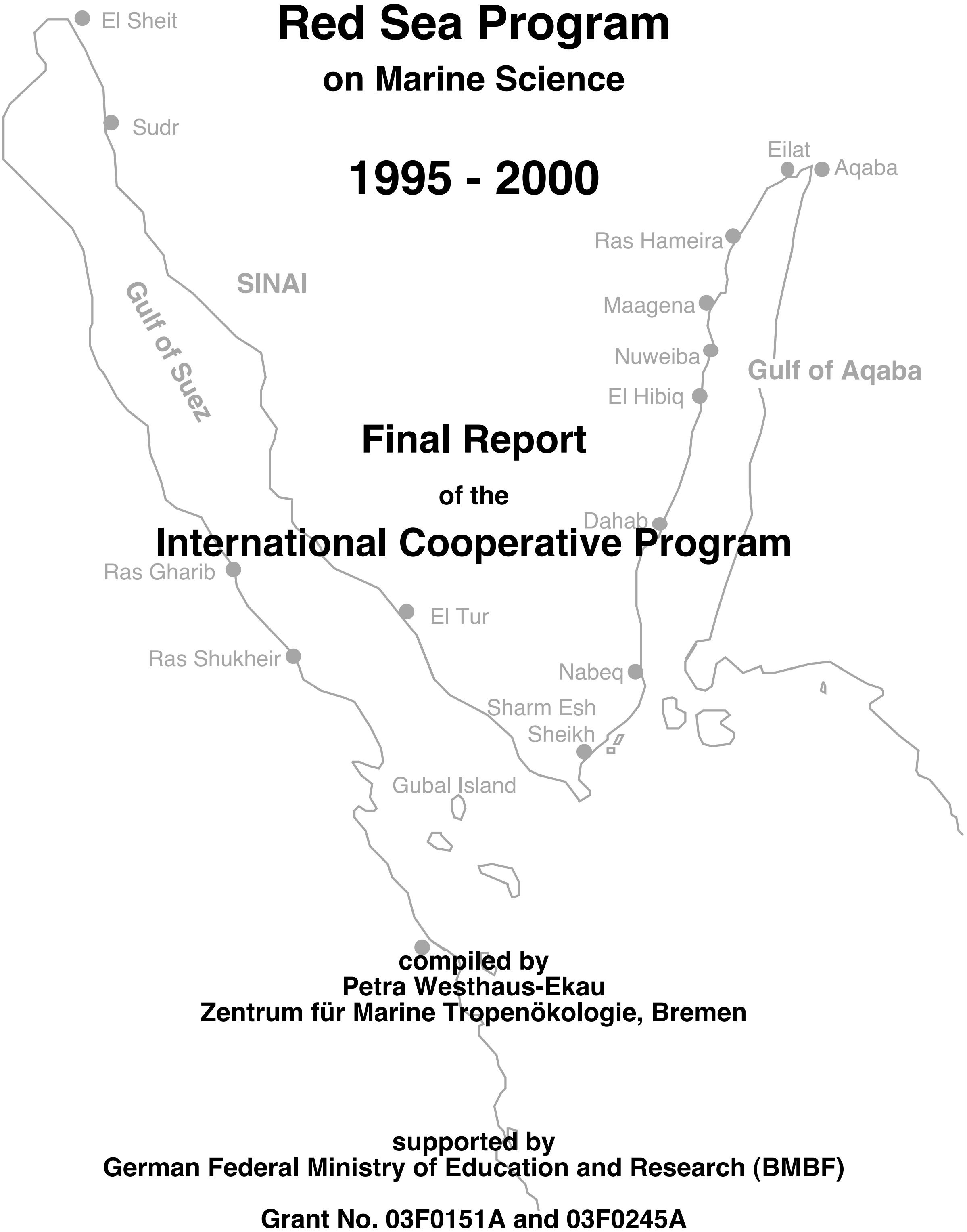

Red Sea Program

on Marine Science

1995 - 2000

Final Report

of the

International Cooperative Program

compiled by
Petra Westhaus-Ekau
Zentrum für Marine Tropenökologie, Bremen

supported by
German Federal Ministry of Education and Research (BMBF)

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Contents

Preface

The marine sciences offer unique opportunities both for interdisciplinary research and for the establishment of international cooperation. In both cases the special role of marine biology has its roots in the nature of the research object. The sea, particularly the Red Sea, strives with interesting forms of life, adapted to the most extreme conditions. Therefore, it is a ‘gold mine‘ for scientists from all the life sciences. On the other hand a common goal – preserving and understanding a fragile ecosystem – and the special working mode of marine sciences – relying heavily on field trips in a vessel – persuade people to collaborate and to develop ties and friendships. With this in mind, I did not hesitate to step in, when Micha Spira approached me in 1995 with the idea of a multinational research project on the Red Sea with two goals: To conduct interdisciplinary research on many aspects of the Red Sea and to promote the peace process in the region. Immediately, we established contacts to leading Egyptian and Palestinian personalities: Prof. Hussein Badawi and Dr. Issa Khater, and at a later stage to Prof. Abu-Hilal in order to put the program on a broad regional base. Interdisciplinarity was fostered by the participation of a broad spectrum of specialists ranging from molecular biologists to physical oceanographers and marine geologists.

When the project started, my view on marine biology was quite limited. I had been before to many marine biological stations, including the IUI in Eilat, since the classical objects of study in neurobiology are marine organisms – squid, aplysia, barnacle, torpedo, limulus – and some of them, like the squid, can only be studied in well equipped stations. However, many other aspects of marine biology were new to me. This was an exciting experience. Not less interesting was the experience about the different approaches and methodologies in the different disciplines participating in the Red Sea Program. The experience that experiments involving cruises requiring sophisticated logistics, and the experience that success of the research plan depended on obtaining valid permits was new to me. Finally it was highly interesting to observe, how research organization and structure differs between the participating nationalities, and it was a challenge to find ways and procedures, which would match the requirements and conform with the regulations of all partners.

The scientific output has been rewarding. Many of our results would not have been possible to achieve without the international structures of the Red Sea Program. Scientific training and capacity building set milestones for future projects. Unfortunately, political developments have prevented, for the time being, success in the other important goal of the program, the furthering of the piece process in the region. However, as biologists we know that seeds have long life. Most seeds have the capacity to hibernate, others overcome long duration periods of drought. The deserts surrounding the Red Sea provide ample examples for that. We are confident that the Red Sea Program has generated seeds of that kind, which will flourish, when times have changed.

Göttingen, December 2000

Prof. Dr. Dr. h.c. Erwin Neher
Chairman, Scientific Steering Committee

Introduction

The Red Sea Program - a unique experience

Gotthilf Hempel

(International Coordinator)

The idea of the Red Sea Program came from a few Israeli and German scientists interested in the organisms and ecology of the Gulf of Aqaba and the Red Sea. A program was then developed in close consultation between Egyptian, Israeli, Palestinian and German scientists and science administrators. The German Ministry for Science and Technology agreed in 1995 to support the proposed multinational program in the region with the dual objective of fostering top class science and promoting the peace process in the region through better mutual understanding. Soon after training of students and young researchers in marine science became a further objective in order to strengthen the academic and research capacity in the region and to develop further competence within the German science community.

RSP and related activities (except "Meteor"-expedition) received 12.8 Mio DM from the German Government. The technical and financial management of RSP was in the hands of the RSP Secretariat at the Center for Tropical Marine Ecology. It was supervised by the Scientific Steering Committee chaired by Prof. Erwin Neher and worked in close contact with the National Coordinators (Fig. 1). An international review group evaluated RSP in its third year and proposed its continuation for two more years (RSP II). Three General Assemblies were held in Egypt, Israel and Germany. A Final Scientific Symposium was planned for November 2000 in Aqaba, Jordan, but had to be postponed until 2001, i.e. after the official end of RSP II on December 31, 2000.

One of the goals of RSP was to link the existing research facilities in the region in order to provide scientists and students from the various participating nations access to neighboring institutions. However, due to the political difficulties in the region, this goal was not fully achieved.

During the first phase of the project, more than 70 scientific partners from several Israeli and German institutes and universities worked together, as well as scientists from several Egyptian National Institutes of Oceanography and Fisheries (NIOF) and the Palestinian Al Quds University (Fig. 2).

After a period of affiliated status over the years 1997-1998 scientists of the Aqaba Marine Science Station (MSS) formally joined RSP II as active partners, recruiting research students from the mother universities in Amman and Irbid (see Annex 1, All Research Participants of RSP).

The Red Sea Program

Scientific Steering Committee:

Chair: Prof. E. Neher, MPIBC, Göttingen

National Coordinators:
Prof. A. Abu-Hilal, MSS, Aqaba
Prof. E. Amin, NIOF, Cairo
Prof. G. Hempel, ZMT, Bremen
Dr. I. Khater, PCG, Jerusalem
Prof. M. Spira, IUI, Eilat

Executive Officers:
Prof. Z. Abdeen, AQU, Jerusalem
Dr. A. Baranes, IUI, Eilat
Mr. A. El-Ibiary, NIOF, Cairo
Dr. C. Richter, ZMT, Bremen

International Coordinator:

Prof. G. Hempel, ZMT, Bremen

RSP Secretariat:

Dr. C. Richter, ZMT, Bremen
Dr. P. Westhaus-Ekau, ZMT, Bremen
Mrs. Petra Hahn, ZMT, Bremen

BEO Secretariat:

Prof. U. Schöttler, BEO, Warnemünde
Dr. J. Harms, BEO, Warnemünde
Mrs. H. Endler, BEO, Warnemünde

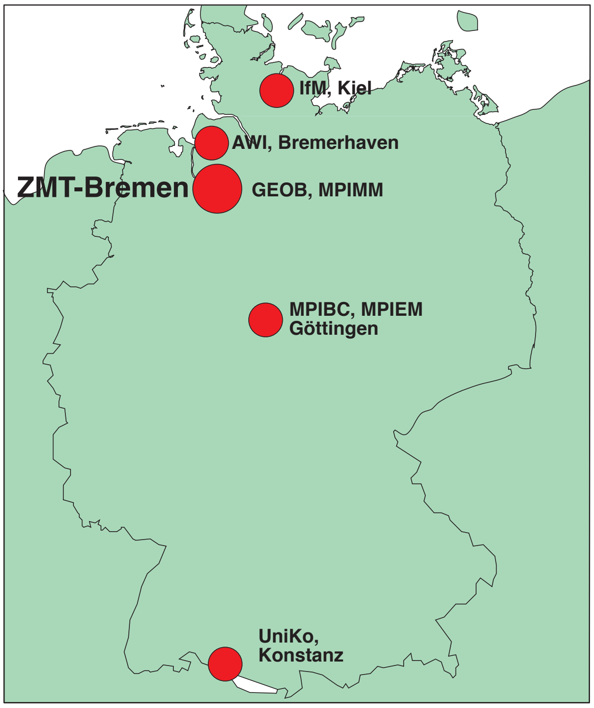
International Review Team:

Prof. B.v. Bodungen, IOW, Warnemünde
Prof. K. Emeis, IOW, Rostock-Warnemünde
Prof. J. Ott, IfZ, Vienna, AU
Prof. D. Richter, INUH, Hamburg
Prof. J.-O. Strømberg, KMRS, Fiskebäckskil, SE
Dr. M. Türkay, FIS, Frankfurt

Fig. 1: The Red Sea Program
Abbreviations: AQU: Al Quds University, Jerusalem; **BEO:** Project Management Organization Biology, Energy, Ecology of the BMBF, Rostock-Warnemünde; **FIS**: Research Institute Senckenberg, Frankfurt; **IfZ**: Institute of Zoology, Vienna, Austria; **INUH**: Institute for Neurobiology, University Hamburg; **IOW**: Baltic Sea Research Institute, Rostock-Warnemünde; **IUI**: Interuniversity Institute, Eilat; **KMRS**: Kristineberg Marine Research Station, Fiskebäckskil, Sweden; **MPIBC**: Max Planck Institute for Biophysical Chemistry, Göttingen; **MSS**: Marine Science Station, Aqaba; **NIOF**: National Institute of Oceanography and Fisheries, Alexandria, Cairo, Hurghada, Suez; **PCG**: Palestine Consultancy Group, Jerusalem; **ZMT**: Center for Tropical Marine Ecology, Bremen

RSP I consisted of 7 projects which were largely independent, in terms of science and scientific personnel. For the extension of the work and synthesis of results during RSP II, the number of themes was reduced to 4, and the subjects within the themes were interlinked (Fig. 3).

RSP research covered the open waters of the Gulf of Aqaba, the physical mixing and stratification in relation to phytoplankton productivity, light and nutrient availability (Theme I), nearshore processes and synecology of coral reefs, particularly life in framework crevices (Theme II), cellular processes of calcification in foraminifera and corals and the use of calcifying organisms as paleo-environmental recorders (Theme III) as well as microbiological and cellular processes in interfaces, particularly microbial mats (Theme IV). All four themes shared common organizational and methodological features; molecular and cellular approaches were used in various themes, as well as newly developed microsensors. Interactions also arose from the



RSP - Partners

in Germany

and Middle East

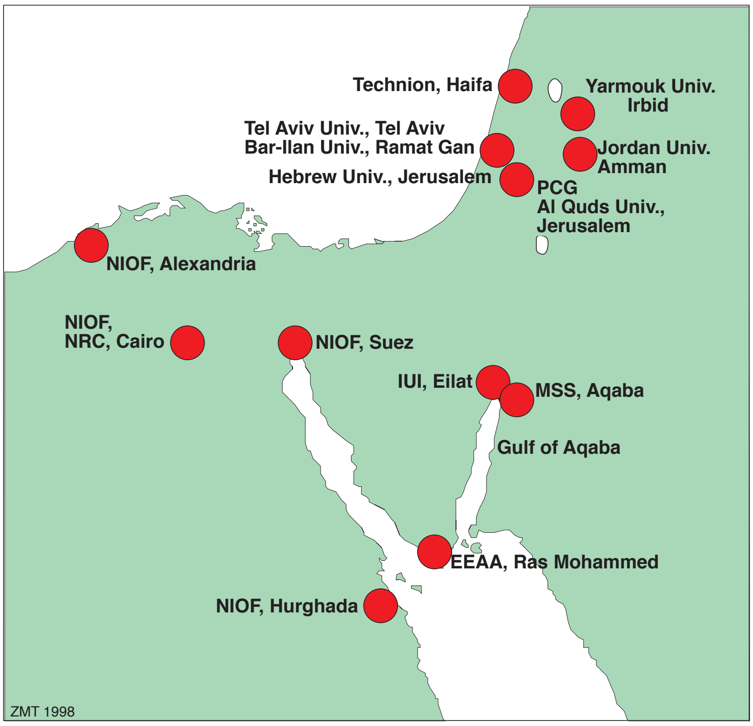


Fig. 2: RSP-Partners

AWI	Alfred-Wegener-Institute for Polar and Marine Research, Bremerhaven
EEAA	Egyptian Environmental Affairs Agency, Ras Mohammed National Park
GEOB	Earth Sciences, University Bremen
IfM	Institute of Marine Science, Kiel
IUI	Interuniversity Institute, Eilat
MPIBC	Max Planck Institute for Biophysical Chemistry, Göttingen
MPIEM	Max Planck Institute for Experimental Medicine, Göttingen
MPIMM	Max Planck Institute for Marine Microbiology, Bremen
MSS	Marine Science Station, Aqaba
NIOF	National Institute of Oceanography and Fisheries, Alexandria, Cairo, Hurghada, Suez
NRC	National Research Centre, Cairo
PCG	Palestine Consultancy Group, Jerusalem
UniKo	University Constance
ZMT	Center for Tropical Marine Ecology, Bremen

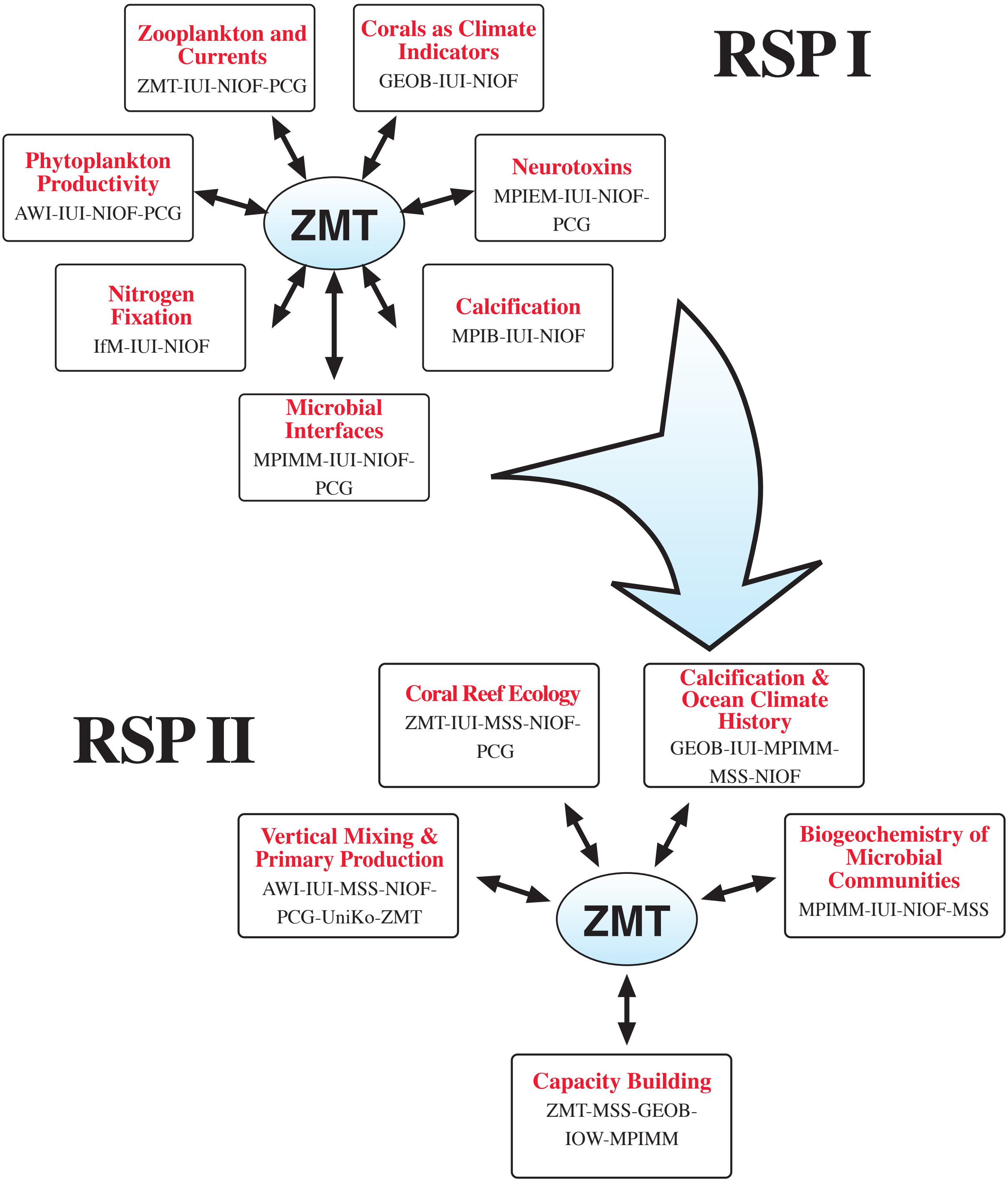


Fig. 3: Scientific structure of RSP I and RSP II
Abbreviations see Fig. 2.

joint use of research facilities in Eilat and Aqaba, as well as from training courses which brought together scientists and students from different research disciplines. All themes extended previous RSP research. Field work was largely completed by end 1999 and data are currently being processed for publication.

Funding in RSP II concentrated mainly on PhD- and MSc-candidates and PostDoc's as well as other activities relating to capacity building, communication, data analysis and preparation of publications. Particularly courses and workshops required substantial funding. By contrast, funds for equipment, consumables and ships were significantly reduced. MSS joined RSP late, requiring additional efforts to build up and extend its existing capacity for marine ecological research. To this effect a special capacity building program was suggested by the RSP review team to carry out innovative research with state-of-the-art equipment, using local expertise as well as external experts for on-the-job-training. MSS provided full logistic support. Mainly near-shore processes were investigated including coral reef ecology, geochemical studies of reef sediments as well as geological studies of corals.

Palestinian marine science suffered strongly from the deteriorating political situation in the region, so that most efforts concentrated on building scientific personnel and extending the Al Quds library for marine science.

The scientific seminars, workshops and training courses planned for RSP II were held in Aqaba and Eilat. Exchange of PhD students, including students from Jordanian universities and MSS, was greatly enhanced during RSP II.

Furthermore, RSP II offered particularly Arabs the opportunity of study periods in Germany to prepare joint publications with their German partners. Besides their direct scientific importance, these steps fostered mutual understanding and training.

We underwent early efforts to set the stage for extending cooperation beyond RSP. In spite of present dramatic worsening of Israeli-Arab relations we still hope that ZMT may act as a contact office mediating and coordinating future projects emerging from RSP. At any rate the German Ministry intends to continue the support for current Arab PhD students who did their field work under RSP.

Research Themes

Research on 'Dynamics and productivity of the phytoplankton and its control by the underwater light field' within Theme I were closely related to the biological leg of "Meteor" cruise 44 to the northern Red Sea and Gulf of Aqaba in spring 1999. It marked the transition from deep-winter mixing to summer stratification and allowed for a quasi-synoptic assessment of various stages of the spring bloom along a north-south gradient from the Gulf waters to the Red Sea proper. Complementing this regional assessment, the RSP studies focused on the temporal evolution of the phytoplankton community in the northern Gulf, extending the time series in the area from previous years. Using the same personnel and equipment allowed for similar methodology for measuring nutrient update, primary production, consumption by herbivores, etc. Micro- and nanoplankton incubation experiments allowed for the first time to assess the role of grazing in the control of the phytoplankton spring bloom.

Freon tracer experiments provided first data on the direct effects of mixing on the vertical distribution of plankton in the water column.

Themes II and III encompass two closely linked research projects on living communities of coral reefs and calcification in response to variable environmental conditions. The synecological investigations of Theme II aimed at the description of cryptic reef communities in relation to the framework morphology, water exchange, food environment and light. Photographic and video observations were supplemented with selected sampling of reference specimen. Two ongoing dissertations have significant relevance to the marine environment: obligate cavity-dwelling sponges are considered highly adapted specialists to extremely oligotrophic environments. Putative increases in food supply due to eutrophication are believed to result in a concomitant shift in the highly interconnected coelobite community away from obligate towards most opportunistic filter-feeding cavity-dwellers. The other investigation relevant to marine conservation addressed the gene-flow of fish populations in the semi-enclosed Gulf of Aqaba.

The working hypothesis was that the populations are highly interconnected so that degraded reef sections are re-colonized quickly by neighboring populations.

Theme III on calcification and use of calcified organisms as paleo-environmental recorders united previously separate projects of RSP I. One of the goals was to understand the cellular mechanisms by utilize calcifying organisms such as foraminifera and corals precipitate calcium carbonate against a strong concentration gradient, the other was to interpret the stable isotope signals in the calcium carbonate skeleton as proxis for environmental changes. Close links existed to the oceanographic work in Theme I concerning the calibration of proxy data in recent corals. Links existed also to sedimentological work carried out on the geological leg of "Meteor" cruise 44. The involvement of the leading institutions in Eilat/Jerusalem and Bremen with mass-spectrometer facilities was particularly valuable in terms of capacity building of young scientists from the region.

Theme IV encompassed microbial processes in the chemoclines of the water column of the Solar Lake during stratification and in the chemocline of the cyanobacterial mats surrounding the lake. Molecular analyses of community structure compared to the physical and chemical changes in the water column developed models of succession of microbial communities across the chemocline during stratification and mixing.

In the cyanobacterial mats the chemocline migrates 2-3 mm diurnally, while 20-30 cm diurnal changes are observed in the chemocline of the water column. This situation requires a high adaptation of the microbial communities due to different environmental conditions. New sampling strategies as well as new measuring methods allowed detailed analyses of the vertical migration and the functional achievements of these communities. Migration may well be a possible solution in the cyanobacterial mats, while it is unlikely to be the case in the water column. Furthermore, the tight physical contact of the microbial community allowed a large spectrum of syntrophic relationship among the microorganisms in the chemocline while this close proximity was absent in the water column. Therefore the comparison of both communities gave a good insight into the various mechanisms by which marine microorganisms cope with environmental changes during diurnal cycles.

Hypersaline lakes exhibit seasonal toxin production by microorganisms, especially at the onset of the stratification period. *Dactylococcopsis salina*, a planctonic Cyanobakterium developing in the upper zone of the chemocline, was the focus for the study of the annual toxin production. Additionally the toxins in mats and in sea anemones were analyzed as to their chemical composition after isolation and purification. Their specific neurotoxic effects of the isolates were investigated.

The microbiological and biogeochemical investigations of Theme IV were based on the results of the very successful collaboration of the Israeli, Egyptian and German scientists of the RSP-Project E. The Al Quds University was linked with Theme IV and with the Solar lake studies in particular by a Palestinian PhD student at Hebrew University. Unfortunately he left the project when he took over a permanent position in community medicine at his home university.

The Marine Science Station participated in the geochemical and microbiological work of Theme IV. Two Jordanian PhD students are enrolled at Bremen University and do their laboratory studies at the Max-Planck-Institute for Marine Microbiology, Bremen.

Concluding Remarks

In terms of marine science RSP was a success. In combination with the "Meteor" cruise in early 1999 it contributed greatly to our understanding of the production processes in the Gulf of Aqaba with its unique oceanographic conditions. Basic insights were obtained in the relative role of light, nutrients and grazing on productivity and community structure in micro- and mesoplankton. The status on the trophic relationships in coral reefs with special reference to the crevices are of similar importance. Breakthroughs in the understanding of calcification in corals and foraminifera were obtained and the climate record of the region was much extended. Studies in the microbial mats of Solar Lake and the application of microsensors in other habitats and communities resulted in an unusually high number of peer-reviewed publications. Molecular-biological methods were also successfully employed in investigations on marine toxins.

The expectation issued in 1995 that RSP would foster the scientific development in the region was fulfilled: RSP provided a unique meeting point for researchers, young scientists and students with different cultural background. The heterogeneous structure of the program as well as the side-by-side of leading scientists and less experienced but highly motivated young scientists proved particularly stimulating and fruitful.

Very impressive is the number of PhD and MSc theses produced under the wings of RSP (see Annex 3). Virtually all of them are based on collaborative work involving scientists and students of different nationalities. Possibly never before there was so much exchange of students and young scientists in the region than in RSP, resulting in a network within the region and in many contacts to the outside world, particularly (but not exclusively) to German science. The senior scientists and the National Coordinators carried a great responsibility in this process. They were also the driving forces for the training courses and workshops which brought together students of all the nationalities involved in RSP (see Annex 5 and 8). Several of the training courses became famous for their success in science training and in human relations.

Technical Report

Claudio Richter

(Program Secretary)

Scientific and technical reports on RSP I have been delivered in April 1999. The major goals of the second phase of the Red Sea Program (RSP II), as outlined in two Scientific Steering Committee meetings in March and October 1999, were to synthesize the results gathered during the first 3 years of RSP, bundle the scientific activities into four themes of research, and build research capacity for future cooperation in the region. The four themes centered around (1) open ocean processes of the Gulf of Aqaba, Red Sea, (2) coral reef ecology, (3) calcification and palaeoclimate, and (4) microbial processes at interfaces and toxins.

RSP scientific results

Large efforts have been devoted during RSP II to the writing up of MSc and PhD theses and to the publication of scientific results. To date, more than 120 titles are listed under the RSP proceedings; 30 theses have been completed. Forty-four papers have been published, 42 publications are in various stages of preparation, and roughly the same number are expected (not listed), after the ongoing research projects are completed (see Annex 2). The four themes differ with regard to the quantity and pace of the scientific output, reflecting in part the number of scientific personnel involved in the projects (e.g. few PhD students and scientists in Theme III vs. a much larger number co-financed from other sources in Theme IV), but also the time-scale of investigation (short-term vs. seasonal). Three quarters of the numerous microbiological and molecular work manuscripts are already published. Progress was slower in the offshore and coastal ecological disciplines, not only because of the larger scale of investigation but also due to the high degree of interdisciplinarity, which required extra efforts in terms of coordination and mobility. This was achieved, on the one hand, by a large number of short-term visits of individual scientists to their partner institutions in Germany and in the region (see Annex 4). On the other hand, RSP also sponsored a number of workshops (see Annex 5), particularly in Themes I and II, where all theme colleagues and students had the chance to come together and discuss the outcome of their work in a broader context. The scientific meetings facilitated the exchange and joint analysis of data and the drafting of a comparatively large number of bi- and multinational publications. Most of those events took place in the Red Sea region.

Field work during RSP II was restricted to daily cruises to station A and nearshore work in Eilat and Aqaba (see Annex 6 and 7). Plans for an expedition to Egyptian waters were shelved because of technical problems. The oceanographic work with the Israeli ship was completed by December 1999, while offshore and coral reef work in Jordan continued all through RSP II due the ongoing work of MSc and PhD students at MSS joining RSP in 1999.

Capacity building

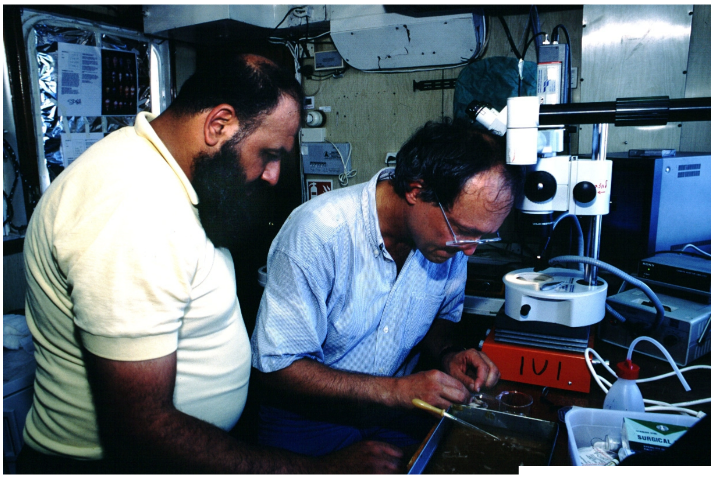
A large number of MSc and PhD studies were sponsored by RSP totaling 25 Israeli, 14 Jordanian, 15 German, 13 Egyptian, 3 Palestinian theses (see Annex 3). Particularly the young Arab scientists remained affiliated to the program, many continuing from MSc to PhD, and from PhD to a faculty position within the RSP network. They take advantage of the equipment provided by RSP and technical skills acquired during training periods abroad, particularly in German laboratories, including such not directly connected with RSP. Important elements of training, but also of cross-cultural exchange were the RSP-Courses (see Annex 8). Junior Courses for undergraduates, which were developed at the Interuniversity Institute in Eilat during RSP I, continued to play a pivotal role in RSP II, this time with Aqaba Marine Science Station as the host. Organized by a skilled board of scientists and administrators pulling together leading scientists and promising students from all RSP nations, the 10-day crash-course not only provided state-of-the-art knowledge in marine ecology, but also a meeting ground for the coming generation of Red Sea scientists. The MSS course had also a strong management component, involving participants of government and NGOs. Two additional courses, in scientific diving and identification of Red Sea coral reef organisms, followed the successful Junior Course in Aqaba. These courses, which also included experts from outside RSP, provided in-depth capacity building for more advanced students in specialized fields.

Coordination

During the second phase of the program, ZMT continued to play its central role as RSP Secretariat. It was responsible for the coordination and implementation of the program activities specified by the Scientific Steering Committee (SSC), in close consultation with the scientific and administrative RSP partners and the funding agency BEO/BMBF.

The main duties were

- to maintain close communication lines with the National Coordinators as well as associated scientists and students to promote the development of scientific cooperation and integration of the various research and training initiatives in the program,
- to administer the program funds in accordance with the research and development goals laid out in the RSP proposal, national needs and government rules, and to produce the financial reports of the program for BEO/BMBF,
- to coordinate and assist in the organization and preparation of SSC meetings and RSP activities, expeditions, exchange programs, workshops, courses and the Final Symposium, in close cooperation with the national secretariats,
- to help RSP visiting scientists and students in Germany,
- to represent RSP in front of other organisations and the public,
- to compile and edit the scientific reports of RSP.



Capacity Building - Three Arab Perspectives

Ekram M. Amin

(Director, National Institute of Oceanography and Fisheries, Cairo)

RSP represents a new trial not only to promote marine science in the area but to accelerate the peace movement between scientists who are in fact the actual policy makers in their countries.

The seven research objects of the program were marked from its beginning in 1995 by its originality. Each of them was a high tech in its fields.

After five years of this program I can summarize its impact on Egyptian marine science in the following:

1) Strengthening the infrastructure of marine sciences,
2) Making available high tech especially in the most modern research fields,
3) Supporting the trend of using research vessels in marine sciences,
4) Accelerating the scientific relation between scientists not only in the area but also on international level,
5) Erecting a solid base for the continuity of scientific cooperation in the different fields of marine sciences.

Acknowledgment

Thanks for Prof. Neher for being the god father of this program, sincere thanks for Prof. Spira for his dedicated efforts to make RSP a reality and cordial thanks for Prof. Hempel and his colleagues for their efforts to reach all the success and to prove that scientific cooperation is the best way to promote science and plant peace especially in our sensitive area. At least we have to admit that without the German generous financial support our fruitful program may not have existed.

Ziad Abdeen

(Dean of Research, Department of Biological Sciences, Al Quds University, Jerusalem)

Palestinians need stronger scientific and institutional capacity to address problems unique to their marine and environmental circumstances. We envisage a pluralistic, regional marine and environmental research program that will nurture productive local scientific groups linked together in transnational networks to address both national and regional marine and environmental problems.

The objectives were to develop Palestinian capabilities in the field of marine biology and to enhance and foster the peace process through collaborative research.

Assessment of Palestinian research problems in marine biology

In spite of the absence of a conducive environment for research due to:

Lack of research culture, weak research infrastructure and scarce financial resources.

From the viewpoint of Palestinians, marine and environmental research is a critical mean of empowerment, enabling Palestinian communities to understand their problems, decide on feasible actions, execute the actions efficiently and effectively, and search for solutions to unresolved problems. Without marine and environmental research, Palestinians will often be flying blind in their attempts to improve marine and environmental issues.

Adopting a sustainable marine research capacity

Our strategy as a University has been to collaborate and go for capacity building at four levels namely:

Personnel level - Develop our critical mass of human resources (Software)

Facilities level - Acquire necessary equipment and back up facilities (Hardware)

Networking level - Ever strengthening networks of research collaboration locally, regionally and internationally

Publication level - Acceptability among the Scientific Community in terms of publications in peer-reviewed journals.

The scientific community

Is not just a place on a map but rather a complex network of relationships founded upon shared values?

Things seem to turn out best for those researchers who can make the best out of the way things turn out. It is not the situation; it is our reaction to the situation.

I for one did not join the research activity, which I loved but learnt to love the research activity which I have joint.

The contribution by RSP

The RSP has helped the Palestinian side namely Al-Quds University in collaboration with the Palestine Consultancy Group (PCG) to achieve its objectives at all levels as stated in our strategy. The outcome of the RSP endeavor has been as follows:

Personnel Level: 1 PhD and 2 MSc students. In addition, many seminars and training courses were specifically organized to address the needs of the Palestinians and have been attended by 19 participants.

Facilities Level: A marine biology laboratory was set up, fully staffed and equipped with basic marine instruments. A back up library specialized in marine and environmental biology which has been approved by the RSP funding scheme is in the process of being established and the list of books and journals have been ordered.

Networking level: A wide array of network has been established with local, regional and national institutions (n=9) and scientists (n=29).

Publication level: More than six papers have been submitted to peer reviewed journals. Many presentations and few posters have been made in international workshops and conferences. Two theses and one dissertation have also been submitted.

This is to show that the sum is much greater than the individual parts. I.e. the contribution of the RSP has been the establishment of a Marine Biology Department at Al-Quds University and a wide coalition of students, researchers and scientists.

Conclusion

Marine research is a system involving people, institutions and processes. Its pursuit depends on systematic analysis, creativity, and exploration. Results from marine research traverse many channels to find their ultimate use. The quality of marine research and research strengthening efforts, as well as their quantity, needs improvement. Specifically: Much longer time horizons should be used for marine research capacity building, and innovative financing strategies such as funding pools and funding intermediaries should be explored.

In the end, although collaboration in the field of marine research has provided me with a multitude of opportunities for pleasure, but has failed to generate joy yet. But I am an optimist.

Ahmad H. Abu Hilal

(Director, Marine Science Station, Aqaba)

The Marine Science Station (MSS) at Aqaba, Jordan was a latecomer to the Red Sea Program (RSP). Beforehand conditions allowed MSS to sign only a bilateral two-year agreement with ZMT on basis of mutual benefits to both institutes. During that initial period 1997-1999 the relationship between the two institutes became excellent and their scientific cooperation has witnessed greater progress than what was anticipated. The Marine Science Station has hosted many graduate students from Germany and Jordan. Meanwhile, German scientists and students have contributed towards the bridging of relations with the partners of the RSP, who had commenced participation in the program a year earlier. The Red Sea Program's administrative body, represented by the International Coordinator and the Secretary, have played a very important role in bringing this stage to success. At the site, the International Coordinator's effort has built a great state of confidence while in the field, the Secretary as scientist, the German students, Jordanian students and researchers' work showed excellent achievement in scientific research and person to person social relations. They were also able to cooperate in all aspects of work. By creating this spirit, the participants were interacting positively in Aqaba and Germany and were able to communicate with other students, researchers, and scientists from the institutes of other RSP participant countries. Jordanian researchers and students have joined cruises, training courses and workshops of RSP in these countries.

The success of the bi-national cooperation has resulted in the MSS joining the second phase of the RSP 1999-2000, as an equal partner. In fact this period witnessed very important activities within the Red Sea Program, where the MSS was the focal point of most of these activities or was very active participant in activities that took place outside Aqaba. By the end of the RSP II, 1999-2000, about 14 German graduates, researchers and volunteers visited Aqaba and worked there on more than one occasion. About 14 Jordanian graduates worked for their theses in Aqaba and at many universities in Germany. They worked under the scientific guidance and supervision of German and Jordan scientists and were able to produce good scientific results quantitatively and qualitatively.

Several workshops for the participants of various scientific research themes, were held at the MSS with attendance of participants from all RSP countries. Training courses in Marine Science, in taxonomy of marine organisms and on five levels of SCUBA diving were held in Aqaba. Aqaba also hosted an important Steering Committee Meeting, which was held during the same period of the visit of the famous research vessel "Meteor" to the Gulf of Aqaba. Jordanian students and researchers were very active participants in various phases of the cruise in February-March 1999.

Jordan and the MSS consider the Red Sea Program a unique cooperative scientific research and training program because of the following :

- The program was able to bring scientist and students from the participating countries of the Middle East to work together, to communicate and know each other and to try and cooperate with one another. Without the program it would have been difficult, if not impossible, to achieve this level of cooperation.

- The program opened the doors for researchers, scientists, students, technicians and other employees from various institutions in Germany and the riparian countries of the Gulf of Aqaba, to exchange useful visits and experiences and also participate in scientific cruises of the Gulf of Aqaba.
- The program has achieved its goals in terms of producing good results of research in each participating country and further results of research with participants from more than one country.
- The program has contributed greatly to the capacity build-up of the participating institutions in terms of modern instruments and other equipment. Some of the laboratory and field equipment was very essential for the research conducted in the Gulf of Aqaba by students and researchers.
- The program opened the door for Jordanian students and researchers to work and/or visit German institutes and benefit from the supervision and/or participation of German scientists in their research. They benefited from the knowledge of the German scientists and from the technology that was made available to them. The students and the the young Jordanian scientists are considered a new blood in MSS and other scientific institutions in Jordan.
- Jordanian graduate students and technicians were able to join very useful courses in Germany and in other RSP countries.

The transfer of technology is one of the most important future fields of cooperation which the MSS is planning to include in any future cooperation program. ZMT and MSS have a common interest in this subject.

It can be stated that the capacity build-up for MSS by RSP was a corner stone in the relation between the MSS and the ZMT within the program. This capacity build-up was a comprehensive one and included the MSS human resources as well as its facilities. RSP is well known in Jordan and particularly at the University of Jordan and the Yarmouk University which cosponsors the MSS as an example of very successful and useful programs, which is based on mutual benefits and respect.

Oceanic System of the Gulf of Aqaba

Seasonal cycle of phytoplankton, mesozooplankton and copepod gut content analysis in the Gulf of Aqaba, Red Sea

Tariq AL-Najjar[1], Ulrich Sommer[2], Nasser S. Abdel Rahman[4] and Mohammad I. Badran[1]

1) Marine Science Station, Aqaba
2) Institut für Meereskunde an der Universität Kiel, Kiel
3) Zentrum für Marine Tropenökologie, Bremen
4) National Institute of Oceanography and Fisheries, Cairo

Seasonal succession among the microphytoplankton was observed in this study. Prochlorophytes dominated during the stable summer stratification period till late of fall season, and it formed about 40% of the photosynthetic biomass, reaching a maximum abundance during August when it formed about 45% of the total photosynthetic biomass. Prochlorophytes did not exceed 5% of the total photosynthetic biomass during December, January and February, whereas in late winter during March they formed less than 1% of the total photosynthetic biomass. Eukaryotic algae dominated during the winter mixing period and formed about 95% of the total photosynthetic pigments, which is much lower than 40% of the total photosynthetic pigments during most of year. The time series record of different phytoplankton pigments analyzed by HPLC shows that Dinophyceae have a low biomass throughout the entire year, which never exceeded 5 ng/l. Cryptophyceae were only registered in the period from November till mid of May, the maximum biomass was (60 ng/l) in December. Prymesiophyceae and Chrysophyceae are evenly distributed over the year, the maximum biomass of Prymesiophyceae was found in winter during January (40 ng/l), while Chrysophyceae reached their maximum biomass (60 ng/l) in spring. Two peaks of Chlorophycea were recorded first in the beginning of winter (88 ng/l) second in beginning of spring (78 ng/l). *Synechococcus* was found around the year with an average of (20 ng/l) and major peak in April (47 ng/l). High biomass levels of Bacillariophycea were detected during spring 158 ng/l in comparison with less than (10 ng/l) in the rest of the year Fig (1).

73 species of zooplankton belonging to 45 genera and 10 taxa were identified. Copepoda outnumbered all other groups forming 87% of the total zooplankton including 56 species within 30 genera. The highest abundance of total zooplankton was recorded in spring with a peak in June (average 1157 ind/m^3), due to the high population of Copepoda (Figs. 2 and 3).

The order Calanoida was represented by 35 species, the dominant species in this order were *Clausocalanus furcatus*, *Mecynocera clausi*, and *Ctenocalanus vanus*. The Cyclopoida were represented by 3 species of *Oithona*, including the dominant *Oithona plumifera*. Fourteen species were identified within the order of Poesilostomatoida dominated by *Oncaea media*, *Oncaea conifera* and *Farranula gibbula*. Harpacticoida were very rare and represented by 4 species.

A number of xanthophylls were found in the gut content of copepods (Figs. 4 and 5). The predominance of peridinin in the copepod gut contents indicates that dinoflagellates were the principal pigmented food source of the copepods studied. The presence of fucoxanthin in both calanoid copepods in spring and zeaxanthin in summer suggest that diatoms were infrequently ingested in spring bloom, however, Cyanophyta were ingested in summer.

Fig. 1: Seasonal pattern of phytoplankton composition in the Gulf of Aqaba.

Fig. 2: Zooplankton community in the Gulf ofAqaba.

Fig. 3: Seasonal variation in zooplankton abundance in the Gulf of Aqaba.

Fig. 4: Gut content analysis (ng/ind) of cyclopoid copepods in the Gulf of Aqaba during the study period.

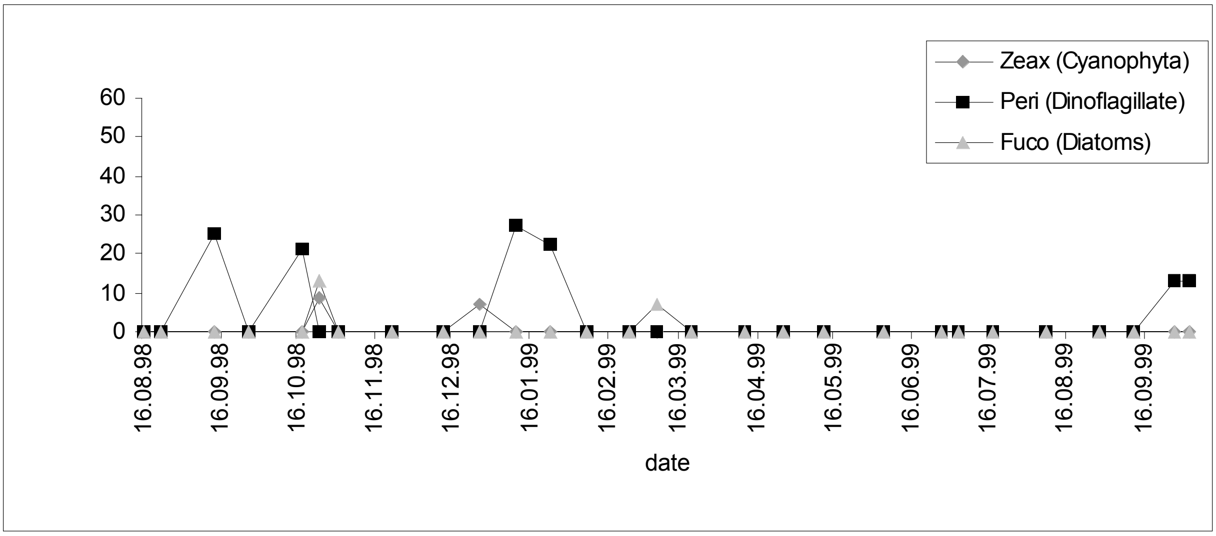


Fig. 5: Gut content analysis (ng/ind) of calanoid copepods in the Gulf of Aqaba during the study period.

Dual limitation of phytoplankton productivity in the Red Sea by nitrogen and phosphorus

Mutaz Al-Qutob[1], Zvy Dubinsky[2], Clivia Häse[3], Max M. Tilzer[4], Jonathan Erez[5] and Boaz Lazar[5]

1) Department of Biological Sciences, Faculty of Science and Technology, Al-Quds University, Jerusalem
2) Department of Life Sciences, Bar Ilan University, Ramat Gan
3) Zentrum für Marine Tropenökologie, Bremen
4) Universität Konstanz, Konstanz
5) Institute of Earth Sciences, The Hebrew University of Jerusalem

The Redfield Ratio, C:N:P=106:16:1, represents the mean proportions of these three elements in marine seston worldwide, indicating the relative nutrient salt requirements by marine plankton. The excess of dissolved phosphate usually found in nutrient poor surface waters of the oceans, and experiments showing nitrate stimulation of phytoplankton productivity led to the conclusion that productivity in the marine environment in general is nitrate limited. Our field data show that the proportion of dissolved nitrate to phosphate in the oligotrophic Gulf of Aqaba, northern Red Sea, is close to the Redfield Ratio even at very low concentrations. The field data together with nutrient enrichment bioassays prove that both nutrients simultaneously control phytoplankton productivity in the northern Red Sea.

The Gulf of Aqaba at the northern tip of the Red Sea receives its water from the Indian Ocean through the Gulf of Aden via two shallow sills: Bab al Mandab (ca. 140 m deep), and 2,000 km to the north, the Straits of Tiran (ca. 250 m deep). This area is sparsely inhabited and surrounded by a desert. Therefore, mainly internal nutrient cycles within the gulf drive its productivity.

The vertical distribution of nutrients in the Gulf of Aqaba is controlled mainly by the alternation of thermal stratification in summer and deep winter mixing. During summer, nutrient salts in the euphotic zone are completely exhausted, and input from deep waters is restricted by the thermocline. By contrast, during winter mixing nutrient salts are entrained into the euphotic zone from deep waters (maximum depth at the sampling site 700 m). However, even in winter nutrient salts are usually depleted. Winter mixing depths vary between years, owing to variable extents of surface cooling. The deeper the mixing, the more nutrients are introduced into the euphotic zone and the more phytoplankton biomass forms during the spring bloom (see Häse et al., this volume). From this we conclude that the overall phytoplankton productivity is controlled by nutrient salt availability.

The question which one of the two nutrients, N or P, is limiting phytoplankton productivity in the Gulf of Aqaba was assessed from ambient N and P concentrations. All available data points from vertical profiles of total inorganic nitrogen and inorganic phosphate during the study period were plotted against each other (Fig. 1). The result was a highly significant linear relationship:

$$N = 15.6\ P + 0.01\ ;\quad r^2 = 0.8902$$

This indicates that

1. N and P vary proportionally, approximately according to the Redfield Ratio, throughout all around the year as a result of uptake by phytoplankton.

