

Phytoplankton and Primary Productivity in Takapoto Atoll, Tuamotu Islands

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Abstract—Takapoto is a virtually closed atoll in the Tuamotu Archipelago, French Polynesia. Planktonic primary productivity was studied there during the southern winter (August, 1974) under several aspects: ¹⁴C in situ uptake, glucose uptake, chlorophyll concentration and phytoplankton counts; stations were located in the southwestern part of the lagoon (5 stations) and outside the reef (1 station). The productivity level in the lagoon, though moderate (125–275 mg C m⁻² day⁻¹), is significantly higher than in the open sea; the same is true for pigment concentration and heterotrophic activity. Phytoplankton composition is quite different in the lagoon (dinoflagellate dominated) and outside the lagoon (where diatoms prevail). Productivity of the atoll as a whole on a yearly basis might be higher, if, as suggested from several considerations, the northeastern (windward) end of the lagoon is more fertile and, on the other hand, if the summer (rainy season) is more favorable. Comparisons are made with the few relevant data available from other atolls of the world, whether open or closed.

Introduction

Surprisingly few studies have been devoted to the planktonic productivity of atolls, as compared to the bulk of researches in various fields of marine ecology as a whole. Even in the case of the Marshall Islands, in which the best known atolls of the world are to be found, direct measurements of phytoplankton photosynthesis are few and somewhat uncertain (Sargent and Austin, 1949; Doty and Capurro, 1961); flow rate studies are generally preferred (Sargent and Austin, 1949; Odum and Odum, 1955; Johannes *et al.*, 1972, and others) though they do not make a distinctive evaluation of benthic vs. planktonic production. Obviously, the assumption that plankton of coral reef areas is relatively impoverished has discouraged efforts. However, one still needs to assess the role of planktonic producers in such reef communities—such elegant ecosystems under both aesthetically and bioenergetically aspects—as atolls.

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Study Area

Takapoto Atoll (about 15°S, 145°W) offers a peculiarity which is nearly an exception among the 75 atolls of the Tuamotu Archipelago and the four odd hundred atolls of the world, namely, it is a virtually closed one with dry land on most parts of its crown (Fig. 1). It communicates with the open sea through a few apertures

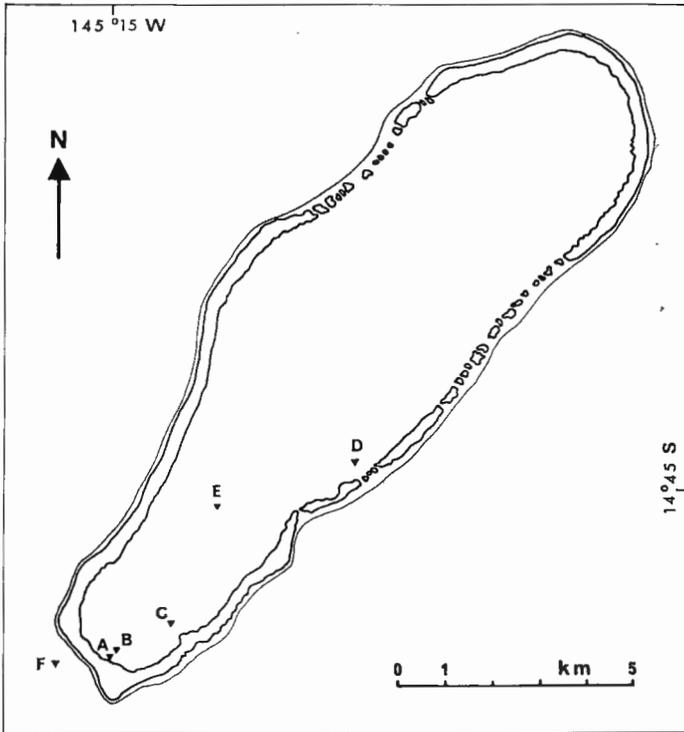


Fig. 1. Takapoto Atoll and the sampling stations.

