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A RESEARCH PROGRAM FOR A TYPOLOGY OF ATOLL LAGOONS: STRATEGY AND FIRST RESULTS

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ABSTRACT

A research program is in progress to relate the morphological characteristics of atolls to the functioning of their lagoons. For that purpose, twelve atolls of contrasting morphology have been selected in the Tuamotu Archipelago, French Polynesia. The chemical and biological characteristics of the water and sediments of each atoll as well as their planktonic, benthic and fish communities were collected during 6 oceanographic cruises. As water parameters differ more between than within lagoons, it is possible to rank the different lagoons using the mean value of each parameter. Their ranking order can be related to the atoll morphology and to the intensity of water exchanges with the open ocean. Macrobenthic and fish communities display a heterogeneous distribution within lagoons according to biotopes, but their structure differs between lagoons when similar biotopes are compared. The results of such a program, relating morphology to functioning, could be applied to many of the other 413 existing atolls in order to provide general framework for a rational management of their lagoons.

INTRODUCTION

There are more than 400 atolls in the world (Bryan 1953; Kinsey and Hopley 1991) displaying a high morphological diversity. Their sizes range from more than 1000 km² to less than one km², with emerged land surfaces high or low. Such a diversity means that extrapolation of existing scientific knowledges on a few atoll lagoons to most of the others is uncertain. There is a need to distinguish different types of atolls, and to relate them to differences in lagoon functioning. This is the approach that is proposed for the research program "Typatoll", with the objective of answering the question: "How does the type of an atoll influence the structure and functioning of its lagoon ?". This program, involving 23 scientists, started in November 1994. In the present paper, we describe the methods, sites and sampling procedures used and justify them *a posteriori* with the first results obtained.

METHODS AND SITES

The comparative method

The comparative method used implies that understanding arises from comparison. Three steps are involved when applied to the Typatoll program.

1 - To select a small number of atolls representative of different morphological types and to characterize them by a few factors that are external to the lagoons (forcing variables).

2 - To measure the internal parameters characteristic of the functioning of the lagoon for each atoll type.

3 - To relate internal parameters to external factors to obtain a functional typology (*i.e.* a classification of the atolls according to differences in their functioning, and the related causes of these differences).

Selection of the external factors

The number of external factors to be examined is restricted by logistical constraints related to the number of atolls that it is possible to study. To compare lagoons characterized by n causal factors taking only 2 values each, 2^n lagoons would have to be studied to cover all combinations. For logistical reasons, the number of external classification factors was restricted to 3. At least 8 atolls will therefore need to be sampled.

The degree of water exchanges between lagoons and the surrounding ocean is likely to be one of the main causes of differences in lagoon functioning. The dominant effect of the residence time of water on primary production has been demonstrated in other ecosystems (Smith 1984; Dufour et al. 1994a). In the One Tree Island lagoon, the amount of dissolved nutrients (Hatcher and Frith 1985) and primary production (Kinsey 1985) were related to the residence time of water. Hamner and Wolansky (1988) demonstrated the dominant effect of hydrodynamic factors on biological processes in lagoons. Delesalle and Sournia (1992) showed that phytoplanktonic biomass in lagoons is positively correlated to the residence time of lagoon waters. Thus, we assumed that the influence of the three selected external factors have to be related to the renewal of lagoonal waters by the oceanic waters.

The first external factor selected is the size of the lagoon, which is related to the volume of lagoonal waters.

The second external factor is the permeability of the atoll rim, which quantifies the level of communication between the lagoon and the ocean. Permeability was estimated as the ratio between the length of the openings to the ocean and the length of the atoll rim.

The third external factor is the "symmetry", which refers to the orientation of atoll openings in regard to the direction of the propagation of the main oceanic swells. In Tuamotu where tides rarely exceed 40 cm, swells induce the main inflow of water into the lagoons. The main swells come from the south and south east (unpublished data of the French Polynesian National Meteorology). With the exception of a few highly closed atolls, the Tuamotu atolls all exhibit lagoon - ocean communications to the south and south est. Some atolls have communications only in these directions, whereas others also have communications in other directions. The factor "symmetry" here is defined as the ratio of the length of openings of the west, north and east sectors to the length of openings of the south sector. The oceanic water flows into the lagoon under the effect of swells until the overflow is evacuated through the openings opposite (in atolls with high symmetry). When there are no (or few) openings in the direction opposed to the water entrances (in atolls with low symmetry), the water level of the lagoon rises until it counteracts the oceanic inflow.