2. Both nutrients are practically exhausted by phytoplankton uptake.

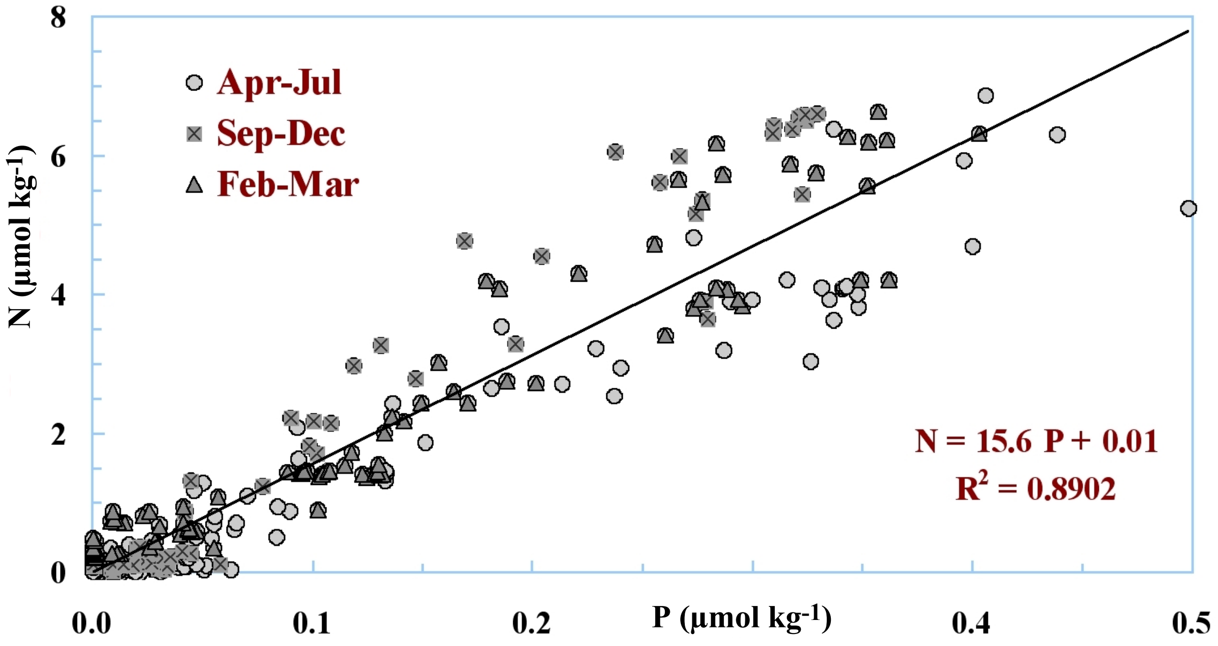
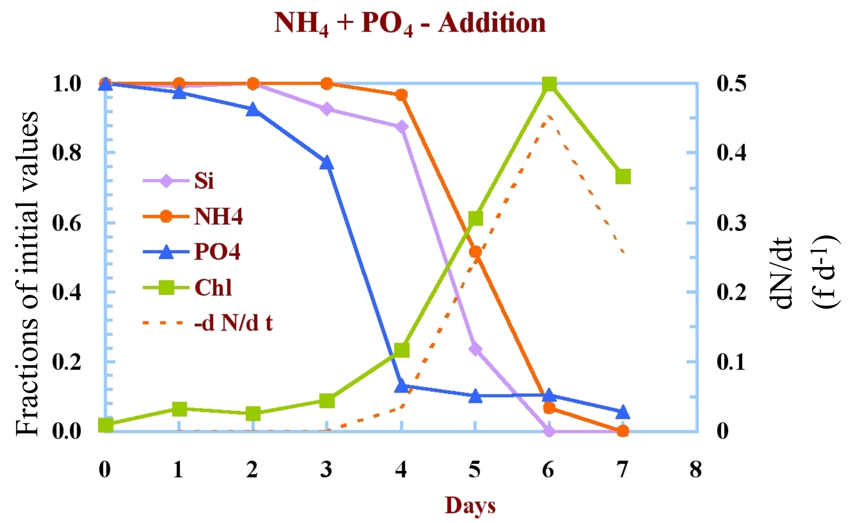


Fig. 1: Relationship between ambient total inorganic nitrogen concentrations ($NO_3 + NO_2 + NH_4$) and inorganic phosphorus (PO_4) in of the northern Gulf of Aqaba (Station A) from 1997 - 2000. Values during winter mixing and spring bloom (February – April) plotted with different signature than values during late summer (August-September). Note that the down panal is an enlargment for the near-surface and euphotic zone water. Note that the slope of the regression line (here representing the N : P atomic ratio) is similar (ca. 15.6) throughout the year and is close to the classic Redfield Ratio of N : P = 16).

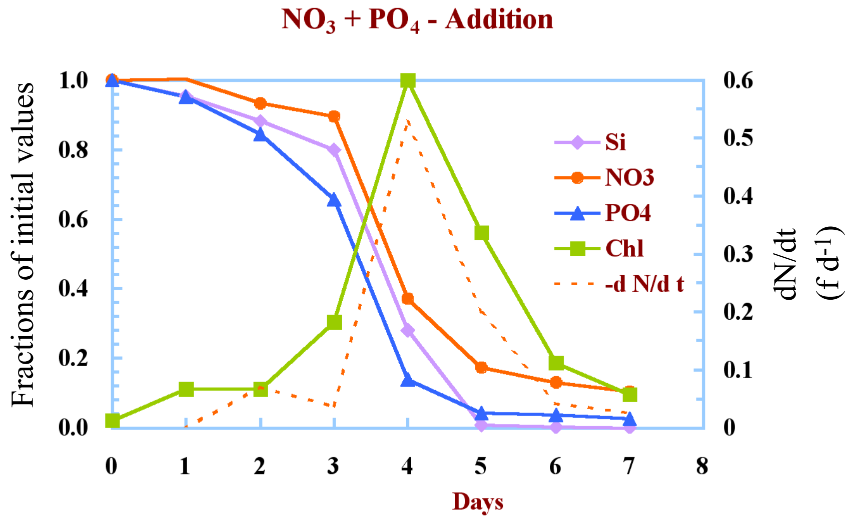
Thus, our field data clearly support the idea of co-limitation of phytoplankton productivity by N and P.

In order to prove this hypothesis, nutrient stimulation bioassays were performed by adding nutrient salts to water samples from the sea surface and the depth of the deep chlorophyll maximum (DCM; ca. 70 m), respectively. Nutrient additions included nitrate, ammonia, and phosphate alone, as well as either nitrate or ammonia together with phosphate. Final concentrations were 0.4 µM P and 6 µM N, respectively. In addition, nutrient-rich deep (600-m) water was added to surface- and DCM-water. Stimulation was monitored by assessing *in vivo* fluorescence as a measure of algal biomass, and nutrient salt concentrations within the experimental flasks that were incubated under natural light conditions for 8 days.

Only additions of both N and P combined, as well as additions of deep water had stimulatory effects on phytoplankton growth, whereas neither N nor P alone elicited any responses (Fig. 2): In the experiments with combined additions of nitrogen and phosphorus, both added nutrient salts as well as silica were completely exhausted within 4-6 days. The development of the *in vivo* chlorophyll fluorescence clearly reflects the nitrate depletion rates (dN/dt). The depletion of silica suggests that diatoms comprised a significant fraction of the phytoplankton involved. However, phytoplankton biomass rapidly decreased after reaching a peak, probably due to grazing by micro-zooplankton (samples were pre-filtered over 65 µm net).



NH_4 + PO_4 - Addition



NO_3 + PO_4 - Addition

Fig. 2: Phytoplankton response to nutrient enrichment

Surface and DCM samples behaved in basically similar fashions. Surprisingly, stimulation was quicker in samples with nitrate than with ammonia additions.

Conclusions

1. In the oligotrophic Gulf of Aqaba the yearly average of the N:P ratio is close to the Redfield ratio, suggesting that neither N nor P alone can stimulate phytoplankton growth significantly. Upon addition of one single nutrient species, immediately the other nutrient would become limiting. This conclusion is substantiated by our bioassay experiments.
2. Generally both nutrients co-limit phytoplankton growth with no indications for productivity restrictions due to either light limitation or iron availability, as in HNLC-regions.
3. When plotting ambient N versus P concentrations within the euphotic zone throughout the year against each other, it becomes apparent that during summer stratification nitrogen is slightly more depleted, whereas during winter mixing this is the case for phosphorus.
4. The fact that the N:P ratio is so close to the Redfield ratio suggests an effective transfer of nutrients between production and regeneration processes in the Gulf of Aqaba, probably due to the restricted nutrient input from the Indian Ocean and the surrounding desert.

Nutrient distribution and dynamics in the Gulf of Aqaba, Red Sea

Mutaz Al-Qutob[1,2], Clivia Häse[3] and Boaz Lazar[4]

1) Faculity of Science and Technology, Al-Quds University, Jerusalem
2) Department of Life Sciences, Bar Ilan University, Ramat Gan
3) Zentrum für Marine Tropenökologie, Bremen
4) Institute of Earth Sciences, The Hebrew University of Jerusalem

Nutrients play a key role in controlling productivity of the world's oceans. In open waters of the oligotrophic Gulf of Aqaba, the overall phytoplankton productivity is controlled by overall nutrient salt availability: The height of the phytoplankton spring bloom was coincident with the maximum of vertical winter mixing during all the years of the study period (Häse et al., this volume). This was attributed to the cumulative entrainment of nutrient salts into the mixed layer from nutrient-rich deep waters with increasing mixing depth.

The nutrient regime in the Gulf of Aqaba was monitored for three years by regular monthly one-day cruises of the Red Sea Program from January 1997 until January 2000, and during the two-weeks cruise of the German research vessel "Meteor" in February/March 1999. Concentrations of ammonia, nitrate, nitrite, phosphate, and silicate were measured by flow injection analysis (FIA) (Figs. 1a-c).

The concentrations of nitrate and phosphate in the upper 100 m were very low almost all around the year. Both nutrients were always depleted within the euphotic zone even during the mixing season as long as the mixing depth was less than ca. 400 m. By contrast, silicate concentration never was depleted in any depth.

The proportion of dissolved nitrate to phosphate in the Gulf of Aqaba was close to the Redfield ratio even at very low concentrations. The field data together with data from nutrient enrichment bioassays proved that both nutrients simultaneously control phytoplankton productivity in the Gulf of Aqaba (Al-Qutob et al., this volume first).

During summer, in the stratified water column ammonia was present (Fig. 1c) and nitrite formed a deep maximum just above the nitracline. During mixing, ammonia concentrations were unexpectedly low, and nitrite was homogeneously distributed throughout the mixed layer.

Within the nitrogen cycle, nitrite plays only an intermediate role as product of biological processes. Nitrite is produced during the decomposition of organic matter by nitrification. Another source is the excretion by phytoplankton which in turn is also able to assimilate nitrite. Under oxic conditions, like in the Gulf of Aqaba, nitrite production by denitrification is negligible.

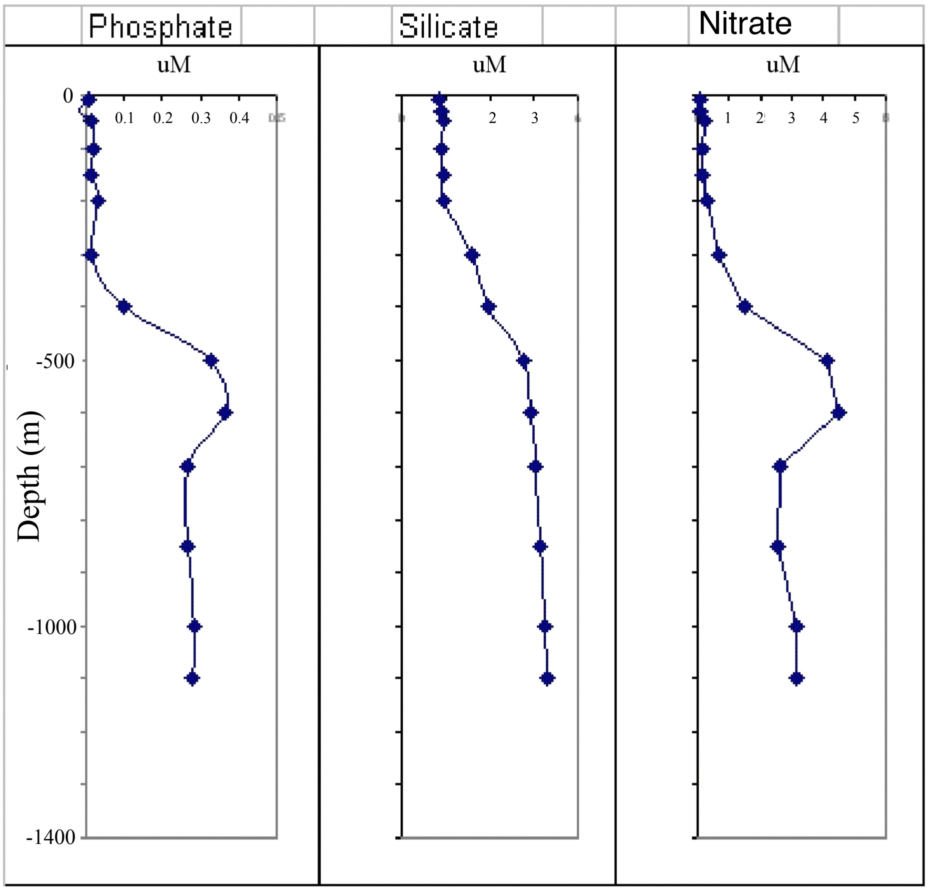


Fig. 1a: Phosphate, silicate and nitrate profiles. Station K 22/2/1999 in the Gulf of Aqaba.

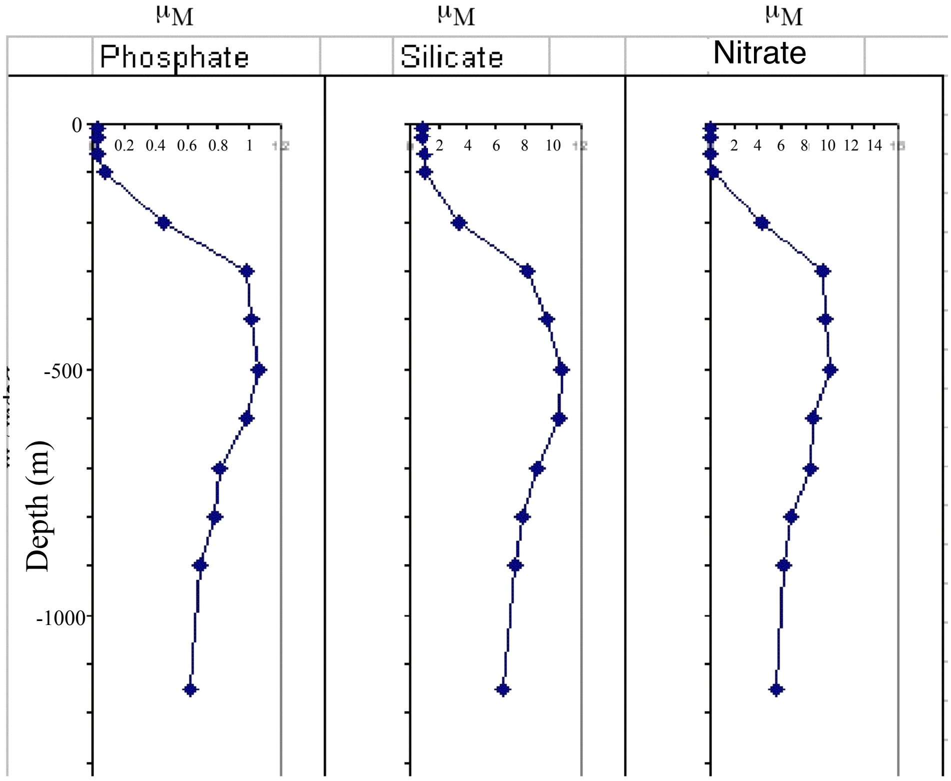


Fig. 1b: Phosphate, silicate and nitrate profiles. 24/2/1999 in the northern Red Sea.

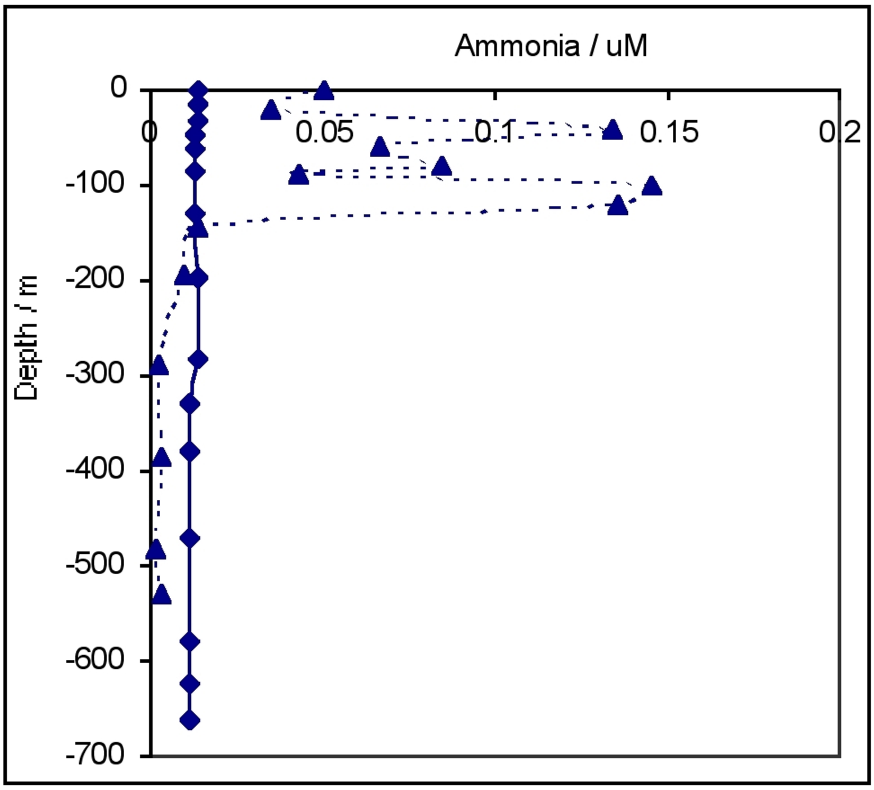


Fig. 1c: Ammonium profiles during mixing (solid line), and during stratification (dotted line). Station A.

During the mixing season, the accumulation of nitrite within the mixed layer was coincident with the development of the phytoplankton bloom as a result of nutrient injection from deep waters. This phenomenon was reproduced by an experiment that simulated the mixing process by adding nutrients to water samples collected at the surface and at the depth of the DCM. The experimental flasks were incubated in 20 m depth, for further details see Al-Qutob et al. (b), this volume. These nutrient enrichment bioassays were performed in September 1999, i.e. at the end of the stratification period. At this time, nitrite in situ was only present in the deep nitrite maximum below the deep chlorophyll maximum. The results of the bioassays are summarized as follows:

1. Nitrite did accumulate within the incubation flasks during the course of the experiment only in the bioassays with dual nutrient additions (N plus P) in which phytoplankton biomass increased markedly. In bioassays with single nutrient additions, no response was elicited (Fig. 2).

2. Nitrite did accumulate in remarkable concentrations only in light samples, not in dark samples.

3. Nitrite accumulation closely followed the development of phytoplankton biomass without a time delay (Fig. 2).

4. Nitrite accumulation in the bioassays with nitrate plus phosphate was faster than in the bioassays with ammonia plus phosphate.

5. The samples from surface and from DCM showed a similar response.

Especially from 4. we conclude, that nitrite production from ammonia via nitrification plays only a minor role during mixing.

Our data clearly prove that the accumulation of nitrite is coupled to the development of phytoplankton biomass. At the present stage it cannot clearly be resolved if the two parameters are coupled directly by phytoplankton excretion or indirectly via grazing and / or decomposition of organic matter. However, from the bioassays we have evidence for direct excretion of nitrite by phytoplankton during the mixing season since no consumption of the added ammonium in the bioassays could be observed within the first days of the experiment, neither by phytoplankton nor by bacteria.

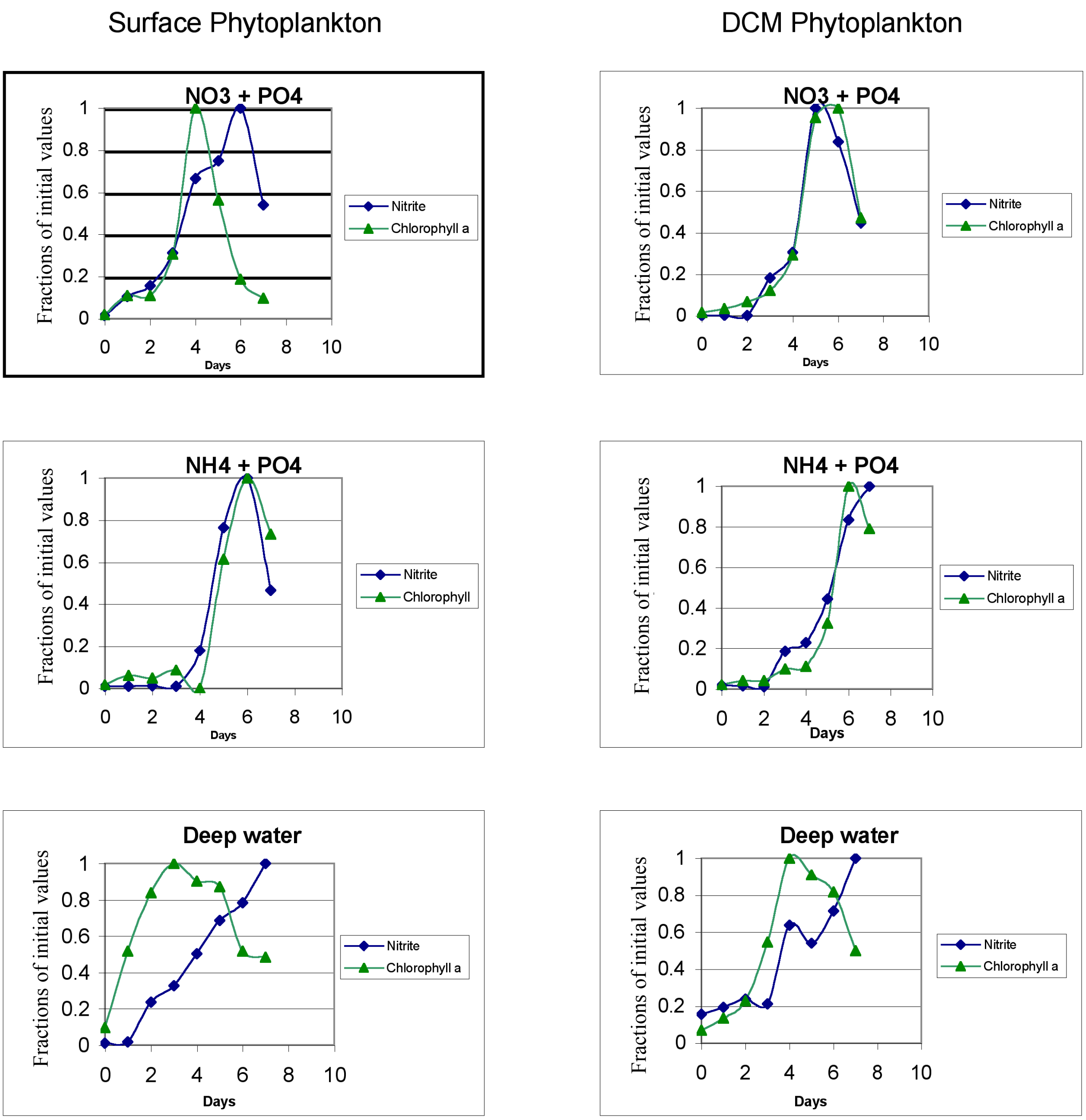


Fig 2: Time course of nitrite concentration and *in vivo* fluorescence during the 8-days incubation of the nutrient enrichment bioassays.

Nutrient chemistry and circulation of waters of the Gulf of Aqaba, Red Sea

Mohammad I. Badran[1] and Riyad S. Manasreh[2]

1) Marine Science Station, Aqaba
2) Yarmouk University, Irbid

Research on nutrient chemistry of the Jordanian waters of the Gulf of Aqaba goes back to mid 1970s. However, it was not until 1994 that reliable analytical methods have been developed and studies covered a significant segment of the water column. Even then the MSS has not been properly equipped with oceanographic tools. The work was manual, exhausting and time consuming. It is thanks to the RSP that supplied the MSS with oceanographic equipment, including an electromechanical winch, GPS, CTD and current meters.

Circulation patterns

Current speed and directions of waters of the north eastern section of the Gulf of Aqaba are summarized in Table 1. The coastal current general direction (~50%) is south/south-east. Speed is mainly between 3 to 10 cm.sec^{-1}. Cross sectional currents in the upper 25 m waters are mainly from offshore to inshore.

Tab. 1: Percent frequency of the water current speed and direction at the north eastern coast of the Gulf of Aqaba during specific periods.

Speed (cm/s)	**04/09/99 to 11/09/99**	**20/10/99 to 26/12/99**	**27/12/99 to 26/01/00**	**26/01/00 to 27/02/00**	**08/03/00 to 21/03/00**	**22/03/00 to 05/05/00**
0--3	5.98	8.73	51.14	78.91	59.08	52.37
3--6	58.68	59.65	33.77	18.66	36.36	35.91
6--9	27.25	21.53	13.84	2.43	4.56	10.17
9--12	6.89	8.2	1.25	0	0	1.5
12--15	1.2	1.89	0	0	0	0.05

Dir. (deg.)	**04/09/99 to 11/09/99**	**20/10/99 to 26/12/99**	**27/12/99 to 26/01/00**	**26/01/00 to 27/02/00**	**08/03/00 to 21/03/00**	**22/03/00 to 05/05/00**
0--45	10.18	11.93	2.21	3.55	11.62	6.06
45-90	18.86	15.56	5.54	8.87	32.32	9.96
90-135	14.07	21.47	34.39	34.49	11.31	17.76
135-180	8.89	9.29	22.01	19.65	1.11	14.6
180-225	21.86	8.2	12.66	10.9	2.07	14.94
225-270	17.96	13.58	15.29	10.55	10.35	21.6
270-315	2.99	13.11	5.47	6.86	19.11	10.56
315-360	5.09	6.87	2.42	5.12	12.1	4.51

Nutrient and chlorophyll *a* seasonal cycle

Since April 1997 records of temperature, nutrients and chlorophyll *a* have been regularly generated on biweekly basis, down to 400 m, at a vertical resolution of 25 m. Fig. 1 shows the annual cycle of the records of temperature, salinity, density, ammonia, nitrate, nitrite, phosphate, silicate and chlorophyll *a*.

Fig. 1. demonstrates that the temperature field has a well-defined seasonal pattern of winter mixing from December to April and summer stratification from May to November. All other parameters closely related to this pattern. Chlorophyll *a* shows a seasonal pattern with a distinct summer peak between 50 and 75 m. Ammonia has been undetectable in the entire

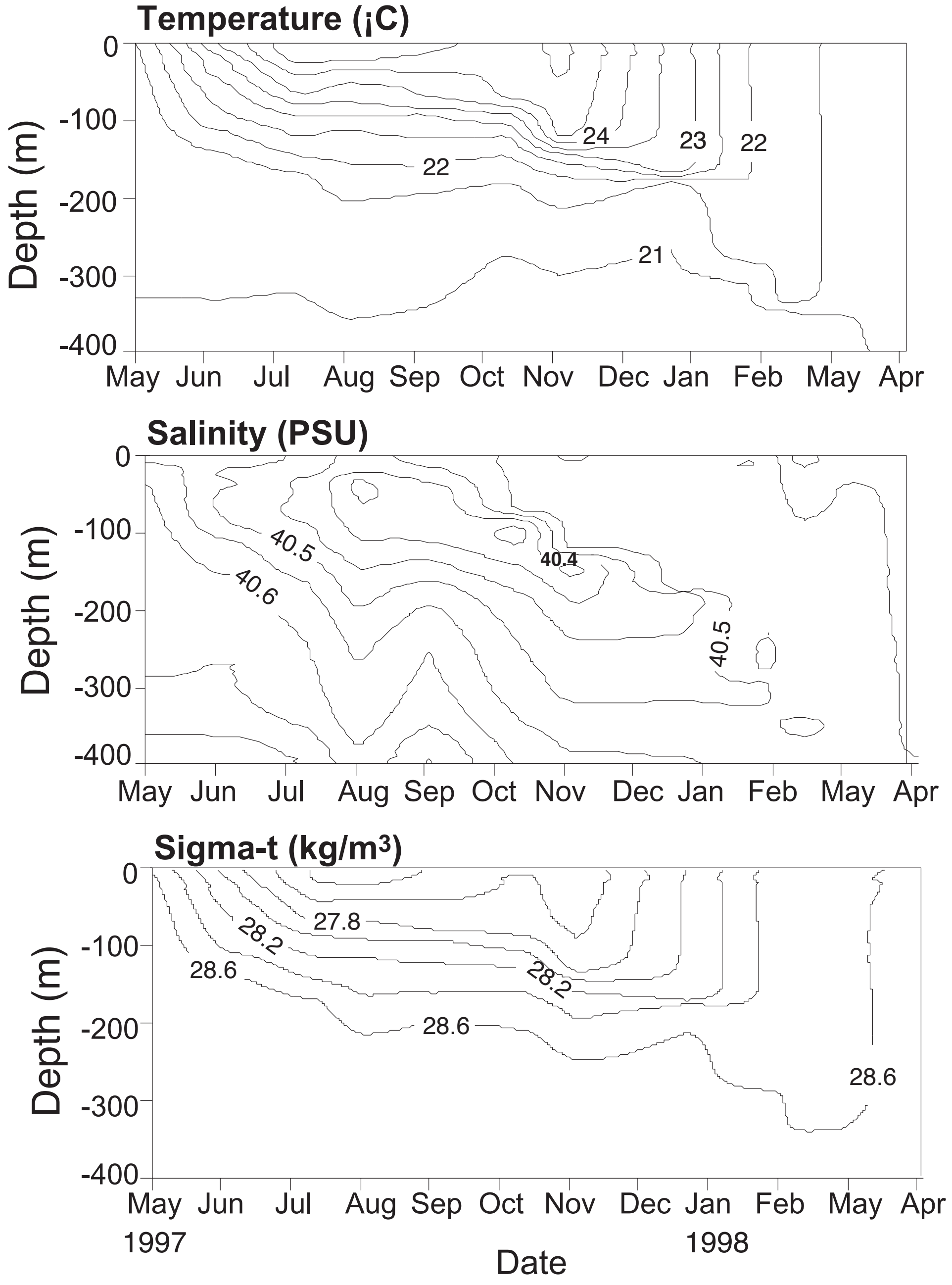


Fig. 1: Annual cycle of water temperature, salinity, density, nutrients and chlorophyll *a* for the 0-400 m water column 3 km offshore in the Gulf of Aqaba, Red Sea.

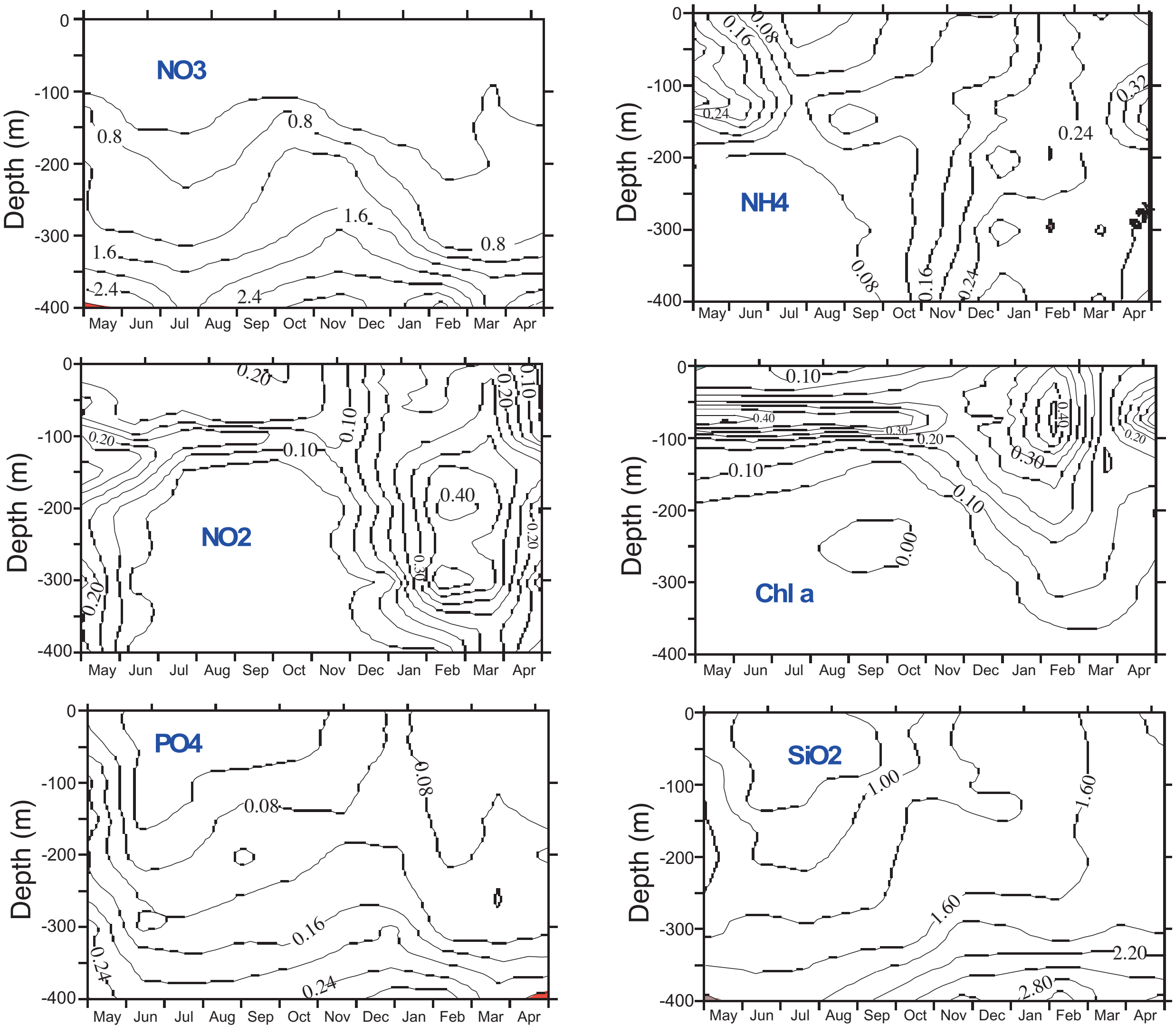


Fig. 1: (continued)

water column during summer and is relatively abundant and homogeneously distributed in winter. Nitrite has a seasonal pattern similar to that of chlorophyll *a* and exhibits a summer subsurface maximum just below that of chlorophyll *a*. Nitrate, phosphate and silicate have similar seasonal patterns characterized by high concentrations in deeper water during summer overlaid by low concentrations in the case of nitrate and phosphate but relatively abundant in the case of silicate. In winter the three nutrients exhibit relatively high concentrations homogeneously distributed in the entire water column.

Nutrients and chlorophyll *a* in the coral reef water

Substantial effort has been made to study the nutrient and chlorophyll *a* behavior in the coral reef waters. Both observational and experimental data have been generated. Fig. 2. shows a comparison between coral reef waters and reference offshore waters with respect to nutrients and chlorophyll *a*. Fig. 3. shows a comparison between waters inside coral reef caves and surrounding waters over the course at a day. Figs. 2 and 3 show clearly that the coral reef water is significantly different from the reference water and that the cave water is significantly different from the surrounding water with respect to nutrients and chlorophyll *a*. This gives rise to the caves being effective production sites of nutrients that sustain the system. Experiments to test the theory of advection being a major source of nutrients to the coral reef have also been carried out.

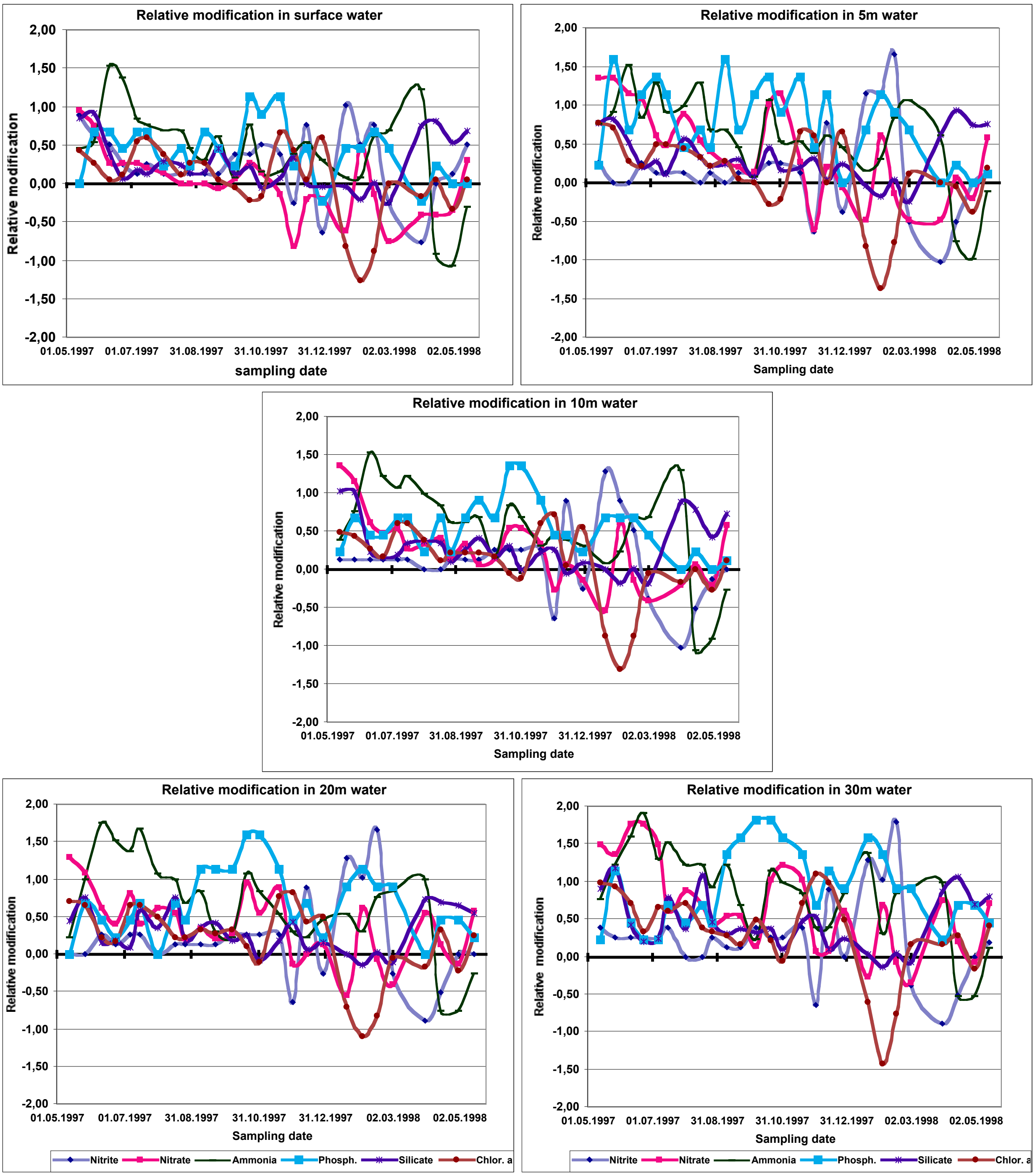


Fig. 2 : Relative modifications of nutrient and chlorophyll *a* concentrations in the surface, 5 m, 10 m, 20 m and 30 m waters overlaying coral reef in the Gulf of Aqaba.

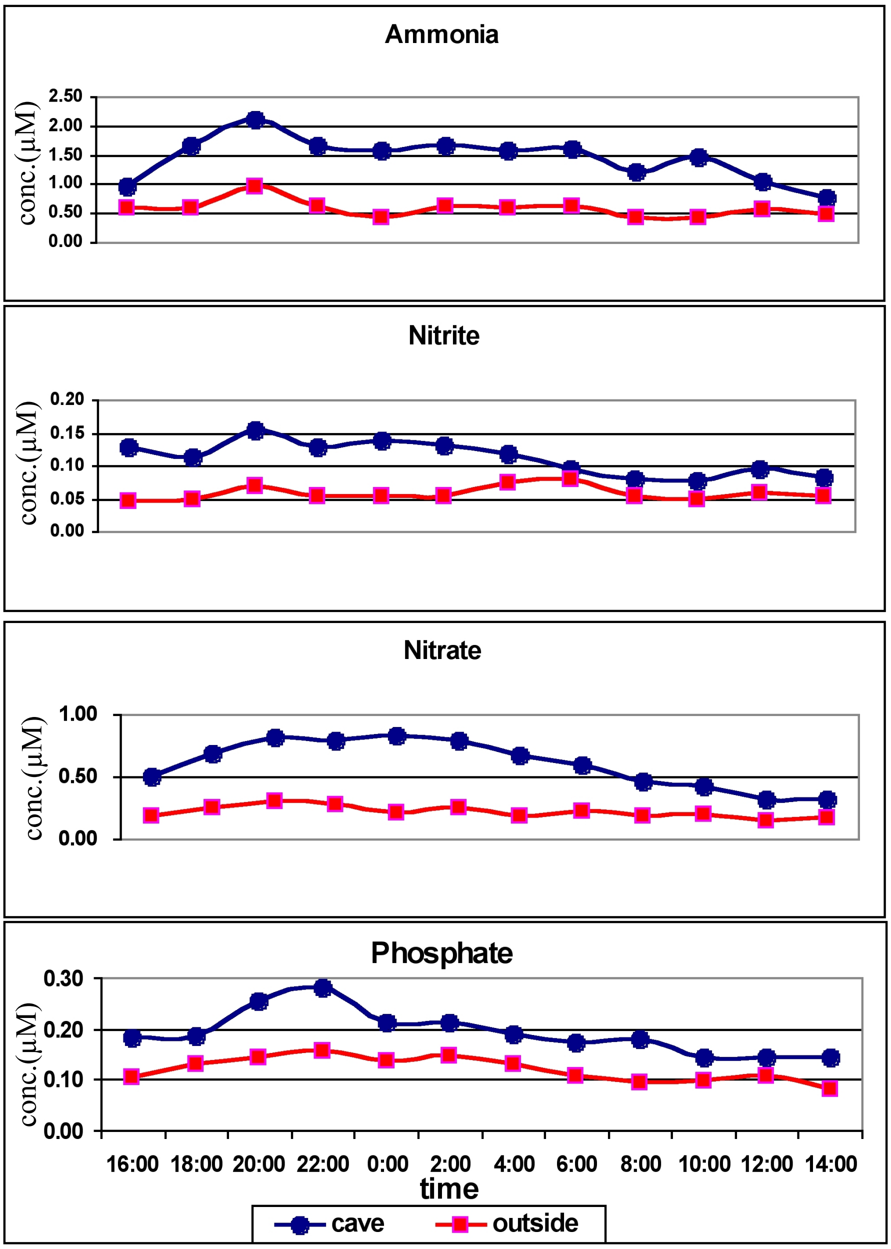


Fig. 3: Comparison between cave waters and the surrounding waters within coral reefs of the Gulf of Aqaba, Red Sea, in the diel course.

Nutrients and chlorophyll *a* in the Gulf of Aqaba and northern Red Sea

The Meteor cruise to the Gulf of Aqaba and Northern Red Sea, February 20th to March 10th 1999 provided an excellent opportunity to generate an intensive data set during the late winter mixing period. Along gulf profiles of temperature, salinity, density, nutrients and chlorophyll *a* are shown in Fig. 4. It is obvious that the well mixed conditions down to the bottom at the northern Gulf of Aqaba, and the gradual decrease in mixing intensity by going south, until pronounced stratification conditions characterize the northern Red Sea proper. This gives rise to the Gulf of Aqaba as a significant source of the deep cooler water mass and that the turn over of deep waters of the Gulf of Aqaba might be much faster than used to be believed before.

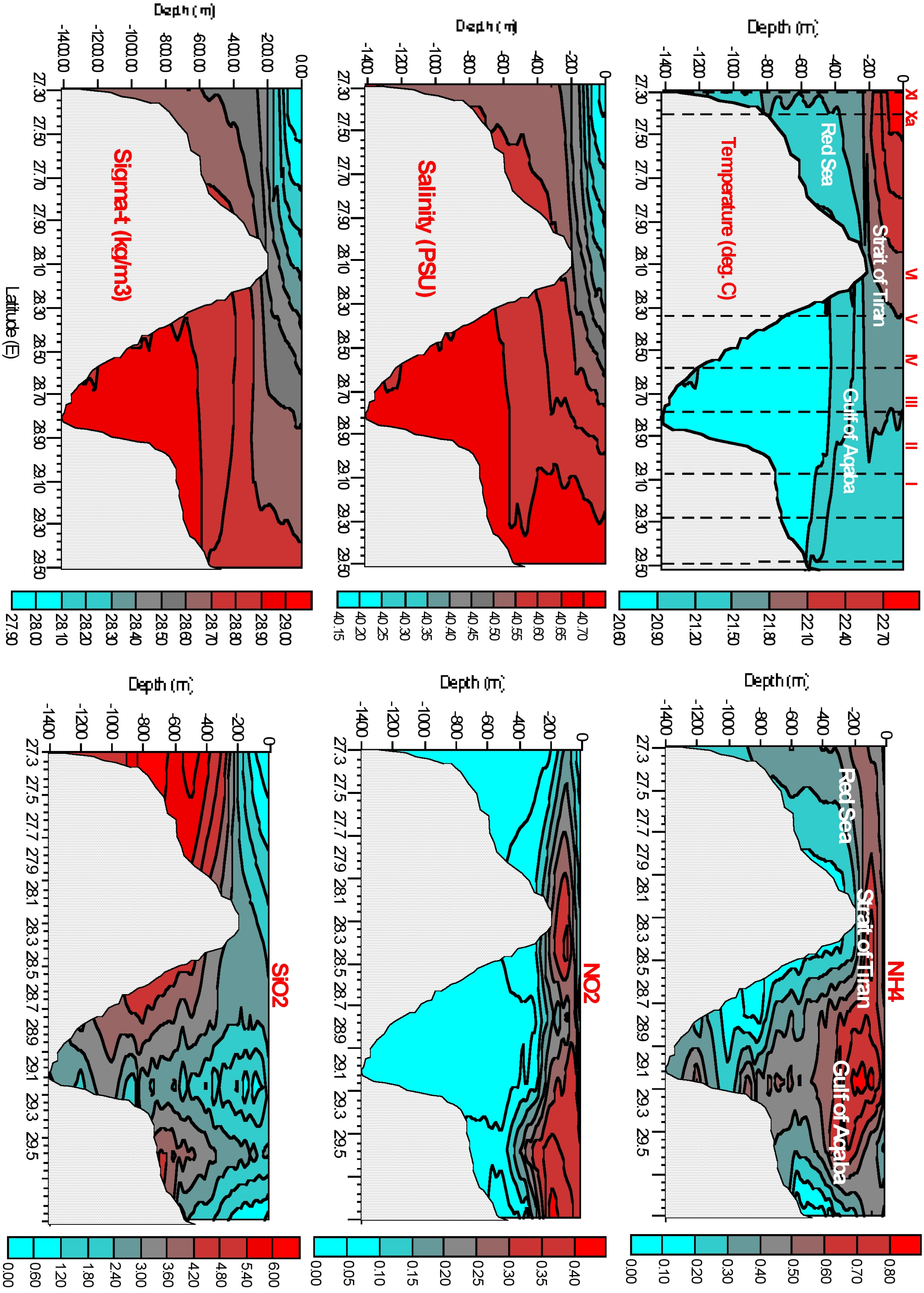


Fig. 4: Records of water temperature, salinity, density, nutrients and chlorophyll *a* along the Gulf of Aqaba and northern Red Sea during February-March 1999.