(Polynesian: "hoas"), most of which—all of them except 2 or 3—are functional under spring tides or storms only; the largest "hoa" (Fig. 2) allows some surface oceanic water to enter the atoll at high tide after crossing over the reef flat.

The main axis is NE-SW and about 16 km long; the lagoon is comparatively deep (down to 45 m in its middle part) though it is dotted with a number of coral patches and pinnacles. Surface temperature ranges from 25–26°C (August) to 30–31°C (February). Surface salinity during our visit, i.e., the dry season, was about 39–40‰ in the lagoon and 36‰ outside.

The atoll is inhabited by a hundred people or so. The only industry, besides copra, is pearl culturing from *Pinctada margaritifera*.

Methods

Primary production of phytoplankton was measured by the carbon-14 method. Bottles, 220 ml pyrex, were suspended *in situ* from sunrise to noon after adding 5 μCi of tracer. They were then filtered on 0.45 μm pore filters. Counting was made two months later on a thin-window counter and then on a scintillation counter, with fairly comparative results. Filters were exposed to fuming hydrochloric acid prior to counting, though we are aware that such a procedure is open to criticism. Total CO_2 content of seawater, as computed from temperature, salinity and pH, was about 25 mg C per liter. Productivity rates were multiplied by a factor of 2 in order to get daily production, since measurements made at Takapoto as well as in other places of French Polynesia (unpublished) had shown us that the rates of the two half-days do not differ significantly from each other.

Glucose uptake experiments were conducted in the same way as above on parallel samples. Since the natural concentration of glucose in the study area is unknown, results will be dealt with here as relative rates.

Phytoplankton pigments were concentrated by filtering three liters of seawater on Millipore HA filters; acidification was prevented by an addition of MgCO_3 powder. Filters were kept frozen at dark for 2-3 weeks before they were extracted in acetone. Then the fluorometric method was followed as reported by Strickland and Parsons (1968); chlorophyll *a* and phaeopigments concentrations were derived from the lectures on unacidified and acidified extracts using a maximum acid-factor of 2.2.



Fig. 2. The main "hoa", at Teavatika, close to Station D. Some ocean surface water flows into the lagoon at high tide.

Seawater was collected for subsequent phytoplankton enumeration on an inverted microscope. Unfortunately, delays (6 months) or fixative (lugol-acetate) or both resulted in unequal preservation of the taxonomic components, so that only diatoms and dinoflagellates (both naked and armored), as well as a few minor groups, were recognizable; obviously coccolithophorids and presumably other flagellates had disappeared.

Stations were located as indicated on Fig. 1. Each of them was visited once, or twice or thrice between August 15 and August 20, 1974. Five horizontal net tows were also obtained for zooplankton studies, the results of which will be published elsewhere by R. Gaudy.

Results

Inside the lagoon, primary productivity in surface water averages $9.7 \text{ mg C m}^{-3} \text{ day}^{-1}$. Individual means at the different stations allow three remarks to be made: 1) rates are the lowest (6.2) at Station A, which is the shallowest; 2) they are relatively low (8.0) also at Station D, close to the entrance of ocean water; 3) these two cases omitted, mean rates for the three remaining stations in the lagoon amount to 12.2. Primary production is apparently light-inhibited in the surface layer since the mean value at 5 or 10 meters depth is 15.2 for the whole lagoon. Integrated rates per square meter for two "average" hypothetical stations 10 and 20-meter deep would be 125 and 275 $\text{mg C m}^{-2} \text{ day}^{-1}$ respectively.

We were able to get only one ^{14}C uptake measurement outside the lagoon, namely, $2.95 \text{ mg C m}^{-3} \text{ day}^{-1}$ at 7 meters (some bottles being lost, a single depth is concerned).

Results of glucose uptake can be summarized as follows: relative rates were greater by one order of magnitude inside the lagoon than outside; station D, in front of the "hoa", showed somewhat in between rates.