The three external factors were calculated from SPOT data recorded in the Polynesian Station of Teledetection (S. Andrefouët, unpublished data). The length of lagoon - ocean communications in each 90° sector of atoll rim were calculated by J. Pagès (1995, unpublished data).

Selection of the atoll types

The Typatoll program is being conducted in the Tuamotu Archipelago, French Polynesia, which comprises 76 atolls, the highest concentration in the world. All the main types of atoll are present in a relatively restricted geographic area, and they are all submitted to the same broad climatic and oceanic environment. Moreover, numerous environmental data were available on two atolls of this region: Tikehau and Takapoto.

To select the atolls for the program, we first excluded the atolls for which no satellite imagery was available or suitable, the largest atolls (over 400 km²) in size, and, for logistical reasons, the atolls located too far from Tahiti. Of the remaining atolls, we selected the ones for which the contrast in the 3 external factors (surface, permeability and symmetry) was greatest. Inside each of the 3 size classes defined, we chose the atoll with the lowest permeability, one atoll with a high permeability but a low symmetry and one atoll with a high permeability and a high symmetry. A few other interesting atolls were added to this selection, giving a total of 14 atoll types selected. (Table 1).

The internal parameters

The internal parameters have to: characterize the structure and functioning of the lagoons well; be as stable as possible to avoid large short-term variations; and be easy to record during a limited survey time. The list of the internal parameters systematically recorded during each survey is given in Table 2.

Sampling surveys

Internal parameters were measured during 2 types of surveys each lasting 21 days.

"Water column" surveys focused upon parameters related to lagoonal waters and sediments. One survey occurred at the end of the dry season, and another at the end of the rainy season. All atoll lagoons were sampled during each survey, with one or two days per lagoon. A preliminary 12 day survey was also carried out in November 1994 to verify that the objectives and sampling strategy of the program were adequate. Chemical and planktonic variables were collected according to Charpy et al. (1990), Charpy and Charpy-Roubaud (1990), Charpy et al (1994), Le Borgne et al. (1989) and Torréton and Dufour (1996) Three "Fish -benthos" surveys involved the sampling of parameters related to fish and macrobenthic (coral, algae, phanerogam, echinoderm and mollusk) communities. All 3 surveys occurred during the dry season to minimize seasonal variations. Three to four atoll lagoons were studied per survey. Abundance and size class structure of the fish populations were estimated by visual censuses performed along 50 meters transects according to the method described in Kulbicki (1988). Species richness, abundance and cover percentages of benthic organisms were recorded at each station in 8 contiguous 5 m² quadrates (adapted from Adjeroud 1996).

Table 1: The 14 atolls of the Typatoll research program. Values (high, medium or low) of their forcing variables (surface, permeability and symmetry). In italics, other characteristics of the choice.

Reka Reka: small size, low permeability
Taiaro small size, low permeability (*scientific reserve since 1972*).
Haraiki, small size, high permeability, low symmetry
Tepoto sud, small size, high permeability, medium symmetry
Tekokota, small size, high permeability, medium symmetry, *tilted atoll*
Takapoto, medium size, low permeability *(well known, not visited but included in data processing)*
Hiti, medium size, high permeability, low symmetry
Hikueru, medium size, high permeability low symmetry *(lagoon with dystrophic crisis)*
Tuanaké, medium size, high permeability, medium symmetry
Nihiru, medium size, high permeability, high symmetry
Kauehi, big size, high permeability, medium symmetry
Marokau, big size, high permeability, high symmetry
Amanu, big size, high permeability, high symmetry
Tikehau, big size, high permeability, medium symmetry *(well known, not visited, data processed)*

Table 2: Main internal parameters recorded during Typatoll surveys

Water column:
- bathymetry
- temperature, salinity, oxygen
- turbidity
- nutrients: NO3+NO2, NH4, PO4, Si
- dissolved organic matter: DON, DOP, DOC
- particulate organic matter: PON, POP, POC
- bacteria: abundance, biomass and production
- nano-picophytoplankton: taxonomy, abundance, biomass and production
- microphytoplankton: taxonomy, abundance, biomass and production
- photosynthetic parameters
- autotrophic and heterotrophic protozoa : abundance
- zooplankon: taxonomy, abundance and biomass
- nutrient control of the seston biomass

Soft bottom
- granulometry, bioclasts
- photosynthetic pigments
- particulate organic matter: PON, POP, POC