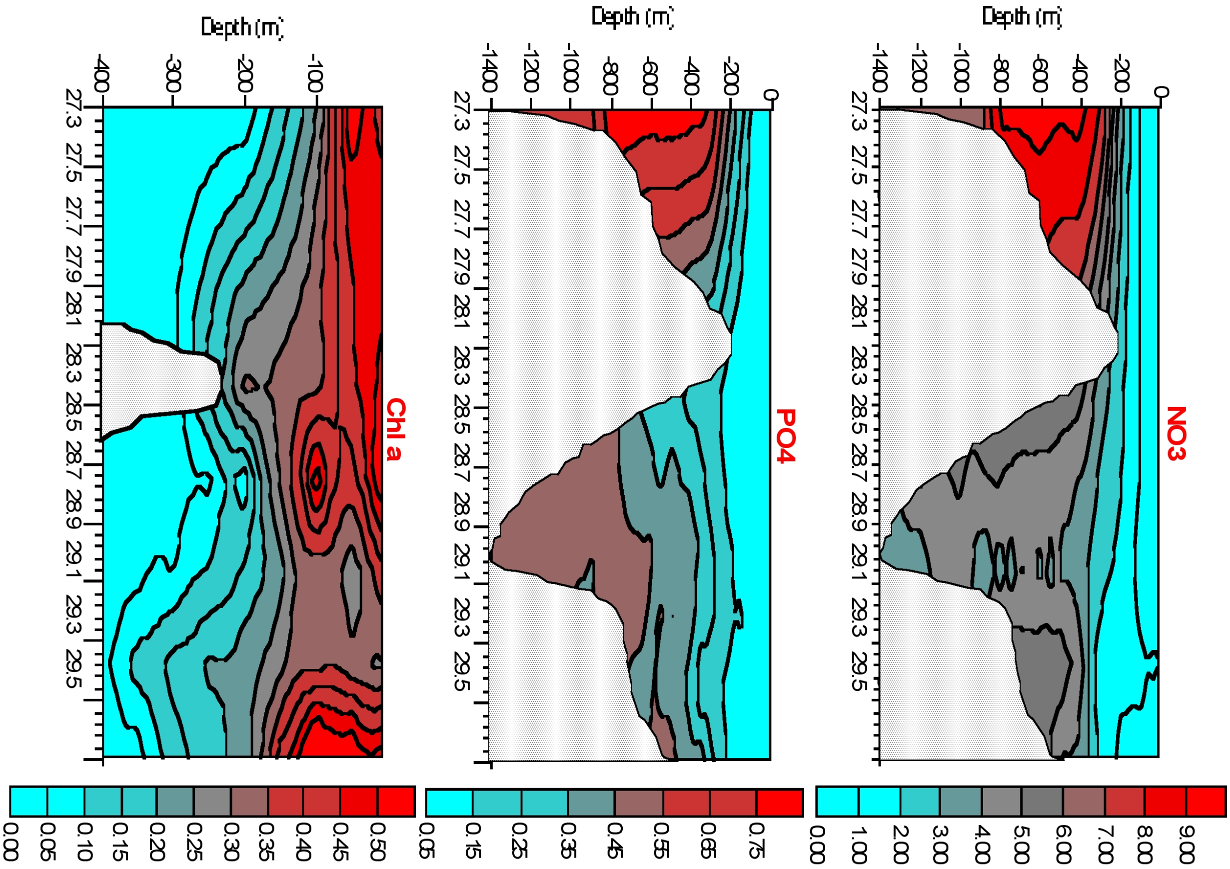


Fig. 4: (continued)

Mesozooplankton communities in the Gulf of Aqaba and northern Red Sea

Magdy Dowidar[1] and Claudio Richter[2]

1) National Institute of Oceanography and Fisheries, Alexandria
2) Zentrum für Marine Tropenökologie, Bremen

A survey was carried out on board r/v "Meteor" during February/March 1999 to study the regional and vertical distribution of mesozooplankton in the northern Red Sea and Gulf of Aqaba during the winter-spring transition period (see Annex 9). Mesozooplankton was collected with a large vertical closing net (maxiMultinet, 9 nets, 0.5 m^2 opening diameter, 150 µm mesh) by means of vertical hauls on a section extending from Aqaba in the northern Gulf along the central axis of the Gulf of Aqaba into the northern Red Sea. Zooplankton was enumerated at 8 stations covering 7-8 depth strata between the surface and 1300 m, yielding a total 66 samples. A total 141 taxa were identified belonging to 10 phyla. Copepods were by far the dominant group, comprising more than half of the taxa, and between 50-95 % of the abundances. Zooplankton densities were highest in the northern Gulf (190 x 10^3 m^{-2}) decreasing to 3-fold lower values in the Red Sea (Fig. 1). Lowest concentrations were found off Dahab (45 x 10^3 m^{-2}) in the southern Gulf of Aqaba. The vertical distribution of zooplankton reflected the density stratification of the water masses in the two regions: Weakly stratified waters in the northern Gulf (St. I-III), with homothermal waters reaching down to 300-400 m coincided with high zooplankton densities at the corresponding depths (Fig. 2). In the Red Sea, by contrast, a marked thermohaline stratification accompanied marked vertical differences in zooplankton abundance, spanning 3 orders of magnitude between the surface and >1000 m. Depth appears to be the main factor determining mesozooplankton community

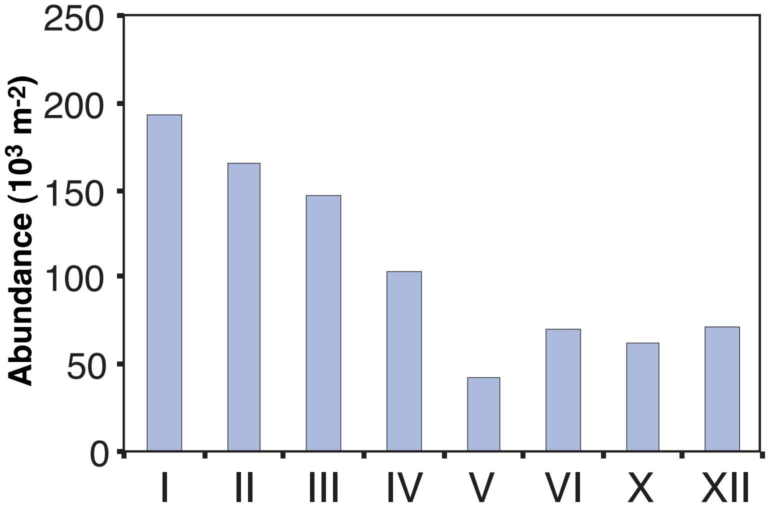


Fig. 1: Integrated mesozooplankton standing stocks in a north-south section (I - XII) between the Gulf of Aqaba and the northern Red Sea (see also Annex 9).

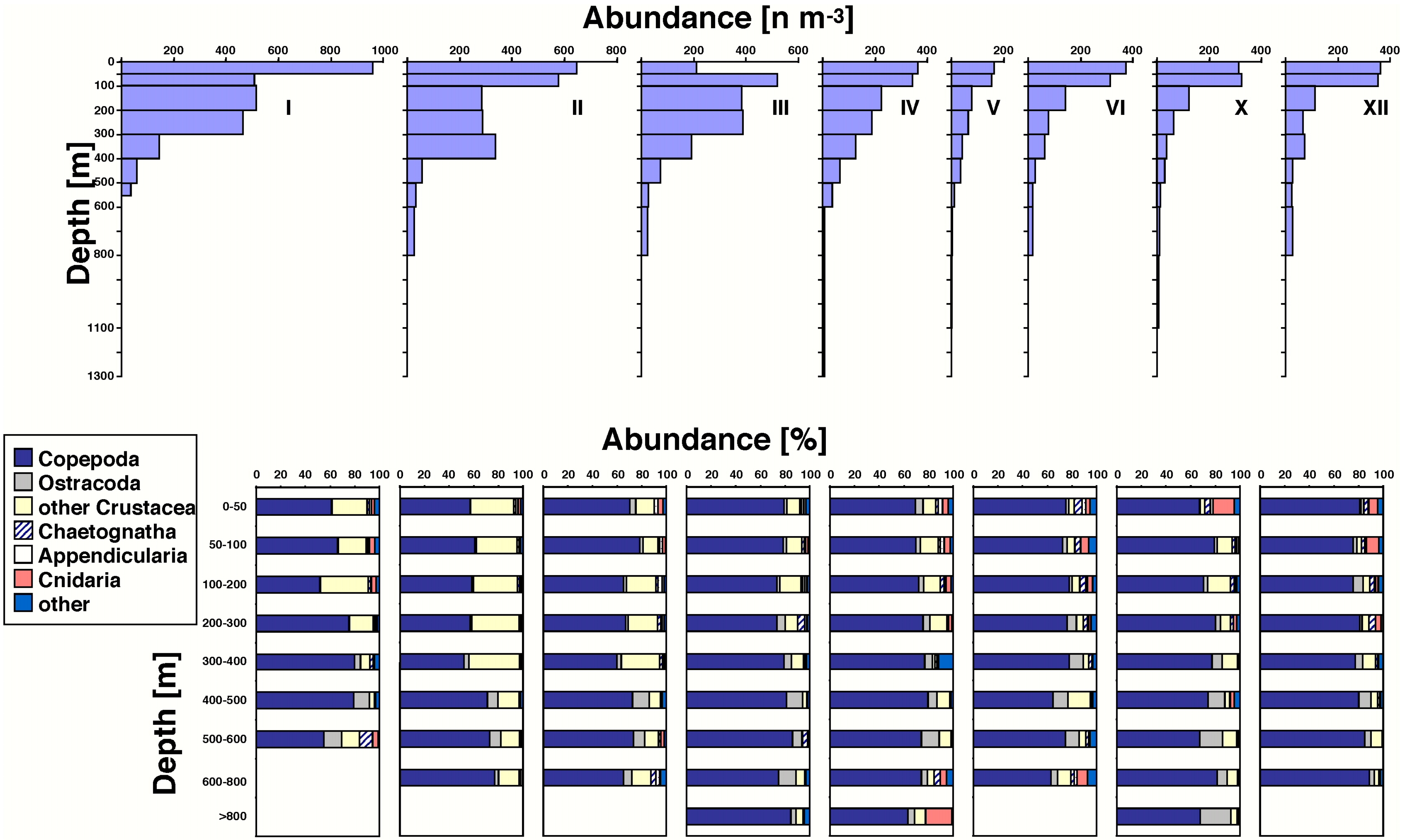


Fig. 2: Vertical profiles of mesozooplankton abundance (upper panels) and taxonomic composition (lower panels) in a north-south-section between the Gulf of Aqaba and the northern red Sea.

structure. MDS analysis carried out on a subset of the 85 most abundant taxa shows a distinct separation of shallow, intermediate and deep water plankton. By contrast, regional differences in community composition appear to be rather negligible, in spite of marked differences in water mass properties between the deep Gulf of Aqaba and Red Sea waters. SIMPER analysis shows that the abundant copepods *Mecynocera clausi, Oithona plumifera*, and *Acartia negligens* along with the rarer *Haloptilus longicornis* account for much of the dissimilarities between shallow and deep samples. The moderately abundant *Oithona setigera* and *Eucalanus attenuatus* account for most of the regional dissimilarities in shallow and deep waters, respectively.

The similarity between zooplankton, phytoplankton and temperature profiles (Fig. 3) suggests a bottom-up control of the vertical and regional differences in mesozooplankton distribution. An exception is the station off Dahab, where the extremely low zooplankton stock may be due in part to predation mortality.

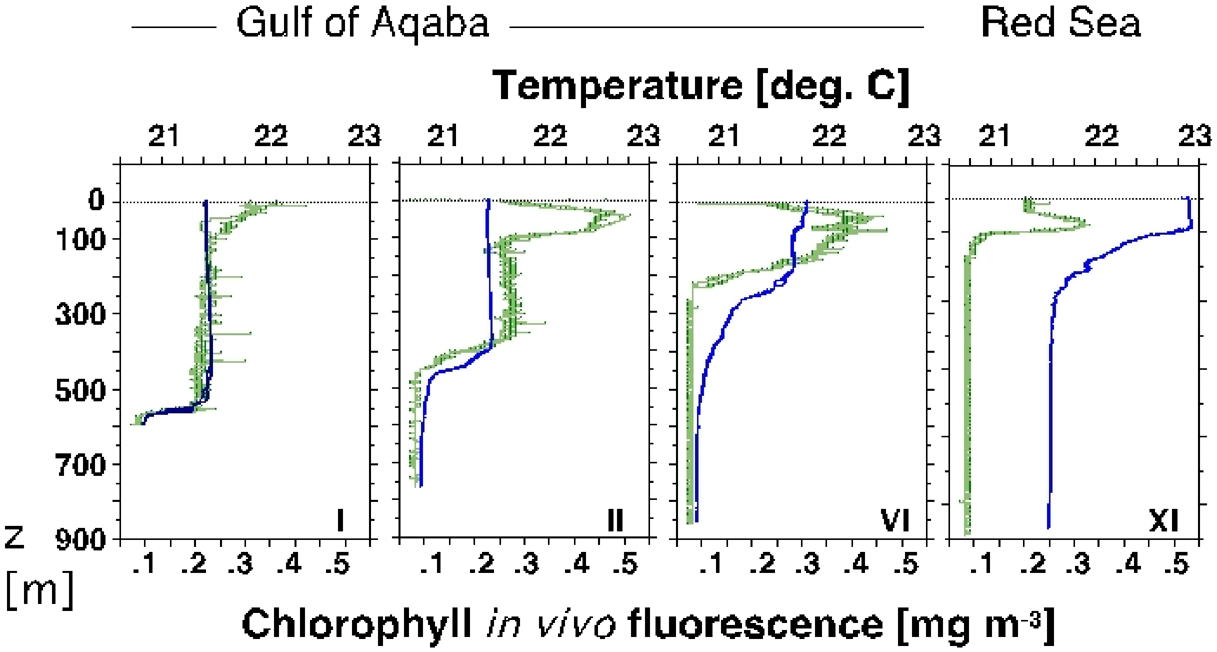


Fig. 3: Vertical profiles of temperature (solid line) and phytoplankton chlorophyll (light line) in a north-south section between the Gulf of Aqaba and the northern Red Sea.

The Type-II Hypothesis: Trophic enrichment of the coastal zone by zooplankton behavior in down-welling currents

Amatzia Genin[1], Claudio Richter[2] and Adel Ali Ahmed[3]

1) The Interuniversity Institute, H. Steinitz Marine Biological Laboratory, Eilat
2) Zentrum für Marine Tropenökologie, Bremen
3) National Institute of Oceanography and Fisheries, Cairo

Ample evidence has been accumulated throughout the past decades indicating that zooplankton becomes aggregated in regions of strong downwelling flows. Examples include both coastal areas and oceanic regions. Earlier observations presented at the proposing stage of this project showed remarkable aggregations of pelagic zooplankton along sandy shores in the northern coast of the Gulf of Aqaba, where predators are scarce. Current measurements at those sites suggested a frequent occurrence of downwelling along the coast. Zooplankton aggregations have also been reported in mid-oceanic fronts. Here the downwelling flow is generated by the sinking of the colder water under the warmer one, producing extensive convergence zones along the fronts. For example, Flament et al. (Nature, 1996) reported an "astounding" increase in the abundance of acoustic backscatterers in an North-Equatorial convergence zone, a site of strong downwelling. Naturally, fishermen have long been following fronts in the ocean in their pursue of rich fishing grounds. As zooplankton aggregates in fronts, so do their predators and the predators of those predators.

The mechanisms generating those aggregations of zooplankton in coastal and frontal zones remained, by and large, unresolved. As the residence time of the water in such highly-dynamic areas is relatively short, mechanisms involved *in situ* reproduction are unlikely. Dynamics models by Shanks, Zeldis, Franks, and others related aggregations of larvae to the occurrence of convergence flow along internal waves, as buoyant organisms (as well as floating objects) would be passively concentrated at the sea surface along the convergence line. However, unlike the case of passive floatation, a mechanism for sub-surface aggregation would require the aggregating animals to swim against the downwelling flow. To the best of our knowledge, there has been no evidence that zooplankters can retain their depth and swim against vertical flows.

The major objective of this project was to test the so called "Type-II Hypothesis", namely, that zooplankton would become aggregated in large densities in coastal downwelling zones due to their ability to actively retain their depth against the vertical flows. Accordingly, this study consisted of three parts, all carried out at coastal habitats in the Gulf of Aqaba : (1) measurements of vertical flows, (2) a characterization of zooplankton distribution across the shore, and (3) a study of the swimming behavior of zooplankton under conditions of downwelling.

Methods

The field study was carried out at two main sites: The coral reef of Eilat and a stretch of sandy habitat at Ras Burka. Supplementary data on both the physics and zooplankton was collected during additional RSP cruises to the northern (sandy) tip of the Gulf (the North Beach of Eilat) and to the coral reefs in Hibiq and Ras Abu Galum.

The distribution of zooplankton was studied by towing zooplankton net (280 µm) aboard a small skiff. The net was equipped with a flow meter, allowing quantitative estimates of zooplankton densities. The samples were preserved in 4 % formalin, and transferred to the laboratory where they were sorted under the microscope to major taxonomic groups (calanoid, cyclopoid and harpacticoid copepods, chaetognaths, appendicularia, mollusks and others). (Detailed taxonomic report of the sampled animals is included in the Interim Report submitted to the Bremen Meeting by the Egyptian group).

The physical part of this study consisted two principal operations: current measurements and temperature-salinity profiling (vertical and horizontal). The currents were measured using electromagnetic current meters (Model S4, InterOcean, USA). Typically two (or more) current meters were deployed in a vertical array including a shallow (5-8 m) and deep (12-17 m, 1 m above bottom) instruments. Occasionally, more current meters were attached to the mooring line in between those two units. The temperature-salinity profiles were carried out by towing a STD (Applied Microsystems, Canada) aboard a small skiff and by swimming with the instrument at shallow regions beyond the reach of the skiff. Typically, horizontal transects were carried out with the STD towed behind the skiff or in front of a swimmer with its sensors at 20-30 cm depth. Each horizontal transect extended from near the shore line out to a site above 60-80 m depth. Each horizontal profile was supplemented with four vertical profiles at bottom depths of 10, 20, 40 and 60 m. Each vertical profile stared at the surface and reached the bottom or to 40 m depth, whichever shallower.

At the core of this study was the *in situ* tracking of individual zooplankters using the FishTV Sonar (hereafter FTV). This multi-beam 1.58 MHz acoustic device, developed by Dr. Jules Jaffe, at the Scripps Institution of Oceanography, USA. Briefly, the sonar includes an underwater sonar array that directs a set of fan beams (0.65 X 20° wide) into slightly different directions. Another set of fan beams, arranged orthogonal to the first, receives the backscattered signal. By pulsing the transmitting array, one transducer at a given time, and receiving on all of the orthogonally arranged receiving beams, one can uniquely decode all points in 3-dimensional space. At an operational range of 2 to 5.7 m, the volume sonified at each "frame" is 0.55 m^3. The resolution in range (distance from the transducer) is 0.77 cm, while the lateral resolution changes from approx. 2.4 to 6.8 cm, at the proximal and distal ends of the operation range, respectively. The maximal frame rate we used was 3 frames per sec.

The first period of this project was devoted to an elaborate testing, re-building of components which following initial tests proved non functioning and an extensive tank-calibration of the FTV. These tests included careful calibration of the acoustic echo strength (Target Strength, or “TS”), monitoring the motions of artificial targets (1 mm diameter beads) in a large (38 m^3) sea-water tank at IUI, and monitoring the motions of individual zooplankters collected at sea and released in the tank. It took about 4 years after the start of our RSP project to reach the current level where the FTV sonar is working reliably, well calibrated and producing top quality data. Our tests of the FTV's sensitivity indicated a capability to record zooplankters larger than about 1.5 mm in length.

The first cruise using the FTV took place in December 1998, at Ras Burka. That cruise was followed by a 1.5 month deployment (February-March 1999) of the FTV in front of IUI, Eilat. In the field, the underwater unit (transducer) was attached to a very large tripod (6 m high), oriented horizontally directly into (or away from) the prevailing currents. Thus, the strongest component of the flow (horizontal, toward or away from the sonar) was oriented along the longest axis of the sonified volume, thereby maximizing the residence time of moving targets within that volume. Each session of acoustic tracking used a frame interval of 3 frames/sec and typically lasted 6-8 min. "Ground-truth" samples were taken once or twice a day using an underwater pump attached on the FTV tripod at the same depth as the sonar.

In order to test whether or not zooplankton was swept with vertical flows, we needed to measure that flow simultaneously with the FTV tracking. The aforementioned S4 current meters measured only the horizontal, not the vertical, currents. To measure the vertical flow, a "fluorscein-video" setup was developed and successfully deployed. This setup included two vertical, taut anchor lines, about 15 m apart. A perfectly horizontal line with clear marks every 1 m was extended between the two vertical lines, exactly at the depth of the water sonified with the FTV, some 10 away. The horizontal line was oriented so that its length would be parallel to the direction of the prevailing long-shore current at the study site.

A video camera was attached on the FTV tripod, also at the same depth, and recorded the paths of "blobs" of fluorescein dye released at a fixed point along the horizontal line. Those blobs were released by a swimmer snorkeling at the surface, injecting pulses of the dye using a large syringe attached to a long (12 m) narrow (2 mm diam.) pipe, the opening of which attached at a fixed point on the horizontal line. The injection was done from the surface (rather than by a scuba diver) to avoid the disturbance to the flow. The syringe was filled with sea-water sucked in situ through the pipe, so that the density of the injected water was the same as the density of the water into which the dye was injected.

The video and the sonar records were transmitted in real time to the ship via underwater cables, allowing simultaneous measurements of the flow (video) and zooplankton motions (sonar).

Altogether, we obtained a few hundred thousands tracks, most of them short (about 1 sec), however, about 10 % of the tracks are over 10 frames (3.3 sec) in length, and about 5 % are longer than 15 frames (5 sec). Given the resolution of the sonar, their occurrence mostly at the proximal two third of the sonified volume (<4 m) where weaker targets were better detected, and the occurrence of vertical flows on the order of 1-2 cm/s, the few thousands tracks longer than 3 sec that we acquired provide the analytical power to decipher down-motion of the animals, if occurring.

Due to the extensive delay in the development of the FTV hardware, we have not yet completed the processing of the enormous data set. This report therefore present the results of the processing of part of the collected data, mostly from the December 1998 cruise. A full report will be completed soon and submitted for publication in a scientific journal.

Results

Both the physical and biological characteristics in the coastal region along the Gulf of Aqaba were highly dynamic. Nevertheless, some general, "typical" trends are becoming clearer as more data are processed. During winter (November-February), the coastal zone is exposed to an on-shore flow component at the surface, downwelling in the near-shore zone, and a consequent return (sea-ward) flow just above bottom (Fig. 1). This trend is in agreement with predictions of the Type-II Hypothesis. Also in accordance with the prediction of this hypothesis is the "typical" (albeit not found at times) gradient of increasing zooplankton density closer to shore at sites where zooplankton feeders (primarily fish) are scarce (Fig. 2). In coral-reef coasts the zooplankton gradient is reversed, with higher densities offshore, primarily due to predation.

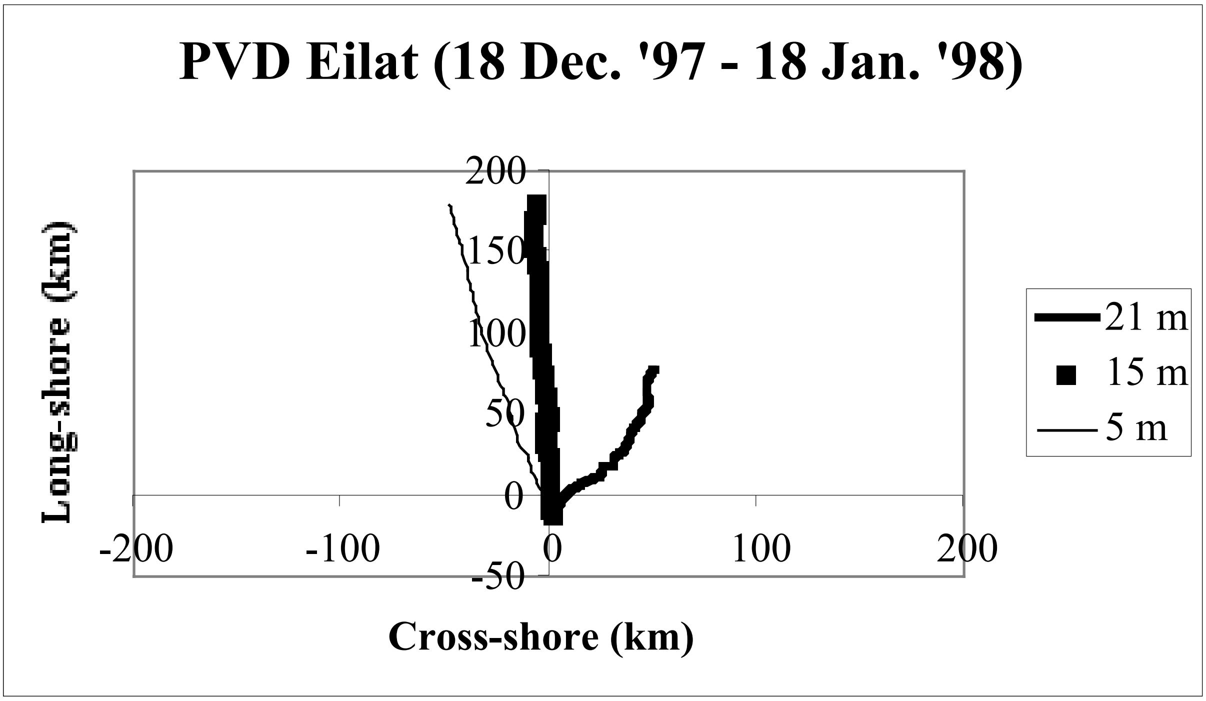


Fig. 1: An example of the flow pattern along the west coast of the Gulf of Aqaba during winter. Plotted are the progressive vector diagrams obtained from a vertical array consisting of three current meters (Model S4) at 5, 15 and 21 m depth (the latter depth was 1 m above bottom). Note the remarkable difference in the cross-shore component, typical for this season: an on-shore in the upper water column and a reversal, sea-ward flow near the bottom. This horizontal pattern reflects a strong downwelling at the coast.

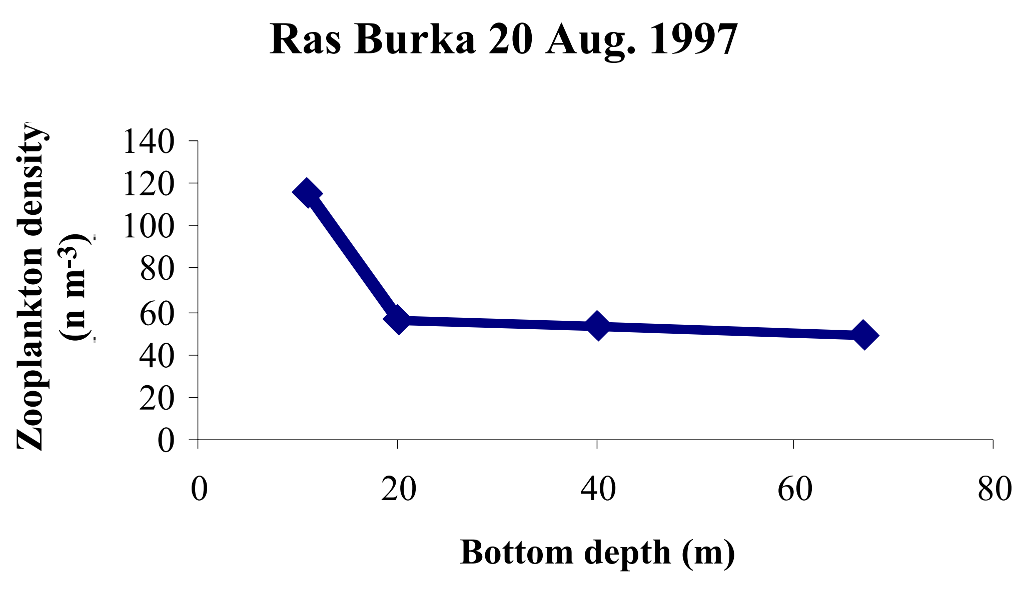
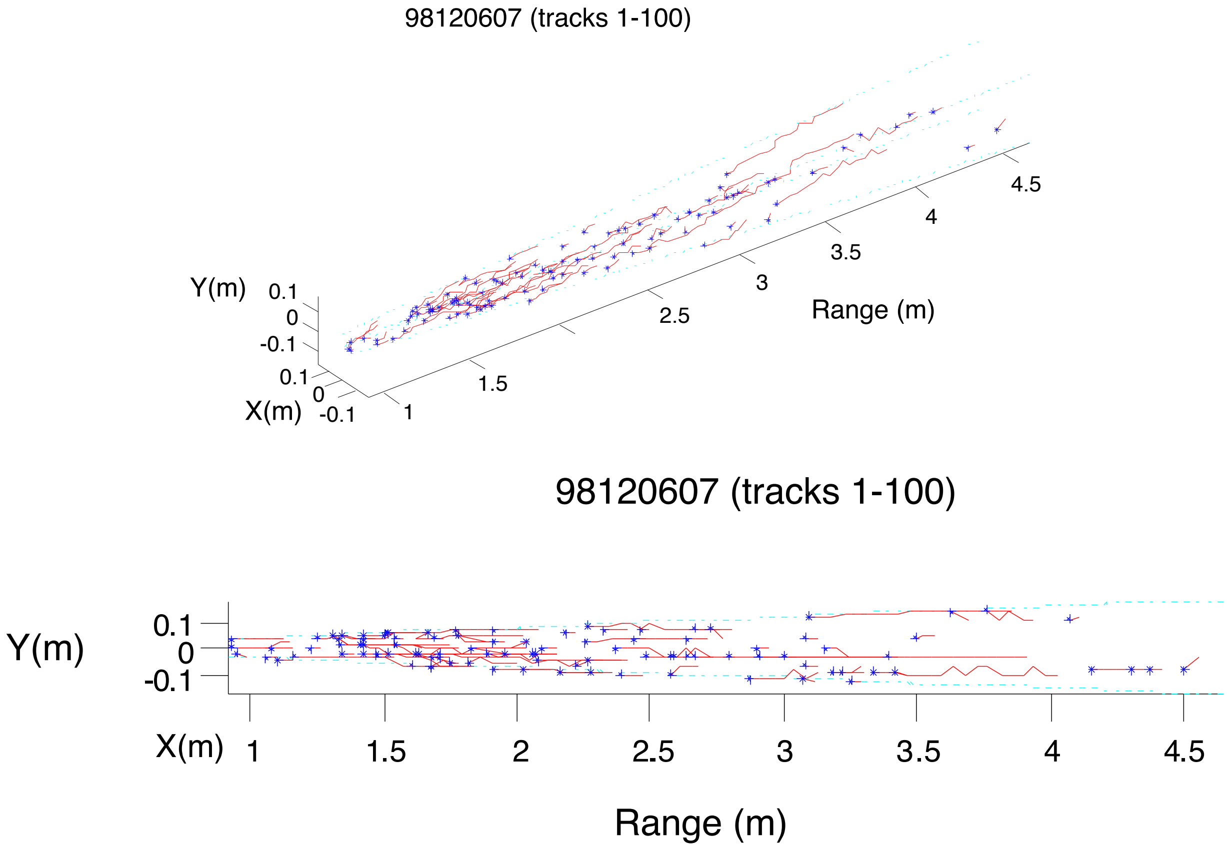


Fig. 2: An example of zooplankton distribution across sandy shores in the Gulf of Aqaba. This profile was carried out at Ras Burka along a horizontal transect from the near-shore point (11 m depth) seaward to a point of 67 m depth. Zooplankton was sampled using oblique, 5 min long tows in lines parallel to the shoreline, with the net sampling the upper meters of the water column. Plotted are the densities of total zooplankton. Note the dramatic increase in zooplankton density at the shoreward-most point (11 m), where the FTV was deployed in the next cruise.

The dynamics of the on-shore flow are in agreement with predictions of the Ekman forcing (Genin and Paldor 1998): The predominantly southward wind brings about an on-shore flow component and downwelling along the western part of the Gulf, while the reversed (off –shore flow near the surface, driving upwelling along the coast) is to be expected along the eastern coast of the Gulf.

In summer, strong stratification seems to effectively suppress the vertical flow, so that occurrences of coastal downwelling are less common and typically last shorter periods, compared with winter. During this season, the differential thermal heating at different distances from shore seems to cause dynamical instability in the cross-shore direction, so that when sea-surface warming is greater near shore (e.g., mid day), the surface water is driven offshore, while when sea-surface cooling is greater near-shore, an on-shore flow would be generated near the surface. The reason for this thermal cycling is that near the shore, a smaller volume of water is being warmed up (or cooled down), compared with the deep water column away from shore. Thus during warm-up periods the water near the shore becomes warmer (i.e., lighter) than the water off shore (and *vice vers*a during cooling periods (Monismit et al., L&O 1990).

Additional mechanisms affecting vertical flows near the coast are eddies, internal waves and the site-specific interaction between the general flow and the local topography. Meso-scale eddies, on the scale of the Gulf's width, may consist a strong on-shore (or off-shore) currents,



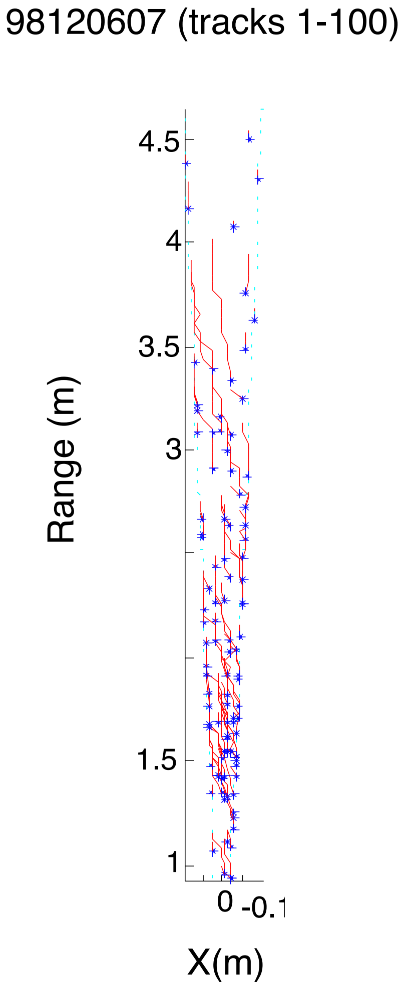


Fig. 3: An example of 100 tracks of individual zooplankters in the size range of 1-4 mm body length obtained with the FTV at Ras Burka (7 Dec. 1998). The starting point of each track is indicated by the dot. All scales are in meters. Top panel: a 3-D plot of the tracks. Mid Panel: a 2-D projection of the tracks showing the verical component (Y) against distance (Z) from the transducer. Bottom panel: a 2-D projection of the plots showing the two horizontal components of the tracks (X and Z). Note the strong horizontal advection of the zooplankton away from the transducer (southward) and to the east (offshore, leftward in the bottom panel), but the lack of clear displacement in the vertical in spite of the prevalence of approx. 2 cm/s downwelling at that time.

inducing coastal downwelling (or upwelling, respectively). Internal waves generate vertical flows on scales from minutes to hours, however, these waves occur when the water column is stratified (i.e., summer), so that their effect in the Gulf of Aqaba is likely to be minimal during winter, when the water column is well mixed down to several hundreds meters. Due to the rugged topography of the Gulf's coast line (e.g., bays, headlands, protruding reef flats, reef walls, etc.), interactions between currents and local topography are expected to result in inter-site variations in the coastal vertical flows.

Based on our overall field work, including two summer cruises, two winter cruises and several shore-based deployments in different seasons, the general pattern emerging is that coastal downwelling prevails along the Gulf's west coast during winter (November-February) and a mixed pattern of both downwelling and upwelling during the other, warmer months. Downwelling prevails year-round at the Gulf's northern tip. Note however, that in each site, during any season, short-term variations (on the scales of minutes to hours) over-composite, so that general trends can be revealed only by long-term (days, weeks) measurements (e.g., Fig. 1). A noteworthy key observation is that vertical currents, either upwelling or downwelling, on the scale of 1-2 cm/s, occur at every site we studied in the coastal zone of the Gulf of Aqaba. (The importance of this observation is explained below).

As mentioned above, at the core of this chapter stands the question of what happens to the zooplankton when exposed to vertical flows of a scales of 1-2 cm/s. More specifically: Do zooplankters retain their depth, swimming against the vertical flow, or are they simply carried along, swept to different depths?

The new technology provided by the FTV, together with our design of solid, stationary deployment of the sonar and the simultaneous measurements of the flow and zooplankton motions allowed the following answer: The average zooplankton retain their depth (Fig. 3). [Note however, that this answer should be considered provisional, as it is based only on 5 runs, or about 5000 individual tracks of zooplankters. The final answer yet needs to await a full analysis of our data set]. Figure 3 shows that under conditions of 1.8 cm/s downwelling, some individuals are swept downwards, others swim upward faster than the downwelling flow, while a few do not change vertical position. The average vertical velocity calculated for the entire population sampled was nearly zero (0.26 cm/s net upward). A similar trend (nearly zero displacement) was found in the other 3 runs under downwelling conditions and one run with upwelling.

The zooplankton community in the size range sonified by the FTV was dominated by copepods (77.5 %) and mollusks (6 %).

Note that to the best of our knowledge, Fig. 3 is the first documentation ever of long *in situ* tracking of meso-zooplankton (mostly copepods) in the ocean. The few published observations of swimming tracks of meso-zooplankton had been, by and large, limited to visual or optical records on the scales of millimeters, or a few centimeters, at best, mostly in laboratory tanks.

Discussion and conclusions

Unlike buoyancy control, which works efficiently to retain organisms (and objects) at the surface or fine-tune their general depth in a stratified water column, the retention of depth under conditions of continuous 1-2 cm/s downwelling flow in a non-stratified (well-mixed) column was possible only due to the zooplankton's active swimming. Thus, a major discovery of this study is that zooplankton (i) senses small changes (of the scale of meters) in its depth and (ii) corrects for such changes by active swimming. Thus, one may infer that individual zooplankters select their residing depth on that scale (meters) and that such selection has some ecological, evolutionary-selective advantage(s). Note, however, that this conclusion, if corroborated by our remaining data, pertains only to the depth range we studied (upper 15 m of the water column). However, other observations on downwelling-related aggregations at greater depths (50-100 m; Flament) suggest that the Type-II mechanism may also work at greater depths. Possible cues for depth determination by the zooplankton include pressure, light intensity and spectrum and possibly other factors (e.g., type or other characteristic of their planktonic food).

Overall, our observations corroborate the predictions of the Type-II Hypothesis: Relatively strong vertical flows occur in the coastal zone primarily in winter, zooplankton actively swims against the vertical flow to retain its depth and is therefore becomes aggregated along the coast. This Type-II enrichment is not a continuous, monotonic process. Seasonality has a major effect, with the downwelling prevailing during winter, but even then, and more so during the stratified seasons, the vertical flows may be intermittent and reverse their direction. As our results indicate, the same mechanism (depth retention) would apply for both cases of down- and up-welling flows.

As a last sentence, we would like to emphasize, again, the provisional nature of the above conclusions, as a full corroboration of the trends should await a complete processing of our entire, most extensive data we have collected during RSP/Project B. If corroborated by the remaining analysis, the Type-II Hypothesis would then become the "Type-II Mechanism" with a far reaching contribution to our understanding zooplankton distributions in the world ocean.

The phytoplankton spring bloom in the Gulf of Aqaba, Red Sea, and its control by light and nutrient availability

Clivia Häse[1], Noga Stambler[2], Mutaz Al-Qutob[3], David Iluz[2], Ezzat A. Ibrahim[4], Mohammed S. Abdel-Karim[4], Ahmed Abdel-Monem[4], Ola E. Taha[4], Zvy Dubinsky[2], Jonathan Erez[5], Max M. Tilzer[6] and Boaz Lazar[5]

1) Zentrum für Marine Tropenökologie, Bremen
2) Department of Life Sciences, Bar Ilan University, Ramat Gan
3) Department of Biological Sciences, Faculty of Science and Technology, Al-Quds University, Jerusalem
4) National Institute of Oceanography and Fisheries, Cairo
5) Institute of Earth Sciences, The Hebrew University of Jerusalem
6) Universität Konstanz, Konstanz

The Gulf of Aqaba at the northern tip of the Red Sea is a highly oligotrophic system with almost no terrestrial runoff from the surrounding desert. The main sources of nutrient input into the gulf are waters from the Red Sea proper through the narrow and shallow Straits of Tiran, and the atmosphere. Within the productive zone, nutrients are depleted almost all around the year. The water of the gulf is extremely transparent with the euphotic zone varying between 80 and 100m. During summer thermal stratification persists, whereas in winter a deep vertical mixing occurs regularly in the Gulf of Aqaba due to surface cooling. The aim of the present study is to examine the implications of the deep winter mixing for phytoplankton productivity in the Gulf of Aqaba.

In the Gulf of Aqaba, the alternation of stratification and mixing controls the seasonal dynamics of phytoplankton productivity, like in temperate open ocean waters. In thermally stratified waters during summer, the phytoplankton cells experience high photon fluxes during the day but are separated from high nutrient concentrations in the deep by the pycnocline. As a consequence, phytoplankton biomass and photosynthetic rates are low during summer. Thus, phytoplankton productivity is limited by nutrient supply. By contrast, during the mixing season nutrients are entrained into the mixed layer from the deep. On the other hand, phytoplankton cells are exposed to very low light levels and even darkness in the deep. Therefore, it depends on the mixing depth and the vertical speed of mixing whether phytoplankton productivity is limited by energy or by nutrient supply.

By contrast, in the northern Red Sea thermal stratification persists, and a deep chlorophyll maximum is present all around the year. During the FS Meteor cruise in spring 1999, which took place during the height of the mixing season in the Gulf of Aqaba, maximum mixing depths of 100m were observed in the northern Red Sea.

Due to the nutrient input into the euphotic zone by deep vertical winter mixing, the chlorophyll content of the water column, and daily photosynthetic carbon fixation reached considerably higher values in the Gulf of Aqaba than in the northern Red Sea (Fig. 1).

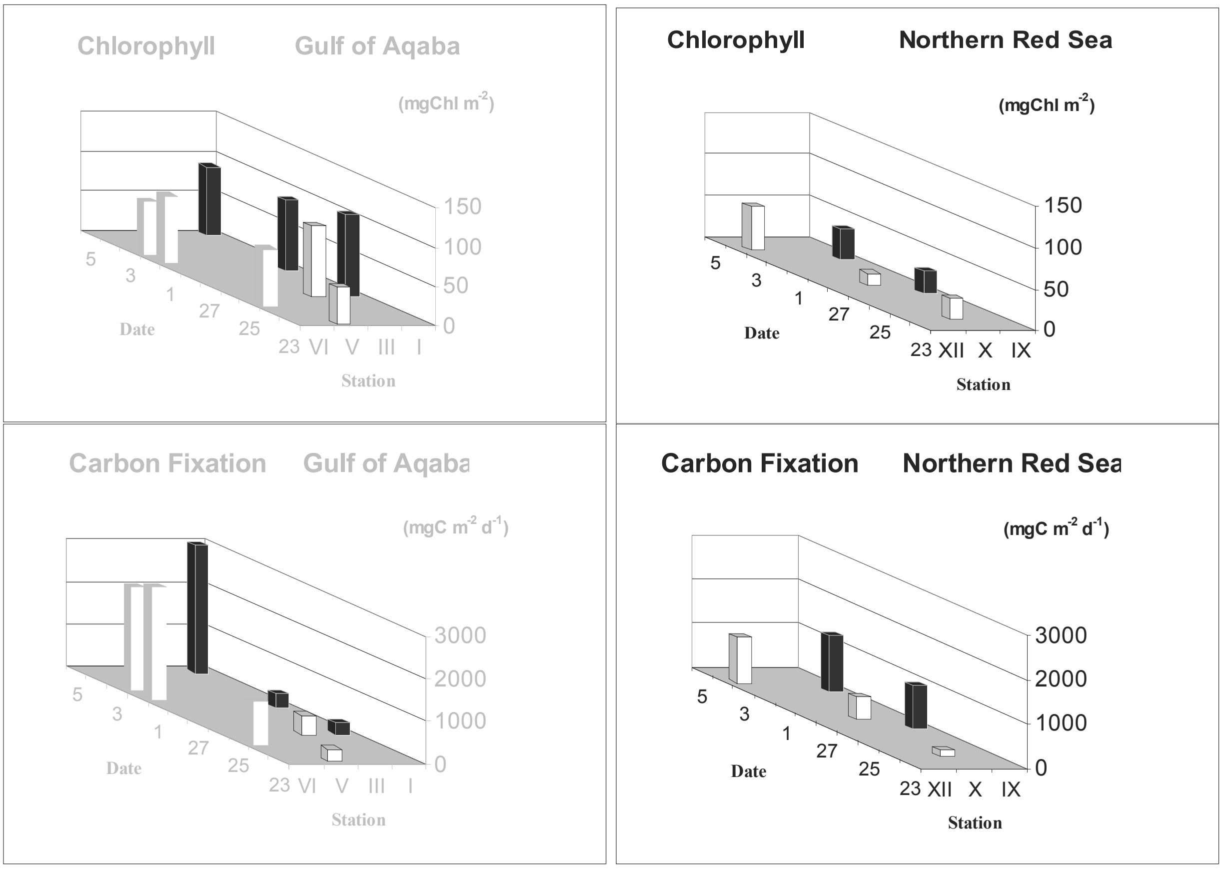


Fig. 1: Chlorophyll content of the water column, and daily photosynthetic carbon fixation in the Gulf of Aqaba (left panels) and in the northern Red Sea (right panels). Data were collected during the r/v "Meteor" cruise in spring 1999 (Feb23-Mar5). StationI (29.492N, 34.951E) is identical with the routine StationA1 in Israeli waters at the northern end of the Gulf of Aqaba. StationsIII (29.084N, 34.767E), V (28.584N, 34.650E), and VI (28.334N, 34.551E) were located on a southward transect within the Gulf of Aqaba. StationsIX (27.416N, 34.666E), X (27.183N, 34.666E), and XII (27.416N, 34.083E) were located in the northern Red Sea.

The common pattern observed in temperate oceans, where deep vertical mixing occurs regularly, is that a phytoplankton bloom is triggered within the euphotic zone by the combination of both high energy supply and high nutrient availability as soon as the mixing stops in spring. Here we demonstrate that, by contrast, in the Gulf of Aqaba the phytoplankton biomass within the water column reached maximum values towards the end of the mixing season, and not thereafter:

During the mixing season in the Gulf of Aqaba, phytoplankton biomass in terms of water column integrated chlorophyll concentrations was linearly correlated with the actual mixing depth (Fig. 2). The same linear relationship was maintained during different years of the study period even though the maximum winter mixing depth varied between the different years due to variable extents of surface cooling.

Moreover, Fig. 2 shows that the chlorophyll content of the water column increased with increasing mixing depth. This implies that phytoplankton grew ‘against’ the energy shortage during deepening of the mixing. However, light limitation may have occurred towards the end

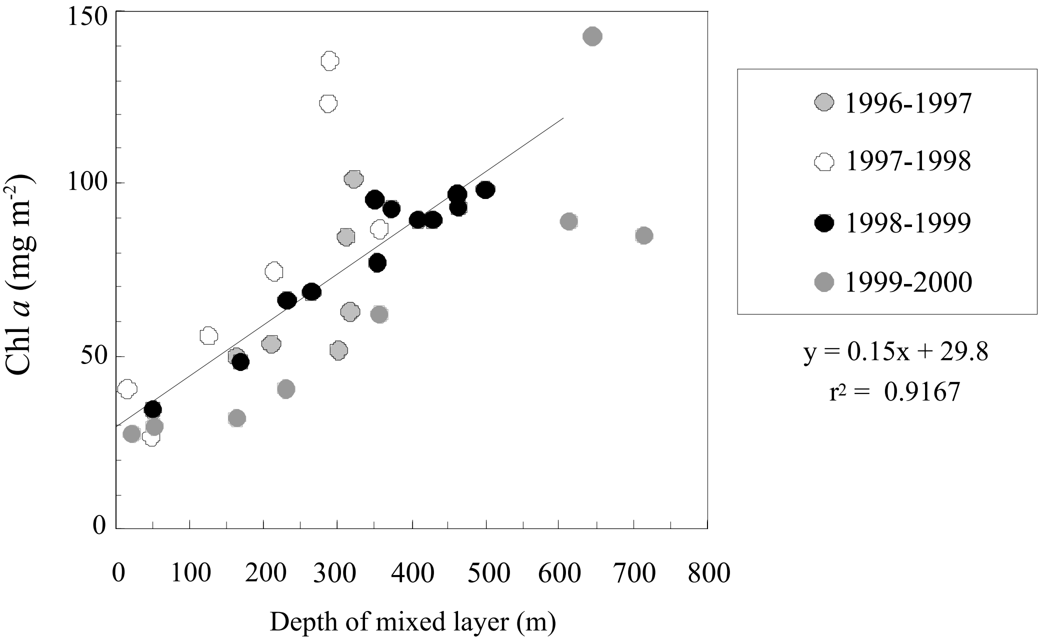


Fig. 2: Relationship between phytoplankton chlorophyll biomass and winter mixing depth at the routine Station A1 in the Gulf of Aqaba. Considered were all data of single sampling dates that were collected during the mixing season from September to April within the study period 1996-2000.

of the mixing season in the year 2000 when the mixing depth exceeded 500m. Therefore, we conclude that the phytoplankton production in the Gulf of Aqaba was limited by nutrient supply as long as the mixing depth was less than 500m.

Furthermore, this finding enables us to estimate the critical depth for positive net production: Apparently, even during vertical mixing down to 500m, phytoplankton was able to harvest sufficient light energy to support positive net production. This we attribute to the high radiative energy input due to the low latitude and little cloud cover in the region, and to fast mixing rates.

Chlorophyll *a* of different phytoplankton fractions at Dahab reef during Summer 1997 and 2000

Ezzat A. Ibrahim

National Institute of Oceanography and Fisheries, Cairo

Two long cruises to Dahab Reef were carried out during the last week of July 1997 and 2000. Three main sampling sites were selected at Dahab Bay, namely back the reef, reef flat and open water (Aqaba Gulf). Water samples were collected from these sites, filtered *in situ* onto glass micro-fiber circles GF/F and kept in dark at –20° C. The samples were transferred to the project's lab at Barrage Station (28 km north west of Cairo). Chlorophyll *a* of different phytoplankton fractions was extracted in 90 % hot methanol (HPLC quality). The extracts were measured with a Turner 10-AU fluorometer equipped with a kit for direct measurements of Chl. *a* without any interference from Chl. *b* and phaeophytine as reported by Welchmeyer (1994).

The total Chl. *a* concentrations recorded in July 2000 were higher than the corresponding values of July 1997, especially at back the reef and reef Flat. The total Chl. *a* values in the selected sites can be arranged in the following descending order: Back the Reef> Reef Flat> Open Gulf Water (Tab. 1).

Concerning the Chl. *a* of phytoplankton fractions, pico-plankton (<2 µm) was the most dominant fraction, constituting from 62 to 82 % of the total phytoplankton Chl. *a*. Net–Plankton (>20 µm) was second in the back, the reef and reef flat, forming 17-31 % of the total Chl. *a*. In Open Gulf Water, Chl. *a* of Nano-Plankton (<20 µm) was higher than net-plankton and comprised 13 % of the total phytoplankton Chl. *a* in both 1997 and 2000 (Tab. 1).

The high Chl. *a* recorded in July 2000 was mainly due to flourishing of *Skeletonema costatum*, while *Nitzschia* spp. and *Chaetoceros* spp. were abundant. We have already uni-algal cultures of these species in the project's lab at Barrage Station.

Tab. 1: Chlorophyll *a* of phytoplankton fractions at Dahab Reef during summer 1997 and 2000 (µg Chlorophyll *a* L^{-1}).

