierata
r.Muntanyeta
NISIN (%)
Time
NISIN (%)
Basins
NISUP (%)
Time
NISUP (%)
Basins
NITHE (%)
Time
NITHE (%)
Basins
NIVI1 (%)
Time
NIVI1 (%)
Basins
NIVI2 (%)
Time
NIVI2 (%)
Basins
NISP1 (%)
Time
NISP1 (%)
Basins
COPGGR (%)
Time
COPGGR (%)
Basins


COPHOR (%)
Time
M A M J J A S O N D J F M
COPHOR (%)
Basins
b.Connectada
E.Túnes
La Rogera
b.Tamariu
La Rierota
r.Muntanyeta
PLOEL (%)
PLOEL (%)
PLJMA (%)
PLJMA (%)
PLLAN (%)
PLLAN (%)
CPLELO (%)
CPLELO (%)
CPLSAL (%)
CPLSAL (%)
RHABB (%)
RHABB (%)
RPACU (%)
RPACU (%)


RPCON (%)
Time
M A M J J A S O N D J F M
RPCON (%)
b.Connectada
E.Tònes
La Rogera
b.Tamariu
La Rierota
r.Muntanyeta
Basins
SEPUP (%)
Time
SEPUP (%)
Basins
STAMP (%)
Time
STAMP (%)
Basins
CSUBRE (%)
Time
CSUBRE (%)
Basins
TAFAS (%)
Time
TAFAS (%)
Basins
THPSE (%)
Time
THPSE (%)
Basins
THWEIS (%)
Time
THWEIS (%)
Basins