Hard coral
- species diversity and spatial cover

Macrobenthos
- species diversity and abundance of echinoderms and molluscs

Algae and phanerogam
- diversity, biomass and spatial cover

Fish
- diversity, biomass, trophic and size structure, demographic strategy

RESULTS

Water column: preliminary questions
During the preliminary survey the sampling procedure focused on the variability within the internal parameters of a lagoon water, in order to answer the following questions:
1 - Are one or two days sufficient to accurately estimate the mean value of each parameter of the water column in relation to spatial variability?
2 - Are the differences of means between atolls high enough not to be masked by small-scale spatial variations within lagoons?
3 - Can the mean properties of the different lagoon types be related to the external factors selected?

Water column: vertical homogeneity
The vertical homogeneity results of the 12 internal parameters within the 9 lagoons sampled during the preliminary survey are summarized in Fig. 1. The mean surface value of each parameter, calculated from all the surface samples in each lagoon was plotted on x-axis, and the mean value of the same parameter calculated from all the deep water samples was plotted on the y-axis. The arrow shows the equality between surface and deep values, where most points were distributed. Such a distribution results from a weak vertical heterogeneity of the lagonal water column.

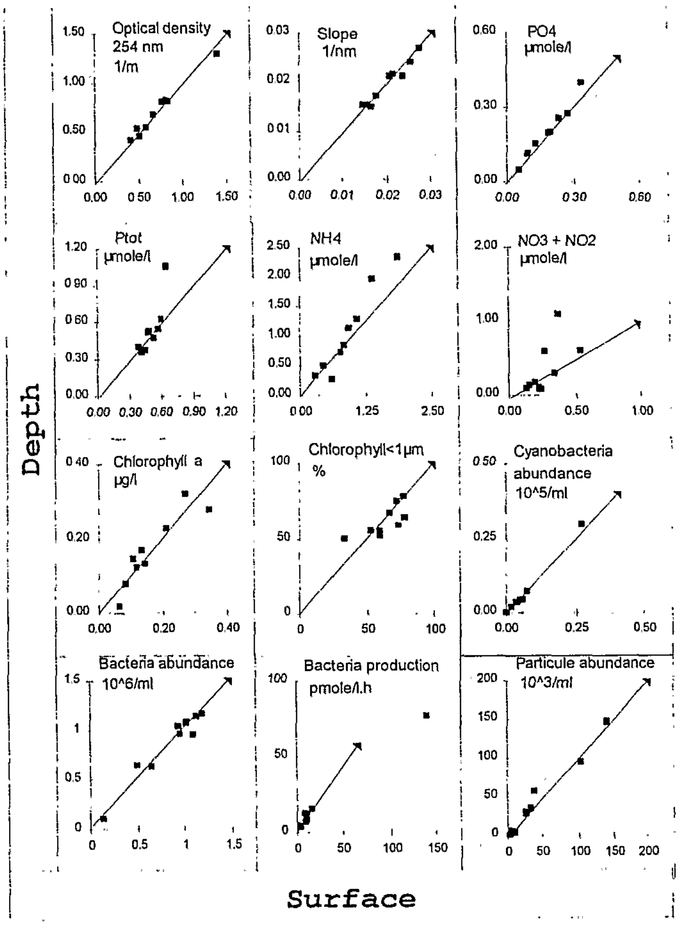

Fig.1: November 1994, internal parameters: relationship between the surface and deep water values. Each point represents the relationship for a lagoon. The arrows show the equality between the surface and deep water values.

Water column: horizontal gradient
During the preliminary survey, water was sampled along a transect from the renewed to the most confined waters, i.e. from the sector with the greatest lagoon - ocean communications to the opposite side. In Fig. 2, the mean values of internal parameters calculated from samples located near the openings are indicated on the y-axis, whereas the mean values of the internal parameters calculated from samples located far from the openings are marked on the x-axis. Each point represents the relationship between contrasting sectors along a confinement gradient. The arrow shows the equality

between the mean values of the two positions. Most of the points are located near the arrow, indicating only weak horizontal heterogeneity of internal parameters within lagoons.