	Summer 1997				Summer 2000			
Sampling Sites	Net >20 µm	Nano <20 µm	Pico <2 µm	Total µg Chl..L^{-1}	Net >20 µm	Nano <20 µm	Pico <2 µm	Total µg Chl..L^{-1}
	%	%	%		%	%	%	
Back the Reef	21	5	74	0.156	17	17	66	0.325
Reef Flat	24	12	64	0.146	31	7	62	0.270
Open Water	5	13	82	0.112	6	13	81	0.121

A simulation model of the plankton community in the Gulf of Eilat

Yury Kamenir[1], Steve Brenner[2], Zvy Dubinsky[1], Mutaz Al-Qutob[3], Boaz Lazar[4], Clivia Häse[5], David Iluz[1], Maxim Shoshani[2], Leonid Sokoletsky[1] and Noga Stambler[1]

1) Faculty of Life Sciences, Bar Ilan University, Ramat Gan
2) Department of Geography, Bar Ilan University, Ramat Gan
3) Department of Biological Sciences, Faculty of Science and Technology, Al-Quds University, Jerusalem
4) The Institute of Earth Sciences, Hebrew University of Jerusalem
5) Zentrum für Marine Tropenökologie, Bremen

A simulation model, describing the plankton community structure and functioning, was developed on the basis of data collected in the oligotrophic Gulf of Aqaba (Eilat), Red Sea. The BATS models, developed for the Sargasso Sea, were used as a close analogue for informational support and comparative analysis. The one-dimensional model describes the vertical structure (down to 200 m depth) for several fractions of phytoplankton (*Prochlorococcus, Synechococcus,* Eukaryotes), and heterotrophs (bacteria, proto- and microzooplankton), as well as chlorophyll, primary production and several parameters of the abiotic environment. Allometry is used to minimize the number of biological parameters allowed for tuning. The groups of objects are described, with the detail level diminishing with the distance from 'the focal point' (primary production); those are grazers (zooplankton),

Structure of the aquatic community

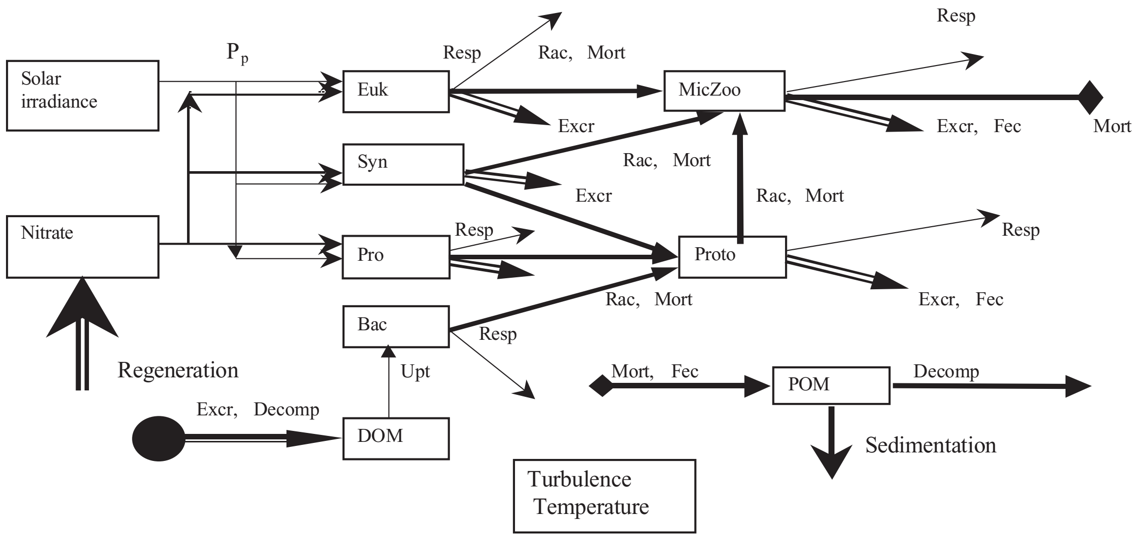


Fig. 1: The model structure (Pro -*Prochlorococcus*, Syn -*Synechococcus*, Euk -Eukaryota, Bac -Bacteria, Proto -Protozoa, MicZoo -Microzooplankton, Pp -Primary Production, Resp -Respiration, Excr -Excretion, Mort -Mortality, Upt -Bacterial DOC-uptake, Regen -Regeneration, Day 1 - corresponds to January, 1st).

abiotic forcing functions (annual dynamics of the solar energy input, temperature, turbulence), and dissolved and particulate non-living components. Simulation runs performed for several consecutive years did produce stable cyclic dynamics of the main parameters. The model output seems to be realistic in description of the seasonal patterns and vertical profiles of the main components for both volumetric and vertically integrated parameters. The variability of the vertically integrated parameters is markedly low in comparison to the dynamics of the corresponding parameters in a specific layer of the water column. The deep chlorophyll maximum (DCM) layer is evidenced during summer stratification at depth of 80-100 m. It is mainly comprised of prokaryotes (Cyanobacteria of the *Prochlorococcus* type) and is characterized with high chlorophyll concentration, primary production, and biomass of microzooplankton. The DCM primary production estimates were high in comparison with the cruise measurement data.

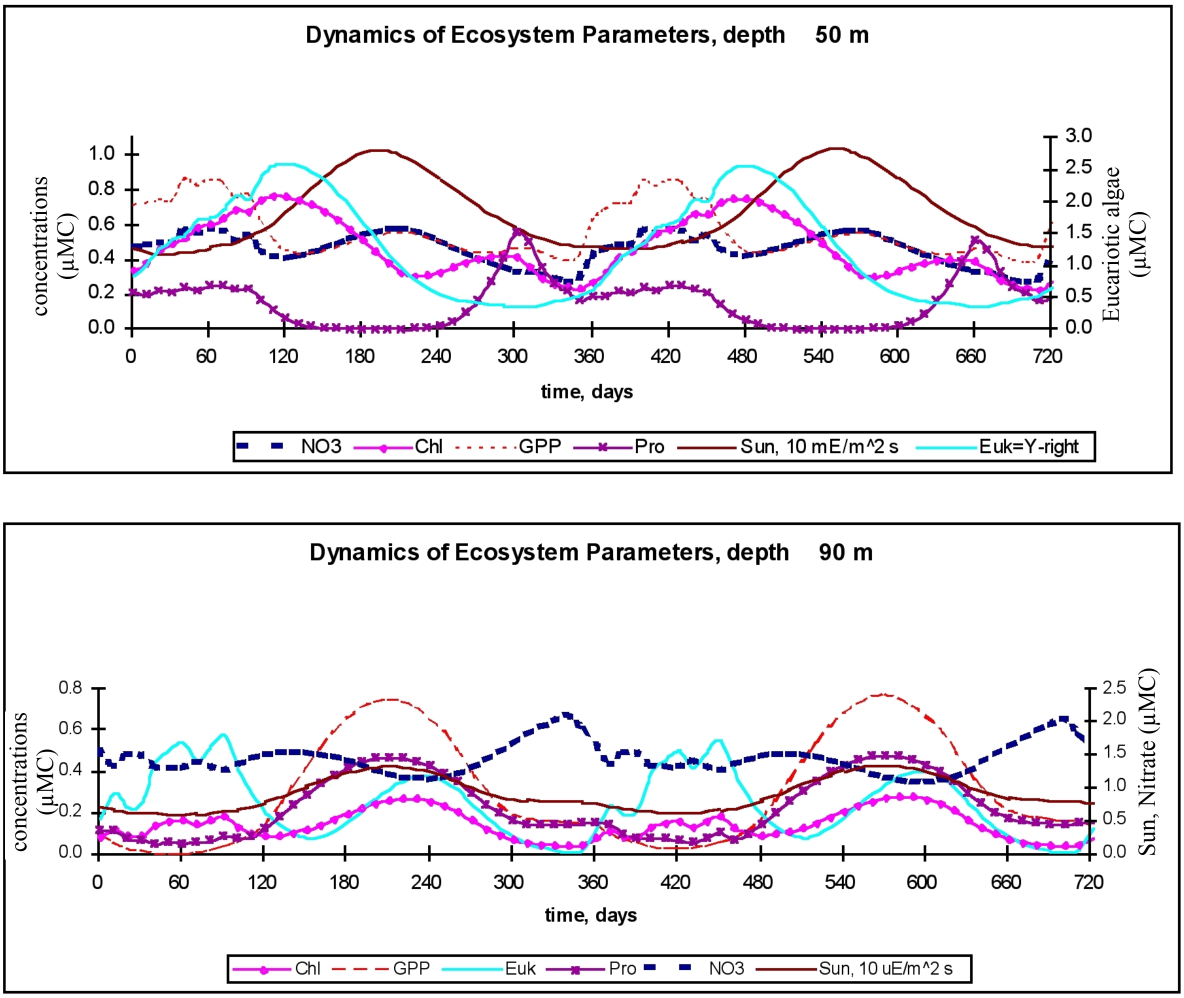


Fig. 2: The model results: Temporal course of community parameters in two fixed depths.

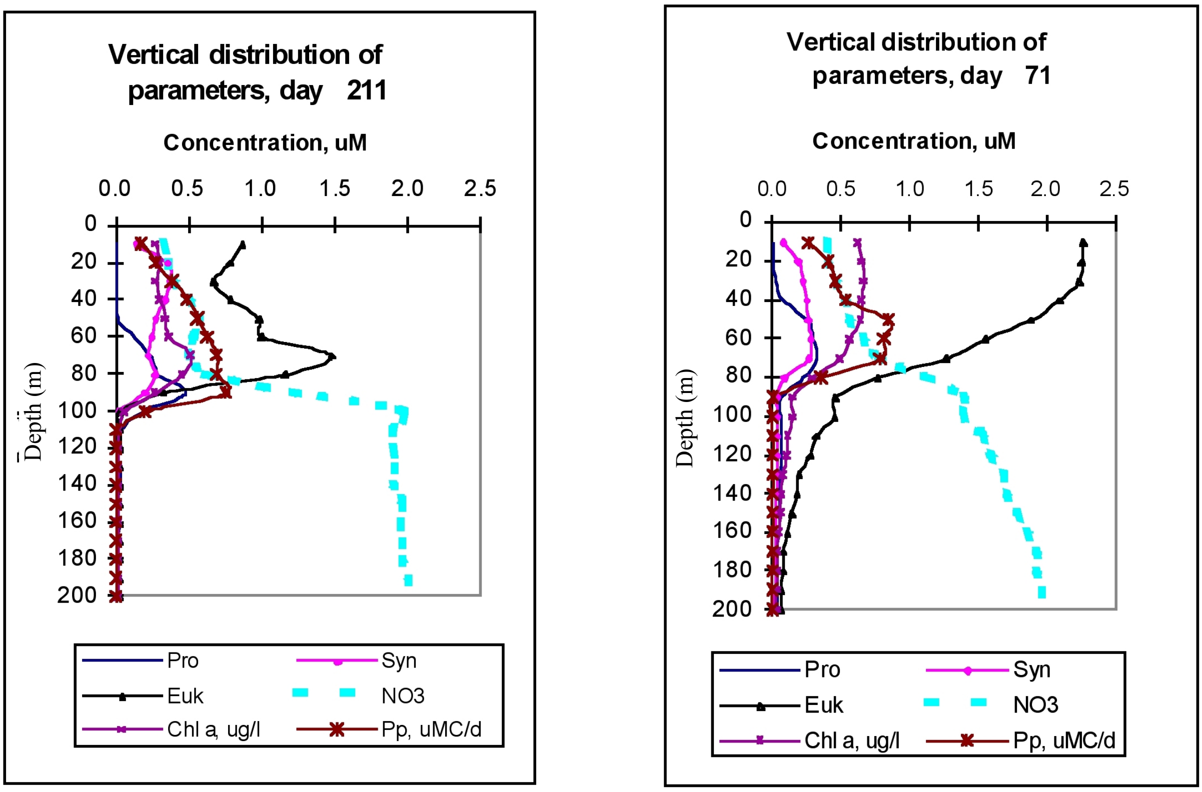


Fig. 3: The model results: Dynamics in the predicted vertical profiles.

Bacteria – phytoplankton – zooplankton interactions

Ulrich Sommer[1], Ulrike-G. Berninger[1], Ruth Böttger-Schnack[1], Thomas Hansen[1], Herwig Stibor[2], Sigrid Schiel[3], Astrid Cornils[3], Meinhard Simon[4], Stephen Wickham[5], Tariq Al-Najjar[6] and Anton F. Post[7]

1) Institut für Meereskunde an der Universität Kiel, Kiel
2) Karl-Ludwigs-Universität, München
3) Alfred-Wegener-Insititut für Polar- und Meeresforschung, Bremerhaven
4) Carl-von-Ossietzky Universität, Oldenburg
5) Universität zu Köln, Köln
6) Marine Science Station, Aqaba
7) The Interuniversity Institute, H. Steinitz Marine Biological Laboratory, Eilat

Introduction

Phytoplankton in the extremely oligotrophic northern Red Sea and in the Gulf of Aqaba (Klinker et al. 1978, Reiss and Hottinger 1984) is characterized by a low biomass (<0.8 mg chlorophyll l^{-1}) dominated (>95 %) by phytoplankton <5 µm (Lindell and Post 1995, Yahel et al. 1998). Except for the early summer and the fall bloom of the cyanobacterium *Trichodesmium*, algae from 5 to several 100 µm are extremely scarce, though not totally absent (during most of the year countable only by plankton nets or by sedimentation of several 100 ml of water; Kimor and Golanski 1992). Similar to phytoplankton, zooplankton is characterized by a low biomass and low abundances. Nevertheless, all major functional and taxonomic groups of marine zooplankton can be found. However, neither total grazing pressure on phytoplankton nor the relative importance of different zooplankton functional categories as grazers of different phytoplankton size classes have been studied so far. The different size classes of phytoplankton and of zooplankton require different methods of grazing measurements. In this article, we synthesize several independent grazing studies performed during the "Meteor" cruise M 44/2 in the Gulf of Aqaba and the northern open Red Sea (15 February to 9 March 1999) together with previous data on zooplankton lipids as a tracer of zooplankton feeding on *Trichodesmium.* The study season was chosen in order to compare plankton from a deeply circulating water column (Gulf of Aqaba, >300 m mixing depth) to plankton from a stratified water column (Red Sea, mixing depth <50 m). This contrast in the mixing regime is quite typical for the study season, while a few weeks later summer stratification begins also in the Gulf of Aqaba (Wolf-Vecht et al. 1992, Genin et al. 1995).

Picoplankton –microzooplankton

Microzooplankton grazing dominated by protozoa on autotrophic and heterotrophic picoplankton was studied by the dilution method of Landry and Hasset (1982). This method rests on a dilution series of natural plankton suspension with filtered sweater. Net growth rates are calculated from cell counts at the beginning and at the end of the incubation period (in our case ca. 36 h). In more dilute samples, the encounter rates of predators with their prey is reduced, resulting in a higher net growth rate of the prey in comparison to less dilute treatments. A linear regression of growth rates on the fraction of undiluted water yields an estimate of the gross growth rate (μ; equivalent to the y-axis intercept) and of the grazing rate (γ; equivalent to the negative slope of the regression). Addition of nutrients in a parallel dilution series prevents nutrient limitation at lower dilutions. It yields an estimate of the maximal growth rate (μ_{max}) and by comparison with μ an assessment of the extent of nutrient limitation.

Numbers of heterotrophic bacteria ranged were in the range to be expected for ultra-oligotrophic environments ($7.07\text{-}8.29 \times 10^5$ ml^{-1} in the Red Sea and $6.75\text{-}6.64 \times 10^5$ ml^{-1} in the Gulf of Aqaba. Flow cytometry reveled considerable differences in the abundance of autotrophic picoplankton, with the smallest group (*Prochlorococcus*) being 10 times more abundant in the stratified Red Sea and picoplankton eukaryotes being 2 times more abundant in the circulating Gulf of Aqaba (Table 1).

Tab. 1: Abundance of autotrophic picoplankton groups (cells ml^{-1}; mean and S.D.) in the Gulf of Aqaba and in the open Red Sea.

Picoplankton group	**cell size (µm)**	**Gulf of Aqaba**	**open Red Sea**
Prochlorococcus	0.6-0.8	18 100±17 400	204 000±45 800
Synechococcus	0.9-1.2	16 500± 7 300	29 100± 8 200
Eukaryotes	1.0-2.0	4 200± 1 240	2 660± 800

Heterotrophic bacteria showed moderately high values of μ (0.62-0.67 d^{-1} in the Red Sea and 0.65-1.40d^{-1} in the Gulf of Aqaba) which was roughly balanced by grazing (= 0.77-0.86 d^{-1} in the Red Sea and 0.91-0.99 d^{-1} in the Gulf of Aqaba). There was no consistent increase of μ with nutrient addition. The growth rates of bacteria in the dilution experiments were higher than those rates (in most case <0.2 d^{-1}) obtained by in-situ incorporation of ^{14}C- labelled leucine (Simon and Azam 1989). Strong differences between results obtained by those principally different methods have been observed elsewhere in oligotrophic waters as well and have not yet been explained satisfactorily.

Autotrophic picoplankton Autotrophic picoplankton showed relatively low growth rates, they were only under moderate grazing pressure and apparently were not consistently nutrient limited.

Nanoplankton – microzooplankton

Grazing of microzooplankton on phytoplankton >5 µm could not be studied by the dilution technique because of the scarcity of medium-sized phytoplankton. Therefore, a factorial combination of release from nutrient stress (addition of N and P or of N, P and Si) and of release from grazing pressure by microzooplankton (sieving of samples through 10 and 20 µm plankton gauze) was used for on-board incubation experiments (Sommer 2000). The response of phytoplankton was studied by calculating growth rates during the first two days of incubation and comparing them with controls.

The results showed a simultaneous control of medium-sized phytoplankton by nutrient limitation and grazing. Nutrient limitation was the more stringent control, because release from grazing did not permit significantly positive net growth rates of most species while nutrient enrichment did. This latter effect is in contrast to the reactions of the picoautotrophs, which were not consistently nutrient limited. A combined release from grazing pressure and from nutrient limitation permitted almost maximal growth rates of medium sized phytoplankton. Grazing rates were inversely related to cell- or colony-size (Table 2).

Tab. 2: Linear regression of grazing rates (d^{-1}) by microzooplankton $\log^{10}$ GALD (greatest axial linear dimension; in µm) of phytoplankton ($g=a+b \log^{10}$ GALD).

N/E; date	**a**	**b**	**r**	**n**	**p**
Southern Gulf; 22.2.		-0.51±0.21	0.47	8	0.042
open Red Sea; 24.2.	1.52±0.19	-0.50±0.13	0.71	8	0.0088
open Red Sea; 27.2.	2.25±0.11	-0.98±0.08	0.96	8	0.00002
Southern Gulf; 02.3.	1.25±0.17	-0.45±0.10	0.77	8	0.0042
pooled data	1.67±0.12	-0.62±0.08	0.66	32	<0.00001

Phytoplankton – mesozooplankton

Mesozooplankton grazing was studied by incubating freshly caught zooplankton with radioactively labelled, cultured food organisms of defined size (1-100 µm length) for 15 minutes and calculating clearance rates from the incorporation of the radioactive label. The dependence of per capita clearance rates of the most important mesozooplankton functional groups on food size is shown in Table 3. *In situ* grazing rates for the different size fractions were calculated by multiplying the per capita grazing rate with abundances of the dominant functional groups and calculating the sum over the different functional groups.

There was a clear differentiation between a microphageous group of zooplankton with optimal

Tab. 3: Clearance rate (ml ind^{-1} d^{-1}) of mesozooplankton for different size (GALD/ESD in µm) categories of food.

	Bacteria	***Chlorella***	**Small penn. diat.**	***Thalassiosira***	***Nitzschia***
	1/0.8	3/2.7	15/8.25	40/22	100/18
Appendicularia	126	113	107	15	3.8
Doliolium	71	86	36	29	17
Ostracoda	19	7.6	7.6	3.8	0.95
Rhincalanus	0	5.5	10	21	91
Calanus	0	1.2	7.8	39	29
small calan.	0	2	9	22	16.5

food sizes of 1-3 µm and a macrophageous group with optimal food sizes > 15 µm cell length (GALD = greatest axial linear dimension) or > 8 µm equivalent spherical diameter (ESD). In the grazing literature, both linear measures are used as an index of effective size and no consensus has emerged so far, which one is more relevant for ”edibility”. The microphageous group comprised tunicates (*Doliolum*, Appendicularia) and ostracods, while calanoid copepods were macrophageous. Calculated *in situ* grazing rates show a surprisingly low impact of copepod grazing on phytoplankton, especially on the dominant small fractions, and a spatially variable, but locally important impact of Appendicularia.

Grazing on *Trichodesmium*

Trichodesmium did not have sufficiently large abundances to perform grazing studies during the season of the "Meteor" 44/2 cruise. It was found in zooplankton net catches from the open Red Sea, but not in the Gulf of Aqaba. In order to show the food-web position of *Trichodesmium*, results of the RSP cruise in June 1997 are included here. During that cruise, different zooplankton taxa were sampled for analysis of their fatty acid composition as a tracer of their diet and compared to fatty acid profiles from cyanobacterial cultures. The picoplankter *Synechococcus* was characterized by an extremely low content of long-chained polyunsaturated fatty acids which is typical for other cyanobacteria as well (Brett et al. 1997, Sargent et al. 1987). *Trichodesmium,* however, had a modest content of the fatty acids C20:5(n-3) (1.7-3.2 % of total fatty acids) and C22:2(n-6) (1.7-2.0 % of total fatty acids). The latter has not been reported or reported in extremely low concentrations (<1 % of total fatty acids) from other phytoplankton taxa (Ackmann et al. 1968, Brett and Müller-Navarra 1997, Reitan et al. 1994). Therefore, it was taken as a biomarker for *Trichodesmium*-feeding. It was found in the large salp *Salpa maxima* (0.65-23.3 %; mean: 6.77 % of total fatty acids) and in the harpacticoid copepod *Macrosetella gracilis* (2.4-5.15 %; mean: 3.33 %). It was not found, however, in calanoid copepods and in the smaller tunicate *Doliolum* sp. *Macrosetella* has been known as a feeder of *Trichodesmium* already before (Böttger-Schnack and Schnack 1989, O’Neill 1998), while large salps have not been reported as *Trichodesmium*-feeders before. Conspicuous blooms of salps, like the one in June 1997, are usually irregular events. Grazing by salps can therefore not be considered as the ”normal” fate of *Trichodesmium*-production.

Discussion

The calculated grazing rates are rather high and show a highly dynamic system in spite of low nutrient levels and low plankton biomass. In order to balance grazing losses, a high production:biomass ratio of phytoplankton is required. This agrees with the high assimilation numbers reported by Häse et al. (pers. comm.). High growth rates balanced by high loss rates at a low standing stocks is the core of Goldman’s (1984) ”spinning wheel” concept for the oligotrophic ocean. He even hypothesized maximal growth rates in spite of low nutrient concentrations (Goldman et al. 1979). Our dilution experiments have shown that phytoplankton dominated by pico- and small nanoalgae are indeed not consistently limited by nutrients while some nutrient limitation was found for stations with a higher contribution of large algae. This agrees too with the experiments by Sommer (2000) who found considerable nutrient limitation for phytoplankton species >6 µm and with Stihl et al. (in press) who found an indication of P-limitation of *Trichodesmium*. Nevertheless, even the medium sized algae are grazed at high rates. It might be concluded, that Goldman's "spinning wheel" operates at maximum speed for the smallest size-classes while it operate at high, but not maximal speed for the larger ones. Given the dominance of small phytoplankton in the region (Li et al. 1993), Goldman's concept appears to be quite realistic at least for the study period. However, the period of deep mixing is the period with the weakest nutrient stress in the Gulf of Aqaba while stronger nutrient stress might be expected for the stratified period (Lindell and Post 1995).

If our results apply to other regions and other seasons of the study region a new paradigm of pelagic food webs for the oligotrophic ocean will be needed. The traditional paradigm has concentrated on the food chain phytoplankton-copepods-planktivorous fish. In the 1970ies the ”microbial loop” (picoplankton and bacteria-heterotrophic flagellates-ciliates-copepods) was proposed as the second major pathway of energy and carbon flow in the pelagic food web (Pomeroy 1974, Sieburth and Davis 1982, Azam et al. 1983). Because of the predominance of picophytoplankton in the oligotrophic ocean (Stockner and Antia 1986, Raven 1986) and the inability of copepods to feed on picoplankton it is assumed that the microbial loop dominated over the classic food chain in oligotrophic systems. We have found grazing rates of pelagic tunicates at least locally comparable to those of the protozoa and clearly higher than those of the copepods. Because of their high efficiency in capturing extremely small food particles, their high clearance rates and their high intrinsic growth rates (Bochdansky and Deibel 1997, Bone et al. 1997, Crocker et al. 1991, Deibel 1982a and b, Heron 1972) we expect them to be similarly important in other systems where the same mechanism operate. Therefore, we suggest that picoplankton feeding by tunicates should be considered as the third major pathway in the pelagic food web.

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Estimation of phytoplankton concentration in the Gulf of Aqaba (Eilat) by bio-optical methods for application in remote sensing

Noga Stambler[1], Leonid Sokoletsky[1], Vladimir Belousov [1], David Iluz[1], Maxim Shoshani[2], Boaz Lazar[3], Max M. Tilzer[4] and Zvy Dubinsky[1]

1) Faculty of Life Sciences, Bar Ilan University, Ramat Gan
2) Department of Geography, Bar Ilan University, Ramat Gan
3) Institute of Earth Sciences, The Hebrew University of Jerusalem
4) Universität Konstanz, Konstanz

The aim of the present work was to examine the relationship between the optical properties of the Gulf of Aqaba waters, and phytoplankton biomass and composition over the course of the year. The underwater light field in the Gulf of Aqaba was characterized on the basis of data collected at station A1 during 1995-2000.

Spectral composition and penetration depth of underwater light was affected by total phytoplankton biomass and by pigment composition. The euphotic zone, as defined by the 1-% light depth, ranged from 70 to 125 m (Fig. 1). The mean vertical light attenuation coefficient

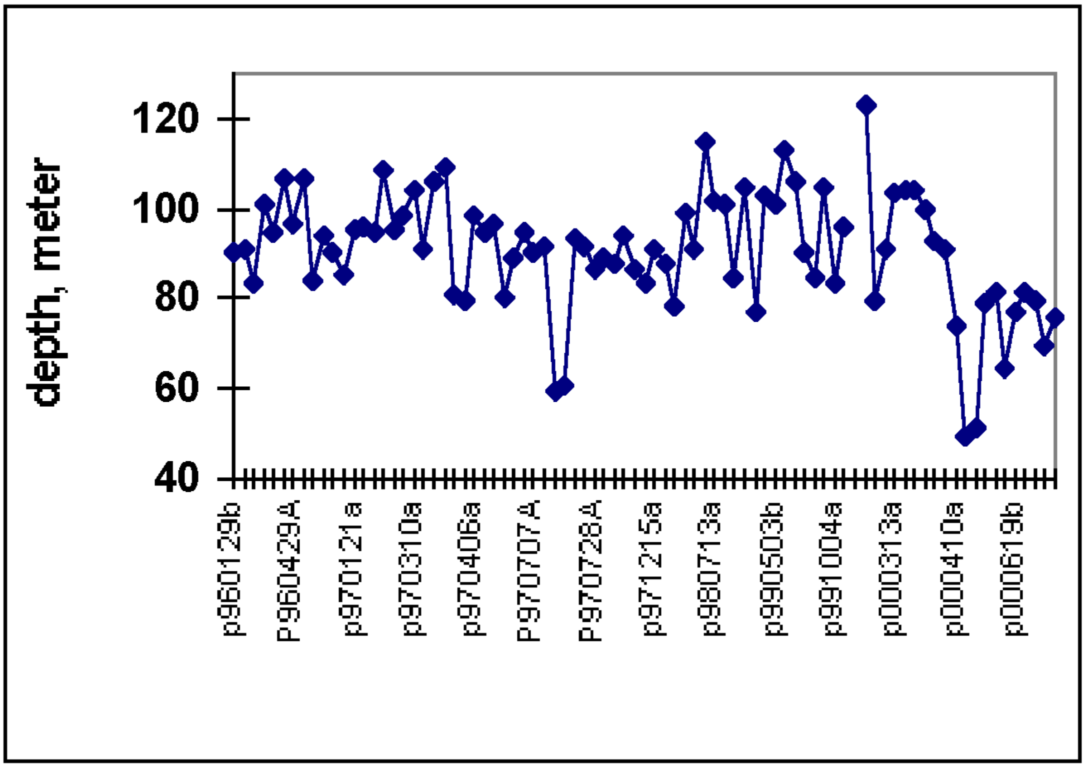


Fig. 1: The euphotic zone at station A1 during 1996-2000.

K_d (PAR), between the water the surface and 110 m depth, showed a summer minimum of 0.04 m^{-1} and a spring maximum of 0.065 m^{-1}. UV (300-400 nm) penetrated down to 69 m depth. The ratio UV/PAR increased from the surface to 10 m depth and declined below, indicating that in shallow waters phytoplankton are exposed to high UV levels. More than 90 % of red light were absorbed in the upper 10 m depth layer which is the reason for the high ratio of UV/PAR in this layer.

K_d (λ) for discrete wavelengths between 400-700 nm was minimal with 0.01 m^{-1} in the blue (440 nm), and maximal with 0.1 m^{-1} in the red (665 and 694 nm). The spectral radiance reflectance, R (λ), varied from less than 1 to 6 % .

During fall, nutrients are introduced to the euphotic zone from below due to water column mixing leading to increasing phytoplankton biomass (see Häse et al., this volume). As a result, phytoplankton biomass increases and the euphotic depth decreases. By contrast, during thermal stratification in summer the nutrient input into the euphotic zone is prevented by the thermocline. Phytoplankton biomass decreases. Consequently, light can penetrate deeper, and the euphotic zone increases. Moreover, small taxa that have a competitive advantage under nutrient-poor conditions. As evidenced by flow cytometry, during mixing eukaryotes are dominant, since there sufficient nutrients in the water. Under stratified conditions, cyanobacteria and prochlorophytes become dominant. Cyanobacteria are dominant immediately after mixing dominant, as soon as the water column begins to stratify in spring. Cyanobacteria are closer to the water surface, while prochlorophytes prefer low ambient light levels in a stable water column. The red fluorescence of the cells is proportional to their chlorophyll content, and thereby provides information regarding the history of the light field to which they are acclimated to. In summer, a deep chlorophyll maximum is present at about 80 m in the Gulf of Aqaba, formed mainly by *Prochlorococcus*. During summer stratification, phytoplankton cells of all three groups showed a marked increase in cellular chlorophyll content with depth as a result of photoacclimation. Photoacclimation was expressed by an increase in all pigments, in particular divinyl chl *a, b* and their relation to chl *a*.

During mixing, eukaryotes, cyanobacteria, and *Prochlorococcus* were found throughout the mixed water column. As a result of homogenous photoacclimation throughout the mixed layer, cellular chlorophyll content did not vary with depth.

In the Gulf of Aqaba, K_d (PAR) values were generally low in comparison to other waters, but showed dependence on pigment concentration, in spite of the low chlorophyll content in the total euphotic zone (0.1-0.6 mg l^{-1}).

Reflectance values were also low as a result of the low concentration of light reflecting particles in the water. By using the reflectance ratio R(440/550 nm), the absorbency of chlorophyll can be distinguished from the absorbency by water itself. In the Gulf of Aqaba, this approach was adequate for the upper 20 m depth layer, whereas the chlorophyll concentration down to 100 m depth was estimated from K_d (490) yielding a highly significant correlation with $r^2 = 0.86$.

The spectral distribution of light at different depths did reflect the seasonal changes in phytoplankton biomass and composition as expressed in the variability of the spectral attenuation coefficients, especially between K_d (440) and K_d (665), and also between K_d (555) and K_d (440) or K_d (694). However, in the Gulf of Aqaba, this effect was small as a consequence of low phytoplankton concentration in general.

Using reflectance ratios at the same wavelengths as used in remote sensing algorithms, we could estimate the chlorophyll concentration quite precisely. The best fit function for the observations in 1995-96 was:

$$\text{Chl} = 0.644^* (\text{R440/R550})^{-1.199}$$

Measured chlorophyll concentrations were highly correlated to predicted chlorophyll concentrations ($r^2 = 0.69$).

In addition, several single-wavelength (at wavelength 443 nm) algorithms for simplified estimations of pigment concentration were developed. The algorithms were derived by analysis of bio-optical data collected during 1996-1998 in the Gulf of Aqaba. Three parameters were considered: Pigment concentration just below the surface (C_0), mean concentration of the ”penetration layer” ($<C_p>$), and the mean concentration of the ”euphotic layer” ($<C_e>$). The analysis showed that:

1) The spectral diffuse attenuation coefficient K_d (443 nm) can be expressed as power dependence on pigment concentration,

2) The spectral backscattering coefficient b_b (443 nm) was almost not influenced by the pigment concentration in the range measured,

3) The spectral water-leaving radiance L_w (443 nm) was proportional to the ratio of incident spectral solar irradiance E_d (443 nm, 0+), and to the spectral diffuse attenuation coefficient averaged over definite water layers [$<K_d$ (443 nm)$>$].

We may summarize that spectral attenuation coefficients of downwelling light and spectral reflectance ratios are useful tool for the estimation of chlorophyll concentrations, even at the low pigment concentrations common to the Gulf of Aqaba.

Vertical distribution of phytoplankton species and their cell densities in the northern region of Aqaba Gulf (St. A)

Ola E. Taha, Mohamed S. Abdel-Karim and Emad H. Sobhy

National Institute of Oceanography and Fisheries, Cairo

During the regular cruises of Project A, water samples were collected from selected depths. The samples were immediately preserved in 4 % formalin and transported to Zamalek Lab. The samples were poured into cylinders and Lugol Iodine was added to facilitate the sedimentation of phytoplankton cells. The volume of each sample was reduced to 50 ml by siphoning the water and 5 ml were transferred to the counting chamber and left for 24 h for extra sedimentation. The counting and identification of phytoplankton species were carried out using inverted microscope (Zeiss Model Axiovert 25 C).

The results were presented as a number of phytoplankton cells per liter. The present data covered the period from March 1997 to March 1998.

Phytoplankton communities in the sampling site were represented mainly by 4 taxa, namely Bacillariophyceae, Dinophyceae, Chromophyceae, and Cyanobacteria. In general, Bacillariopyceae were the dominant group, represented mainly by *Chaetoceros compressum, Leptocylindrus danicus, L. minimusan, Nitzschia longissima, N. closterium, Pseudonitzshia delicatissima, Skeletonema costatum* and *Thalassiosira angulata*.

Dinoflagellates were the second abundant group and were represented by *Amphidinium crassum, A. latum, Exuviella compressa, E. apora, Gymnodinium albulum, G. minor, G. minutum, Oxytoxum diploconus*.

Chromophyceae were the third abundant group and represented by *Hillea fusiformis, H. marina, Rodomonas salina* and *Rhinomonas fulva* .

Cyanobacteria were the last group represented by the pico-plankton species, the chroccocal Cyanobacterium *Synechococcus*.

The results indicated that in March, June and July 1997, phytoplankton cells were concentrated at 20 m depth, reaching a maximum of 11,538 cells. L^{-1} in March 1997. In May and December 1997 and February and March 1998, the population densities of phytoplankton cells were high at depths from 80–100 m with a maximum value of 13,400 cells l^{-1} in February 1998. It is noteworthy that the euphotic zone in the sampling site extended to about 110 m (Fig. 1).

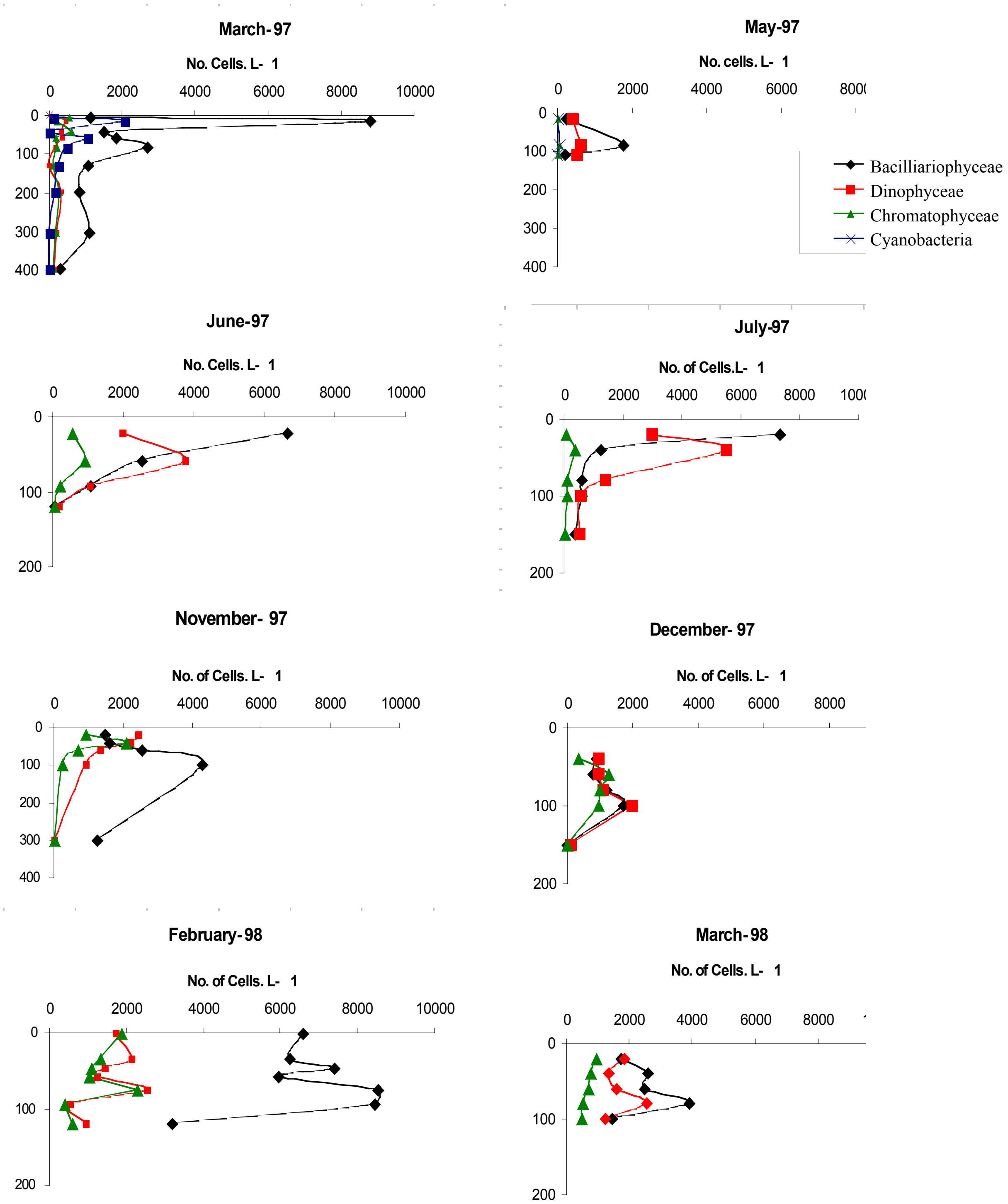


Fig. 1: Phytoplankton concentrations at various depths in 1997 and 1998.

Assessment of fish stocks with emphasis on Scombridae in the Gulf ofAqaba (Jordan)

Nidal Odat[1], Sayeeda Mir[1], Maroof Khalaf[2] and Mohammad El-Zibdeh[2]

1) Department of Biological Sciences, Yarmouk University, Irbid
2) Marine Science Station, Aqaba

Abstract

The goal of the present study was to assess stocks of commercial fishery in the Gulf of Aqaba. Special emphasis was given to the Scombridae family. The study was conducted over a period from July 1999 to June 2000. Assessment of the major fish stocks was conducted on a daily basis. Samples of the two commercially valuable species of scombrids, *Katsuwonus pelamis* and *Euthynnus affinis*, were collected for aging, length weight relationship (LWR) measurements and for stomach content analysis. The logarithmic form of the equation $W=aL^b$ was established. The LWR indicated that growth was of an isometric form for all the investigated species. Values of the constant b were found to be close to 3. It was found that Scombridae and Siganidae were among the most commercially valuable families represented the major fish landings during the investigated period in the Gulf of Aqaba. Data on catch indicated that more than 60 % of the total catch was belonging to Scombridae. It is essential therefore that the population dynamic of this family and factors affecting it should be investigated for better management and sustainable use of these commercially important fish stocks. Amongst the factors are food availability, environmental conditions and catch season. The combination of numerical, frequency of occurrence, and gravimetric methods of stomach analysis for the two examined species of the Scombridae revealed that the variation in food items is related to presence or absence of the major food item *Atherinomorus lacunosus* and that other food items such as the planktonic crustacean and/or molluscs became a second priority.

Introduction

Resources of coral reef fishery are intensively exploited all over the world and in many cases they are overfished. In spite of recent progresses in the ecological understanding of these communities, many aspects of their exploitation dynamics still remain obscure, and that successful assessment methods suited to these highly complex fisheries are still to be designed (Appeldoorn 1996, Russ 1991, Pauly 1988).

Because Jordan has a short coastline (27-km) and narrow continental shelf, the fishery resource is limited to artisanal methods. Jordan fishermen operate few number of medium and small fishing boats, using simple fishing gear such as hand-lines and gill nets. Their fishing grounds became very limited, mainly due to political complication. In the past they were allowed to go as far as Tiran Island and other fishing grounds in Saudi-Arabian and Egyptian waters in the southern part of the Gulf of Aqaba. Now the use of those waters is not allowed for any fishing purposes. Fishermen are using small fishes like sardines as baits. Trolling lines, hooks and seine nets are used by the artisanal fishery. Trolling lines are used to catch relatively large fishes that command high prices such as tuna and dolphin fish.

The family Scombridae includes 15 genera with 49 species. They are found in tropical and subtropical waters. Mackerels and tuna are fast swimming, usually pelagic fishes, having two dorsal fins, with finlets behind the second dorsal and anal fins. Caudal peduncle is slender with lunette caudal fin. Tuna and tuna-like species are extremely valued commercially, especially the albacore, the bigeye tuna, the bluefin, skipjack, and the yellowfin tuna.

The literature clearly reveals a major gap in studies describing the fisheries structure and the assessment of the fishery resources in the Jordanian sector of the Gulf of Aqaba. Therefore, the present study aimed to gather recent information about the status of the local fishery resource there. Data collecting was based on information obtained by interviewing fishermen, description of fishing devises and selected parameters of stock assessment records. Special attention was given to investigate some biological aspects of two species of tuna fish, *K. pelamis* and *E. affinis*.

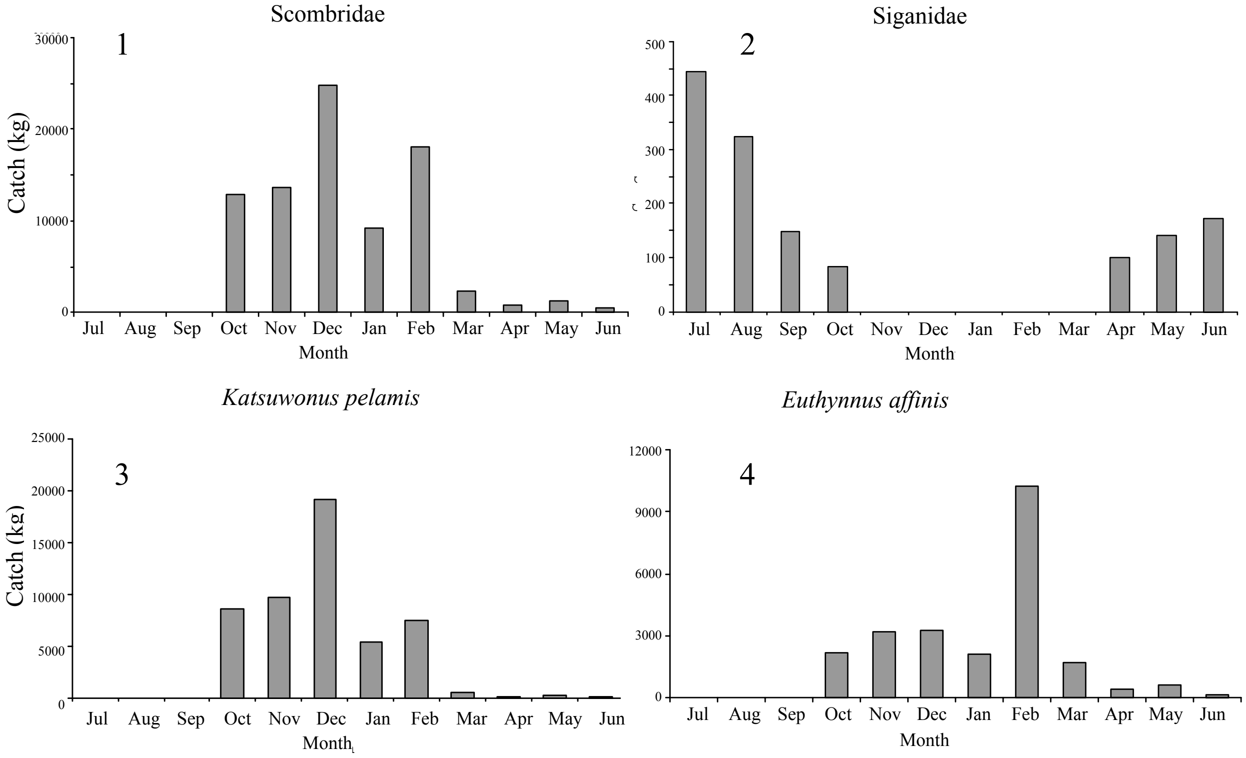
Methodology

The framework of the present study was carried out over a period of 12 months, from July 1999 to June 2000. Landing sites and catch of the main families, length weight relationship and fishing effort were analyzed. Data on marketing and commencing policy of the commercially fishes were gathered from the local fish markets in Aqaba. Data on number of fishermen, number of boats, the time spent at sea during the fishing day, number of fishing trips, and areas where the active fishing was carried out were collected from the Jordanian Coast Guard Forces check points at the two landing sites located in the north and south of Aqaba. For laboratory investigations fifteen specimens from each species, *K. pelamis* and *E. affinis* were collected for aging, LWR measurement, gonadal index and stomach content analysis. Data on food items were analyzed by a combination of numerical, frequency of occurrence and gravimetric methods (Hyslop 1980).

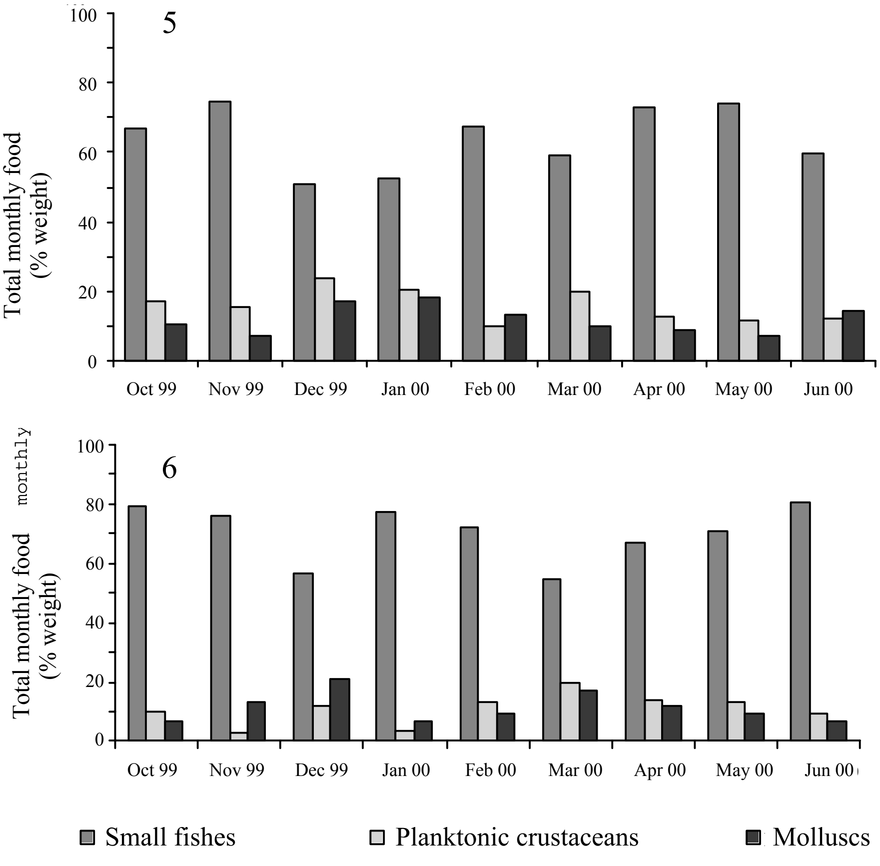
Results and discussion

The results indicated that the family Scombridae appears in the Jordanian water during the period from October until June and disappears during the period July till September (Fig. 1). This may be related directly or indirectly to some oceanographic and biological factors in the Gulf of Aqaba such as temperature and the biological productivity of the sea.

Two species of tuna are mainly caught in the Gulf of Aqaba, *K. pelamis* and *E. affinis*. These two species, usually caught by hand line and sometime with gill nets, appeared during nine months of the year from October till July (Fig. 3 and 4). Specimens of the other important fam-



Figs. 1-4: Monthly catch of Scombridae, Siganidae, *Katsuwonus pelamis* and *Euthynnus affinis* in the Gulf of Aqaba.



Figs. 5-6: Seasonal variation in the diet composition of *Katsuwonus pelamis* (5) and *Euthynnus affinis* (6) as percentage of total food items by weight.