The average concentration of chlorophyll *a* in the lagoon is 0.10 mg m^{-3} . Individual stations behave in the same way as described above for ^{14}C uptake. Outside the lagoon, the mean of three measurements is 0.05 mg m^{-3} . The acid-ratio is slight though significantly higher in the lagoon (1.66 as a mean) than in the open sea (1.48); hence the respective concentrations of phaeopigments are 0.09 and 0.08 mg m^{-3} .

On either sides of the atoll, phytoplankters amount to ca. 2,500 cells per liter. In spite of the inadequacy of the countings (see above), it is noteworthy that these numbers consist essentially of:

Inside: dinoflagellates (a wide variety of them, including naked as well as armored species, both large- or small-sized; the dominant species is *Peridinium ovum*, a tropical and temperate plankter;

Outside: diatoms, mostly benthic or tychoplanktonic.

Discussion

This first assessment of planktonic primary production in Takapoto Atoll

(and in the Tuamotu Islands as well) suffers from two gaps. First, only the southwestern half of the atoll has been sampled. Due to prevailing NE tradewinds, one might expect an upwelling or some mixing to occur in the northeastern edge of the lagoon, according to Von Arx (1954) model of circulation; in this connection, Wiens (1962) states that the windward part of an atoll is usually more productive and that, more than a coincidence, fishermen villages are usually set on this side rather than on the other one (in this respect, Takapoto example is misleading: the village is SW today, but it was first settled NE until it was destroyed by a storm). Thus, enigmatical enough is an earlier observation by Rose (1953) who has published the first plankton data on Takapoto, namely a brief comment on two zooplankton catches from the two opposite ends of the lagoon; one sample is reported to be impoverished and the other one quite rich, but their respective locations are not mentioned.

Our second concern is about seasonality, since the present study merely depicts the winter or dry-season conditions. It has been pointed out (Sournia, 1969) that the alleged homeostasis of yearly conditions in the tropical seas is an oversimplified postulate. Physical considerations would rather lead to a careful examination of seasonal variability (Von Arx, 1954). Furthermore, according to some crude biological observations at Takapoto (Y. Morizur and other local sources, unpublished), a spectacular bloom of "a medusa" occurs every year in the lagoon from November to March; a similar event is reported from Mururoa, another atoll in this area (Michel *et al.*, 1972; and Michel, pers. comm.), and minor blooms of phytoplankton, whether periodical or not, are known from Rongelap, Marshall Islands (Johnson, 1954) and Rangi-roa, Tuamotu Islands (Michel *et al.*, 1972).

Few as they are (^{14}C samples: 26; pigment extracts: 14), the present measurements still make up the most consistent series of data on planktonic primary production from any atoll. Some comments and comparisons may thus be presented.

Phytoplankton standing stock and production are both moderate in the lagoon waters, however they are significantly higher than in the open sea, as it results from the few measurements we made outside (Station F) and from oceanic data in this area of the Pacific Ocean (Koblentz-Mishke *et al.*, 1968, 1970; Desrosières and Wauthy, 1973). On the other hand, our glucose experiments may be reasonably interpreted as an increased heterotrophic activity in the lagoon as compared to the ocean, in agreement with the direct bacterial countings made by Johannes *et al.* (1972) in the Marshall Islands. Phytoplankton offers another contrast, since its composition is drastically different on both sides of the atoll; however, we were not able to evaluate the coccolithophorid component, which seems to be prominent in such areas (Fournier, 1970; Desrosières, 1971; Michel *et al.*, 1972).

Though the inflow of ocean water is quite limited, the various parameters that we measured at station D show somewhat intermediate values between oceanic and lagoonal conditions. It may thus be predicted that detailed budget studies there would be rewarding.

Most of the data on atoll productivity originate from Eniwetok (Marshall

Islands) which is widely open to oceanic conditions by means of passes and submerged reefs. Photosynthetic rates were measured there by Sargent and Austin, 1949 (oxygen method) and by Doty and Capurro, 1961 (^{14}C method); in spite of being poorly conclusive, they do agree with the present data. Chlorophyll values, on the other hand, are fully reliable and compare closely with the present ones (Gerber and Marshall, 1974) or exceed them by 2-4 times (Doty and Capurro, 1961; Marshall, 1965). The two latter works, however, apply to total chlorophyll; no doubt subtracting phaeopigments would reduce the discrepancy or cancel it.