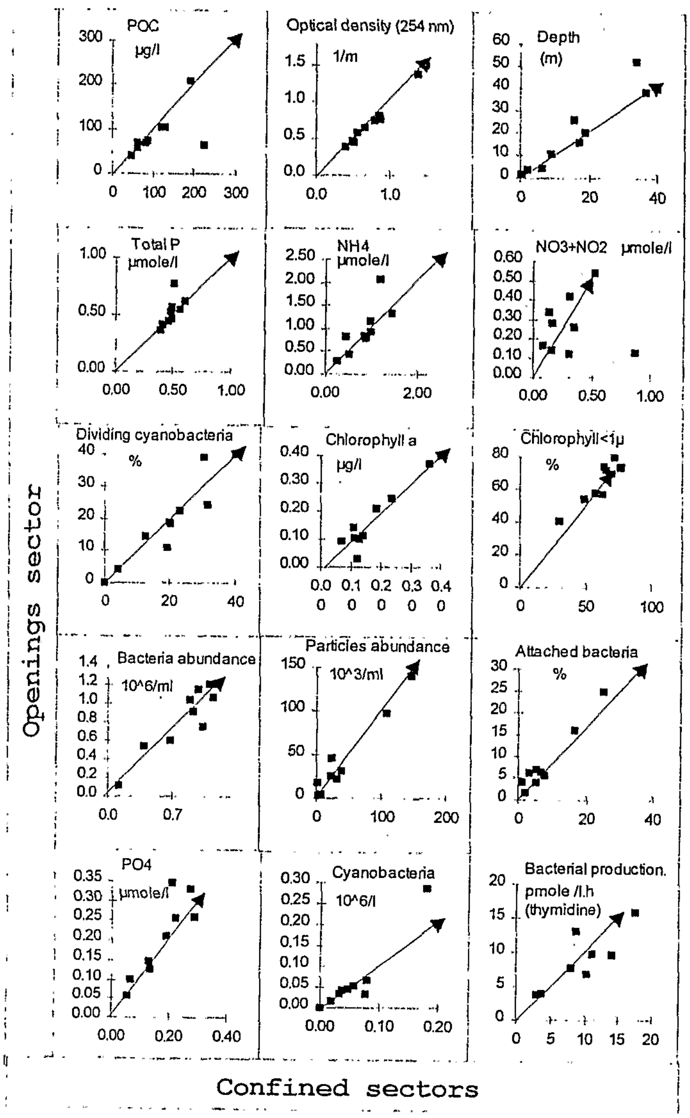

Fig.2: November 1994, internal parameters: relationship between the mean value near the openings and the mean value within the confined sectors. Each point represents the relationship for a lagoon. The arrows show the equality between the openings and confined sectors.

Water column: inter- and intra-lagoonal variations

The mean variation of internal parameters within lagoons was compared to the variation of the means of the same parameters between lagoons. From the preliminary survey, we calculated the coefficients of variation (CV = standard deviation/mean) of all samples within each lagoon. Each CV estimates the within-lagoon variability The mean of the 9 CVs represents the mean within-lagoonal variability. For each parameters we also calculated the CV of the 9 lagoonal means, which is indicative of the between lagoon variability. In Fig. 3, most of the inter-lagoonal CVs plotted on the y-axis exceed the intra-lagoonal CVs plotted on the x-axis. Such a result proves that the inter-lagoon variability is higher than the intra-lagoon variability. We conclude, then, that the sampling design performed allows different lagoons to be compared, as inter - lagoon variability is not masked by variability within individual lagoons.

Water column: relationship between internal parameters and external factors

Are the means of the internal parameters of the different types of lagoons related to the designate external factors which caracterize the atolls?