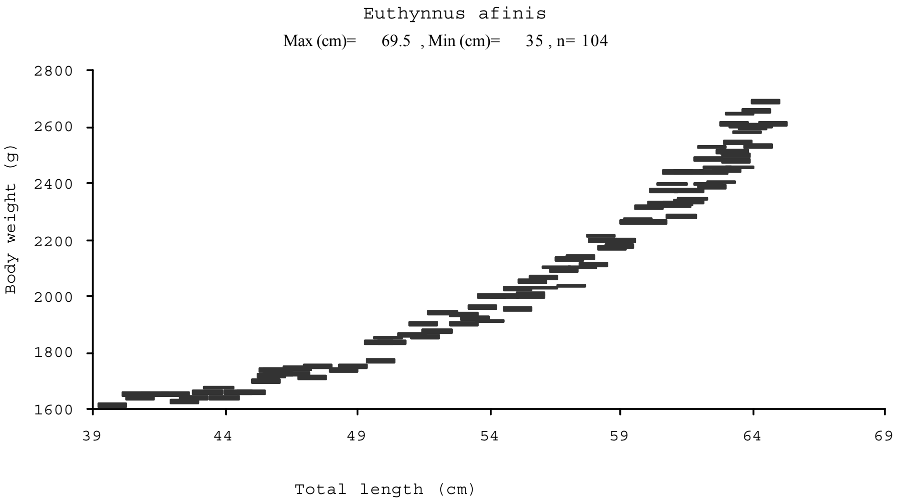


Fig. 7: Length weight relationship for *Euthynnus affinis.*

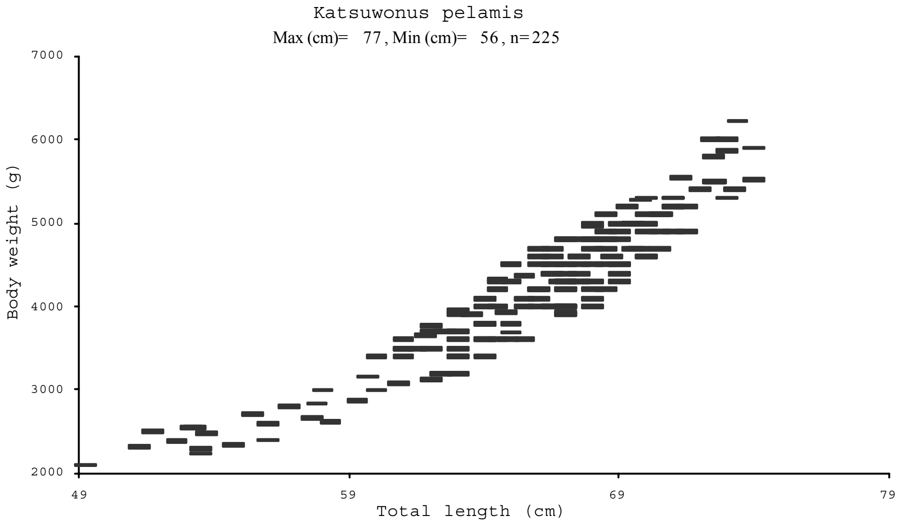


Fig. 8: Length weight relationship for *Katsuwonus pelamis.*

ily Siganidae are caught all around the year except for the period from November till March (Fig. 2). In this period the fishermen completely pay their attention to utilize other fishes like tuna. Variation in the food items was found in the stomach of the two species of tuna *K. pelamis* and *E. affinis*. Small fishes (*Atherinomorus lacunosus*) were the major food items for these two species. The appearance of these small fish in stock the Gulf of Aqaba during the period of the year, where tuna represent most of the fish in the Gulf, may indicate that the distribution and the migration of tuna to the Jordanian waters is related directly to their need of these small fishes as a preferable diet component. Crustacean and molluscs were also found in the stomachs of these two species of tuna (Fig. 5 and 6).

The results for the length weight relationship of the two species showed that the growth is isometric. The regressions were highly significant with the values for the constant b close to 3. The coefficient of determination (r^2) for *K. pelamis* was 0.8123 and 0.8991 for *E. affinis*. The LWR for the two species is given in (Figs. 7 and 8).

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The status of Jordan's marine fisheries in the Gulf of Aqaba

Mohammad El-Zibdeh and Ahmed Abu-Hilal

Marine Science Station, Aqaba

The study aimed to evaluate the actual status of Jordan's marine fishery resource for a better management and utilization of the Jordanian Gulf of Aqaba. Scattered data and information on marine fisheries, fishing efforts expended by Jordanian fishermen, total catches, imports and consumption from 1956 to 1998 were gathered, compared, statistically treated and analyzed. Gradual decline with fluctuated pattern of commercial fish production was observed during the investigated period despite the apparent increase in number of registered boats and fishermen. The maximum annual catch was 191.9 t in 1966 and minimum catch was 18.7 t in 1980. It was observed that fish production does not exceed more than 0.8 % of the total fishery consumption of Jordan. Percentage of fresh fish to the total consumed fish fluctuated between 0.65-17.85. The *per capita* fish consumption of Jordanian is low (1.5 kg/head/year). However, demand for marine fish is large and being expanded as learnt from the substantial increase of fish imports in recent years. It was concluded that the marine fishery resource would continue to decrease in the future if the past and present practices are to continue. Suggestions for improving marine fishery and mariculture in Jordan are discussed.

Introduction

Jordan has a coastline of only 27 km long on the northeastern side of the Gulf of Aqaba. Most of the coastal strip is rocky with a fringing coral reef system and deep waters are close to the shore. The waters within this northern portion is characterizes by its low productivity (Levanon-Spanier 1979). The marine environment in this area had suffered for sometimes before 1970 from the illegal use of dynamite for fishing purposes. It was further affected from the use of underwater bombs made by neighboring military forces. The environment suffers from port activities and industry expansion. During the last three decades, intensive industrialization, and trading and recreational activities have adversely affected the shallow water community including the fringing coral reef. The Jordan’s short coastline certainly limits commercial fishing to artisanal methods, which centers mostly on reef-associated and some pelagic fish species. Therefore, commercial fishing in Jordan is of little significance to the GNP. A gradual decline of commercial fish production has been observed during the last few years. Fishing grounds of Jordan’s fishermen vary from time to time, mainly due to political restrictions. Few years ago they were able to go as far as Tiran Island and other fishing grounds in Saudi-Arabian and Egyptian waters in the southern part of the Gulf of Aqaba. Now the use of those waters is restricted for any fishing purposes which was negatively reflected on the Jordan fish catch from the Gulf despite the efforts made to benefit from the various programs to develop the fishery resources for countries surround the Red Sea (FAO UNDP, Arab Fishing Company, the Arab League and the FAO project; RAP/18/1002) and development of fisheries in areas of the Red Sea and Gulf of Aden (Bartkowiak 1955, Braid and Kahlidi 1962, Dabaj 1980, Eriksen 1957, Gilberg 1966).

Methods

The scattered data on fish catches (landings) were obtained from the fish inspector statement and files of the Ministry of Agriculture Office in Aqaba (Kilani, pers. comm.). The fish imports for 42 years (1956-1998) were obtained from previous reports (Gilberg 1966, Dabaj 1982, Department of Statistics in Jordan Exterma; Trade, 1966-1968, 1979-1982; Ministry of Agriculture 1996, 1998). Data on human population were obtained from the Statistical Yearbook (1998) published by the Department of Statistics in Jordan. Number of fishermen and fishing boats were obtained from the official files of the licensing office in Aqaba Port Authority. The number of fishing trips per boat were obtained from the files of the Jordanian Coast Guard Forces.

Results and discussion

Fig. 1 represents the annual catches of marine fishes from the Gulf of Aqaba by Jordanian fishermen from 1956 to 1996. It shows the highest catches were in the period between 1960 and 1966 with maximum landings in 1966. The catches decreased in 1967 and 1968, and then increased during 1969 then decreased again in 1970 and 1971 when the catches were only 35.3 t. In 1972 another period of small and gradual increase in the landings occurred but only for 3 years, after which a period of dramatic decrease in landing started in 1975 but remains more or less fluctuated around the average as estimated in the successive years. Many reasons were behind this fluctuation in the total marine catches. Amongst the reasons are the followings:

1) Wars in the region, together with the political conditions created by it. The 1967 war had affected the landings until 1969. The 1970 local troubles had affected the fishing operation to the end of 1971. The 1973 "October War" had also affected the movements of the fishermen who were unable to fish in the southern regions in the Gulf of Aqaba, particularly in the Egyptian coastal waters along Sinai coasts.

2) The strict security measures by Jordan and neighboring countries and the difficulties in getting fishing permissions had also affected the number of trips to the fishing grounds in the southern portion of the Gulf.

3) The Jordanian "fishing law" No. 25 for 1943 and the law of Agriculture No. 20 for 1973, which prohibit the illegal use of dynamite for fishing purposes, were enforced and strictly applied after 1970. The fishermen stopped the use of dynamite in- and outside Jordan waters, consequently the catches decreased.

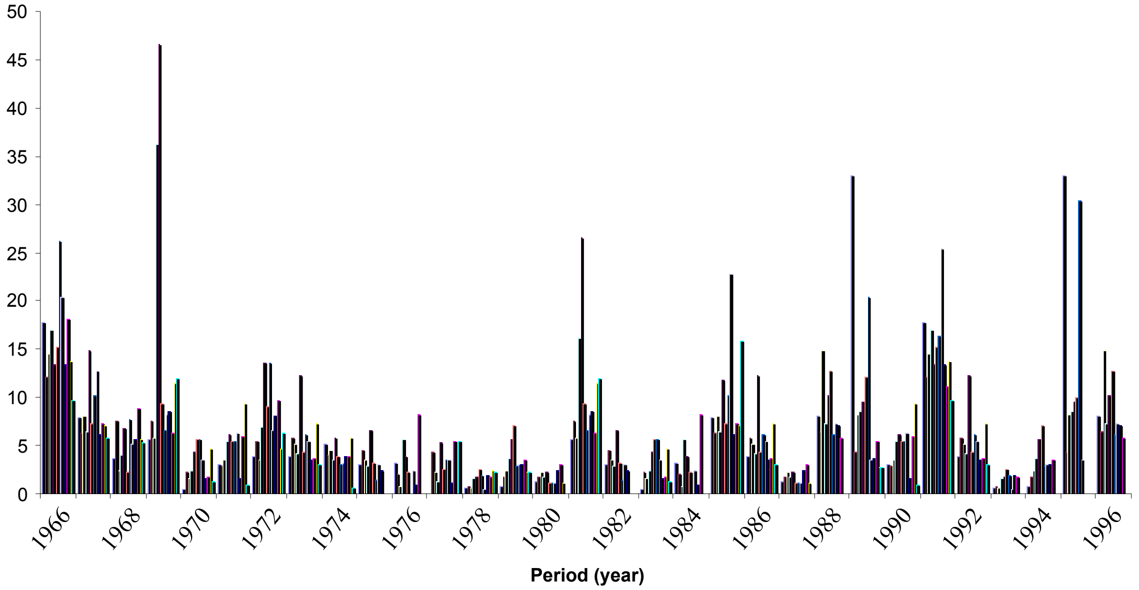

Fig. 1: Annual landing (tons) from the Jordanian Gulf of Aqaba in the period between 1966 and 1996

4) Many licensed fishermen and many fishing boats were out of work, mainly because of the above-mentioned reasons. Furthermore, many fishermen had left fishing to a better income from the new jobs created by the increased activities in the port and in the private companies.

5) The most prominent observations on the deterioration of fishery production in recent years is the depletion of soft bottom communities with a serious decline in macrofauna such as echinoderms and gastropods and the dominance of nematodes and polychaetes in the Gulf of Aqaba.

Monthly and seasonal landing

The average monthly catches for the period between 1966-1982 showed general seasonality. May is the month of the maximum catches. This is in agreement with a similar conclusion reported in Saudi Arabian Red Sea by Kedidi (1984). Spring is the season of the highest catches and winter is the season of lowest catches. The highest catches during spring could be attributable to the relatively high productivity during this time of the year, which is considered as the spawning season for most of the fish species in the Red Sea area (Kedidi, 1984). Many species of the family Scombridae usually appear in large schools in the northern part of the Gulf of Aqaba during April, May, June, and July (Ben Tuvia 1962). The big *Thunnus albacares* form the bulk of the catch during this season.

Relation between catches and number of fishermen and fishing boats

Fig. 2 shows the catches and the number of fishermen from 1970 to 1996. It shows an increase in the number of registered fishermen and a paralleled increase in number of fishermen actu-

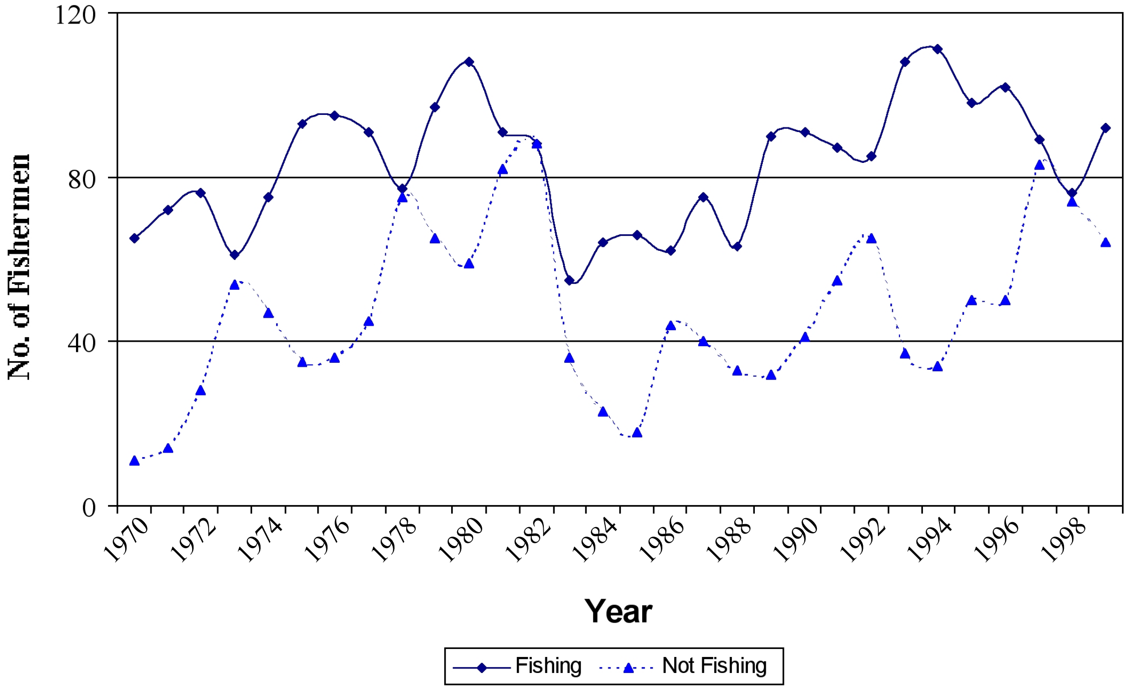

Fig. 2: The registered number of Jordanian fishermen (fishing and not fishing) during the period 1970 - 1999.

ally at work. However, not all of fishermen who registered are actually practice fishing because regularly around 30-40 % are used to leave fishing looking for better income jobs. It can be said that the increase in the number of registered fishermen (and fishing boats) was a false increase because a high percentage of these fishermen were not practicing fishing and many of the boats were not used in fishing trips. It is therefore not surprising that the increase in the number of fishermen was found not to significantly contribute to the total catches. However, the statistical analyses of the available shows that number of trips are more indicative and more important in affecting the total catches. The calculated correlation coefficient (r) between total catches and number of trips was high (r = 0.70).

Fish catches and imports

The annual fish import from 1956 to 1982 and from 1990 to 1996 indicates that fish importation is increasing continuously. The last decade recorded the highest in fish imports to Jordan (Figs. 3 and 4). However, the catch/import ratio is still at its minimum and that reflected on the average fish per head (fish/head/year) in Jordan, which is lower than the world average (13 kg/ head) and even lower than the average reported for many Arab countries (Juma et al. 1981), such as south Yemen (51.6 kg) Oman (22 kg) and Saudi Arabia (4.2 kg). The highest fish/head in Jordan was 3.6 kg in 1993 and the lowest was 0.6 kg in 1981. The average fish/head for the period from 1968 to 1982 was 1.43 kg, of which 1.38 kg as imported fish.

Mariculture in Jordan

Potentials of inland aquaculture development is very limited due to the water shortage in Jordan. Mariculture however, has a strong possibility to be improved and developed in good har-

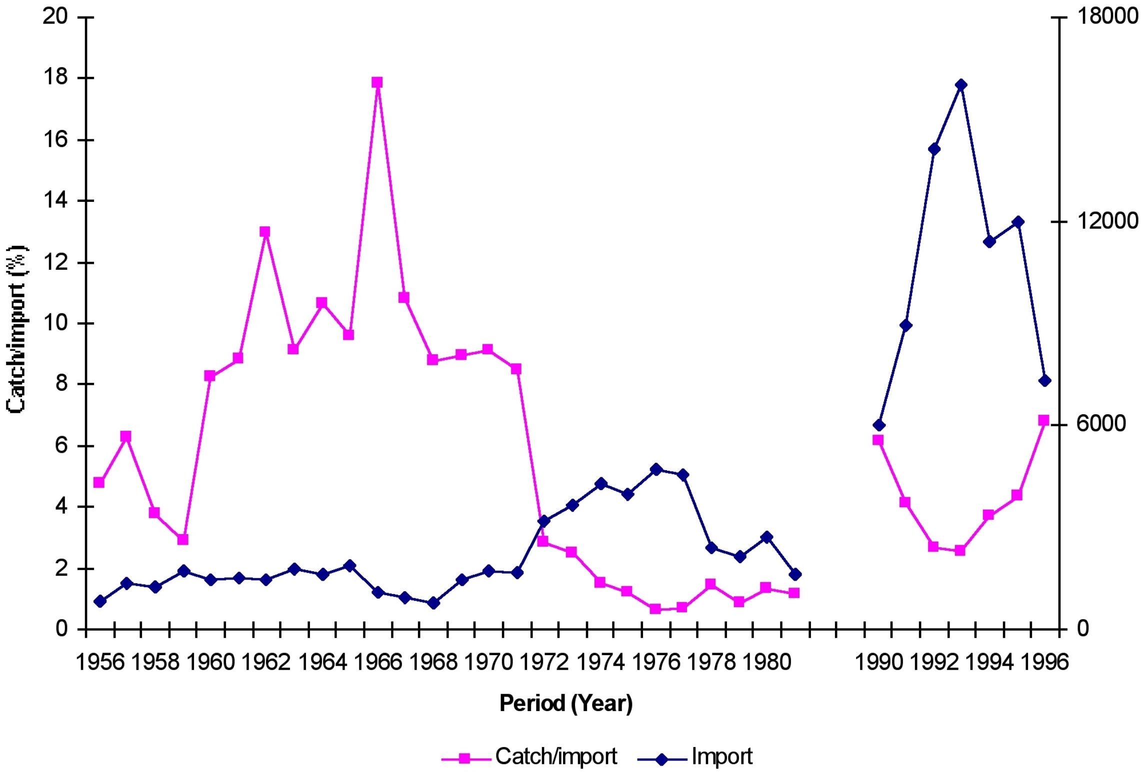

Fig. 3: Fish import and percentage of annual catch per import.

mony with marine environment. As of today, there were limited research and development projects in mariculture in the Aqaba region and none of these were geared to commercial scale. The Marine Science Station is currently the main center of marine fisheries in Jordan and therefore a natural focus for any activities in research and development of mariculture and the most appropriate base on which staffing and facilities are built. A previous study noted the

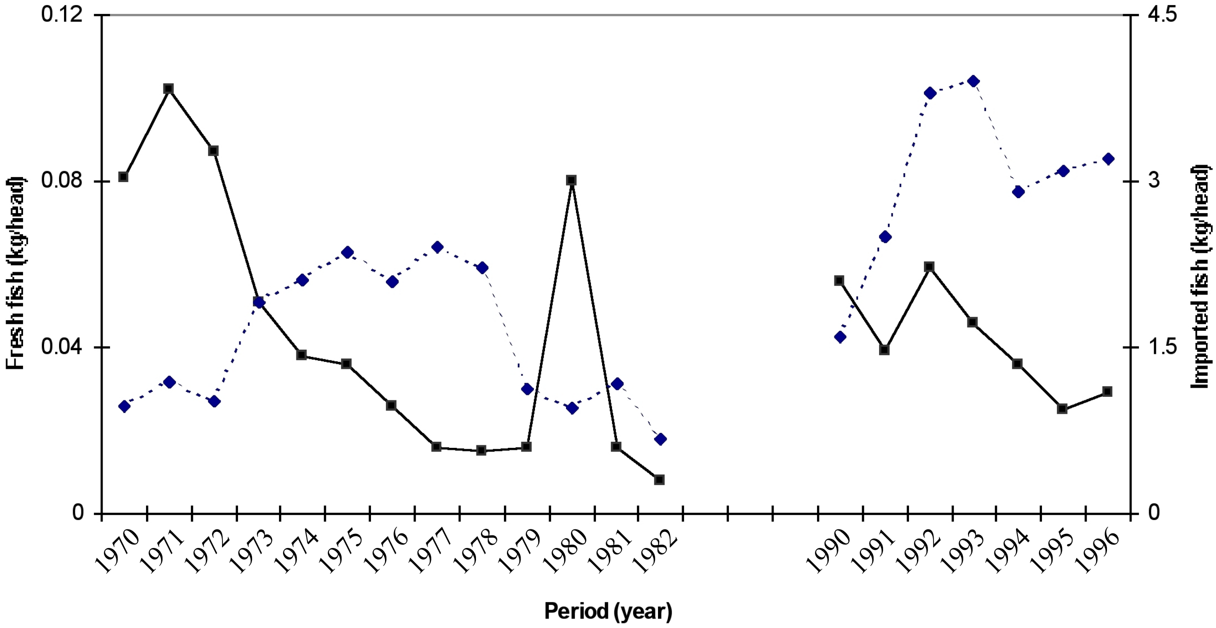

Fig. 4: Imported and fresh fish per capita in Jordan during the period from 1970-1996.

potential of the Jordanian coast in the Aqaba Gulf for practicing different aspects of mariculture (FAO 1974). Only some experiments were conducted at the Marine Science Station. Pilot experiments on culturing sea bass *Dicentrarcus labrax*, rabbitfish, *Siganus* sp. and red tilapia, *Oreochromis* sp. were conducted to investigate the technical and economical feasibility of these species in the Gulf of Aqaba. Early experiments have started at the Marine Science Station about ten years ago. A major pilot experiment was conducted in collaboration with a French team (Joubert 1990). The Mediterranean species *D. labrax* was introduced into the Jordanian waters of the Gulf of Aqaba. The experiment was heavily based on imports. The expertise, fry, raw material and feed were all imported from France, which resulted in high costs. A large fraction of the costs went for importing fingerlings and feed. The aim of the experiment was to investigate the technical and economic feasibility of culturing sea bass and to compare between two raising systems, inland race ways and floating cages under Aqaba Gulf conditions. Encouraging results have been reported in terms of adaptation, growth and mortality and that the environmental conditions in the Gulf would be exceptionally suitable for culturing these species.

Conclusion

Figures indicate that Jordan will continue to depend mainly on the imported fish to provide the local market with its needs if no effort was made to improve and develop fishing methods and gear and increasing the fishing grounds outside Jordanian waters.

Fishing grounds available for Jordanian fishermen are very limited. Agreements with Egypt and Saudi-Arabia to increase fishing grounds organize fishing activities and to facilities is a necessity. Therefore organizing and improving the fishermen activities is also necessary. A fisherman's co-operative organization will help solving many problems and organizing fishing efforts.

There is a need for a marine fishing center connected with the fishermen's co-operative to gather information on fisheries, fishing methods, catches, fish species and gear. The data will be useful for fisheries development.

The local, Arab and international private sectors should be encouraged to establish a fishing company and finance the purchase and operation of modern fishing boats as well as to finance and operate fish farming projects. It is necessary to cooperate with Arab League, United Nations Organizations and Programs and with all interested International Institutions to help in:

1) Provision of a transport boat which could collect the catches of small tradition boats used by the fishermen and from other fishing boats and bring it to Aqaba. It will provide fishermen with their needs such as food water and ice. This will help them to stay at sea for long periods.

2) Provision of a fishery survey vessel equipped with necessary fishing gear, equipment for fish location, navigation, enough storage space (-20° C) and small scientific laboratory.

3) Training of a fisheries officer and enough crew to work on the boats.

4) Securing a fishing gear technologist or master fisherman to train fishermen and researchers on the most suitable fishing operations.

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Ecology of Coral Reefs

Human impacts on coral reefs of the northern Egyptian Red Sea

Abdel-Hamid Abdel-Rahman and Ahmed H. Nawar

National Institute of Oceanography and Fisheries, Cairo

The effects of human activities on coral reefs were studied at seven locations along the Northern Red Sea of Egypt, extending from El-Ain Al-Sukhna in the north (Gulf of Suez) to Gasos1 (20 km south Safaga Port). We investigated the effects of increasing sedimentation rates, high levels of petroleum pollution, increasing sewage discharges and enhanced recreational activities on coral community structure and population density of Zooxanthellae. Occurrences and distribution of four coral diseases (Coral Bleaching, White Band Disease, Black Band Disease and Bacterial Infection) were determined as indicators of reef health. Live hard coral cover, species diversity, hard coral density and population density of Zooxanthellae decreased significantly with increased sedimentation rates and concentration of petroleum hydrocarbons. In contrast, dead coral cover was significantly increased with elevated levels of oil pollution and sedimentation. Macroalgal cover was significantly negatively correlated with live hard coral cover. The increased dissolved nutrient concentrations, as a result of enhanced sewage discharges, significantly increased the percentage of macroalgae which compete with hard corals for substrate space and overgrow living coral tissues. Coral breakage was found to be the most common damage in the reefs exposed to higher visitor frequency. Boat anchors, SCUBA diving, trampling on reef flats and destructive fishing practices were the main causes of coral breakage. It is suggested that the interactions between natural and anthropogenic factors were the probable causes of enhanced coral diseases in the area of study. Some coral species such as *Stylophora pistillata*, *Acropora pharaonis*, and *Galaxea fascicularis* showed greater resistance to increasing sedimentation rates, high levels of oil pollution and sewage discharges.

Coral Reef Sponges in the Gulf of Aqaba (Jordan)

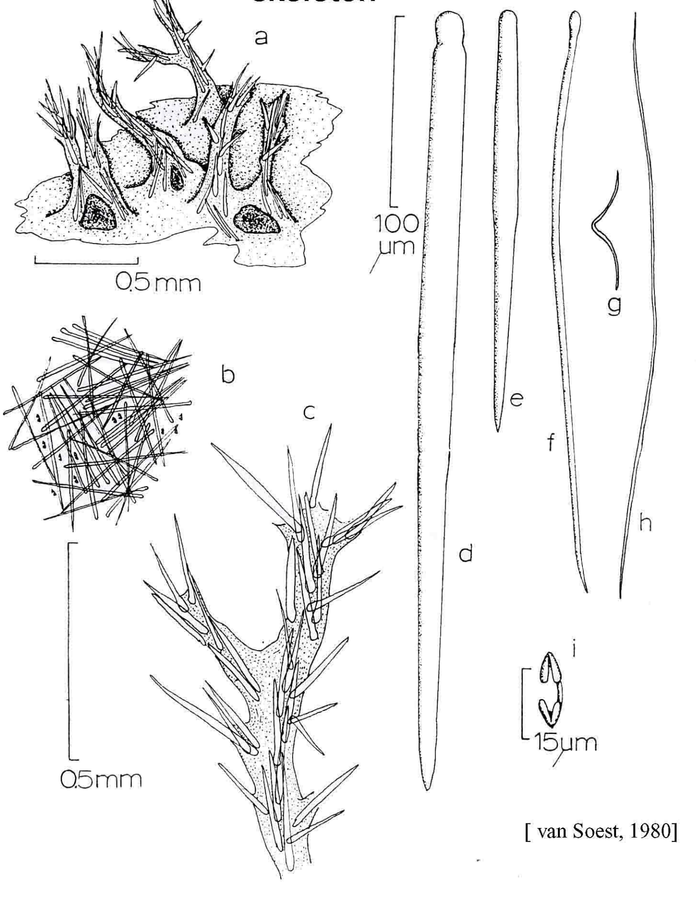
Ahmed Al- Sabi[1], Salim Al-Moghrabi[2] and Mohammed Al-Adhami[1]

1) Yarmouk University, Biology Department, Irbid
2) Marine Science Station, Aqaba

The Gulf of Aqaba is one of the two V-shaped branches at the northern tip of the Red Sea. Its fringing coral reefs harbor highly diverse communities at the most northern latitudinal distribution of reefs worldwide. Sponges are an important component of coral reef benthic communities and their biomass may exceed those of the reef building communities. Sponges have a considerable impact on their environment by effectively filtering large quantities of water, modifying the reef framework, competing for space and serving as food source and shelter for numerous fishes and invertebrates.

The phylum Porifera or "sponges" consist of four classes: Demospongia, Calcarea, Hexactinellida and Sclerospongia. Demospongia comprise the largest class (95%); they possess a skeletal network of siliceous spicules divided into megascleres (large spicules) and microscleres (small spicules), that frequently supplemented or entirely replaced by spongin

Fig.1. Typical Demospongia skeleton



[van Soest, 1980]

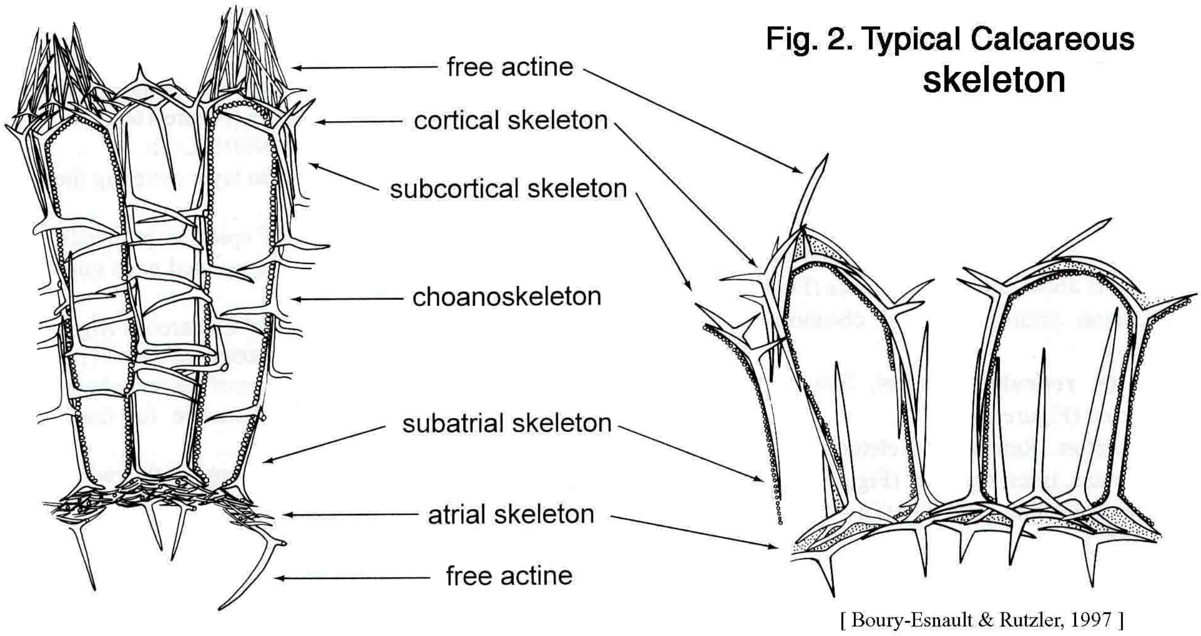


Fig. 2. Typical Calcareous skeleton

[Boury-Esnault & Rutzler, 1997]

fibers (Fig. 1). Calcarea are composed of separated calcareous spicules, one-, three-, or four-rayed spicules (Fig. 2). The combination of spicule size, type, distribution and their relationship to the fibrous skeleton is often used for their identification. It is important to combine the histological and morphological characteristics with habitat aspects since the morphological nature of sponges shows great plasticity in response to local and geographic environmental variables (Bergquist 1978 and Deload 1996). Almost all attributes to sponge structure vary within wide limits, thus making description and definition of species very difficult and more subjective than that of most other invertebrate groups.

Studying the biodiversity of the coral reef sponge community is an important step in understanding the coral reef ecosystem. Sponges are valuable indicators for monitoring, the health and rehabilitation of coral reefs. Sponges are interesting for their bioactive compounds. Large efforts are undertaken worldwide to extract and identify these for medical purposes.

Fig. 3. *In situ* photo of *Tethya seychellensis* (Demospongia); Tetractinomorpa, Hadromerida, Tethyidae), 14 m depth.

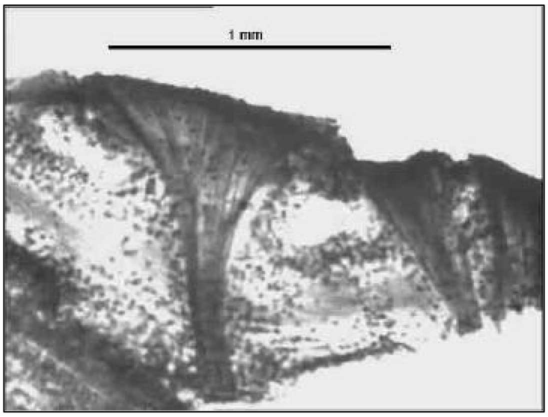


Fig.4. Tangential section of *Tethya seychellensis.*

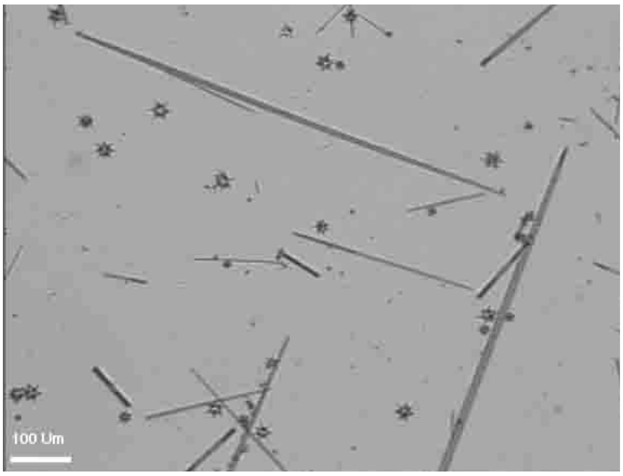


Fig. 5. Spicule preparation of *Tethya seychellensis.*

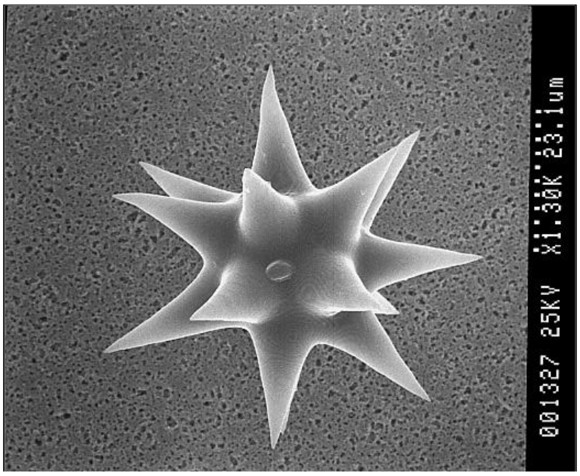


Fig. 6: SEM photo of microscleres (Astrose form) of *Tethya seychellensis* .

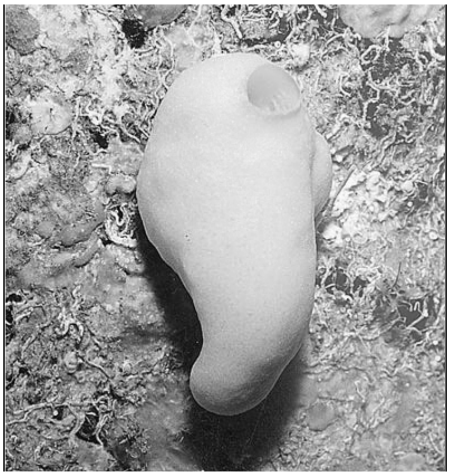


Fig. 7: *In situ* photo of *Leucetta chagosensis* (Calcaria: Calcinea, Clathrinida, Leucettidae), 12 m depth.

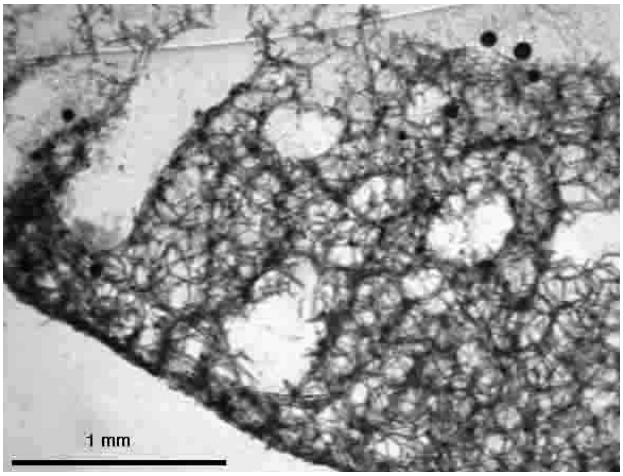


Fig. 8: Tangential section in *Leucetta chagosensis*.

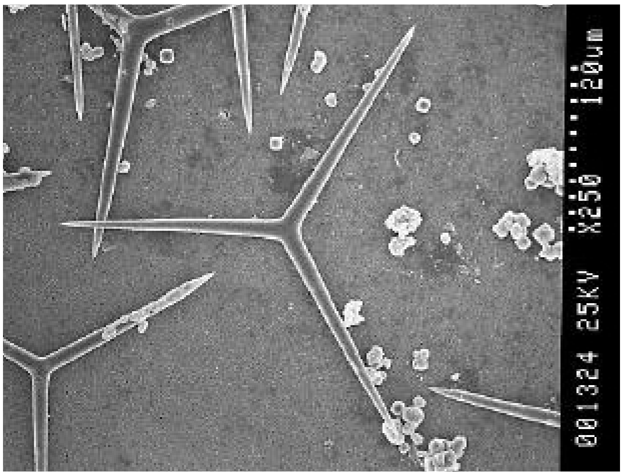


Fig.9: SEM photo of triad spicules of *Leucetta chagosensis.*

Studies of sponges of the Gulf of Aqaba and the Red Sea are rare. Burton (1952) reported on sponges collected from coastal and shallow habitats during the MANIHINE expedition in 1949. The collection included 33 species. Levi (1965) reported 43 species from the southern Red Sea, five of which were reported by Burton (1952). Fishelson (1971) listed 23 species from muddy bottoms, subtidal rock, and mangroves and Goren (1979) found 7 species colonizing artificial substrata in Eilat. Most other references date back to the late 19th century using already preserved specimens.

This work aims to fill the gap by documenting the taxonomic composition of the sponge community in the coral reefs of the Jordanian coastal waters of the Gulf of Aqaba using a combination of underwater photography and histological methods.

140 samples were collected from 13 stations along the Jordanian shores of the Gulf (29° 30.0' N, 34° 59.5' E to 29° 21.6' N 34° 57.8' E) by SCUBA diving. The following parameters were noted prior to each sampling: Documentation of morphology, life color, texture, surface, dimensions, water depth and type of habitat. After alcohol preservation, each sample was dissected and spicules and sections were mounted onto microscopic slides. Taxonomic description of each specimen was done for each family sample representative and SEM of major types of spicules was carried out.

Out of 140 collected specimens, 78 different specimen were identified at least to the family level, 14 specimen were not sponge (encrusting algae, bryozoa and tunicates) and the rest were doublets. With 73 species (94 %) demospongia were dominant (2 subclasses, 10 orders, 32 families, 47 genera). Five species (6 %) belonged to the class Calcarea (2 subclasses, 2 orders, 3 families and 3 genera). Hexactinellida and sclerospongia were not studied. Based on observations on sponge fauna distribution it was noticed that abundance and diversity decreased in the north site due to pollution and human affect damaging the coral reef habitat. The diversity increased in the reservation area of the Marine Science Station habitats in the southern site. Some species could be recommended as references for coral reef monitoring (e.g: *Grayella cyathophora*).

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Octocorallia (Coelenterata) in the Gulf of Aqaba

Wael Al-Zereini[1], Salim Al-Moghrabi[1] and Mohammed Al-Adhami[2]

1) Marine Science Station, Aqaba
2) Yarmouk University; Biology Department, Irbid

The Gulf of Aqaba is one of two appendages at the north tip of the Red Sea. It embraces highly diverse reef structures of the fringing type, which represent the most northern latitudinal distribution of coral reefs in the Indian Ocean. Octocorallia is one of the biota dominating marine environments, particularly coral reefs, and is occupying space on the coral reefs in tropical and temperate waters. Their role in the formation of coral communities on the reefs is often as important as that of the scleractinians. They may harbor many different invertebrates-commensals, symbionts, and parasites (Sorokin 1995). Octocorals comprise six orders: Alcyonacea, Gorgonacea, Penatulacea, Telestacea, Stolonifera, and Coenothecallia. Alcyoncea (Fig. 1), are lobate or massive colonies with fused internal spicules, and are associated with symbiotic dinoflagellate (zooxanthellae), except the Dendronephthya and Scleronephthya species that are an azooxanthellate animals. Gorgonians are arborescent, bushy or whip like colonies that have variant colors and a calcareous or horny skeleton (Fig. 2). Telestacea colonies consist of simple or branched stems that bear elongated polyps on its sides and termination (Fig. 3a). Penatulacea are elongated colonies that has one end embedded in the

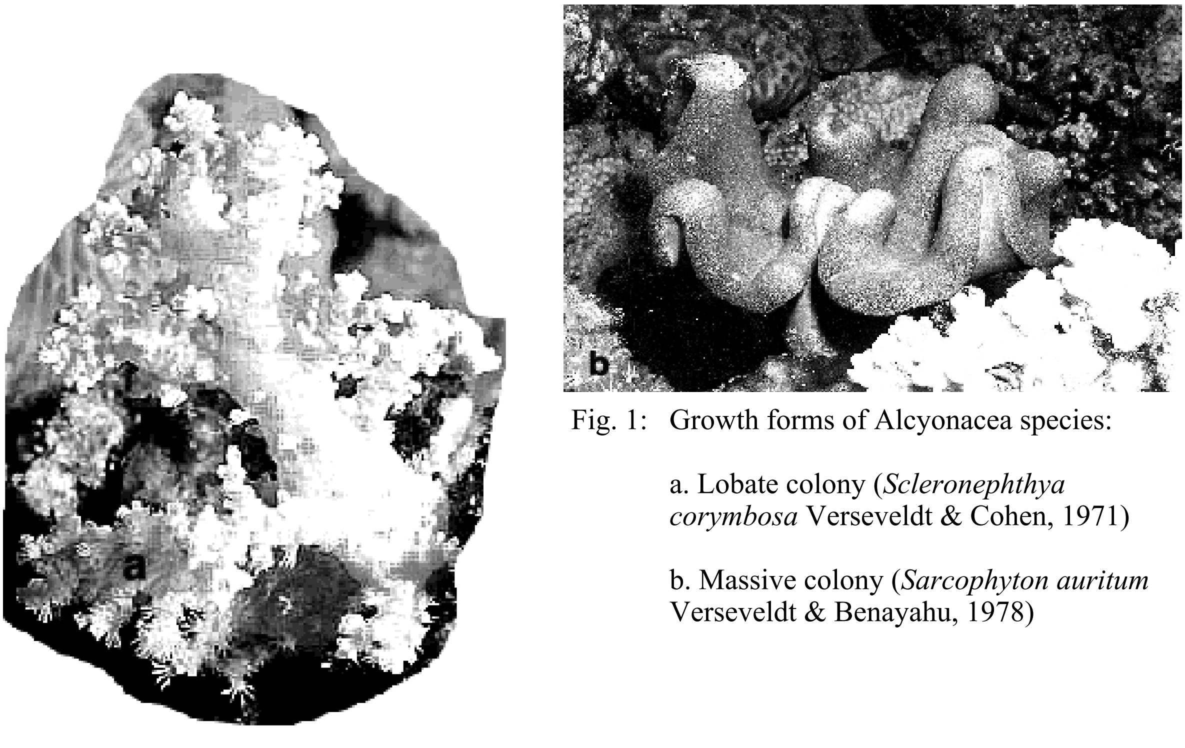

Fig. 1: Growth forms of Alcyonacea species:

a. Lobate colony (*Scleronephthya corymbosa* Verseveldt & Cohen, 1971)

b. Massive colony (*Sarcophyton auritum* Verseveldt & Benayahu, 1978)

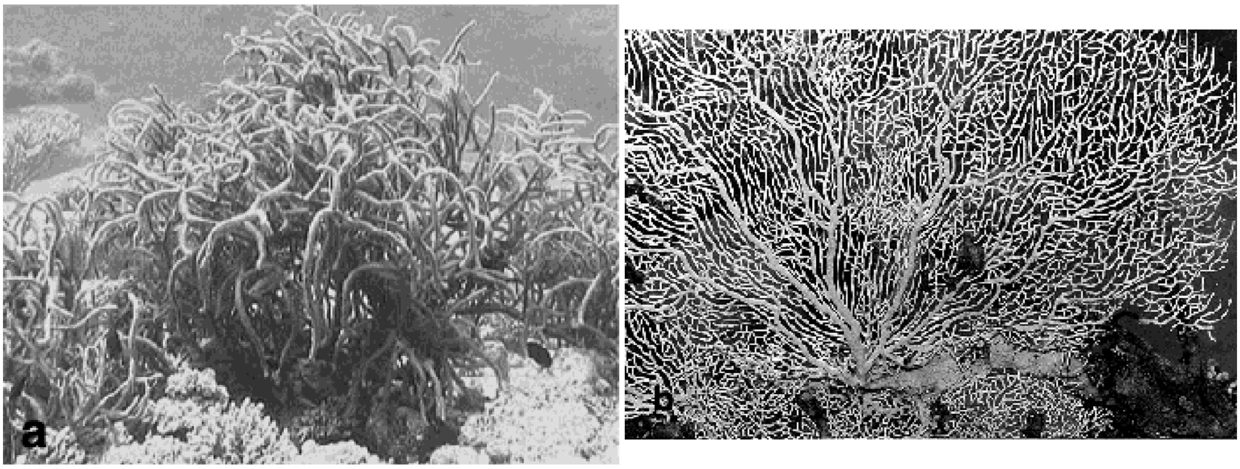

Fig. 2: Growth forms of Gorgonacea species:
a. Bushy shaped gorgonian (*Rumphilla torta* Klunziger, 1877)
b. Fan shaped gorgonian (*Annella mollis* Nutting, 1910)

mud, while the opposite or distal end bears the polyps, which are situated on a lateral (leaf like) extensions, for most species, or on a main capitate polyparium (Fig. 3b). Five of the aforementioned orders have species flourishing in the Red Sea (Gulf of Aqaba). The Coenothecallia is an Indo-Pacific order, but was not found in the Red Sea. Of the other orders, the Stolonifera is represented in the Red Sea by two species only, which are: *Tubipora musica* Linné, 1758, and *Clavularia hamra* Gohar, 1948; the Xeniidae species, from the Alcyonacea, had been studied extensively in the Red Sea (Eilat), ecologically and taxonomically (Benayahu 1985 and 1990, Reinike 1997).

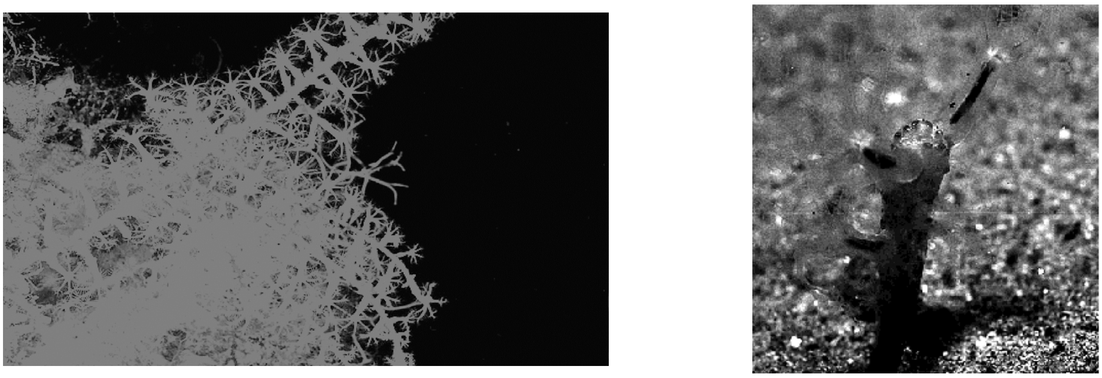

Fig. 3: a. *Carijoa* sp. (Telestacae, Telestidae) b. *Cavirnulina* sp. (Pennatulacae)

Although diverse communities of octocorals are widely distributed in the Gulf, few studies have dealt with their taxonomy. Versevldt and Benayahu (1983) had described sixteen soft coral species from the Red Sea, eight of them exist in the Gulf of Aqaba. Reinicke (1997) described nineteen species of Xiniidae in the Red Sea, eleven of them flourish in the Gulf of Aqaba. Grasshoff (1976) described five gorgonian species from the Gulf of Aqaba (Eilat) representing three genera (Acabaria, Clathraria, and Acanthogorgia). In addition, Grasshoff (2000) studied and identified the gorgonians collected by Israeli and German researchers from the Sinai coast and the Strait of Gubal in the last three decades (in print).