About half-way from Eniwetok and Takapoto is Fanning Atoll (Line Islands) which has been intensively studied in the recent years. It is nearly as landlocked as Takapoto; both islands are about the same size but Fanning lagoon is shallower. Carbon-14 uptake was measured around noon at a single station and on a single day (Gordon *et al.*, 1971; see also Gordon, 1971); other attempts were unsuccessful due to abnormally high dark counts (Krasnick, 1973). Fortunately, a valuable set of chlorophyll measurements is available (Krasnick, 1973). In the whole, phytoplankton biomass and production per cubic meter are higher by several times in Fanning Atoll, but, considering the respective depths, one may state that the two lagoons are equally productive on a surface basis. Phytoplankton counts are not absolute either; it seems that dinoflagellates were dominant inside the lagoon (Gordon *et al.*, 1971) while coccolithophorids prevailed outside (Fournier, 1970).

Turning our attention again to the Tuamotu Islands, a brief mention can be made of Hao Atoll in which chlorophyll concentrations proved to be roughly equal (Michel, 1969) to those observed at Takapoto. Except from some notes about phytoplankton at Wake Island (Marshall, 1968), no other comparison relevant to our subject is available from the Pacific Ocean. In the Indian Ocean, Kawaratti Atoll, still an "open" one, has been visited by Qasim *et al.*, 1972 (see also Qasim and Sankaranarayanan, 1970); their ^{14}C figures are uncertain with respect to methodology, but chlorophyll data come fairly well into the range for Pacific atolls and, once again, the productivity level is higher in the lagoon than in the open sea.

So little do we know about planktonic productivity in so few atolls of the world . . . , in spite of the theoretical interest of such studies (e.g., endemism and budget studies) and their practical perspectives (aquaculture).

ACKNOWLEDGEMENTS

This work is part of the program "Man and Biosphere" (Theme VII: Ecology and rational uses of insular ecosystems); funds were made available from the "Territoire de la Polynésie Française" and FIDES. Help was offered for pigment analysis at the "Centre O.R.S.T.O.M. de Nouméa" (New Caledonia). Carbon-14 countings were kindly made by Dr. J. Brouardel and Mrs. M. Joseph (Paris) and we are similarly indebted to Dr. G. Jacques (Banyuls s/mer) for the glucose data. Most valuable also is to find friends on an atoll; we did.

Résumé

Les paramètres suivants ont été mesurés dans l'atoll de Takapoto (Polynésie Française) en août 1974: assimilation photosynthétique (méthode du ^{14}C), contenu chlorophyllien (méthode fluorimétrique) et composition taxinomique du phytoplancton, ainsi qu'assimilation hétérotrophique (glucose marqué).

Entre le lagon et la mer ouverte apparaissent des différences marquées, tant qualitatives que quantitatives. Bien que la biomasse et la production phytoplanctoniques soient modestes à l'intérieur de l'atoll ($0,10 \text{ mg chlor. } a \text{ m}^{-3}$; $125\text{--}275 \text{ mg C m}^{-2} \text{ j}^{-1}$), elles sont significativement supérieures aux niveaux observés à l'extérieur et au grand large; de même, l'assimilation hétérotrophique, évaluée en unités relatives, est bien supérieure dans le lagon.

Takapoto, atoll presque clos, se prêterait particulièrement bien à des études de bilan. Comme il était prévisible, celle des stations située dans le lagon mais en face du principal "hoa" (interruption de la couronne récifale), présente des caractères composites.

Les données relatives aux autres atolls du monde sont recensées. Très peu nombreuses, elles laisseraient penser actuellement que l'importance quantitative du phytoplancton ne varie guère d'un atoll à l'autre.

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