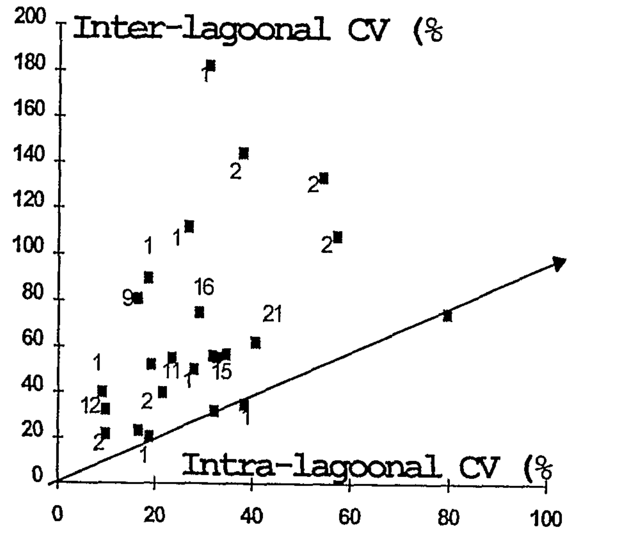

Fig.3: Relationship between intra-lagoonal variability and inter-lagoonal variability for measured water column parameters. The arrow shows the equality of the two variabilities. Numbers represent for 1 and 2: absorbence characteristics of water; 3: particulate organic carbon; 4: PO_4; 5: NH_4; 6: total phosphorus; 7: dissolved organic phosphorus; 8: NO_3; 9: primary production (PP); 10: PP>3µm; 11: PP from 1 to 3µm; 12: PP<1µm; 13: Cyanobacteria abundance; 14: dividing cyanobacteria; 15: total chlorophyll a (Chl); 16: Chl>3µm; 17: Chl from 1 to 3µm; 18: Chl<1µm; 19: Bacteria production; 20: bacteria abundance; 21: dividing bacteria; 22: attached bacteria; 23: particle abundance; 24: bacteria production/cell.

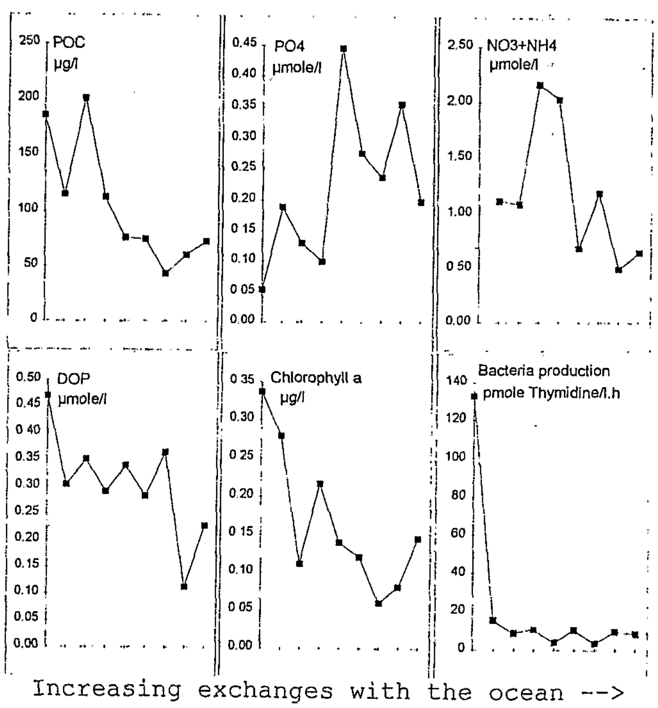

Fig. 4: November 1994: selected internal parameters in relation to different lagoons ordered along x-axis according to the intensity of their exchanges with the ocean. Each point represents the mean of the samples for a lagoon.

Different combinations of the 3 external factors, size, permeability and symmetry were tested to obtain an index of lagoon-ocean exchanges. One of the simplest is the product of permeability x symmetry which results in the following order, from the most to the least confined lagoon visited during the Typatoll surveys: Taiaro, Reka Reka, Hiti, Haraiki, Tepoto Sud, Hikueru, Kauehi, Tuanake, Tekokota, Marokau, Nihiru, Amanu. The results of the preliminary survey indicated that the internal parameters were correlated to the intensity of water exchanges between the ocean and the lagoon when estimated as above (Fig.4). The more the lagoons are confined, the more they are depleted in PO4. The reverse is observed for dissolved mineral nitrogen. The most confined lagoons are characterized by the highest planktonic biomass and bacterial production.

Similar results were obtained during the "water column" survey that followed, indicating differences are persistent. For example, the chlorophyll concentrations in November 1995 also decreased with the increase in the opening level of the lagoon (Fig.5).

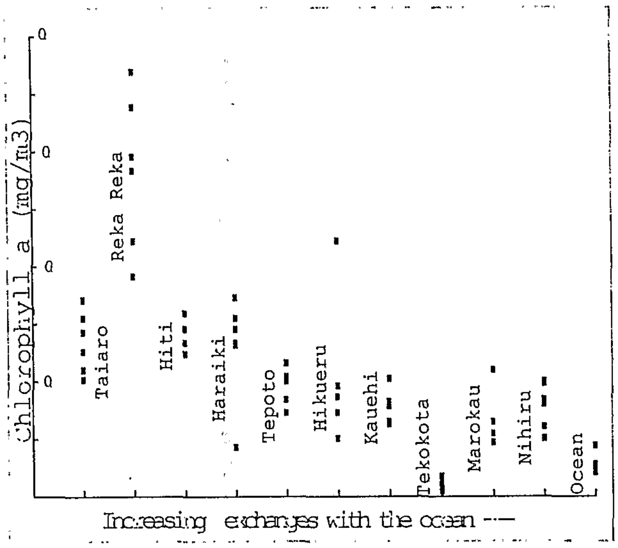

Fig.5: November 1995: Chlorophyll a concentrations within different lagoons ordered according to the intensity of their exchanges with the ocean. Each point represents a sampling site.