This is the first study that deals with the identification of Octocorallia in general and

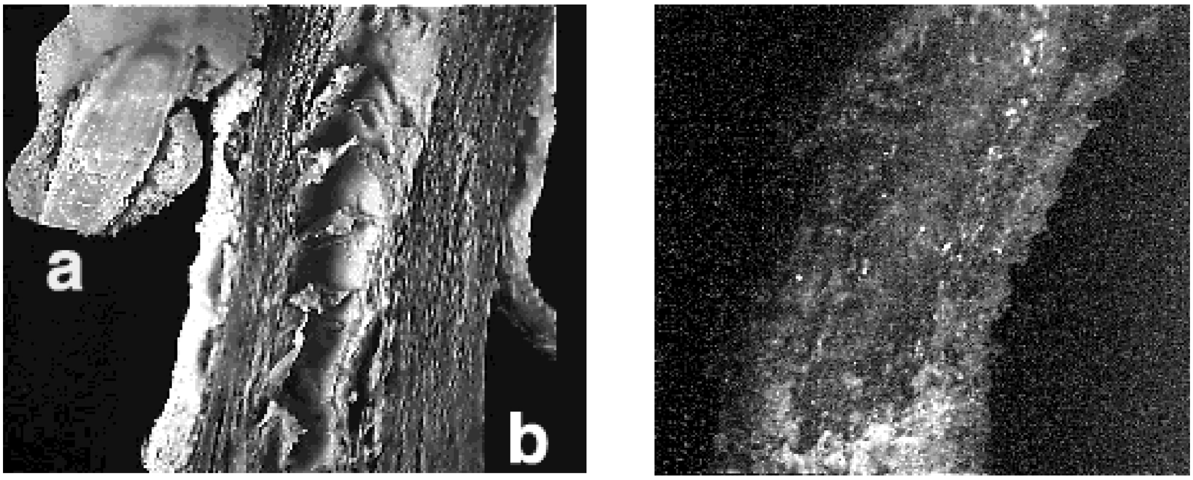

Fig. 4.: Axial structure of the Gorgonacea:

1- Holaxonia: a proteinous axial support more or less extensively permeated by $CaCO_3$. a) Calaxonia: Axial support doesn't have a chambered central core but is solid. b) Holaxonia I: Axial support has a hollow, cross-chambered central core.

2- Scleraxonia: Skeleton consists only of sclerites, free or more or less firmly cemented together by horny or calcareous material, but sometimes absent entirely.

Gorgonacea in particular from the Gulf of Aqaba (Jordan). Octocorallia samples were collected from fifteen sites along the northern coast of the Gulf (29°27.865' N, 34°58.865' E to 29°21.605' N, 34°57.815' E). Morphological characteristics, including color, shape, dimensions of each colony were done *in situ* and in the laboratory on preserved samples. Furthermore, several underwater photographs have been made for each sample. The classification is used according to Bayer (1981) and Williams (1990); the terminology used is based on Bayer et al. (1983). Taxonomic descriptions of these species are based on closer investigation of axial structures (Fig. 4), external morphology, lobe shape (for soft Alcyonacea), and sclerite forms (Fig. 5). Collected samples were found to represent:

1) Twenty-two species of Gorgonacea possessing monomorphic polyps representing eleven genera and six families (Plexauridae, Gorgoniidae, Acanthogorgiidae, Melithaeidae, Subergorgiidae, and Ellisellidae); all identified.

2) Twenty-eight species (25 identified) of Alcyonacea possessing dimorphic polyps representing eleven genera and four families (Alcyoniidae, Xiniidae, Nidaliidae, and Nephtheidae).

3) Four Penatulacea species (2 identified) representing four genera and three families (Virgulariidae, Pteroeididae, and Veretillidae).

4) Two species of Telestacea (1 identified) representing two genera and one family (Telestidae).

Most of the gorgonian samples were found in surge-protected locations (artificial reefs), but in zones of some current due to tidal flow. Elastic gorgonids can withstand the force of the water and occurred over the whole depth range, whereas, the brittle ones were only found in the deep

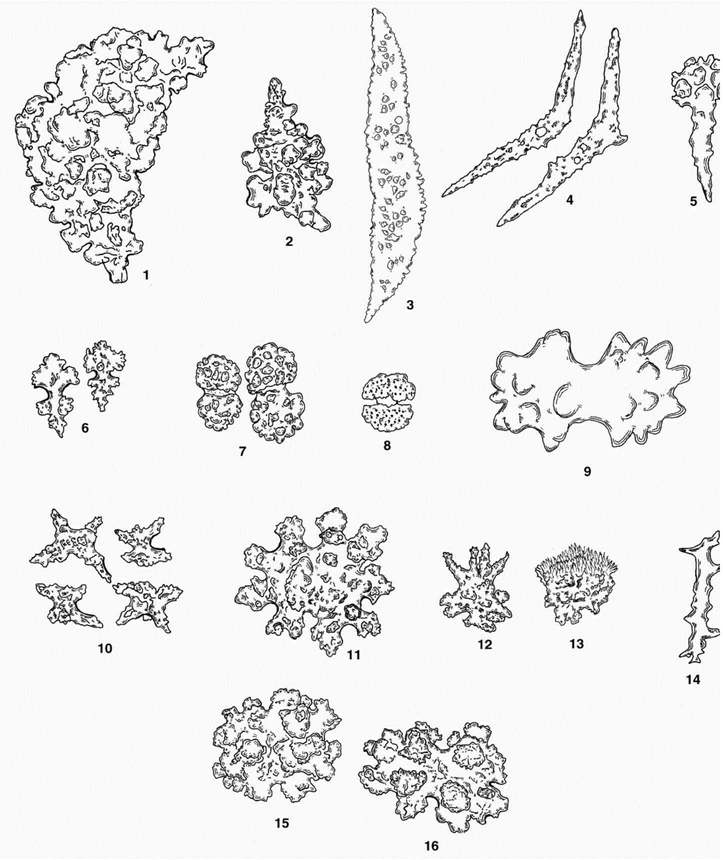

Fig. 5. Major sclerite forms in the Gorgonacea:
Spindle forms:
1. Thick spindles (*Acabaria pulchra*), 2. Unilaterally spinose spindles (*Acabaria sinaica*), 3. Fusiform sclerites (*Astrogorgia lea*). 4. Hockeystick spindles (*Acanthogoria spinosa*, tentacle sclerite), 14.Anastomosing branches spindles (*Carijoa* sp.).
Club- shaped sclerites:
5. Clubs (*Sinularia* sp.), 6. Clubs (*Rumphilla torta*).
Double-head sclerites (capstans):
7. Capstans (*Ellisella marisrubri*), 8. Capstans (*Anella mollis*), 9. Double-stars (dumbbell sclerites) (*Cladiella* sp.).
Radiated sclerites:
10. Six-eight radiates (*Acanthogorgia spinosa*), 11. Radiated spheroids (*Bebryce studr*), 12. Antler-like sclerites (*Bebryce sulfurea*), 13. Rosette sclerites (*Bebryce studri*).
15. Ellipsoid sclerites (*Euplexaura nuttingi*)
16. Double head ellipsoids (*Euplexaura* sp.)

furrows, *Acabaria* spp., where they grew close to the more continuously flushing entrances. Sea pens and alcyonian were found in the natural reefs. Morphological variation in the colonies was found, which is due to environmental effects, especially within the soft corals. Sinularias, Cladiellas, and Dendronephtheas species, show that they are a strong colonizers. This baseline study is highly important for better management of the unique resources in the Gulf of Aqaba and it is a first step in applied research (e.g. pharmacology and medicine).

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Fish communities in the coral reefs of the Gulf of Aqaba

Avi Baranes

The Interuniversity Institute, H. Steinitz Marine Biological Laboratory, Eilat

Introduction

Research on fish communities in the Gulf of Aqaba was integrated into RSP II, as part of a project on larvae dispersal and genetic flow in populations of coral reef fishes in the northern Red Sea.

The planning of an effective colonization or recolonization of coral reefs by fishes is of crucial importance. However, there is still very little knowledge concerning the dispersal of the fish larvae in the current region of the northern Red Sea. It should also be emphasized that almost no knowledge is available on the systematic of the different stages during the development of ichthyoplankton. The only literature available concerns very few species of fishes, mostly non-coral inhabitants, which have been studied in sporadic occasions. Therefore, any study of larval dispersal should be proceeded by cataloguing fish species in the ichthyoplankton. Knowledge of the growth rate of each species in correlation with current mapping will serve as an information about the recruitment rate in the coral reef.

The relationship between the coral reef and its fish inhabitants has been very well documented. Using the monitoring of some species, their distribution and abundance may be correlated to those of the coral species. If the corals are adversely affected by stressful environmental conditions such as chronic pollution, their health will deteriorate. This deterioration should be detected by the fishes which feed on them. The corals are sessile and cannot avoid stress, whereas the fishes are mobile and can emigrate to healthier regions of the reef. In contrast to the complicated analyses of pollutants in the reef, simply counting the abundance of colored coral reef fishes using conventional census techniques is a relatively simple task.

In recent investigations conducted in the northern beach of Eilat it has been shown that shallow sandy beaches serve as a nursery ground for some coral reef fishes. In the project we proposed to investigate whether the Gulf of Suez itself can be considered as a nursery ground for the Gulf of Aqaba and the Red Sea proper.

The present study was seriously hampered by political and financial constraints, preventing extension of the work beyond the end of RSP II and comparative sampling in Egyptian reefs and waters in the Gulf of Aqaba and Gulf of Suez.

Results

The fish biodiversity in the Eilat region is presented by E. Brokovich (this volume) who actually performed the research within the frame of an MSc thesis at Tel Aviv University. The main conclusion one may draw from his research is that fish may certainly be used as bio-indicators of the coral reef ecosystem health. It is obvious that the coral reef of Eilat is under severe stress due to pollution, development of tourism and organic enrichment of the seawater (aquaculture and human sewage). Adequate methods and database should be made available to environmental investigations in the future.

Conclusions

It is regrettable that the objectives of the planned research were not fulfilled. The results of the fish biodiversity are crucial for the understanding of the ecosystem in the Gulf of Aqaba. I strongly believe that in order to produce a scientific paper, it is necessary to go on in evaluating the situation along the Sinai coast and in the Aqaba region. Census of fish populations was performed in the past in the Nuweiba region (30 years ago) and up-to-date data will show if there is an impact on the ecosystem following the tourism development in that region.

The increase of reports on the occurrence of large sharks (*Galeocerdo cuvier*) near the northern coast of the Gulf of Aqaba certainly indicate that if the natural food of these predators is affected through the deterioration of the ecosystem, we may face in the near future problems of shark incidents.

Reef fish communities and biodiversity in Eilat's reefs

Eran Brokovich[1], Avi Baranes[2] and M. Goren[1]

1) Tel-Aviv University, Tel Aviv
2) The Interuniversity Institute, H. Steinitz Marine Biological Laboratory, Eilat

Introduction

Fishelson (1995) describes species disappearance and reduction in abundance of a large number of animal taxa in the northern part of the Gulf of Aqaba. The suspected cause of this stress comes from anthropogenic sources related to the development of the area: Phosphate loading in the harbor, oil harbor, town sewage and sand (added to the beaches by the municipality) contribute to the pollution (Hawkins and Roberts 1994, Fishelson 1995, Dubinsky and Stambler 1996, Abelson et al. 1998, Wilhelmsson et al. 1998). Furthermore, the hundreds of thousands of tourists cause deterioration of the reef (Fishelson 1995, Wilhelmsson et al. 1998, Zakai 1998), divers and snorklers on the reef break corals and cause re-suspension of sediment. Such damages have a devastating impact on the environment by altering species composition, leading to communities dominated by opportunistic organisms. The decrease in spatial complexity of the reef caused by the destruction of corals leads to a reduction in both species richness and diversity of reef fishes. Coral destruction may also be followed by a reduction in fish settlement (Rilov and Benayahu 1998) and abundance (Sano et al. 1984).

Mariculture fish cages in the north of the gulf are an additional factor of pollution spreading also fish diseases (Diamant et al. 2000). In order to supply decision-makers with facts about the pressing need to establish and conserve marine parks, the arguments of the scientific community must be objective and well documented. This requires thorough study and collection of data regarding the sites to be protected, as well as their specific fish and invertebrates communities and their behavior (Fishelson 1999).

Among marine organisms, fish have received large attention. Many publications appeared over the years and contributed to the knowledge of the area (Ben-Tuvia et al. 1983, Goren 1993). More than 1280 species belonging to 157 families are listed (Goren 1993, Goren and Dor 1994, Khalaf and Disi 1997; Khalaf and Kochzius, this volume).

The Israeli part of the Gulf of Aqaba is characterized by variable habitats. Sandy bottom areas, mostly in the North Beach area; fringing reef areas, from the Nature Reserve southwards to the border with Egypt, and patches of corals and knolls which are found in-between these areas and in deeper waters. Different habitats in the reef area supports different assemblages of fishes (Russell et al. 1978, Sano et al. 1984). A number of habitats parallel to the shore in the reef area are defined from shallow water to 15 meters of depth (Bouchon-Navaro 1980, Edwards and Rosewell 1981, Harmelin-Vivien and Bouchon-Navaro 1981). Loya and

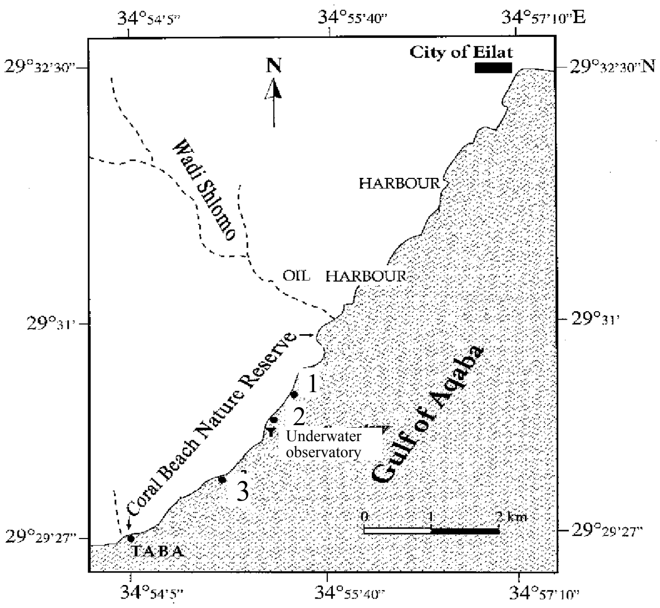

Fig. 1: The northern area of the Gulf of Aqaba (Red Sea) and the census sites (1-3). North nature reserve site is marked "1", south nature reserve is marked "2" and the cave site is marked "3".

Slobodkin (1971), Mergner (1971) and Fishelson (1999) defined habitats for the benthos communities and mainly for corals.

Most of the reefs in the area of Eilat are part of the Nature Reserve and reef fish are protected. The survey method to be used should be non-destructive. The visual census technique has been in use for that reason since the early 50’s (Schmitt and Sullivan 1996, Watson and Quinn 1997, Rilov and Benayahu 1998, Golani and Diamant 1999). This method is accurate for most fish species, although a certain underestimation of both the cryptic and most abundant species can occur (McCormick 1994, Hickford and Schiel 1995, Gledhill et al. 1996, Watson and Quinn 1997). The method presented also causes some bias due to the activity of the diver; his subjectivity; and as a result of fish behavior (Bortone et al. 1989, Parker et al. 1994, Sale 1997, Watson and Quinn 1997).

Because of the high mobility of the fishes, recording data on underwater tape has been found to be the most accurate (Greene and Alevizon 1989, Bortone et al. 1991) and efficient (Chapman et al. 1974, Greene and Alevizon 1989) method of fish data collection. It has advantages over writing on a plastic slate or recording on a video recorder (Sale and Sharp 1983, Greene and Alevizon 1989).

Little is known about of fish communities' composition in the Gulf of Aqaba. Rilov and Benayahu (2000) have compared the natural reef with an artificial reef but that was the only recent research on natural reef fish communities in Eilat area. Another research (Golani and Diamant 1999) relates to an artificial reef and an early research by Ben-Tuvia et al. (1983) was done in Sinai, Egypt.

The composition and structure of reef fish communities are important aspects of reef ecology (Branden et al. 1986): The species abundance and diversity is the core of community structure analysis and monitoring of environmental quality (Sanderson and Solonsky 1986). It may also reflect the overall reef condition (Schmitt and Sullivan 1996) and ”health” (Bortone et al. 1989).

Research objectives and impacts

1. The aim of this research was to investigate the fish community structure in the different reef habitats, from very shallow waters to a depth of fifteen meters. The collected data will be placed in a data base of Eilat’s reef fish community and will thus be available to decision makers. In addition, data relating to species diversity and abundance will also be available.

2. The main significance of the proposed research is creating a basic, reliable and up to date reference to other researches now and in the future. Monitoring the fish communities in the future, we could observe changes that could tell us about the fish condition and the ecological condition of the reef as a whole. It will also be possible to use the community data for monitoring environmental quality by using Fish as bio-indicators (Bortone et al. 1986, Fausch et al. 1990, Bortone et al. 1991).

3. As a whole, fish have ecological and economical value. They are economically important to tourism: Diving, snorkeling and visiting the underwater observatory, and to some extent to the fisheries industry. They are ecologically important as being a large and important part of coral reef organisms.

Methods

The census followed seven months of preliminary studies (February to August 1999). During this time sites were chosen, habitats were defined, transects were marked, numerous dives to practice fish identification to the species level were performed and training in order to evaluate fish abundance was done. Also, underwater recording system was built and dives were conducted to test it and to train in using it.

Study sites

For this research, three sites along Eilat’s reefs (Gulf of Aqaba, Red Sea, Fig. 1) were chosen. In each site the fish community was surveyed from shallow water to a depth of fifteen meters. The sites chosen are regarded as typical representatives of reefs in the area. In all of them there are a developed shallow continuous fringing reef in the shallow waters and coral patches on the sandy slope in deeper water. The three sites have different amount of tourism related stress level (Zakai 1998):

1. The northern part of the coral reserve (”north reserve”) is a stressed area with many snorklers and divers.

2. The southern part of the coral reserve (”south reserve”) is an area with regulations limiting the number of divers and prohibiting snorklers. It is similar to the reef at the northern site but is separated for nature conservation and management reasons.

3. The area north of The Princess Hotel ("caves") relatively to the north reserve has low stress level of snorklers and divers.

Definition of habitats

Habitats were defined as follows:

1. Lagoon: Shallow waters between the shore and the reef flat; mostly sandy bottom with some coral patches.

2. Reef flat (table): Horizontal flat area of the reef separating the lagoon and the open waters.

3. Fore reef: The seawards face of the reef flat appears as a vertical wall of corals or a steep and complex coral area; from 0- 5 m depth.

4. M. slope (moderate slope): a sandy, moderate angle slope covered with some coral patches; from 5-10 m depth.

5. S. slope (steep slope): a sandy, steep angle slope covered with coral patches; from 10- 15 m depth. In the area of the ”caves” there is no lagoon habitat and the steep slope starts at 6-7 m instead of 10 m.

Census techniques

In our work, scuba divers set up a double line transect in the study area (measuring tapes connected on both sides of a two-meter P.V.C pipe, Fig. 4a) (Sale 1997). The transect was 2 m wide (Chabanet et al. 1995, Watson and Quinn 1997) and 50 m long (Chabanet et al. 1995, Watson and Quinn 1997). Data collection was done using an underwater tape recorder to record all the fishes [following McManus et al. (1981) and Bortone et al. (1991)].

The divers first counted large, fast swimming fishes, while deploying the measuring tapes (Fowler 1987), looking forward and 1 m to either side. The census started after five minutes to allow the fishes to resume their natural behavior (Carpenter et al. 1981). In the next 2 m wide transect all the fishes seen were counted except those counted before. Finally, going over 1 m of the transect width (half the width, inside the tapes boundary), the smaller and the more cryptic species were meticulously searched for and counted (Edwards and Rosewell 1981, Fowler 1987). This made the counts more accurate (Sale 1997).

The counts were made according to Bortone et al. (1986, 1991): Only the fishes in front of the diver were counted. If a fish which is a part of a school crossed the transect, the whole school was counted.

All estimations of fish abundance were made by the same diver (B. E.). In order to prevent biases caused by different divers.

Fish identification was done by comparing observed fish to photos from literature: Randall 1983, Randall et al. 1990, Debelius 1993, Lieske and Myers 1994, Randall 1995, Allen and Steene 1996, Khalaf and Disi 1997, Debelius 1998.

Three repetitions were made in each site, in each of the habitats. The primary transects were deployed without previously surveying the sites.

To include most of the physical parameters characterizing each habitat in the transects, the transects were deployed (where possible) at a predetermined angle to the beach. This incorporated maximum of the width of the habitat (habitats were not usually wide enough to make a transect perpendicular to the beach).

To investigate seasonal affects on the fish community, each transect was sampled 4 times a year at different seasons. To ensure studying of the precise same locality (for seasonal repetitions), the transect starting point and end point were marked by a small red float and a small sign which were anchored to dead corals.

In addition to the transects, we conducted "arbitrary" swimming census in the area, to add species to our species fish list (Russell et al. 1978, Branden et al. 1986, Fowler 1987, Sale 1997).

Data analysis

Fish community and its indices:

Community indices, including fish abundance (total number of individuals), species richness (number of species), Shannon-Wiener Diversity Index [$H'=\Sigma P_i \ln(P_i)$] and Pielou's Evenness Index [$J'=H'/\ln(S)$] were calculated for each habitat for every season. The indices were calculated pooling together 9 transects (900 m^2) in each habitat. The indices of the lagoon were done over 6 transect each season due to the absence of a lagoon in the caves site.

When the data were normally distributed and there was homogeneity of variance, ANOVA tests have been used, otherwise non-parametric test (Kruskall-Wallis) have been used.

Similarity between fish communities in the habitats and sites:

Multidimensional scaling (MDS) was applied to the averaged transects in each habitat for each of the sites. This MDS was used to reveal the relationships between the different habitats and the different sites. The MDS method was based on the Bray-Curtis similarity matrix.

The stress level coefficient indicates how much of the variation is explained by the dimensions examined in the analysis. The lower the value, the greater the variance explained by the chosen dimension. Data were Log (x+1) transformed to reduce the affects of highly abundant species.

Results

In the present study we found 257 fish species belonging to 49 families. 229 of the species were seen in the transects and the other 28 were observed in random swims in the area.

Fish community and its indices

All significant differences identified were at P level of less than 0.05. The number of species was significantly higher at the fore reef (S=132) than at the other habitats. There were 113 species at the m. slope, 101 species at the reef flat and 99 at the s. slope. Significantly fewer species were found at the lagoon (S=74) than the other habitats (Fig. 2b). The same pattern was seen in the average number of fishes which was highest at the fore reef (N=6939) and lowest in the lagoon (N=890) (Fig. 2a). The most diverse fish assemblages were on the reef flat (H'=3.54) and the fore reef (H'=3.47), the least diverse were the m. slope and s. slope with H'=3.12 and 3.1 respectively (Fig. 2c). The lagoon was in-between the two groups (H'=3.34). Looking at Pielou's Evenness, the lagoon and reef flat had a significantly higher index than all the other habitats (J'= 0.78 and 0.77) but were not significantly different from each other. The fore reef (J'=0.71) had a significantly higher index than the m. slope (J'=0.65) (fig. 2d).

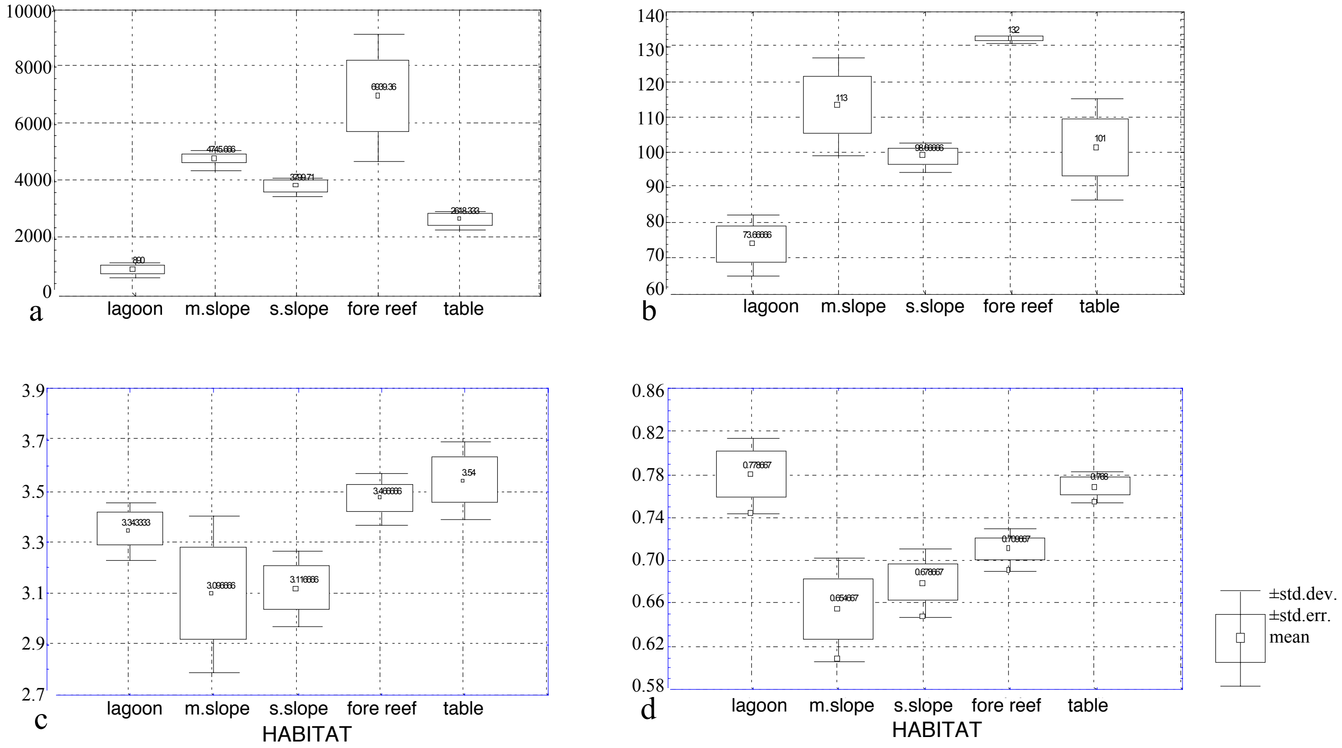

Fig. 2a: Fish abundance in different habitats; 2b: Number of species in the different habitats; 2c: Shannon-Wiener Diversity index of the different habitats; 2d: Pielou's Evenness Index of the different habitats. All indices are calculated for 900m^2 of reef in each habitat (except lagoon, 600m^2).

Similarity in fish communities between the habitats and sites

The MDS analysis was applied to the data in order to analyze the relationships between the fish assemblages among sites and habitats (Fig. 3). The low value of the stress level (0.09) corresponds to a good ordination with no real prospect of a misleading interpretation. The fish communities appear to group according to the different habitats: The lagoon above the reef flat, the fore reef in the middle, the moderate slope to the left and the steep slope furthest to the left.

Discussion

This research creates a fish community database for future reference. The methods used are repeatable, easy to apply by trained researches and supply plentiful data.

Fish community indices

The present study demonstrates the differences between the fish assemblages in the different habitats. Fishes are most abundant at the fore reef. The fore reef also holds the largest mean number of species and it is also one of the two most diverse habitats, even though the Pielou's Evenness Index shows us that the fore reef is not the most homogenous habitat. A homogenous community is one with a similar amount of fishes from every species. The reason of the less homogenous community at the fore reef is probably attributed to large schools of planktivorous fish that were counted in that habitat. The fore reef is considered a much more complex habitat with numerous holes and crevices, corals and rocks that are used by the fish for cover.

The lagoon holds the smallest mean number of fish species and individuals. Nevertheless it has a relative average diversity, probably attributed to the high homogeneity (evenness) of the habitat.

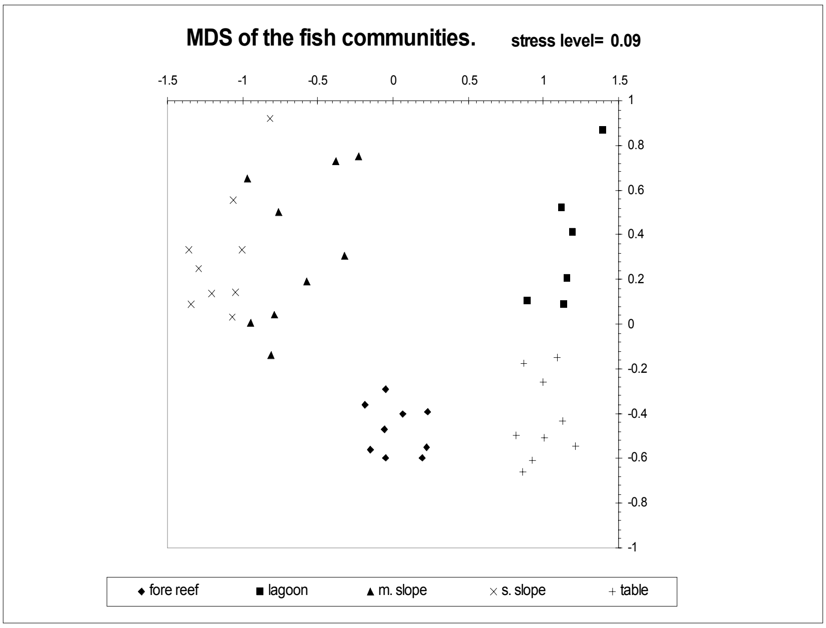

Fig. 3: MDS analysis on the fish community data from the different habitats in the different sites during the year. Stress level = 0.09. Data were log(x+1) transformed.

There might be strong connection between the physical structure of the coral reef and the fish assemblage in the habitat.

Khalaf and Disi (1997) reported about 322 reef associated fish species across the reefs of Aqaba. Comparing with the 257 species in 148 genera and 50 families found in the current research the situation on the other side of the Gulf seems better. A better comparison (in Jordan and in Egypt), using exactly the same methods, was deprived from us due to political reasons.

Similarity between habitats and sites

A number of researchers have already shown similarity in fish assemblages between analogous zones of reef (Letourneur 1996, Rilov and Benayahu 2000) in our study it is possible to distinguish between different assemblages in different habitats. From the MDS representation it is possible to see separation on two axes. Looking at the fish indices and the MDS representation it seems possible that on the X-axis community evenness might be part of the reason for the separation and on the Y-axis it might be species diversity.

A different MDS analysis of standardized data (relative abundance) showed very similar results. This leads us to believe that the main differences between the fish communities in the different habitats is due to species composition of the habitat rather than differences in the fish abundance or the number of species in a habitat.

Loya and Slobodkin (1971) showed that the average number of colonies and percentage of living corals were highest in the fore reef, then in the m. slope, s. slope and finally the reef flat. Fish abundance in this study shows similar trends and suggests a connection between fish abundance to the number of coral colonies and percentage of living corals.

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Fish larvae from the Jordanian coast of the Gulf of Aqaba, Red Sea

Tawfiq Froukh

University of Jordan, Amman / Marine Science Station, Aqaba

The Gulf of Aqaba is located at the northeast branch of the Red Sea and is characterized by extensive fringing reefs, which provide wide range of niches. Fishes are the dominant group of coral fauna with regard to both biomass and diversity. Although the ichthyofauna of the Gulf of Aqaba is quite well known, there are few studies on fish larvae in the Gulf of Aqaba and no previous studies concerning the Jordanian coast.

Coral reefs are inhabited by thousands of fish species, most of them pass through a pelagic larval stage (Leis and Goldman, 1987). Little is known about the history of this pelagic stage (Leis, 1986). According to Sale (1980), the pelagic phase of coral reef fishes have a strong effect on the population structure of the demersal adult phase. Most of the ecological, behavioral, and taxonomic works about reef fishes of the Gulf of Aqaba deal with the adult populations (e.g. Khalaf and Disi 1997, Wahbeh and Ajiad 1985 and Fishelson 1964, 1966, 1970, 1977).

The present study is the first taxonomic and ecological research on fish larvae in this area.

Light traps were used for the collection of the fish larvae in front of the Marine Science Station, Gulf of Ababa, Jordanian side, for one year from June 1999 to June 2000 (weekly). After preservation fish larvae were stained, drawn and identified using references for the Indo-Pacific region.

This study indicated 11 different species belonging to 31 different genera out of 25 different families. The following drawings of the most common fish larvae are presented here as first results of the ongoing MSc thesis.

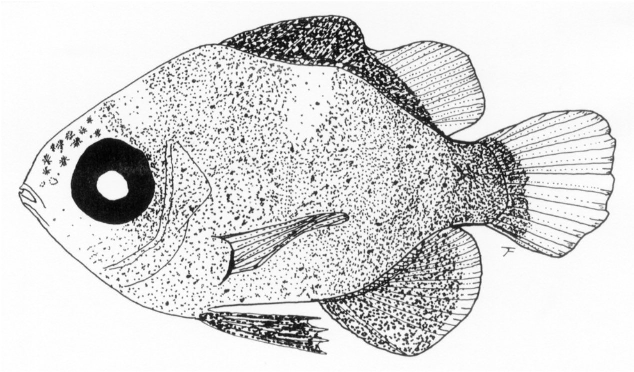

Fig. 1:

Amphiprion bicinctus,
TL 12.5 mm, SL 9.7 mm

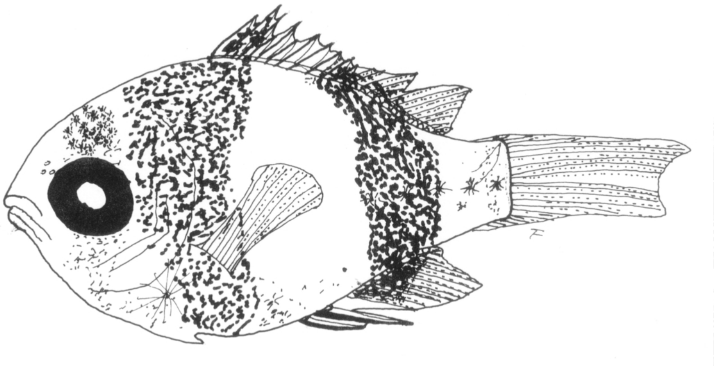

Fig. 2:

Dascyllus aruanus,
TL 10.1mm, SL 7.5 mm

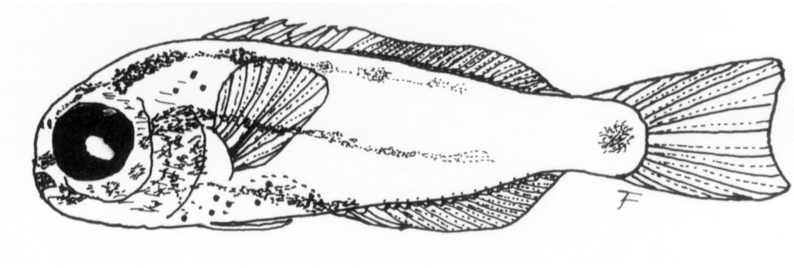

Fig. 3:

Meiacanthus nigrolineatus,
TL 12.8 mm, SL 10.4 mm

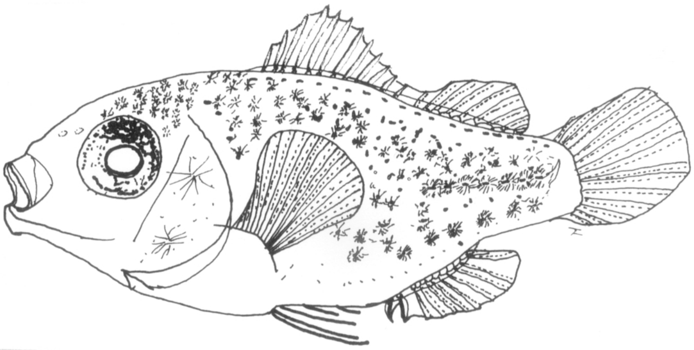

Fig. 4:

Choridactylus multibarbus,
TL 9.5 mm, SL 7.8 mm

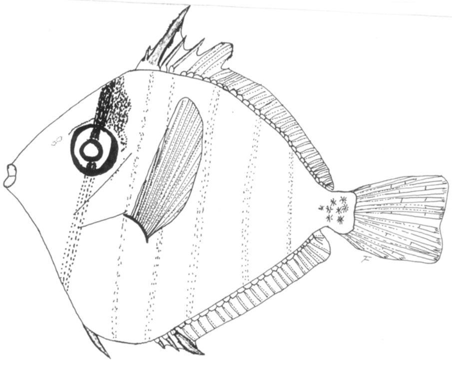

Fig. 5:

Zebrasoma veliferum,
TL 20.3 mm, SL 16.7 mm

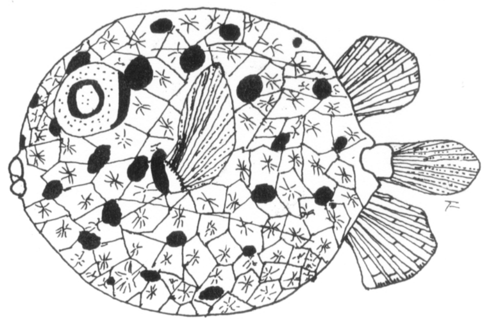

Fig. 6:

Ostracion cubicus,
TL 11.3 mm, SL 8.8 mm

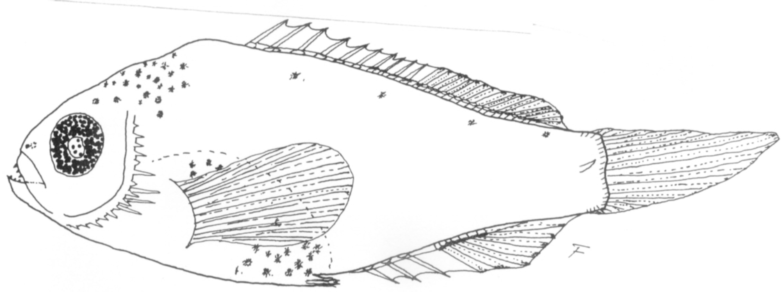

Fig. 7:

Plectranthias winniensis,
TL 19.5 mm, SL 14.5 mm

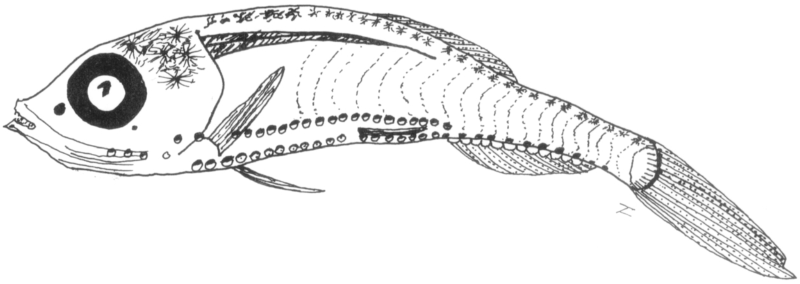

Fig. 8:

Vinciguerria mabahis
TL 14 mm, SL 13 mm

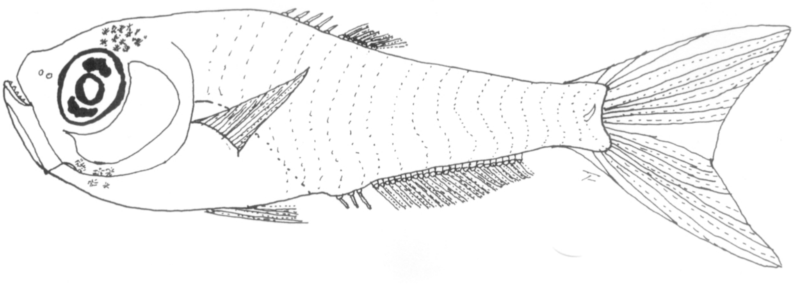

Fig. 9:

Parapriacanthus ransonnari,
TL 17.5 mm, SL 15.3 mm

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Small-scale structure of zooplankton, phytoplankton, temperature and currents in the coral reefs and adjacent open waters, Gulf of Aqaba

Raed Ghrayeb[1], A. Karim Farrah[1], Amatzia Genin[2] and Ziad Abdeen[1]

1) Department of Biological Sciences, Faculty of Science and Technology, Al-Quds University, Jerusalem
2) The Interuniversity Institute, H. Steinitz Marine Biological Laboratory, Eilat

Introduction

One of the most ubiquitous characteristics of oceanic plankton is its high level of temporal and spatial variations, termed "patchiness". Causes for zooplankton patchiness include physical and biological processes. For example, large oceanic eddies near the Gulf Stream entrap zooplankton in highly defined patches which move across the ocean. Localized upwelling events may lead to the formation of phytoplankton patchiness which, under conditions of sufficient residence time, can lead to corresponding patchiness of zooplankton. Similarly, localized predation can generate patches "void" of prey. Ample evidence for such predation-related patchiness was recently documented above isolated underwater mountains in the Pacific Ocean. While low-frequency fluctuations (millennia, decadal, seasonal) are fairly well documented, rapid changes, on the scale of minutes to hours, are poorly understood. Possible reasons for high-frequency fluctuations in plankton abundance include physical advection, localized population growth, interactions with patchy food or predators, and behavior.

Coral reefs are sites of intense, localized predation on zooplankton and phytoplankton, generating sharp reef-ward gradients of declined plankton abundance. Zooplankton feeders at the reef include numerous species of fish and invertebrates (e.g. corals, anemones, echinoderms), while major phytoplanktivores include sponges, bivalves, polychaetes and ascidians. Some of these predators are active during the day (e.g. damsel fish), while other are nocturnal (e.g. corals). Some of the predators are highly aggregated (e.g. fish schools), while others are more homogeneously dispersed. The temporal and spatial dynamics of this predation and their effects on plankton patchiness are poorly understood. As food replenishment to those benthic, site-attached grazers and predators totally depends on currents, the short-term temporal and spatial patchiness of their planktonic prey is a complex outcome of physical advection, distribution of predators, and biological processes such as predation behavior and functional responses.

The major objectives in this study were to quantify the short-term (minutes to weeks) variations of phytoplankton and zooplankton over a coral reef and at a near-by, open-water site, and to evaluate the roles of currents, behavior and localized predation in the generation of the observed variations.

Methods

Water samples were obtained with two large (132 l/min) submersible pumps, delivering the pumped water to shore via 45 mm diameter PVC pipes. Both pumps were deployed at 8 m depth: One at the reef, 40 m off shore, attached to a tripod with the intake opening suspended 0.75 m above bottom, and the other at the open waters, 163 m off shore, where the pump was attached to a mooring line with its intake positioned 34 m above bottom (42 m depth) (hereafter "Reef" and "Away" sites, respectively).

Phytoplankton abundance was estimated using measurements of Chlorophyll *a* and phaeopigments, supplemented by occasional microscopic cell counts. Chlorophyll *a* was measured using a Turner Designs TD-700 fluorometer. Phaeopigment concentrations were measured with a Turner Designs AU-10 fluorometer, using the acidification method. Microscopic counts of *Synechococcus* and pico-eukaryotes were made immediately after collection using a Nikon epifluorescence microscope.

Zooplankton samples were obtained by filtering the pumped water through a 1 m long, 36 cm diameter, 100 µm mesh net, submerge in a large (135 l) container to avoid drying and damage of the trapped animals. Each sample was obtained by filtering water for about 1 h, with an average (± sd) volume filtered of 8.25 m^3 (±0.68). The sample was immediately transferred to the laboratory where it was separated into two parts: One aliquot (10.4 % of the sample) was separated using a Stempel Pipette and preserved in 4 % buffered formalin for later microscopic counts, while the rest of the sample was combusted for 4 h at 450° C and weighed again, producing the ash-free dry weight of the sampled organisms (hereafter "AFDW"). Microscopic counts were made using a dissecting microscope (x40 magnification). The counted animals were sorted to the following taxa: (a) calanoid and cyclopoid copepods combined, (b) harpacticoid copepods, (c) copepod nauplii, (d) molluscs, (e) appendicularia, (f) chaetognaths and (g) polychaetes.

The sampling plan consisted of four different interval-schedules, carried out during a 54 days period. A "sample" in the following two sections indicates a pair of water samples, one from the Reef and the other from the Away site. The daily schedule consisted of one sample a day around 10:00 am obtained 5 days a week (Sunday through Thursday). Twice a week, a nocturnal sample was added, producing a 15 pairs of day-night samples. Once every two weeks, hourly samples of phytoplankton and 16 to 17 samples of zooplankton were taken throughout a 24 h interval (a zooplankton sample every approx. 1.5 h), producing four series of samples of diel cycles. In addition, during each of those four sampling days, quarter-hourly chlorophyll samples were taken: Consisting 16 samples (a sample every 15 min) taken during two 4-hour long series, one during mid-day and the other around mid-night.

Overall, during the 54 days of our field sampling at the two sites, a total of 222 single samples were processed for zooplankton biomass, a total of 102 zooplankton samples were sorted under the microscope, 532 samples were processed for phytoplankton pigments and 14 samples were counted under the epifluoresence microscope.

Currents and temperature data were measured using two electromagnetic current meters

(Model S4, InterOcean, San Diego, USA) equipped with a temperature sensor. One current meter was deployed at the Away site, attached to a separate mooring line at 6.5 m depth, while the other instrument was deployed at 8 m depth the Reef site. Each current meter was positioned about 10 m away from the pump. The current meters were set to record the average current speed and direction and temperature of a 1 min interval every 10 min. However, values measured precisely at our plankton sampling times were used for the analysis of the temperature variability on corresponding scales (e.g. a single temperature value measured daily at time of sampling [between 08:00 to 10:00] were was used to calculate the daily variance of temperature on the scale of our 54 day-long series).

The Coefficient of Variation (CV) was used throughout as our principal parameter of temporal variations in the plankton. Statistical analyses were made using Statistica for Windows (Version 99).

Results and Discussion

Zooplankton

Over our entire time series at the two sites (N=222), zooplankton density varied between 549 to 11282 individuals in m^3, with a corresponding variation in biomass from 1.16 to 11.69 g AFDW m^{-3} (Fig. 1). The overall averages were 5630 individuals m^{-3} and 3.96 g AFDW m^{-3}. Values of coefficient of variation (CV) over the entire time series were 36% for the density and 52 % for the biomass (Tab. 1).

The CV of zooplankton biomass during the day (daytime samples throughout our 54-day long series) at the Away and Reef sites were 48 and 36 %, respectively, while the CV values of the nocturnal samples were 37 and 38 %, respectively. The variations of biomass during a single day were much smaller than the variation during the 54 day-long series, with the average CV for the single sampling days (N=4 single days, each consists of 16-17 samples) equal to 24 and 27 % for the Away and Reef sites, respectively (Tab. 1). Although the biomass and density of zooplankton generally co-varied (Fig. 1) and were significantly correlated one with another, only less than half of the variance in the biomass values was explained by the numerical density. Adult and copepodite stages as well as nauplii copepods dominated (74 %) the sampled zooplankton community, which together with molluscs and appendicularia formed over 92 % of the collected specimens.

A general increase in zooplankton density took place at the two study sites, both in the diurnal and nocturnal samples, from the start of our sampling in early October to its end in the beginning of December (Fig. 1). This increase was more evident in the density, particularly in the day-time, than in the biomass data. The increase in zooplankton biomass was largely due to a quasi-monotonic increase in copepods (calanoids, cyclopoids and harpacticoids), but not in other taxa. Zooplankton abundance co-varied at the two sampling sites, both in terms of density and biomass. A significant ($P<0.001$) correlation between the two sites, with Pearson Correlation Coefficient $R \geq 0.7$, was found for the total zooplankton biomass, the total density, copepods (cyclopoids and calanoids combined) and harpacticoids.

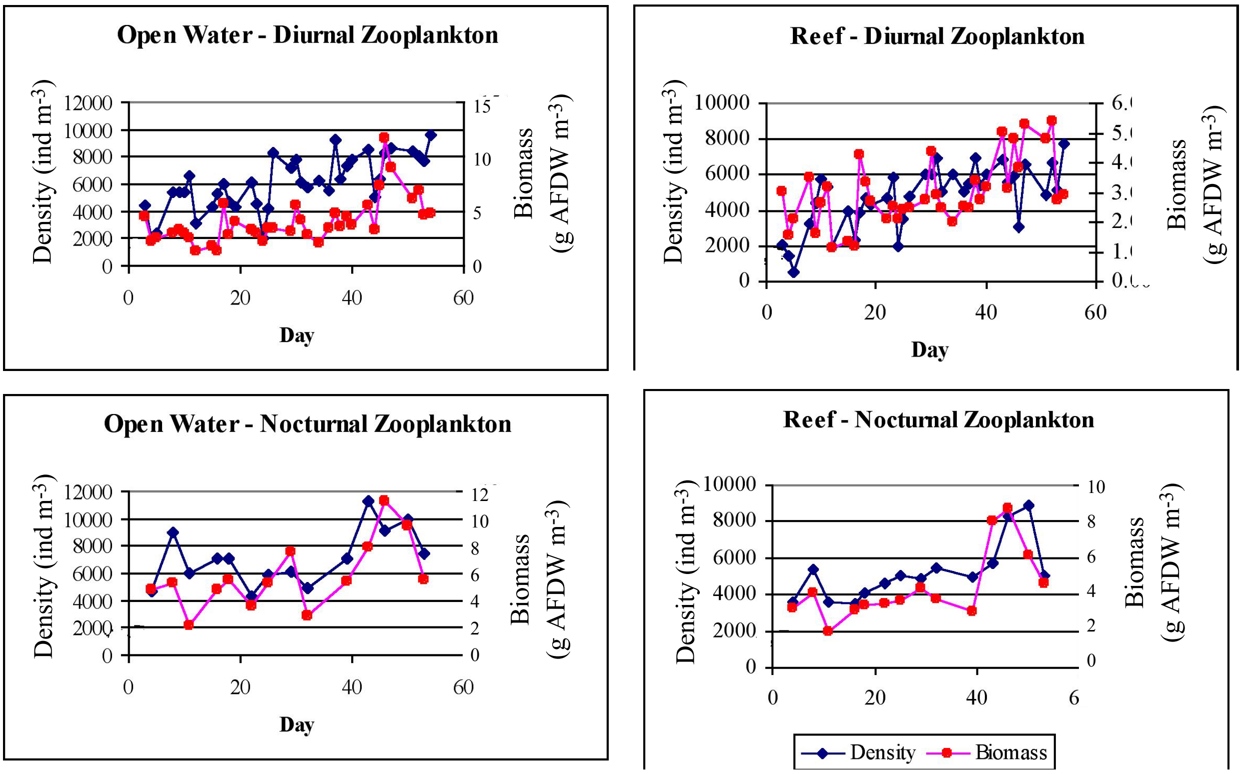

Fig. 1: Time series of total zooplankton density and biomass in the Open Water (= Away site) and the IUI Coral Reef (=Reef site) in Eilat in autumn 1999.

The zooplankton biomass and the densities of the total zooplankton and each of the three dominant taxa (cyclopoids and calanoids copepods [combined], harpacticoid copepods and copepod nauplii) were significantly higher ($P<0.0001$, Paired t-test) at the Away site than at the Reef. On the average, the zooplankton density and biomass at the reef were equal to about 75 % of those found at the open-water site. The taxonomic composition of the zooplankton community was similar at the two sites, except for calanoid and cyclopoid copepods which, in addition to their higher density in the Away site, consisted a significantly (Paired t-test, $P< 0.0001$, $N=51$) higher proportion of the zooplankton community at that site.

That zooplankton abundance co-varied at the two sites was evident on both the scale of the entire 54 day-long series as well as on the scale of hourly samples within days. The correspondence in zooplankton biomass between the Reef and Away site in the whole series was slightly higher ($R^2=0.7$) during the day than at night ($R^2=0.6$).

A clear diel cycle was observed in the zooplankton biomass both at the Reef and the Away site, with nearly a doubling of biomass during night. The pattern is most apparent when the zooplankton biomass is normalized relative to the average biomass during the corresponding day. A sharp increase in zooplankton abundance occurred around 16:00, remaining high until about 04:00 am, when it declined back to the low diurnal values. During our sampling period the sunset time changed from 17:16 p.m. at the beginning of our sampling to 16:41 p.m. at the end of our series. The corresponding change in sunrise time was from 05:38 am to 06:17 am. Darkness was reached some 30 min after sunset.

Tab. 1: The Coefficient of Variation (CV) of zooplankton (biomass and density), phytoplankton (concentrations of chlorophyll *a* and phaeopigments), current speed and temperature at different sites, times at different temporal scales.

Scale	**Time**	**Site**	**Chl.**	**Phaeo.**	**Zoo. Biomass**	**Zoo. Density**	**Current speed**	**Temp.**
Overall measurements		0.18	0.32	0.42	0.36	0.63	0.023	
54 days	Diurnal	Away	0.22	0.35	0.48	0.33	0.66	0.024
		Reef	0.22	0.33	0.36	0.36	0.77	0.023
	Nocturnal	Away	0.29	0.53	0.37	0.29	0.73	0.024
		Reef	0.28	0.54	0.38	0.31	0.65	0.024
Diel		Away	0.07	0.19	0.24	-	0.52	0.003
		Reef	0.08	0.23	0.27	-	0.35	0.005
10-15 min		Away	0.04	0.11	-	-	0.48	0.001
		Reef	0.05	0.14	-	-	0.41	0.003

Phytoplankton

Chlorophyll *a* concentrations varied throughout our time series from 135 to 509 ng l^{-1}, with an average of 312 (N=532) (Fig. 2). Corresponding changes in phaeopigment concentration ranged from 13 to 270 ng l^{-1}, with an average of 81 (N=529). The concentration of both chlorophyll and phaeopigments generally increased from the start to the end of our time series. Variations in chlorophyll were generally much smaller than those of zooplankton, while those of phaeopigments were similar to the latter. The CV values of chlorophyll ranged 22-29 % for the whole series and 4-8 % for the 15 min and diel series. Those of phaeopigments ranged 35-54 % for the whole series, and 11-23 % for the diel and 15 min series (Tab. 1).

Overall the concentrations of chlorophyll and phaeopigments at the Reef and Away sites were highly correlated. However this correlation was very high on the scale of our 54 day long series of daily samples (Pearson Correlation Coefficient R=0.95 and 0.71 for chlorophyll and phaeopigments, respectively), less so for the scale of hours (R=0.53 and 0.51, respectively) while weak (and not significant, P>0.05, in 6 of the 8 series) correlation was found for the scale of 15 min. As in the case of zooplankton, the concentration of chlorophyll was slightly (5.2%) but significantly (P<0.0001, Paired t-test) higher at the Open waters than at the Reef, while no significant difference (P>0.14) between the two sites was found for phaeopigments.

The phytoplankton community was dominated by *Synechococcu*s, which formed over 97 % of the cells counted. As in the zooplankton time series, an overall increase in the cell density, chlorophyll *a* and pheopigments was observed throughout our 54 day-long series.

A clear diel cycle was observed for both the chlorophyll and phaeopigments at the two study sites. Pigment concentrations generally increased in late afternoon (14:00-17:00 p.m.) and started to decline in early night (around 20:00 p.m.) reaching low values around midnight and remaining low throughout the rest of the night and the morning. The diel cycle in chlorophyll

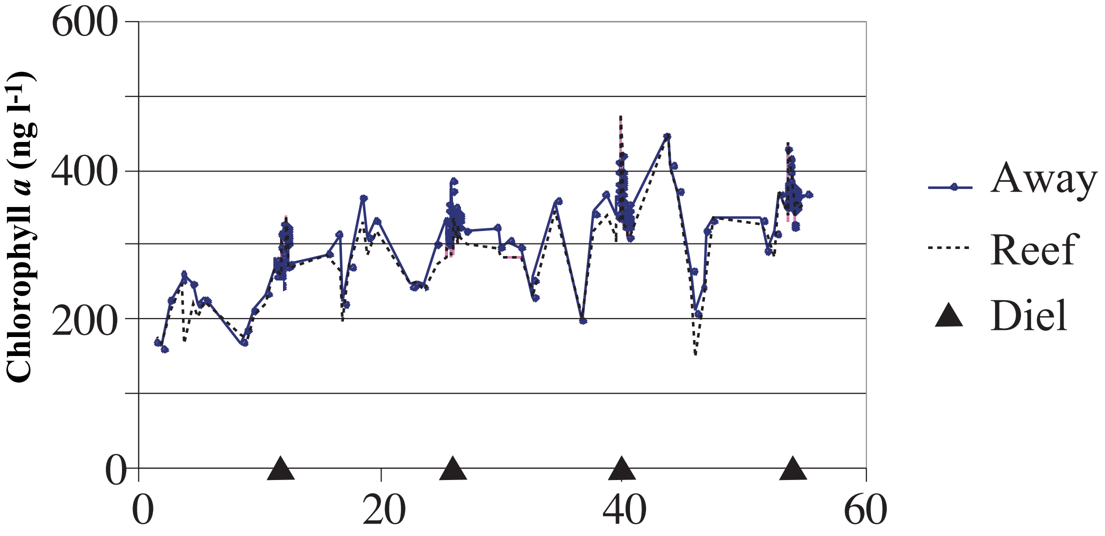

Fig. 2: Time series of chlorophyll *a* concentrations in the Away site (=Open) and IUI Coral Reef in Eilat. The triangle symbols on the horizontal axis indicate the days of daily and 15 min sampling schedules.

can be attributed to the well-documented synchronous daily reproduction cycle of *Synechococcus* and other phytoplankton taxa. Our findings indicate a peak of cell growth in late afternoon. The diel pattern in phaeopigments seemed to follow that of chlorophyll with a short time lag, as expected in predator-prey relationships where the predators, in this case filter feeders, exhibit a linear functional response.

Combined zooplankton and phytoplankton data

Although zooplankton and phytoplankton exhibited a generally similar trend of increasing values with advent of our time series, the correlation between these two planktonic groups was weak. In fact, only zooplankton density ($R=0.48$; $P<0.02$), not biomass ($P>0.05$), was significantly correlated with chlorophyll. The apparent reason for the weak correlation was the much higher variation of the zooplankton throughout the time series.

Temperature

As expected for the fall season, the *in situ* temperature generally decreased with time, except a short (3 days) of warming near the end of our time series. During the day, the temperature at the Reef was about 0.2° C higher than at the Open waters, while at night similar temperatures were measured at the two sites. Overall, temperature varied the least of all the parameters measured in this study (Tab. 1), with CV values smaller than 2 % on all scales, from 54 days to 10 min.

Currents

The flow regime during our field study consisted of relatively medium-weak currents, with an average flow speed (scalar) of 9.7 and 5.3 cm/s at the Open-water and Reef sites, respectively. Thus, one can conclude that the sampling point at the Reef was located within the benthic boundary layer, where the flow is weaker than the free flow aloft. Overall, the flow at the height of our pump at the Away site was northward with a weak (0.8 cm^{-s}) component of on-shore flow, while at the reef, the flow was directed straight off shore, with a net advection of about 1.8 cm^{-s}. This pattern resulted from the occurrence of downwelling near the shore, generated by a wind-driven, on-shore current at the upper water column (recorded by our current meter at the Away site), with a return, off-shore current near the bottom (recorded by our near-bottom current meter at the Reef). This pattern is also reflected in the negative correlation between the cross-shore components at the two sites, so that the stronger the on-shore flow at the Away site, the stronger is the off-shore flow at the Reef. The level of variation in current speed (scalar) was the highest of all parameters measured in this study, with values exceeding 65 % for the daily measurements throughout our 54 day long series, 35-52 % for the diel scale and 41-48 % for the 10 min scale (Tab. 1). Thus, of the six parameters we measured, current was the only one with high variation on the scale of 10 min.

Currents and plankton

A general trend of increasing chlorophyll and zooplankton abundance under conditions of stronger on-shore currents at the open-water site, was apparent at both sites. This trend corroborates the consideration of the coral-reef as a “sink” for both phytoplankton and zooplankton. Thus, under conditions of stronger on-shore flow aloft, the reef is exposed to higher flushing rate by effluent waters originated at the open sea. When no cross-shore flow occurs, or when it is reversed, both sites are exposed to greater proportions of reef water, which had been depleted of planktonic prey.

Conclusions

The temporal variations, or “patchiness” on the scale of daily samples during our 54 day long series was about 1.5 higher (in terms of CV) for zooplankton than for chlorophyll (phytoplankton), both at the coral reef and the open waters. This difference between phytoplankton and zooplankton is similar to that found in a 80 km transect in the North sea (Mackas et al. 1985). Thus, on the scale of 54 days, both the zooplankton and phytoplankton abundance were fairly predictable, with CV values around 25-50 %. On that scale organisms inhabiting the coral reef and its adjacent waters are exposed to moderate changes in the abundance of their planktonic food.

1) On the scale of hours (within a day) the difference between the temporal patchiness zooplankton and phytoplankton was much larger, approximately by a factor of 3. This increase in the difference between the two planktonic groups was due to a dramatic decrease in the phytoplankton patchiness, rather than an increase in the variability of zooplankton. Two factors seem to contribute to this difference: The vertical migration of zooplankton (not shared by phytoplankton) and the diel cycle of predation. Most of the zooplanktivores at the reef are visual predators, feeding during the day only, while most of the phytoplanktivores at the reef are filter feeders, which do not exhibit diel feeding patterns. Consequently, the peak-to-peak difference during the diel cycle is a factor of 2 for zooplankton, merely ca. 0.2 for phytoplankton. As the intense predation is considered the main ultimate cause for the

remarkable vertical migration of zooplankton in the reef, our findings form an excellent example for the effect of predation on plankton patchiness.

2) The patchiness of zooplankton and phaeopigments were of similar magnitude, much greater than that of chlorophyll. This is not surprising, as phaeopigments are the product of predation (grazing) on phytoplankton. Again, predation is apparently a major cause for patchiness, even on scales as small as 15 minutes, where the level of phaeopigment patchiness was 2-3 times greater than that of phytoplankton, primarily at the reef.

3) Of the two physical parameters measured in this study, temperature and currents, the former was the least and the latter was the most “patchy” variable among all those measured, on scales from 54 days to 10 minutes. The implication is that organisms in the coral reef and its adjacent waters need to be adapted to high variance and frequent changes in the flow but only small changes in temperatures.

4) The currents’ high variability on the scales of minutes is not reflected in the corresponding trends of plankton abundance. Thus, minute-scale currents apparently have no significant effect on plankton patchiness.

5) Both phytoplankton and zooplankton were significantly less abundant at the reef than at the Open-water station, located only 130 m seaward. Together with the current-meter data, this inter-site difference of planktonic abundance can be best interpreted in terms of intense phytoplankton grazing and zooplankton predation at the reef. As described by Genin et al. (1998), our current measurements show the prevalence of a typical circulation for the west coast of the Gulf, where the near-surface water is moving along shore (northward during the period of our study) with a clear on-shore component, generating downwelling along the coast with a strong return off-shoreward flow just above bottom. Thus, open water, rich with phytoplankton and zooplankton is advected onto the reef at the upper layers of the water column. This water replenishes food for the benthic grazers and predators at the reef, causing the return waters to be relatively depleted of plankton.

6) The observed gradual increase in phytoplankton and zooplankton abundance coincided with the ensuing fall mixing and seasonal eutrophication in the northern Gulf of Aqaba (Genin et al. 1995). This seasonal change in overall abundance was due primarily to the increase of copepods. The increase in chlorophyll was due to an increase of both the *Synechococcus* and eukaryotic taxa.

7) Variations in the abundance of zooplankton near the coral reef of Eilat are affected by four major factors: Seasonality (scale of 54 days), predation and currents (scales of days and diel cycle) and behavior (scale of diel cycle).

8) Variations in the abundance of phytoplankton near the coral reef of Eilat are affected by four major factors: Seasonality (scale of 54 days), predation and currents (scales of days and diel cycle) and reproduction cycle (diel).

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Fish communities on Jordanian coral reefs and adjacent habitats in the Gulf of Aqaba, Red Sea

Maroof A. Khalaf[1] and Marc Kochzius[2]

1) Marine Science Station, Aqaba
2) Zentrum für Marine Tropenökologie, Bremen

Introduction

The Red Sea ichthyofauna is quite well known compared to other parts of the tropical Indo-Pacific Ocean. Goren (1993) recorded 1248 fish species from this semi–enclosed northern extension of the Indian Ocean. A further 11 new records were added to the fishes of the Gulf of Aqaba by Baranes and Golani (1993). Randall (1994) added 22 new records and Khalaf et al. (1996) added 4 new records. To date more than 1280 fish species are known from the Red Sea. Ichthyological research in the Red Sea dates back more than 200 years to the collections and descriptions of fishes by Peter Forsskål (Klausewitz 1964, Nielsen 1993). Despite a long tradition of taxonomic work (e.g. Forsskål 1775, Klunzinger 1884), as well as biosociological and ecological studies on certain families, such as damselfishes (Pomacentridae) (e.g. Fishelson et al. 1974, Fricke 1977) and butterflyfishes (Chaetodontidae) (e.g. Bouchon-Navaro 1980, Bouchon-Navaro and Bouchon 1989, Roberts et al. 1992), surprisingly few studies are published on the general community structure of Red Sea shorefishes (Ben-Tuvia et al. 1983, Brokovich 2000, Rilov and Benayahu 2000). Other investigation deal with fish communities on artificial reefs (Rilov and Benayahu 1998, Golani and Diamant 1999) or give short species lists for certain areas (Clark et al. 1968, Tortonese 1983).

Several studies on the autecology (e.g. Wahbeh and Ajiad 1985a, 1985b) and population ecology (e.g. Bouchon-Navaro and Harmelin-Vivien 1981, Bouchon-Navaro 1986) of fishes were conducted along the Jordanian coastline of the Gulf of Aqaba, but no synecological approach has been conducted to date. This study investigates for the first time the fish communities of shallow water habitats along the Jordanian coast to get ecological information for a proper management of the Red Sea Marine Peace Park and adjacent waters.

Material and Methods

Transects of 50 m by 5 m were marked at six sites along the 27 km Jordanian coast, Gulf of Aqaba, Red Sea. At each site visual censuses were conducted along three transects at 6 m and 12 m depth, respectively. At five sites (Cement jetty, Marine Science Station, Tourist Camp, Jordan Fertilizer Industries and Jordan Fertilizer Industries jetty) three censuses were conducted at each depth. In Al Mamlah Bay 39 censuses were conducted at 6 m and 43 census at 12 m. In addition three censuses were done at 20 m depth at two stations near the Jordan

Fertilizer Industries. All fishes on the transects were identified to species level and recorded. All counts were done by the first author to prevent observer bias. The survey of the benthic habitat was conducted by the line-intercept method, recording percentage cover of live hard coral, soft coral, dead coral and rock, sand and seagrass (English et al. 1994).

Multivariate analysis of the data (hierarchical clustering) and ANOSIM (Analysis of similarities) significance test were performed with PRIMER 4.0 software (Carr et al. 1994). Hierarchical clustering is based on Bray–Curtis similarities. Transformation and standardization of data are indicated at the figures (Clarke and Warwick 1994). The ANOSIM significance test compares similarities of species compositions between the samples and can give evidence for differences. ANOVA (Analysis of variances) significance test was performed with STATISTICA software (Anon 1993).

Results

So far 348 species have been recorded for the Jordanian Red Sea coast (Khalaf and Disi 1997). In this study 202 shallow water species belonging to 123 genera and 43 families were identified. Most individuals belong to the families Serranidae, subfamily Anthininae (37.1 %; 2 species), Pomacentridae (22.3 %; 18 species), Labridae (8.0 %; 41 species), Apogonidae (6.2 %; 9 species), Caesionidae (6.2 %; 3 species) and Atherinidae (5.0 %; 1 species). The most abundant species are *Pseudanthias squamipinnis* (36.8 %), *Pomacentrus trichourus* (6.0 %), *Atherinomorus lacunosus* (5.1 %), *Paracheilinus octotaenia* (3.7 %), *Dascyllus marginatus* (3.6 %), *Chromis pelloura* (3.3 %) and *Caesio lunaris* (3.2 %). The ten most abundant species made up for more than two third of all individuals. In terms of frequency of appearance the most common species are *Pomacentrus trichourus* (87.3 %), *Amphiprion bicinctus* (79.7 %), *Pseudanthias squamipinnis* (79.7 %) and *Coris caudimacula* (78.8 %), as well as *Chaetodon paucifasciatus*, *Chromis dimidiata* and *Dascyllus marginatus* (all 72.9 %).

Cluster analysis of the sites shows three main clusters: The seagrass dominated Al Mamlah Bay and the 6 m and 12 m transects of the coral dominated sites (Fig. 1). This indicates different fish communities at 6 and 12 m depth as well as in the seagrass dominated Al Mamlah Bay. Confirmation of this pattern is evidenced by an ANOSIM significance test. Only one site (cement jetty 6 m) is assigned to the 12 m transects, indicating no difference between the two depth at this site. This picture can be connected to the benthic substrate. Cluster analysis of the benthic habitat composition gives the same pattern. This suggests that habitat composition and depth are the main influencing factors for the structure of fish communities in shallow water habitats along the Jordanian coast. Analysis by species shows two main clusters, one representing fishes of the coral habitat, the other fishes of the seagrass beds. Within the coral habitat the are two sub-clusters, representing 6 m and 12 m depth (Fig. 2).

Fish abundance is significantly higher (ANOVA: $p=0.003$; $F=10.39$) at the coral dominated transects at 12 m depth (1508.3 fishes/250 m2; SD 1016.3) than at 6 m depth (683.7 fishes/250 m2; SD 388.9). The same pattern can be observed in the seagrass dominated Al Mamlah Bay (ANOVA: $p<0.001$; $F=21.21$), with 3397.0 fishes/250 m2 at 12 m depth (SD 1440.7) and

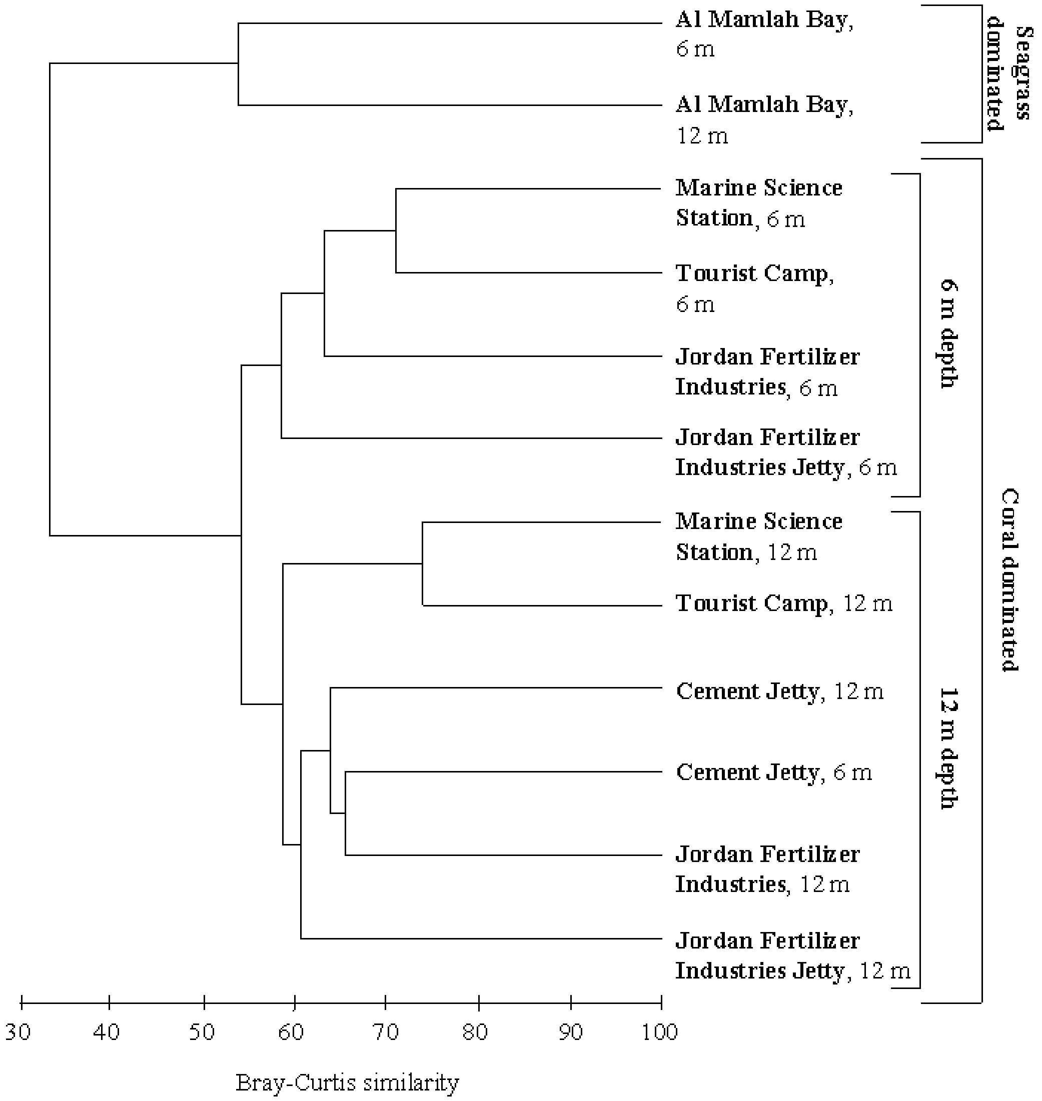

Fig. 1: Relationship of fish communities at different sites along the Jordanian Red Sea coast, Gulf of Aqaba (Bray-Curtis similarity; log(1+y) transformation of data; standardisation; group average).

856.3 fishes/250 m2 at 6 m depth (SD 1342.1). Comparison of fish abundance between the 12 m transect at the seagrass dominated Al Mamlah Bay and the coral dominated stations show a significantly higher fish abundance for Al Mamlah Bay (ANOVA: $p<0.001$; $F=20.84$). In terms of species richness and Shannon-Wiener diversity a significant difference is detected between 6 m and 12 m depth in Al Mamlah Bay (ANOVA: $p<0.001$; $F=24.45$ [diversity]; F= 285.48 [species richness]), with lower values in the shallow water seagrass meadows.

A biogeographic comparison based on presence/absence of species showed decreasing similarity of fish communities from the northern tip of the Gulf of Aqaba going south through the Red Sea proper into the western Indian Ocean (Fig. 3).

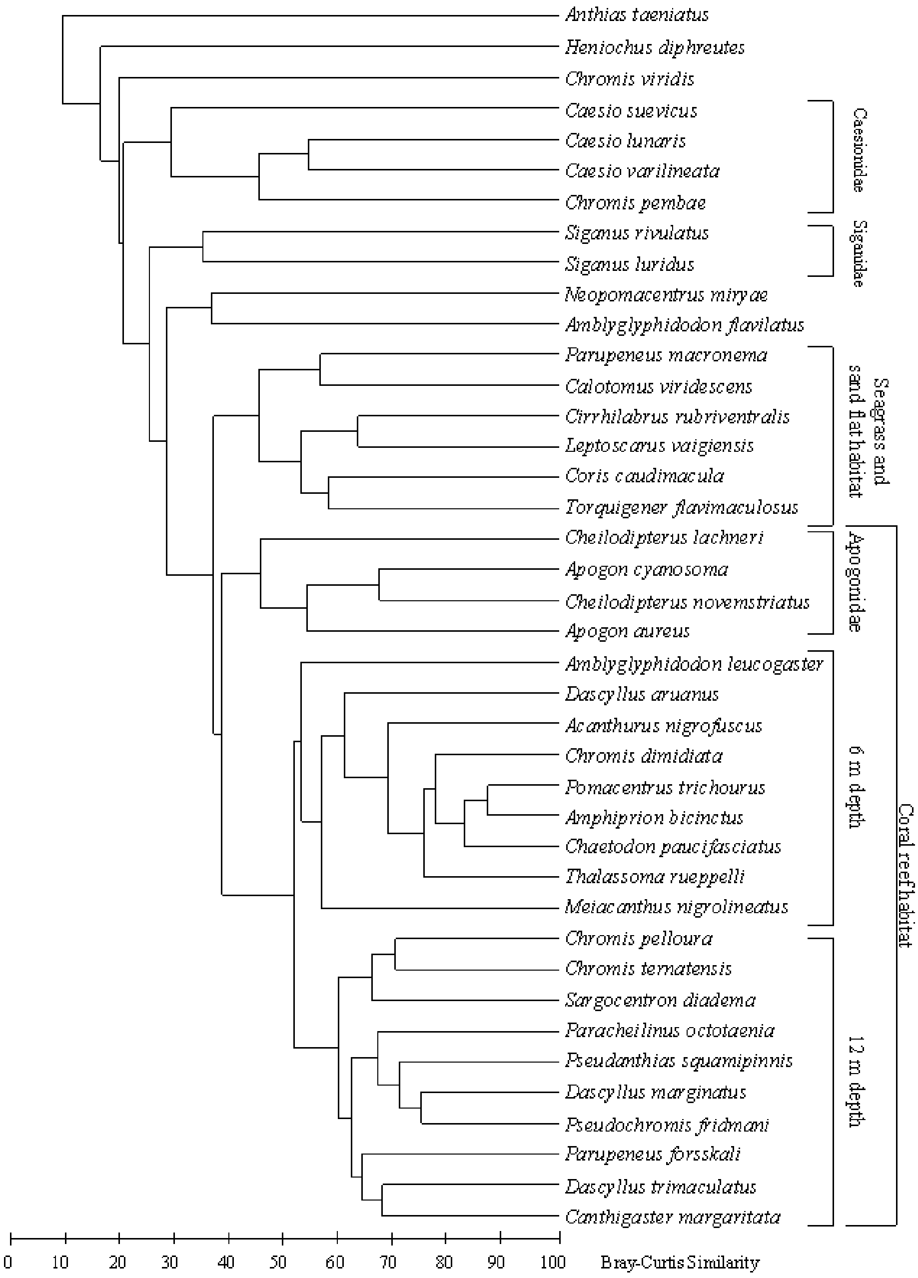

Fig. 2: Fish communities at the Jordanian Red Sea coast, Gulf of Aqaba. Species with at least 0.2 % of total abundance (no pelagic species; square root transformation of data; standardisation; group average).

Discussion

All drawn conclusions are restricted to day active and non cryptic species. As discussed by Brock (1982) and DeMartini and Roberts (1982), dwarf, cryptic and nocturnal species are underestimated by the visual census technique. Nevertheless, the visual census technique is widely applied and accepted for fish ecological studies on coral reefs. To minimize bias in comparing data of other studies, only information of visual transect counts were utilized.

The shallow water fish fauna of the Jordanian coast shows a high diversity with 202 species compared to other studies in the Red Sea. In a fringing reef near Sharm El Sheikh (Sinai)

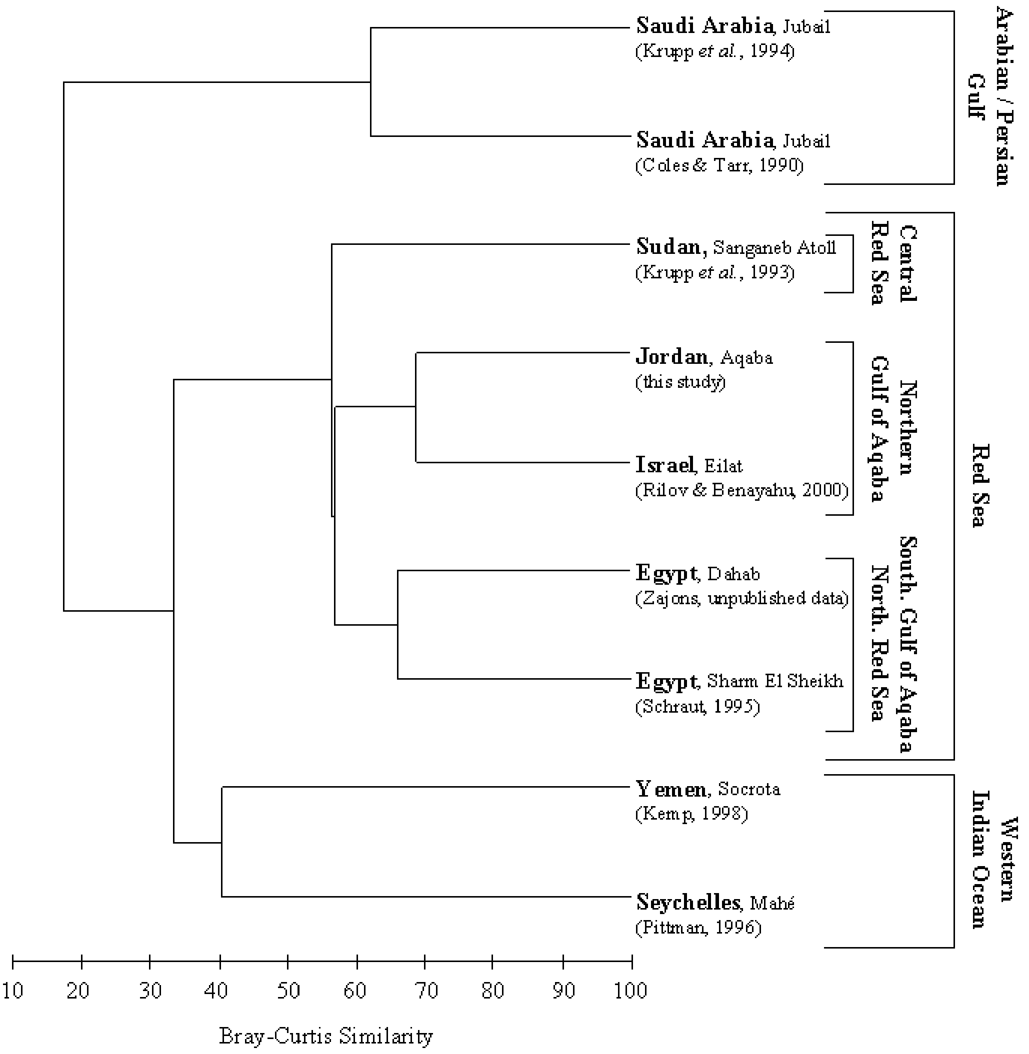

Fig. 3: Biogeographic relationship of the fish assemblages on Jordanian coral reefs to other geographical regions.
(Bray-Curtis similarity based on species presence/absence; exclusion of pelagic species).

Schraut (1995) recorded 176 species, in Dahab (Gulf of Aqaba) 162 species were identified (Zajons, unpubl. data), Krupp et al. (1993) recorded 121 species on the Sudanese Sanganeb atoll and in Eilat (Gulf of Aqaba) Rilov and Benayahu (2000) counted 142 species. These differences have to be taken with caution, because the observed species richness in an certain area is influenced by sampling intensity and the timeframe of the investigation. *Pseudanthias squamipinnis* is the most abundant species on Jordanian coral reefs as well as in the "Japanese gardens", Eilat (Rilov and Benayahu 2000), at Nuweiba in the Gulf of Aqaba (Ben-Tuvia et al. 1983) and at Sanganeb atoll, Sudan (Krupp et al. 1993). Other species with more than one percent total abundance in Jordan as well as at Sanganeb atoll (Krupp et al. 1993) are *Chromis dimidiata, Chromis ternatensis* and *Caesio suevicus*. Compared to the "Japanese gardens" in Eilat (Rilov and Benayahu 2000), the following species belong to the ten most abundant species at both sides of the Gulf of Aqaba: *Pomacentrus trichourus, Paracheilinus octotaenia, Dascyllus marginatus* and *Neopomacentrus miryae*.

The relatively high similarity of the fish communities in Aqaba and Eilat is also demonstrated by the hierachical cluster analysis of species presence/absence data from other localities in the Red Sea, western Indian Ocean and Arabian/Persian Gulf. There is a pattern of decreasing similarity of fish communities going south from the Gulf of Aqaba through the Red Sea proper into the Indian Ocean. These differences in the structure of fish communities on northern and southern Red Sea coral reefs are shown for several families, such as butterflyfishes (Chaetodontidae), angelfishes (Pomacanthidae), damselfishes (Pomacentridae), surgeonfishes (Acanthuridae), parrotfishes (Scaridae), wrasses (Labridae), emperors (Lethrinidae) and snappers (Lutjanidae) (Sheppard et al. 1992, Roberts et al. 1992). Differences in the community structure within the Red Sea might be due to north-south differences in habitat as well as an abrupt increase in turbidity south of around 20° N (Sheppard et al. 1992, Roberts et al. 1992). The low similarity of Red Sea fish communities to the Indian Ocean is caused by two barriers: The shallow connection of the Red Sea to the Gulf of Aden at Bab El Mandab strait and the reef-free section between Somalia and India, separating the Red Sea from the Indian Ocean (Roberts et al. 1992). The Gulf of Aqaba has different oceanographic properties compared to the northern Red Sea and shows a different vertical zonation for certain fish species. Due to the narrow and shallow Straits of Tiran the connection to the northern Red Sea is restricted. Therefore the Gulf of Aqaba can be considered as a distinctive zoogeographic region within the Red Sea (Sheppard et al. 1992), which is supported by the biogeographic relationships in our analysis (Fig. 3).

Cluster analysis (Fig. 1) and comparison of total abundance show significant differences between 6 m and 12 m depth as well as the habitat composition at the Jordanian coast. In Al Mamlah Bay the habitat at 6 m is dominated by seagrass beds and therefore shows a lower fish abundance, species richness and diversity than at 12 m depth. At 12 m depth the habitat is composed of seagrass, corals and sandy areas Due to the lack of shelter between the short blades of the seagrass and predators from the adjacent coral habitat, only a low number of individuals and species can utilize the seagrass meadow. The characteristic species of the seagrass and coral reef habitat are reflected in the species dendrogram (Fig. 2). Due to the high productivity of the seagrass meadows and feeding migrations of fishes from the coral reef to the seagrass beds (Kochzius 1999), the total abundance of fishes at 12 m depth is significantly higher in Al Mamlah Bay than at 12 m depth in the coral dominated sites. Studies in the Caribbean have shown that the biomass of fishes is higher in coral reefs adjacent to seagrass meadows than in reefs without seagrass beds (Birkeland 1985). Comparison of fisheries from different coral reef regions suggested that coral reefs with extended shallow water habitats, such as seagrass meadows or mangroves, yield the highest catch. Reefs with a ratio of shallow water habitat to coral reef of 1:1 or more are very productive (Marshall 1985). Despite the lack of biomass data in this study, the high abundance of fishes in Al Mamlah Bay supports this findings. Before the recent closing of this area, it was the favorite fishing ground for local fishermen, indicating a high standing stock and high productivity of fish. Our results support the importance of Al Mamlah Bay as a high productive area along the Jordanian Red Sea coast and its important role as part of the protected “Red Sea Marine Peace Park”.

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Effect of the reef framework and bottom sediment on nutrient enrichment in a coral reef of the Gulf of Aqaba, Red Sea

Mohammed Rasheed[1,2], Mohammad I. Badran[2], Claudio Richter[3] and Markus Hüttel[1]

1) Max-Plank-Institut für Marine Mikrobiologie, Bremen
2) Marine Science Station, Aqaba
3) Zentrum für MarineTropenökologie, Bremen

Summary

Inorganic nutrients and chlorophyll *a* concentrations were measured biweekly in a transect across a coral reef in the Gulf of Aqaba over a period of one year. The nutrient and chlorophyll concentrations were compared to those in offshore waters (400 m depth) seaward to the reef. In reef and offshore waters, nutrient (ammonia, nitrite, nitrate, phosphate and silicate) and chlorophyll *a* data showed seasonal changes with higher concentrations in winter and low concentrations in summer. However, throughout the summer, nutrient concentrations in the coral reef waters exceeded those in the offshore waters significantly while in winter this difference was less pronounced. The evaluated nutrient levels in reef waters were caused by nutrient release from reef framework and coral sand. In the reef framework water, ammonia, nitrate, nitrite and phosphate concentrations were 1.2-2.3 fold higher than those in the surrounding waters and the fluxes from the framework would amount to approximately 14.5 mmol m^{-2} d^{-1} for ammonia, 7.7 mmol m^{-2} d^{-1} for nitrate, 0.9 mmol m^{-2} d^{-1} for nitrite, 1.3 mmol m^{-2} d^{-1} for phosphate. Likewise, nutrient concentrations in the pore water of the carbonate sediment adjacent to the corals exceeded those of the reef water by a factor of 18-76. Here, the calculated minimum fluxes were 0.06 mmol m^{-2} d^{-1} for ammonia, 0.03 mmol m^{-2} d^{-1} for nitrate, 0.01 m^{-2} d^{-1} for nitrite, 0.01 mmol m^{-2} d^{-1} for phosphate, and 0.07 m^{-2} d^{-1} for silicate. We suggest that reef framework and coral sand act as filters for particulate organic matter and that the decomposition products of trapped material increase the nutrient concentrations in the reef water.

(full text submitted to "Marine Ecology Progress Series")

Fig. 1: Average nutrient concentrations (µM) in the framework of cavities of the coral reef (cav= cavities; hatched columns) and in the surrounding waters (ref=reference; white columns).

The cross-shore conveyor and the fate of plankton in the coral reef

Claudio Richter[1], Mohammad I. Badran[2], Britta Munkes[1], Mohammed Rasheed[2], Helge Niemann[1], Khaled Al-Sokhny[2], Riyad Manasreh[2], Alexander Voigt[1], Iris Kötter[1], Mark Wunsch[1], Mohammad El-Zibdeh[2], Maroof Khalaf[2], Gotthilf Hempel[1]

1) Zentrum für Marine Tropenökologie, Bremen
2) Marine Science Station, Aqaba

Summary

Several lines of evidence from collaborative work in the fringing coral reef in Aqaba, in terms of plankton and current measurements, video tracking of particles and temperature readings, show that offshore plankton-rich water enters the reef via the surface, becomes denser near-shore due to evaporation and night-time cooling and exits the reef via downslope density currents. In the course of this conveyor, the water becomes modified: stripped of zoo- and phytoplankton via fish and invertebrate filter feeders and enriched in nutrients by remineralization of organic material produced and imported into the reefs. Zooplankton uptake by fish amounts to ≈1 g C m^{-2} d^{-1}. Phytoplankton and bacteria are taken up at similar rates by benthic filter feeders, mostly cavity-dwelling sponges. Organic debris is either trapped in the framework or ends up on sand, so that at times the entire sandy area bordering the reef edge is virtually carpeted with faeces egested by zooplankton-feeding fish. Ensueing remineralization provides an important source of new nutrients for reef corals and algae, but also for the adjacent pelagic system. We postulate that the Gulf of Aqaba fringing reef is a trophodynamically open system with significant cross-shore exchange of material between the coral reef and the oligotrophic waters at large.

Background

Coral reefs are considered essentially closed systems, where the bulk of the material is recycled within the systems' boundaries with an only minor exchange of material between the reef and the open sea, land and atmosphere, respectively.

However, studies carried out in Aqaba and elsewhere often show pronounced gradients in the concentrations of nutrients, phytoplankton and other material between the coral reef and the open sea. In Aqaba, for example, nutrients are enriched throughout the year in coral reef waters as compared to offshore waters (Fig. 1). Also phytoplankton pigments are higher near the reef than offshore, except during the spring bloom where offshore waters are richer in phytoplankton. As inputs from land are non-existent in this desert enclosed sea, the increase in nutrients and chlorophyll near the coast must be due to upwelling of nutrient-rich deep water, remineralization of zooplankton and/or other organic matter advected onto the reef, or a combination of both.

Results and Discussion

A field study carried out over the shelf break in front of the Marine Science Station (Fig. 2) shows a net onshore flow of surface water towards the coral reef, and a net offshore flow in deeper water, particularly during the night (Fig. 3A). Associated with the surface inflow are higher backscatter intensities (Figs. 3B and 4), indicative of higher concentrations of zooplankton and other particles. Offshore surface currents show lower backscatter intensites, indicating removal of backscattering particles near the reef (Fig. 4). Higher backscatter intensities near the bottom (Fig. 3B) indicate offshore transport of echo-reflecting inorganic particles near the sea-bed, but may be due partly also to reverberation near the sloping bottom. Lateral currents appear to be driven by differences in the windfield, as well as by tidal and thermohaline effects. Current meter deployments near the sea bed show both, periodical and temperature-related variations in downwelling intensities (Fig. 5). These results are corroborated by ongoing long-term deployments near the reef.

The quality and quantity of organic particles exchanged between the ocean and the coral reef is affected by a diverse and dense assemblage of coral reef suspension feeders. Large zooplankton is effectively consumed by planktivorous fish and corals. Fish are visual predators which feed mostly during day. Corals, by contrast, extend their stinging tentactles mostly during the night to feed on the abundant zooplankton in the coral reef. The 'wall of mouths' of planktivorous fish is in fact a series of 'fences', of diminishing mesh size as one approaches the reef from offshore: Caesionids patrol the outer reaches of the fore-reef, whereas the smaller Pomacentrids and small Serranids (Pseudanthias) shoal nearer to the reef (Fig. 6). Sometimes very large warms of small Atherinids congregate near the reef edge, egesting large amounts of feces to the sea bed. Cross-shore distributions of zooplankton show significant depletions, coinciding with abundant fish and intense community feeding (Fig. 7A-B). Rapid remineralization of the rain of faeces (Fig. 7C) as well as gill excretion locally enhance the concentrations of dissolved inorganic nitrogen (Fig. 7D) which are rapidly metabolized nearshore, as evidenced by falling TIN levels and proportionally higher ammonia levels (Fig. 7E).

Phytoplankton is taken up by passive suspension feeders, such as some soft corals (e.g. the beautiful Dendronephthya), but above all, by active suspension feeders, like sponges or ascidians, which create a water stream through their bodies. Cryptic habitats like holes and cavities within the coral reef framework provide a large substrate for suspension feeders in coral reefs which deplete the through-flowing water of minute phytoplankton and bacteria (cf. Richter et al., this volume).

Nutrients regenerated from the organic material ending up in coral reef cavities are recycled back to the sunlit autotrophic coral reef community, fuelling an important part of the primary production (cf. Rasheed et al., this volume).

Fig. 1: Cross-shore distribution of inorganic nutrients and chlorophyll *a* in the Aqaba Marine Science Station coral reef (MSS). (Source: Rasheed, MSc thesis 1998)

Mucus net feeders sitting on the reef edge such as the worm-like snail Dendropoma scavenge both, zoo- and phytoplankton from the water, but also trap epibenthic animals and algae in their sticky nets (cf. Kappner et al. 2000).

Conceptually, as a water parcel proceeds from the open sea towards the fringing reef, it passes through three 'filters': it is first selectively screened for large 'macro- and meso'-zooplankton by visually predating fish. Nearer shore the smaller 'meso- and micro'-plankton are eaten rather indiscriminately by smaller fish and invertebrates. Cryptic suspension feeders, finally, constitute the main filter for the very small 'picoplankton'. Inorganic nutrients are formed, washing out towards the open ocean, fuelling pelagic production, closing the cross-shore cycling of material between the ocean and reef.

Fig. 2: Bathymetric map of MSS showing current meter moorings (crosses) as well as the cross-shore transect (line). (Source: Niemann, MSc thesis in prep.)

Fig. 3: Vertical profiles of cross-shore current velocities (A) and time-varied gain (TVG) corrected acoustic backscatter intensities (B) during day- and night-time hours. Downward-looking 300 kHz ADCP, moored at 16 m over 100 m bottom in front of MSS (cf. Fig. 2).
(Source: Manasreh, PhD thesis in prep.)

Fig. 4: Diurnal variations in backscatter intensities in on- and offshore flowing waters.

Fig. 5: Time series of temperature and downwelling current velocities near the sea bed, as determined with acoustic current meter in front of MSS, December 1999.

Fig. 6: Cross-shore distribution of main groups of zooplanktivorous fish in front of MSS. (Source: Munkes, Diploma thesis in prep.)

Fig. 7: Cross-shore distribution of size-fractioned zooplankton dry-weights (A), zooplanktivore abundances (B), feeding intensities (C), fish egestion rates (D), total inorganic nitrogen (TIN) (E) and ammonia (F) in front of the MSS. (Source: Munkes, Diploma thesis in prep.)

Dense populations of cavity-dwelling sponges deplete phytoplankton in Red Sea coral reefs

Claudio Richter[1], Mark Wunsch[1] and Mohammad I. Badran[2]

1) Zentrum für Marine Tropenökologie, Bremen
2) Marine Science Station, Aqaba

Abstract

Using an endoscopic camera, we discovered a rich assemblage of filter-feeders encrusting the labyrinth of crevices interlacing Red Sea coral reefs. At a flushing time of ≈5 min. water flow supports dense populations of sponges which cover up to 56 % of cavity walls. Biological filtration removes up to 74 % of phytoplankton entering framework cavities, corresponding to an uptake of ≈0.8 g C m-2 d-1, or an estimated 20 % of the community metabolism of the entire reef. Ensuing remineralization is a key source of new nutrients supporting coral and algal growth.

Results

Efficient conservation and rapid turnover of limiting resources enable coral reefs to thrive in nutrient-poor waters. However, material cycling does not proceed without losses so that reefs depend on a compensatory inflow of extrinsic material (Erez 1990), to a large part in the form of <5 µm phytoplankton and bacteria (Ayukai 1995, Yahel et al. 1998). How this 'ultraplankton' is taken up by the reef community remains enigmatic, because ultraplankton feeders such as sponges or ascidians are rather scarce on the outer surface of the reef (Yahel et al. 1998) or may be entirely missing (*).

In dark places such as overhangs and caves, filter-feeders are quite common (Logan et al. 1984, Jackson and Winston 1982, Jackson et al. 1971, Vasseur 1974) and field experiments show their ability to capture small particles very efficiently (Buss and Jackson 1981). However, attempts to quantify their abundance and filtering activity have been thwarted by the methodological difficulty of accessing the narrow crevices and cracks which interlace coral reefs (Wunsch and Richter 1998).

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*Lazar, B. (unpublished material) found chlorophyll *a* depletions over denuded reef sections in Sinai peninsula (Egypt), Red Sea.

Fig. 1: Cryptic sponges abound in coral reef crevices in the Red Sea. *Batzella sp.* (nearly black, in the middle and at the bottom left), *Arenosclera sp.* (white at right, featuring black exhalant opening) and other unidentified species fill out the entire frame in this 50 x 37 mm close-up taken at 150 cm distance from the entrance in a cavity at Aqaba, Jordan. Video images were obtained with the CaveCam (Wunsch and Richter 1998), a diver operated 25 mm diameter endoscopic camera reaching up to 4 m into coral reef cavities. (Sponges were identified by R. van Soest, Amsterdam)

Here we provide evidence that coelobite suspension-feeders are a major sink for phytoplankton in coral reefs. In a first quantitative assessment with the endoscopic CaveCam carried out as part of the Red Sea Program (Wunsch and Richter 1998, Kaiser 1998), we explored the cryptic biota in coral reef crevices from 3 fringing reef locations in the northern Red Sea. A total of 17 cavities, 20-80 cm in diameter, were investigated at Ras Mohammed (Egypt), Eilat (Israel) and Aqaba (Jordan) between 2 and 14 m water depth. We observed high densities of coelobites up to the maximum 4 m range of the video probe (Fig. 1). Quantitative analysis of the high-resolution images reveals a rich coelobite community harboring a total 362 taxa, including 197 varieties of sponges (Wunsch, unpubl.).

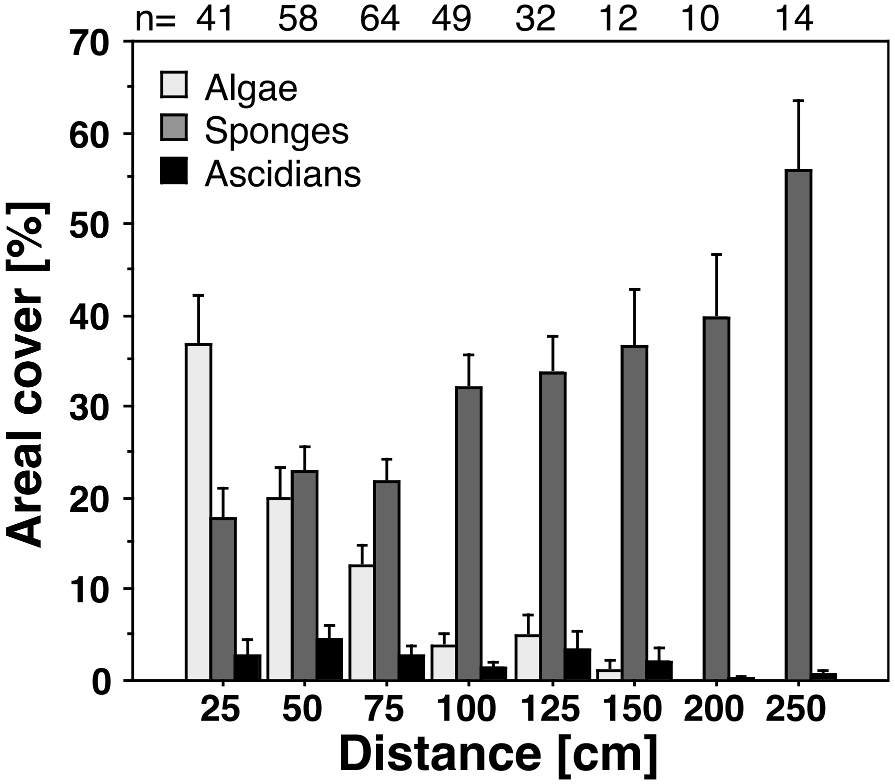

Fig. 2: Encrusting red algae dominate the coelobite community near the entrances, while filter-feeding sponges increase towards the dark inner sections of the cavities. Results are based on image analysis of a random subset of 280 video frames (50 x 37 mm) from 17 cavities investigated with the CaveCam in Ras Mohammed (Egypt), Eilat (Israel) and Aqaba (Jordan) (Wunsch unpubl.). Error bars denote standard error of the mean areal cover for each taxon.