Fish-benthos: preliminary questions
One of the aim of the Typatoll program is to obtain a characteristic index value for the fish and macrobenthic communities representative of each lagoon type. However, the high spatial heterogeneity of fish and benthic communities has been demonstrated by many authors (review in Sale 1991). If such a spatial heterogeneity is not taken into account, the values obtained may be highly biased by the sampling design and the calculation of a truly characteristic mean for each lagoon type will not be possible. The first survey devoted to the study of fish and benthic communities was completed for 3 lagoons in September 1995, and from the results an adequate sampling strategy was thus defined.

Fish-benthos: within - lagoon heterogeneity
Three factors influencing the community distribution were distinguished: the morphology of the reef rim, the localization of sites related to prevailing winds, and the depth of the lagoon at each site. Six categories were defined according to reef morphology: vegetated and emerged rim (islands), unvegetated and temporally immersed rim, pass, reef - flat spillways, pinnacles and deep soft bottom. Two levels of localization were distinguished according to wind exposure (windward and leeward) and two main classes of depth: shallow (<10m) and deep (>10m).

Fish-benthos: within - lagoon variability
Three gradients of spatial distribution of fish and benthic communities within a lagoon were differentiated, which all displayed a similar nature, organization and hierarchy in the three atolls studied. Whatever the atoll, the most diversified and numerous communities were associated with pinnacles and passes when the morphological factor is taken into account, with a shallow depth where depth is concerned and with windward zones when exposition to wind is considered. Contrary to what was observed for water column parameters, the spatial distribution of fish and benthos communities within lagoons is highly heterogeneous but organized along three different gradients. Thus, to obtain means representative of each type of lagoon the sampling strategy must take into account the different strata distinguished.

Fish - benthos: between lagoon differences
When the within-lagoon variability of spatial distribution was considered in a similar way for all lagoons, the comparison of means between lagoons could be carried out.

In the three atolls studied, Kauehi, Nihiru and Tepoto Sud, 31 species of hard corals, 22 species of mollusks, 7 species of echinoderms and 262 species of fish were identified. Whatever the morphological zone considered, the total number of species recorded was the highest in Kauehi and the lowest in Tepoto Sud for all the groups considered, except for the echinoderms which were most diverse and numerous in Nihiru (Fig. 6 and 7). The mean number of species and the mean density of reef fishes followed the same gradient: high in Kauehi, medium in Nihiru and low in Tepoto Sud. The mean biomass of fish was also highest in Kauehi, but was similar in Nihiru and Tepoto Sud (Fig. 6). The percentage cover of living corals and the density of mollusks resulted in the same ranking order: Kauehi > Nihiru > Tepoto Sud (Fig. 7). Moreover, the percentage cover of macroalgae and the density of echinoderms were higher in Nihiru than in Kauehi, Tepoto Sud always displaying the poorest communities.

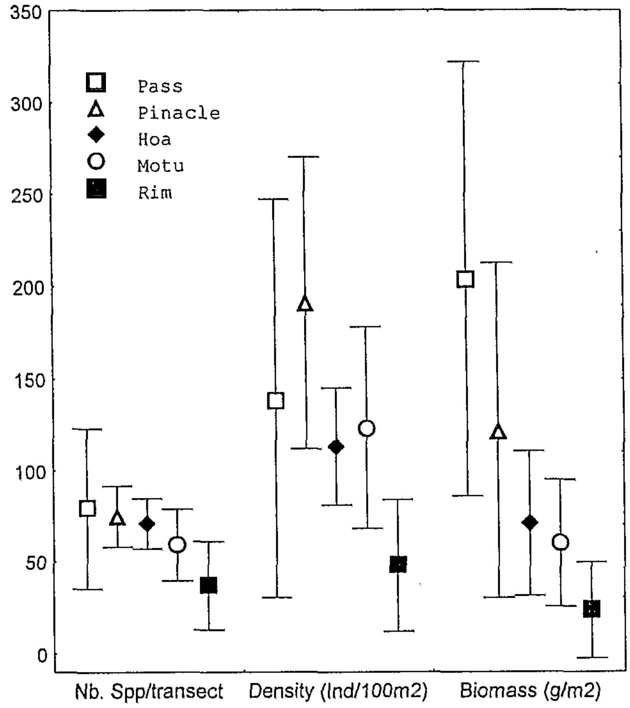

Fig. 6 : Mean number of fish species, of fish density and of fish biomass according to morphological zones for the 3 atolls combined

Thus for most group and community parameters, the between-lagoon differences might be related to the ranking of atolls in size or exchanges with the ocean, as these 2 external factors decrease from Kauehi to Tepoto Sud. The fact that Nihiru is the only one of the three atolls without a pass may suggest that the absence of pass favors macroalgae and echinoderms. These first results demonstrate that the different groups of organisms studied reacted differently to the same external factor which may either favor or hinder the diversity of communities.

The study of other atolls will either confirm or invalidate the results obtained from the first three atolls to better understand the influence of external factors on the structure of the various groups studied.

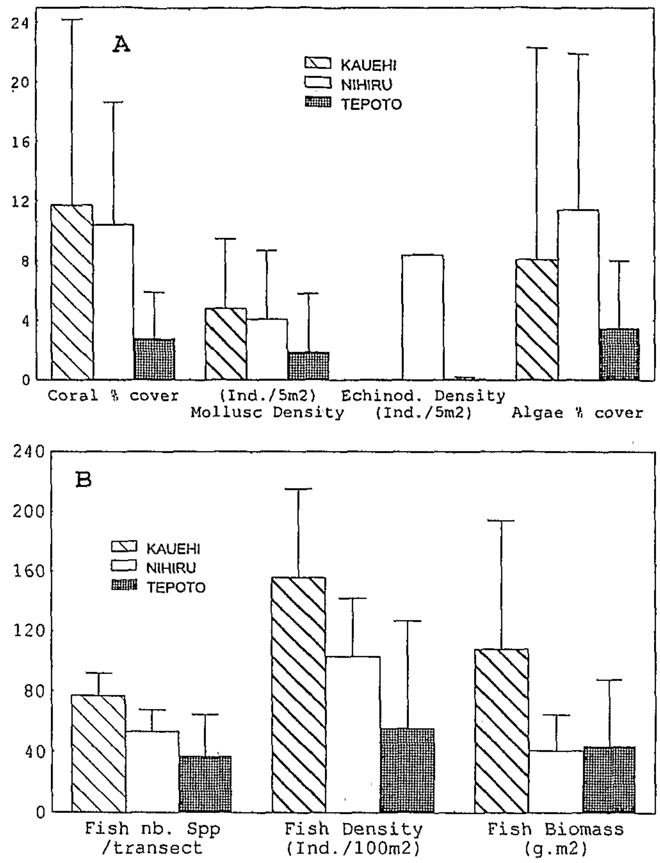

Fig. 7 : Difference in benthic community parameters (A) and in fish community parameters (B) between Kauehi, Nihiru and Tepoto lagoons.

DISCUSSION AND CONCLUSION

1 - The aim of the present paper is to explain the scientific procedures developed in the Typatoll program and to justify the chosen sampling strategy by the analysis of the first results obtained.

2 - There is no evidence that the scheme developed here for classifying lagoonal systems will work outside the Tuamotu. The ability to extent the classification depends upon the availability of suitable data on atolls lagoon in other regions.

3 - The comparative method is easier to use when the ecosystems studied are clearly delimited and isolated from each other. Canadian and Soviet scientists have used this method to study the ecology of lakes (in Le Cren and Lowe-McConel 1980). The approach was well adapted for the study of atolls in Tuamotu which are well limited ecological units, independent from each other and influenced by the same climatic and oceanic environment.

4 - The Typatoll program was aided by the knowledges previously acquired on 2 Tuamotu atolls, Tikehau (for example, Harmelin-Vivien 1985, Intes 1990) and Takapoto (Salvat and Richard 1985; Buestel et al. 1995). These studies allowed the identification of the most effective external factors, the selection of the less variable internal parameters, the determination of the time periods and sampling sites the most representative of average conditions, and the attribution of confidence intervals to limited spatio - temporal data.

5 - The choice of external factors was directed by the previous results found in the literature, and by the necessity to limit their number. Some important factors like vegetated surfaces or human activities were not considered.

6 - The index of lagoon - ocean exchange used to rank the atolls is not the water residence time. Research is in progress to estimate the lagoon water residence times using other forcing variables like the energy and direction of swells, internal parameters like the shape of the lagoon, its volume, the depth of its passes and spillways, and different methods like salt balance or cesium concentrations.

7 - The Typatoll program does not seek to explain the spatial and temporal variations within lagoons. The intra lagoonal variations of the internal parameters are only considered so that indices, reliably representative of each lagoon, can be obtained and are not due to transient states or particular zones. A critical question in this program is "Does the low sampling effort devoted to each lagoon allow integration of the main intralagoonal variations?". Different answers arise according the different groups of parameters recorded.

For fish, benthos and sediments, the solution lies in the sampling of the various biotopes or strata present within the lagoon. The final means of the internal parameters for each lagoon will be calculated taking into account the respective surfaces of the various biotopes. These surfaces are determined by the analysis of SPOT satellite images for shallow waters, and by scuba diving surveys for deep waters.

For the water column, data collected during 2 surveys clearly point to a low within-lagoon variability which had already been observed in Tikehau and Takapoto atolls. A vertical homogeneity of temperature, salinity, nutrients, chlorophyll a, bacterial biomass and production has been generally observed (Sournia and Ricard 1976; Charpy - Roubaud et al. 1990; Charpy and Charpy - Roubaud 1991, Dufour and Torréton 1993; Buestel et al. 1995). Buestel et al. (1995) demonstrated the highly isotropic structure of the Takapoto lagoon. In the Tikehau lagoon, the CVs for particulate organic C, N and P, and for chlorophyll a among samples collected during several surveys range from 0.07 to 0.27 (data in Charpy and Charpy - Roubaud 1991). The CV of bacterial biomass and production recorded between ten sites of the Takapoto lagoon were only 0.13 and 0.17 (Dufour et al. 1994b). The intralagoonal coefficients of variation obtained during the preliminary survey are of the same order of magnitude (Fig. 3).

In Tikehau and Takapoto lagoons, Charpy and Charpy - Roubaud (1991), Dufour and Torréton (1993), Charpy et al. (1994) and Dufour et al. (1994b) recorded low seasonal variations of phytoplanktonic, phytobenthic and bacterioplanktonic biomasses and production. The sampling design of the "water column" surveys of the Typatoll program which comprises one survey in the dry season and one in the wet season, should thus take into account the eventual seasonal variations of the lagoonal water parameters. The day to day variations of these parameters cannot be integrated into this program. Nevertheless, their influence is limited as the coefficient of variation of daily measures ranged only from 0.07 to 0.24 for bacterioplankton biomass and production in Tikehau and Takapoto (Dufour and Torréton 1993; Dufour et al. 1994b). It is nevertheless important to avoid storm or hurricane periods.

8 - The sampling effort completed for fish and benthos communities was not the same in all biotopes , but proportional to the surfaces occupied by each biotope and it focused more on shallow (<10m) than deeper zones as the highest density of fish occurs in shallow waters. An accurate record of pelagic species was not attempted. As most fishes in atoll lagoons are associated with coral substrata (Caillart et al. 1994) which have been well sampled in the Typatoll program, there should not be a serious underestimation of fish biomass due to bias in pelagic species estimates.

In conclusion, the sampling designs defined for the water column and the fish and benthic communities are well adapted to the scientific problem studied in the Typatoll program as they provide evidence of significant differences between lagoons that are representative of a mean intra-lagoonal structure. The external factors seem to have been "robust" as they allowed atolls with significantly different lagoon structure and functioning to be selected.

Disturbance factors related to human activities were consciously discarded, but were likely to have been of little importance in this program, as all the selected atolls, except for Takapoto, were sparsely or not at all populated. The logical procedure consists of understanding first the natural state of the lagoons before trying to discern the effects produced by a growing human pressure on these ecosystems. The results of the Typatoll program may be used as reference points for further specific studies on the effects of human disturbances on the functioning of atoll lagoons. The ultimate aim of the Typatoll program is to relate the morphological characteristics of the atolls to the functioning of their lagoons, in order to provide a general framework for rational management of their resources. Atoll lagoons appear to be particularly sensitive ecosystems, and the results of this program may help us to understand, for example, why some lagoons are more subjected to dystrophic crisis than others, or why some lagoons have a high production of fish and others of bivalve mollusks.

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