Coralline algae and other photoautotrophs predominate near the cavity entrances, but algal cover rapidly declines towards the inner reaches of the cavities, giving way to a heterotrophic community dominated by filter-feeders (Fig. 2). Sponges alone cover between 18±3 % and 56±8 % (mean ± SE) of the cavity walls, with an increasing share towards the inner reaches of the cavities. Ascidians occur regularly but in lower numbers, covering <5 % of the substrate between 25-150 cm and <1 % beyond. The ensemble of other filter feeders (bivalves, brachiopods, bryozoans and polychaetes) rarely exceeds 2 % of the available space, with the exception of the soft coral *Scleronephythya* sp. which may locally attain up to 25±7 % of the total cover. Although nephtheid corals are reported to ingest phytoplankton (Fabricius et al. 1995, Fabricius et al. 1996), they are passive suspension feeders restricted to well-flushed areas and, hence, largely absent in framework cavities.

Determination of coelobite biomass is a daunting task due to the cryptic nature of the organisms and the complex 3-dimensional structure of the cavity system. Our observations, however, comply with the general assumption that the surface area provided by anastomosing crevices and cracks exceeds by far the projected reef area (Logan et al. 1984, Jackson et al. 1971, Ginsburg and Schroeder 1973). Assuming a conservative ratio of 2:1 between the actual and projected area (Gischler and Ginsburg 1996), we estimate a coelobite biomass of ~45 g C m^{-2} for sponges alone (**). This is >50 % of total reef biomass (Sorokin 1995).

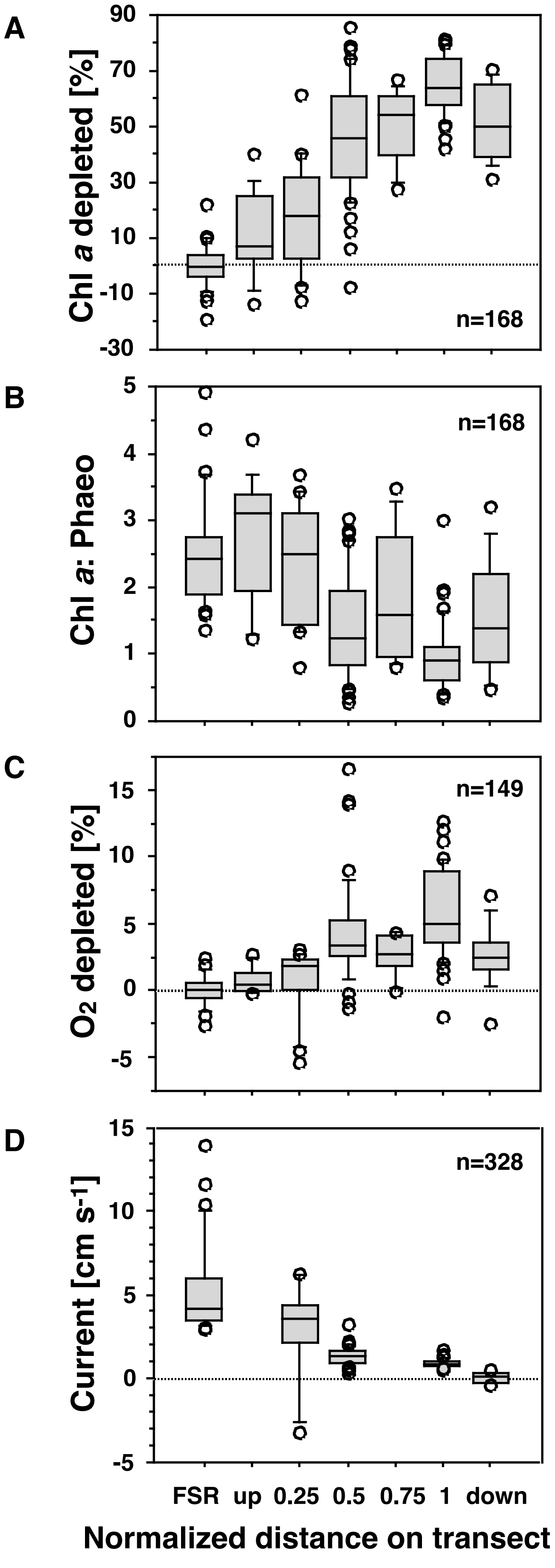

Fig. 3: Small-scale distribution of (A) chlorophyll *a*, (B) chlorophyll *a*: phaeopigment-ratio, (C) oxygen and (D) water currents between the freestream reference (FSR) ~2 m away from the reef and reef framework cavities. Distance from the upstream entrance (up) is given as fraction of total cavity length. Box plots are composites of a total 15 small-scale transects carried out between 0.6-4.0 m long, 0.1-1 m wide cavities and FSR in Ras Burka, Ras Abu Galum (Egypt) and Eilat (Israel) between 2 and 16 m depth. Data for downstream exits of tunnel cavities (down) are available for 5 transects. Boxes encompass 50%, whiskers 95% of the data, center lines of boxes denote the median. Water samples were collected with 100 ml syringes. Oxygen was measured by Winkler titration, pigments were determined fluorometrically after filtration through GF/F filters and acetone extraction (Parson et al. 1984). Currents were determined videographically by tracking the displacement of suspended particles in a scaled video plane, using CaveCam and conventional underwater video techniques (Wunsch and Richter 1998).

In order to assess the activity of the filter-feeding community, we measured the small-scale variations in phytoplankton pigments, oxygen and water flow between randomly selected framework cavities and freestream waters in the fringing reefs of Eilat (Israel), Ras Abu Galum and Ras Burka (Egypt).

Our results show strong depletions of chlorophyll *a* in the inner quarters of the cavities (64±8 % median ± MAD above the reef) (Fig. 3A), alongside with marked decreases in the chlorophyll *a* : phaeopigment ratio (Fig. 3B) indicating heavy grazing (Currie 1962). The downstream openings of the cavities feature reversals of the above patterns, due to mixing above the reef.

Oxygen depletions are small but significant (5±2 %, Fig. 3C; Kruskal-Wallis tied $p<0.0001$), reflecting the overall heterotrophic nature of the coelobite community.

Water flow decreases with increasing distance from the cavity entrance (Fig. 3D), proceeding at a speed of 0.9±0.1 cm s^{-1} or 21 % of freestream values through the framework (one sample sign test, $p<0.0001$).

Dye experiments confirm that water exchange is generally rapid. 95 % of fluorescein dye injected into 48 randomly selected cavities is washed out in less than 5 minutes (simple regression of log-transformed fluorescence Y [%] versus time t [s] yields:

$$Y= 1.866 - 0.004 \times t \; (n= 240; R^2 = 0.46).$$

Variations in ambient flow affect the magnitude of chlorophyll *a* depletions, which may range between 40 % and >70 % for a given set of cavities (Fig. 4).

For the upper first meter of framework we calculate an uptake by the coelobite community of 0.80±0.05 g phytoplankton C m^{-2} d^{-1}, equivalent to 20 % of the gross reef production (Erez 1990). Our figure is based on a mean (±SE) concentration difference of 0.15±0.01 mg chlorophyll *a* m^{-3} between cavity and freestream waters (this study), a water renewal rate of ~300 times d^{-1} (this study), a minimum volume fraction of cavities of 30 % (Gischler and Ginsburg 1996), and a carbon:chlorophyll *a* -ratio of 60 (Legendre et al. 1988).

This flux of extrinsic material along with other sources of organic matter is rapidly metabolized in the cavities as evidenced in significant enrichments in phosphorous (∂P) and nitrogen (∂N) relative to freestream waters, high levels of ammonia (42 % of total inorganic N) and $\partial N : \partial P$-ratios (15.5) near the Redfield ratio (Redfield et al. 1963). Remineralization of the filtered phytoplankton accounts for up to 16 % and 17 % of the dissolved inorganic phosphorous (∂P) and nitrogen (∂N) regenerated in the cavities. Although this is a moderate fraction of the total nutrient flux emanating from the cavities, these new nutrients constitute an effective gain for the reef ecosystem, enhancing net growth of the overlying coral and algal community.

** Biomass calculations are based on an average sponge thickness of 3 mm (unpublished material), 45.8 mg ashfree dry weight (AFDW)/ml sponge [H. M. Reiswig, Journal of Experimental Marine Biology and Ecology 14, 231-249 (1974)] and 0.5 g C/g AFDW [T. R. Parsons, M. Takahashi, B. Hargrave, Biological oceanographic processes (Pergamon Press, Oxford, 1984)].

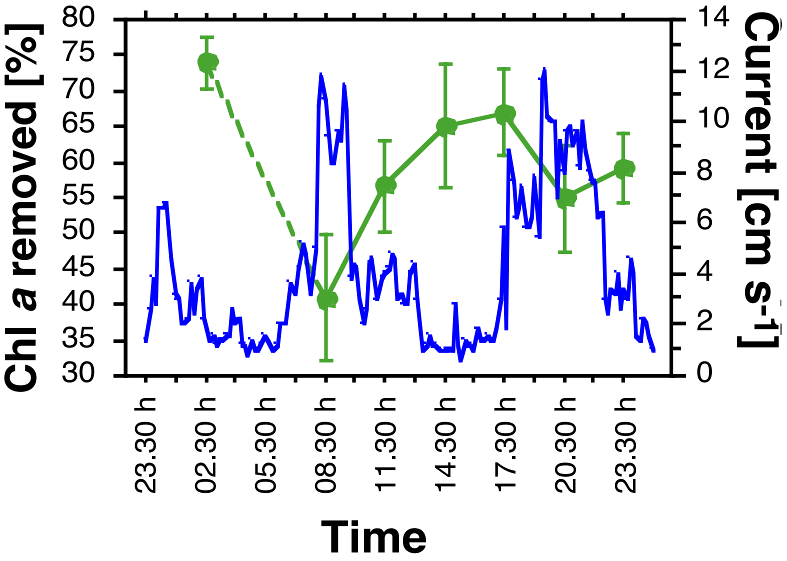

Fig. 4: Diel variation of currents (line) and chlorophyll *a* depletions (symbols) in coral reef cavities. Water samples for chlorophyll *a* were simultaneously taken every 3 hours from 8 haphazardly selected 0.5-0.8 m long, 0.1-0.3 m wide cavities in a fore-reef pinnacle in front of the Aqaba Marine Science Station, Jordan, between 5 and 10 m water depth. Reference samples were taken from the surrounding water 5 m away from the pinnacle. Error bars denote the standard errors of the mean. Currents were recorded every 5 minutes with a Sensordata SD-6000 current meter moored 5 m away from the pinnacle.

The widespread occurrence of phytoplankton depletions over coral reefs (Ayukai 1995, Yahel et al. 1998, Legendre et al. 1988, Glynn 1973) indicates that pelagic-benthic coupling through sponge-dominated coelobite communities may be a major pathway through which essential elements are channeled into coral reefs.

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Coelobite (cavity-dwelling) communities in Red Sea coral reef crevices

Mark Wunsch[1], Salim Al-Moghrabi[2], Iris Kötter[1], Claudio Richter[1] and E. Saadalla[3]

1) Zentrum für Marine Tropenökologie, Bremen
2) Marine Science Station, Aqaba
3) Egyptian Environmental Affairs Agency, Ras Mohammed National Park Headquarters, Sharm El Sheikh

Abstract

The morphology, size, light regime, water exchange and community structure of 25 Red Sea coral reef crevices were investigated using traditional and novel techniques, including the video-endoscopic CaveCam and the LightSheet system. Analysis of a total 3066 video images from cavities in Aqaba (Jordan), Ras Mohammed (Egypt) and Eilat (Israel) revealed rich sessile macrobenthic communities, encompassing 386 taxa (including 156 species and/or genera) and covering about two thirds of the substratum. The zonation of the coelobite communities along the cavity axis was governed by the distance from the cavity entrance and the resulting strong light gradient (0.005-16.5 % of the surface irradiation), as well as the great variation of the water exchange (0.9-5.5 cm s^{-1}).

Cavities were estimated to at least double to triple the substrate area compared to a reef without caves, providing living space for coelobites that equals or exceeds the outer reef surface area. These findings emphasize the importance of coelobite communities for coral reef ecology.

Introduction

The coral reef framework is usually riddled with holes and crevices providing extensive substrate for a wide range of sessile organisms and shelter for many vagile animals. Crevices, cracks and small caves (0.05-1 m in diameter) are the most common cryptic coral reef habitats, providing probably more than half of the total available settling surface in coral reefs (Jackson et al. 1971, Logan et al. 1984).

However, these small cavities have remained virtually unexplored being inaccessible for divers. Recently the development of the CaveCam (Wunsch and Richter 1998), a diver operated endoscopic underwater video-system, enabled the exploration of these hidden habitats.

Site and cavity description

Two main study sites were selected at the opposite ends of the north eastern extension of the Red Sea: (1) The Marine Science Station (MSS) in Aqaba and (2) Ras Mohammed on the southern tip of the Sinai peninsula bordering the Red Sea proper. Twelve cavities were chosen randomly at each site, 4 at 2-4 m, 11-13 m and 19-20 m respectively. In Aqaba they were located on the upper and lower fore-reef slope and in the shallow ‘Coral Garden’, a fringing reef with prolific hard coral growth. In Ras Mohammed the reef is a drop-off to more than 70 m. Cavities at the third site, Eilat, did not match the size and depth criteria. However, the survey of a 4 m long cavity in ‘Moses Rock’, an isolated reef pinnacle in the "Coral Beach" marine reserve provided a case study for a large tunnel cavity. Cavities were 1.25-2 m long and < 0.7 m wide at the entrance.

Methods

The sessile communities lining the cavity walls were studied with the CaveCam. It consists of a high-resolution finger camera in an underwater housing connected to a video recording and a control unit. 5 pictures were recorded systematically from the ceiling, left and right wall and bottom respectively in 25 cm increments along the cave axis. The longer Moses Rock cavity was surveyed in 50 cm increments from 0-350 cm.

3066 images representing an area of over 80.000 cm^2 were analyzed on a computer for percent coelobite cover. Distinct organisms that could not be identified to species level were recorded as 'taxa'. Data were analyzed with the Primer 4.0 software package for community based studies (Plymouth Marine Lab). For mathematical reasons only the 37 more abundant species (total cover per species >250 area units or total of individuals >150) qualified for the multivariate community analyses. 198 coelobites were photographed in situ for the ground-truthing of video images and sent to taxonomists for identification.

Cavity volume, surface area and morphological features were assessed by means of the LightSheet, a CaveCam based 3-D underwater surveying system (Wunsch, submitted). Other parameters measured include light intensity (employing a custom-built small light meter) and water exchange, measured with blocks of gypsum that dissolve according to the ambient water motion (‘clod card’ dissolution technique, Jokiel and Morrissey 1993). These were employed simultaneously for 3 consecutive times for 48 h along the cave axis. The frequency and size of caves at the 2 main sites was surveyed along line-transects.

Results

Reef porosity

With 42 % of voids along the transects, a large portion of the Ras Mohammed reef was eroded in contrast to only 28 % in Aqaba. Aqaba reefs were riddled with many small cavities (e. g. 30 cavities ≤ 0.1 m per 50 m) whereas cavities at Ras Mohammed were generally larger. The

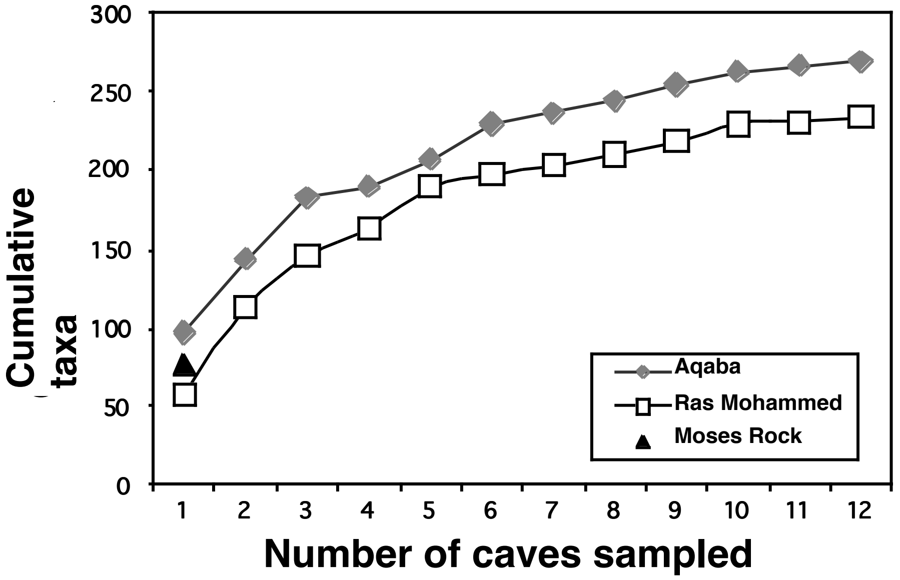

Fig. 1:

Cumulated number of taxa versus no. of cavities for sessile coelobite communities in Aqaba, Moses Rock and Ras Mohammed.

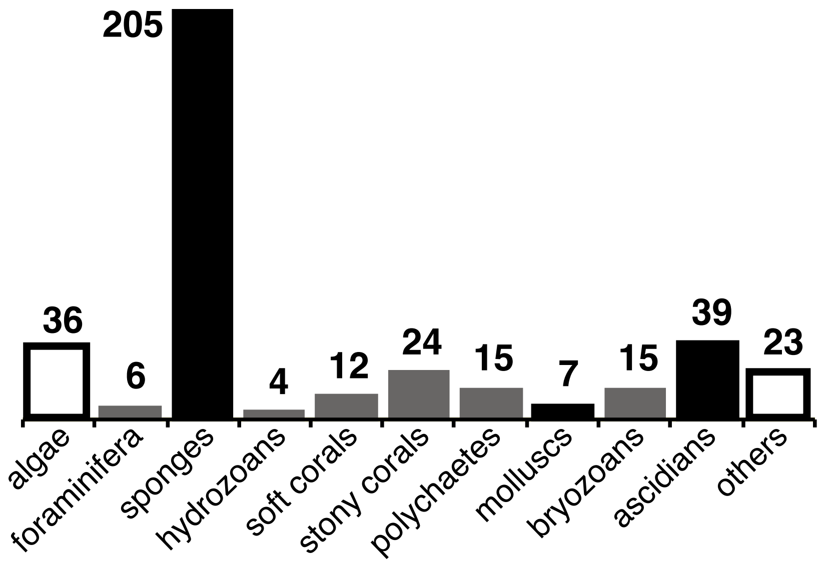

Fig. 2:

Number of taxa distinguished per major taxon.

cavities provided a roughly 5-fold increase in substrate for coelobites compared to the plain reef surface. Calculated with an average coelobite cover of 65 %, the organisms would occupy an area much larger as the plain outer surface area of the reef!

Diversity and abundance

Diverse cryptic communities were encountered at all three sites. All together, 386 taxa were distinguished. Fig. 1 suggests that sampling had been adequate to account for the common coelobite taxa. Increasing sampling efforts would have been needed to find increasingly rarer species. The diversity was found to be lower by 40 taxa in Ras Mohammed than in Aqaba which could be explained by the rather uniform environment at the former site. With 205 taxa sponges were by far the most diverse group followed by ascidians with 39 taxa (Fig. 2).

The sponge *Chondrilla sacciformis* was the single most important animal species (Fig. 3). The colonial ascidian family Didemnidae represented almost one third of the ascidians but

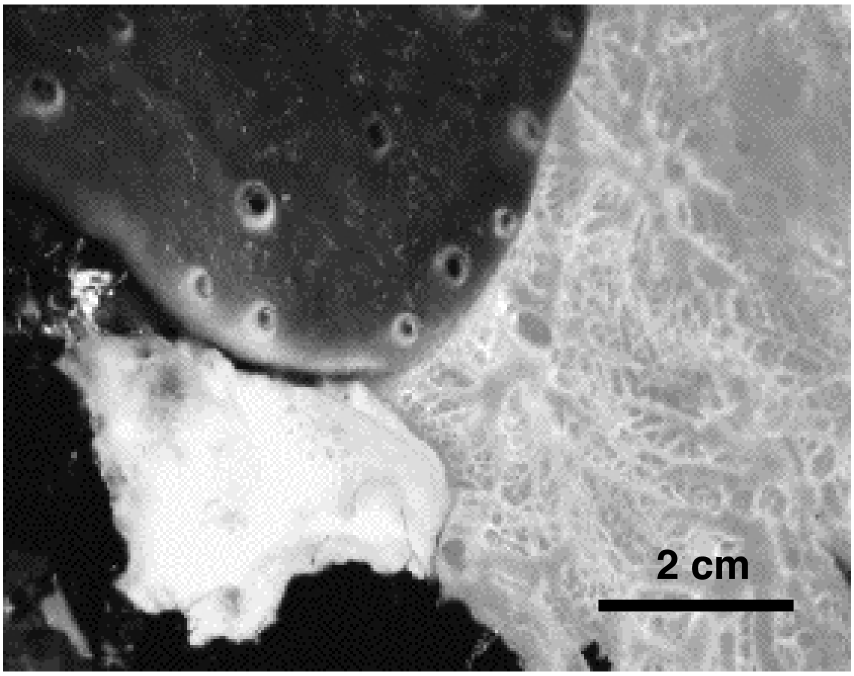

Fig.3:

The most important coelobite, the sponge *Chondrilla sacciformis* (dark) grows over a *Clathria* sp. and an unidentified sponge.

Tab. 1: Relation between coelobite distribution and combination of environmental variables (Bio-Env analysis) between cavities (A) and along the cavity axis (B). Thecombinations yieldingthe best explanation are highlighted.

		Environmental factor	Correlation factor	
A	all cavities at Aqaba and Ras Mohammed	Site	0,40	**combined 0,42**
		Depth	0,22	
		Water motion	0,18	
	Aqaba	Depth	**0,66**	combined 0,58
		Water motion	0,47	
	Ras Mohammed	Depth	0,30	**combined 0,33**
		Water motion	0,29	
B	Aqaba	Depth	0,29	**combined 0,43**
		Distance from entrance	0,27	
	Ras Mohammed	Distance from entrance	0,20	**combined 0,28**
		Light	0,19	
		Water motion	0,06	

comprised over 85 % of their colonized area, four didemnid taxa alone accounted for 76 % of the ascidian cover. Polychaetes were abundant and can occur in monospecific crusts. They reached an average cover of 5.6 %. Ascidians, scleractinians and octocorals were patchily distributed (1.3 –1.8 % overall cover). The complete picture is provided in Fig. 4.

Environmental factors

The Multi-Dimensional Scaling plot (MDS) in Fig. 5 of the community data shows a clear grouping according to depth and site. This is corroborated by the so-called BIO-ENV (Primer 4.0) that reveals the environmental factors and combinations of these governing the

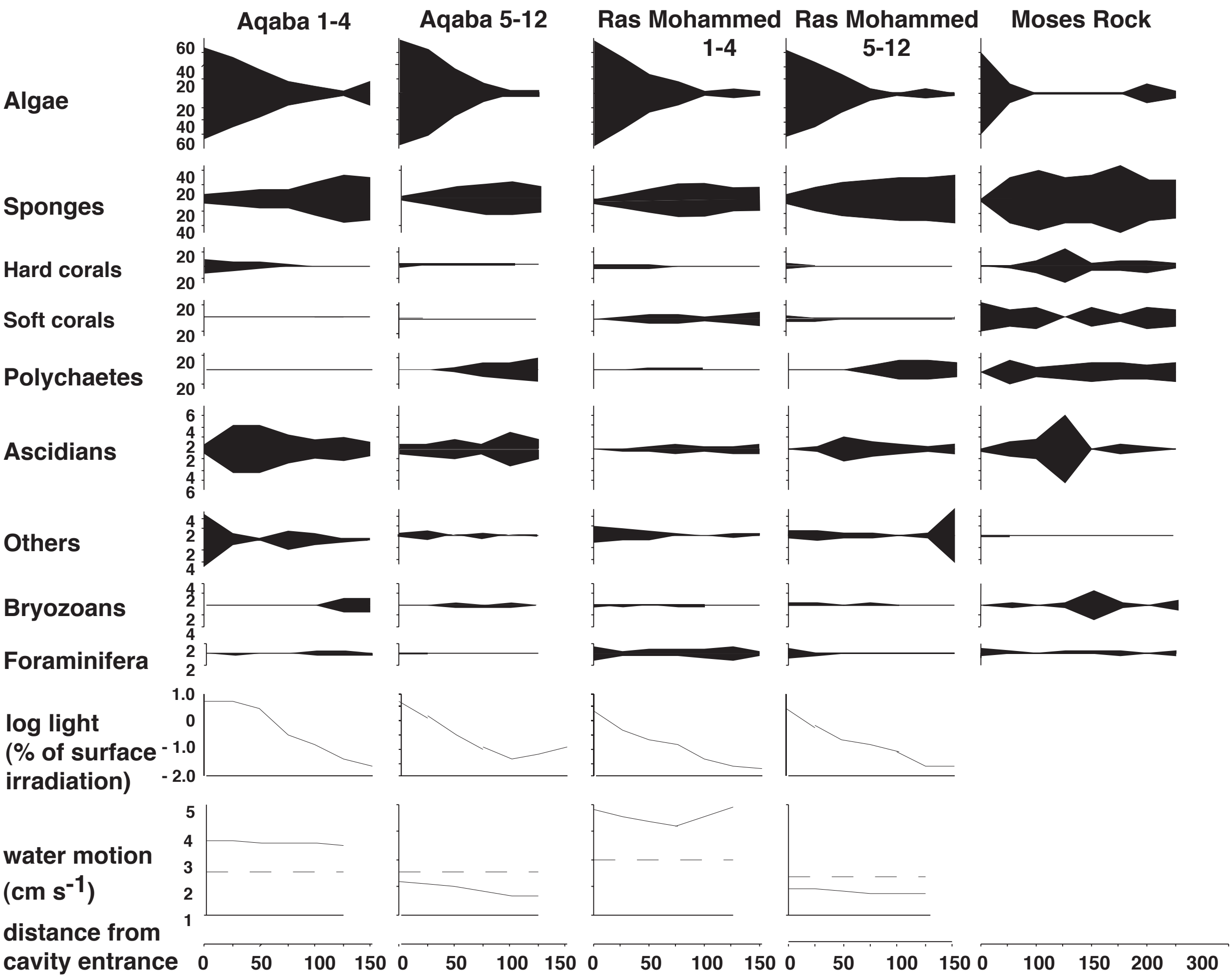

Fig. 4: Distributon of coelobite communities for groups of cavities determinded by statistical analysis. Note the ten-fold magnification of the abundance scale of rarer taxa, starting with ascidians. Error bars have been removed for the sake of clarity. Light and water motion could not be measured at Moses Rock.

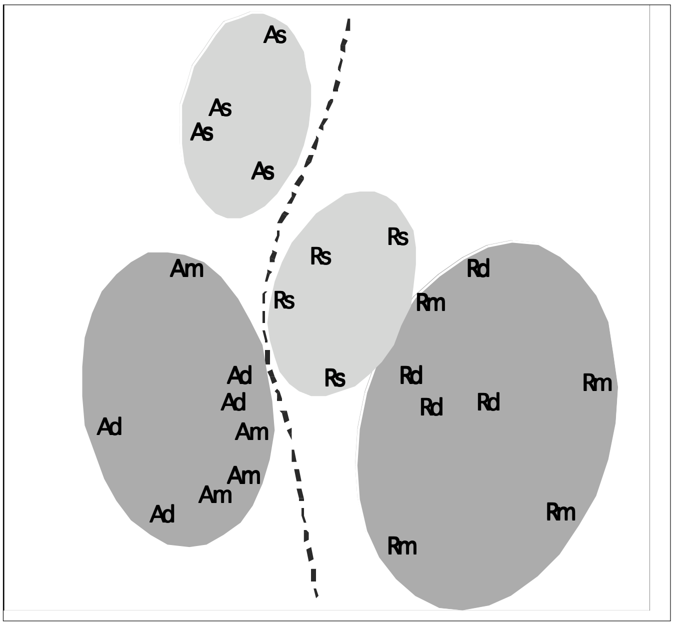

Fig. 5

Non-parametric MDS ordination plot of the 24 cavities at Aqaba (A) and Ras Mohammed (R), labeled according to depth (s=shallow, m=medium, d= deep). Based on 4th-root transformed abundances (=cover) of the 37 most abundant taxa and Bray-Curtis similarities (stress= 0.18).

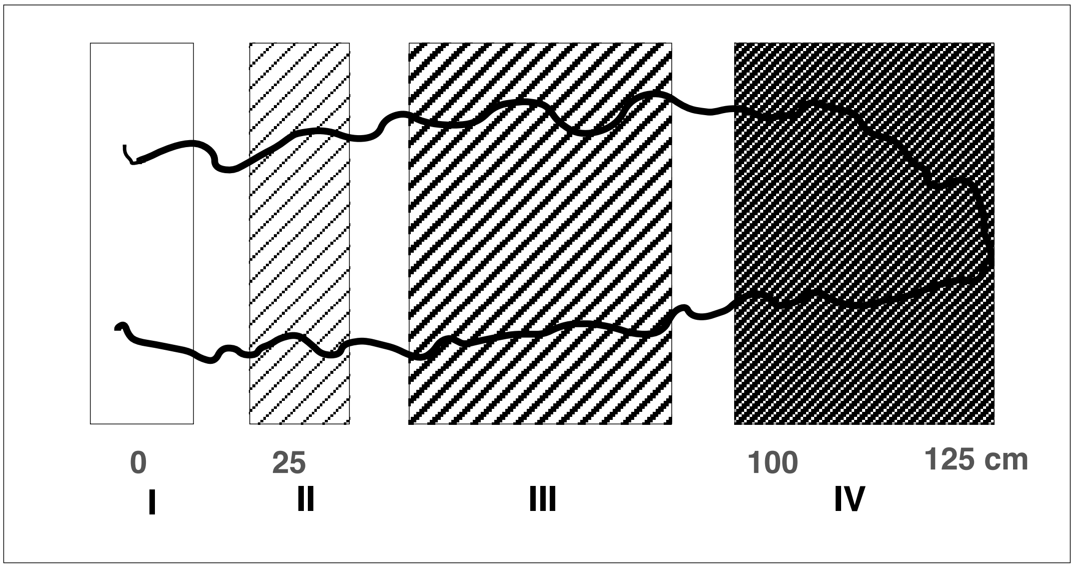

Fig. 6: Zonation of coelobite communities: The similarity analysis of the community structure for each slice for all cavities revealed a distinct zonation from the cavity entrance into the reef. The exposed entrance (0 cm) was dominated by encrusting algae (Zone I) which gradually became less important with diminishing light and increasing seclusion of the following slices. Zone II was still rich in algae but significantly different from the neighbouring slices. From 50 cm onwards animals took over and the slices were more similar. Consequently Zone III and IV were composed of two slices each.

composition of a community by calculation of the correlation factor ρ_H (Tab. 1). Looking at all cavities as a whole (1 cave = 1 community) the factor site (Aqaba or Ras Mohammed) combined with depth accounted for the highest correlation (ρ_H =0.42). Depth and water exchange rates were the 2nd and 3rd most important factors (Tab. 1). For Aqaba cavities alone, depth is a very strong determinant (ρ_H=0.66), whereas for Ras Mohammed a combination of depth and water motion gave the best, although not very clear explanation for the community composition (ρ_H = 0.33).

The same analysis was run separately for the community structure along the cavity axes for Aqaba and Ras Mohammed. In Aqaba depth was still the dominating factor (ρ_H=0.29) which may me explained by the very different reef structure and exposition compared to the steep reef wall at Ras Mohammed. Aqaba cavities were governed 2nd most by the distance from the cavity entrance, which itself was highly influenced by a combination of water motion rate and light level (Fig. 4). In Ras Mohammed the picture was less clear. The combination of distance from entrance with light and water exchange provided the best but still weak explanation for the different communities (ρ_H=0.28).

Zonation

The diversity along the cavity axis showed lowest numbers of taxa near the entrance, a maximum at 50 cm from the entrance and a slight decrease in number of taxa towards the inner cavities. Similarity analysis between the communities of the 25 cm-sections of all cavities suggested 4 distinguished 'zones' as shown and described in Fig. 6: The algae dominated community in the entrances gradually transformed into animal (sponge and polychaete) dominated communities in the sheltered inner reaches of the coral reefs.

Conclusions

- Coral reefs can be highly porous and their cavities of different sizes and shapes provide enormous settlement space for benthic organisms.
- The CaveCam and the LightSheet system proved to be invaluable tools for the exploration and documentation of reef cavities, providing detailed accounts of their structure and communities.
- Coral reef cavities represent densely populated and highly diverse habitats with sponges as the most important organisms. They have to be accounted for in any functional reef model or calculation of trophic fluxes.
- Differences in depth, exposition, water exchange and light lead to large variations in community composition along and between cavities, even in semi-enclosed waterbodies such as the Gulf of Aqaba/northern Red Sea.

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Mass removal of dissolved organic carbon by coral reef invertebrates

Gitai Yahel[1,2], Jonathan Sharp[3], Dominique Marie[4], Clivia Häse[5] and Amatzia Genin[1,2]

1) The Interuniversity Institute, H. Steinitz Marine Biological Laboratory, Eilat
2) Department of Evolution, Systematics and Ecology, The Hebrew University of Jerusalem, Jerusalem
3) Graduate College of Marine Studies, University of Delaware, Lewes, Delaware
4) Station Biologique, CNRS, INSU et Université Pierre et Marie Curie, Roscoff
5) Zentrum füt Marine Tropenökologie, Bremen

Over 90 % of the organic carbon in the ocean is found in the dissolved (DOC) pool (Wangersky 1965). Early in this century, Potter (1909) proposed that marine animals should utilize this immense resource of nutritious matter. However, except for bacteria (Azam et al. 1983) and some invertebrate larvae (Wright et al. 1989), direct evidence of bulk utilization of DOC in the ocean is lacking. Using a new *in situ* technique for clean sampling of the seawater inhaled and exhaled by benthic suspension feeders we measured mass removal of DOC in four common coral-reef invertebrates. In two sponges and a tunicate, a concentration threshold was apparent, above which an average of 9.4-9.8 µM DOC was removed by the animals, accounting for at least 56-67 % of the total carbon the animals gained from the water they filtered. In a third sponge, DOC comprised >40 % of the total carbon gained, with no apparent threshold. Intermittent occurrences of rich DOC patches at the coral reef allowed those benthic animals to gain an order of magnitude more organic carbon than in the total living phytoplankton and bacteria they removed. This study revealed an important nutritious pathway in two evolutionarily-remote phyla. It may require a reconsideration of our understanding and future investigations of carbon fluxes in marine benthic communities.

(Report on ongoing studies)

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Long-term, fine-scale distribution and vertical migration of zooplankton over coral reefs, Eilat, the Red Sea, using a multi-beam 3-d sonar (FTV)

Ruthy Yahel[1,2], Jules Jaffe[2] and Amatzia Genin[1,2]

1) The Interuniversity Institute, H. Steinitz Marine Biological Laboratory, Eilat
2) Department of Evolution, Systematics and Ecology, The Hebrew University of Jerusalem, Jerusalem
2) MPL, Scripps Institution of Oceanography, La Jolla

Changes in the distribution of zooplankton on scales from centimeters and minutes to months were studied with the FTV, 1.6 MHz multi-beam imaging sonar over a coral reef. The study was supplemented with physical measurements and additional zooplankton sampling using nets, pumps, and demersal traps. The water over the reef was heavily populated with drifting oceanic plankton. The density of the diurnal, but not the nocturnal zooplankton was positively correlated with phytoplankton concentrations. Small pelagic species dominated the diurnal community. Demersal plankton emerged at dusk, at a constant light intensity, exactly at the same time visual zooplanktivorous fish stopped their activity. The abundance of zooplankton at the beginning of the night was about twice that during the day, primarily due to the ascent of large demersal forms from the reef. Advection processes and the entrainment of pelagic vertical migrators to the reef's water modified the community structure during the course of the night. Nocturnal zooplankton was most abundant a few meters above bottom, with a depleted layer found just above the coral bed. Unlike the ascent, the descent of the zooplankton at dawn was gradual.

(Report on ongoing studies)

Studies in Calcification and Paleoclimate

Geomorphology, facies analysis and diagenesis of Quaternary coral reefs, Red Sea coast, Egypt

Mohammed Abd El-Wahab[1], Ahmed H. Nawar[1], E. Abd-El Shafy[2] and A. S. El-Sorogy[2]

1) National Institute of Oceanography and Fisheries, Cairo
2) Geology Department, Zagazig University

Summary

Quaternary coral reefs of the northern part of the Egyptian Red Sea coast comprise one submergent (modern) and three emergent (Pleistocene) units. According to the biofacies analysis, the modern unit is differentiated into different morphological terraces and zones. It is separated by sandy bottom embayments, corresponding to Wadi mouths. The Pleistocene reef units exhibit different elevations above the present sea level. Microscopic analysis of the studied limestones revealed the presence of mudstones, wackestones, packstones, grainstones, boundstones and floatstones microfacies types. Four stages of diagenetic alteration can be traced from the living to the Pleistocene reefs. They are decomposition of organic tissues, introduction of marine cements, leaching of sclerodermities under subarial conditions and precipitation of low-magnesium calcite through meteoric fresh water. Quantitative composition of skeletal and non-skeletal grains from thin sections indicates upward reduction in the number of biota, specially the aragonitic ones. The analysis of aragonite, Mg-calcite, calcite and dolomite represent the common mineral composition in the present reefs. Contents of Sr and Mg are about average of world reefs concentrations.

Temperature dependence and coupling of photosynthesis, respiration and calcification in scleractinian corals measured with microsensors for O_2, Ca^{2+} and pH

Fuad A. Al-Horani[1,2], Dirk de Beer[1] and Salim Al-Moghrabi[2]

1) Max-Planck-Institut für Marine Mikrobiologie, Bremen
2) Marine Science Station, Aqaba

Coral reefs are one of the most productive and diverse of all natural ecosystems; they have been regarded as the marine equivalents of rain forests (Bourlier and Harmelin-Vivien, 1989). They are tropical shallow water ecosystems largely restricted to the seas between the latitudes of 30° north and 30° south of the equator, where temperature ranges between 20 and 30° C. Currently, coral reefs are suffering from global warming that leads to the loss of their symbiotic dinoflagellates (bleaching) and eventually their death. Massive coral bleaching has been reported from several parts of the world. The situation is likely to deteriorate as the sea water temperature is increasing still (Hoegh-Guldberg 1999).

The main biogeogenic processes of corals are photosynthesis (O_2 production, CO_2 binding), respiration (CO_2 release) and calcification (Ca^{2+} uptake, CO_2 release). Obviously the balance between these is crucial for the net exchange between corals and seawater. It is thought that calcification can balance the pH effect of photosynthesis, and thereby alleviate the CO_2 limitation for photosynthetic activity. The effect of temperature on the metabolic rates was studied by the use of entire colonies with inherent variation in phenotype and genotype. A better comparison of experiments became possible by the recent use of microcolonies originating from the same mother colony (Al-Moghrabi et al. 1993). Previous analysis could not reveal the mechanisms in detail, or assess the physiological variations between different parts of the colony. The new application of microsensors permitted the measurement of many parameters at a µm scale and with high temporal resolution (de Beer et al, 2000, Kühl et al. 1995). Both advancements were combined to investigate the impact of temperature on the physiology of the Scleractinian coral *Galaxea fascicularis*. In addition, a mechanistic study of the coupling between photosynthesis and calcification was undertaken.

Galaxea colonies were collected by SCUBA diving from a depth of about 5 m from the Gulf of Aqaba (Jordan) south of the Marine Science Station. Collected colonies were transported to the Max-Planck-Institute for Marine Mikrobiology in Bremen/Germany where they were kept in a 540 l tank with artificial seawater (26° C, 130 $\mu E.m^{-2}\ s^{-1}$ sunlight spectrum lamps). *Favia* spp. colonies were collected by SCUBA diving from a depth of 5 m from the Red Sea in front of the Moshe Shilo center. The colonies were brought in the laboratory and kept in a flowcell with an 80 l recirculation tank, with seawater that was changed daily.

Temperature dependence

Single polyps of *Galaxea* were fixed to glass vials with underwater epoxy resin. After regeneration into microcolonies they were used for microsensor measurements of photosynthesis, respiration and calcification at 6 different temperatures (17-35° C). Gross photosynthesis (GP) was highest at temperatures of 23 and 26° C, close to the prevailing temperature (Fig. 1A). At 35° C gross photosynthesis was irreversibly inhibited as the microcolonies bleached (expulsion of zooxanthella and/or photosynthetic pigments). Profiles of O_2 and Ca^{2+} showed a strong temperature effect on the three processes (Fig. 2). The net photosynthesis (gross photosynthesis minus respiration) rapidly decreased with temperature and became negative at temperatures above 29° C (Fig. 1A). Light respiration showed a similar trend as the GP curve, with temperatures of 23 and 26° C being optima. Light respiration is tightly coupled to photosynthesis, thus the low respiration at 35° C were attributed to the loss of the symbiotic zooxanthella.

The Ca^{2+} concentrations measured at the polyp surface also showed temperature dependence of Ca^{2+} uptake (Fig. 1B). In the dark and below 29° C, the Ca^{2+} surface concentration was temperature independent. It was 2-5% below the seawater concentration due to dark calcification. Light clearly increased the concentration difference between seawater and tissue surface, thus increasing calcification rates. During illumination, the Ca^{2+} surface concentration showed a dip at 26° C (>10% below seawater calcium level) indicating maximum uptake rates at ambient temperature. However, at 32° C and higher, Ca^{2+} was higher at the tissue surface than in the seawater, both in the light and in the dark, due to calcium dissolution.

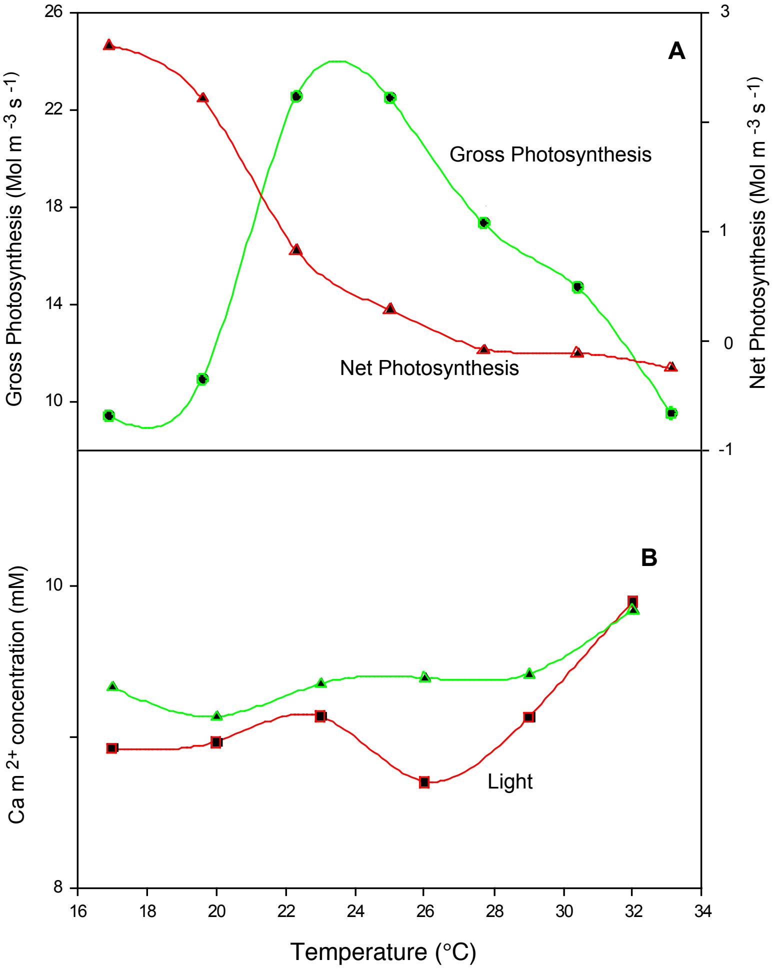

Fig. 1: Gross and net photosynthesis (A) and levels of Calcium at the tissue surface during light and dark incubation (B) in the scelactinian coral *Galaxea fascicularis* at different temperatures.

The surface pH measurements during light and dark incubation at different temperatures confirmed the measured rates of respiration and gross photosynthesis. During light incubation, the pH increased gradually with temperature until 23° C, then remained constant until 29° C. At 32° C the pH be-

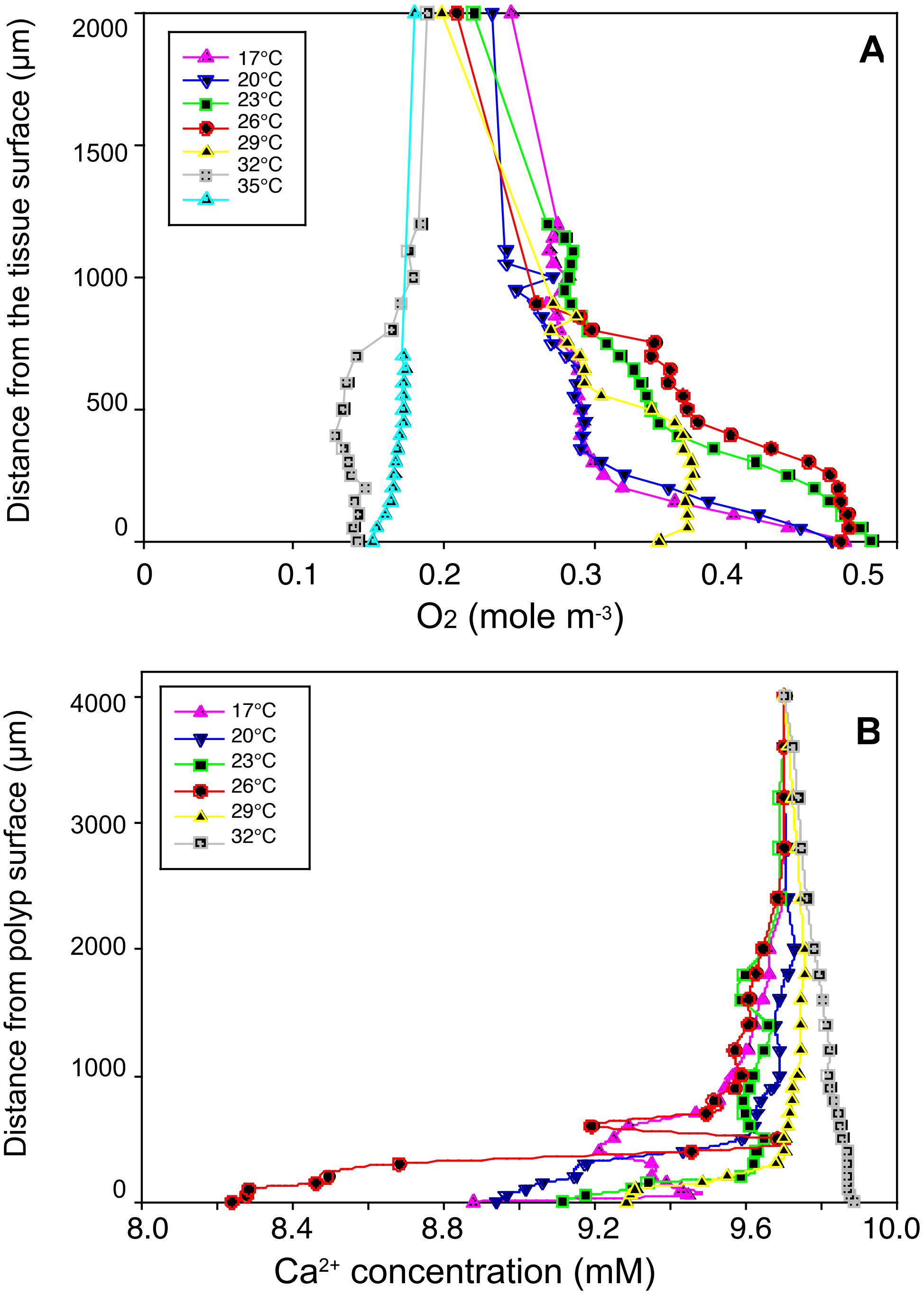

Fig. 2: Oxygen profiles (A) and Ca^{2+} profiles (B) in the scleractinian coral *Galaxea fascicularis* at different temperatures.

came slightly acidic compared to the water phase, probably due to a decrease in the uptake of CO_2 by photosynthesis. The largest difference in pH between light and dark incubations occurred at temperatures between 23 and 29° C, indicating high rates of photosynthesis and respiration at this range of temperature. The observed O_2 uptake at this temperature supports this observation.

Conclusion: Although photosynthetic activity is maintained up to rather high temperatures (32° C), corals at super-optimum temperatures (above 26° C) consume more O_2 than they produce, decalcify and produce CO_2.

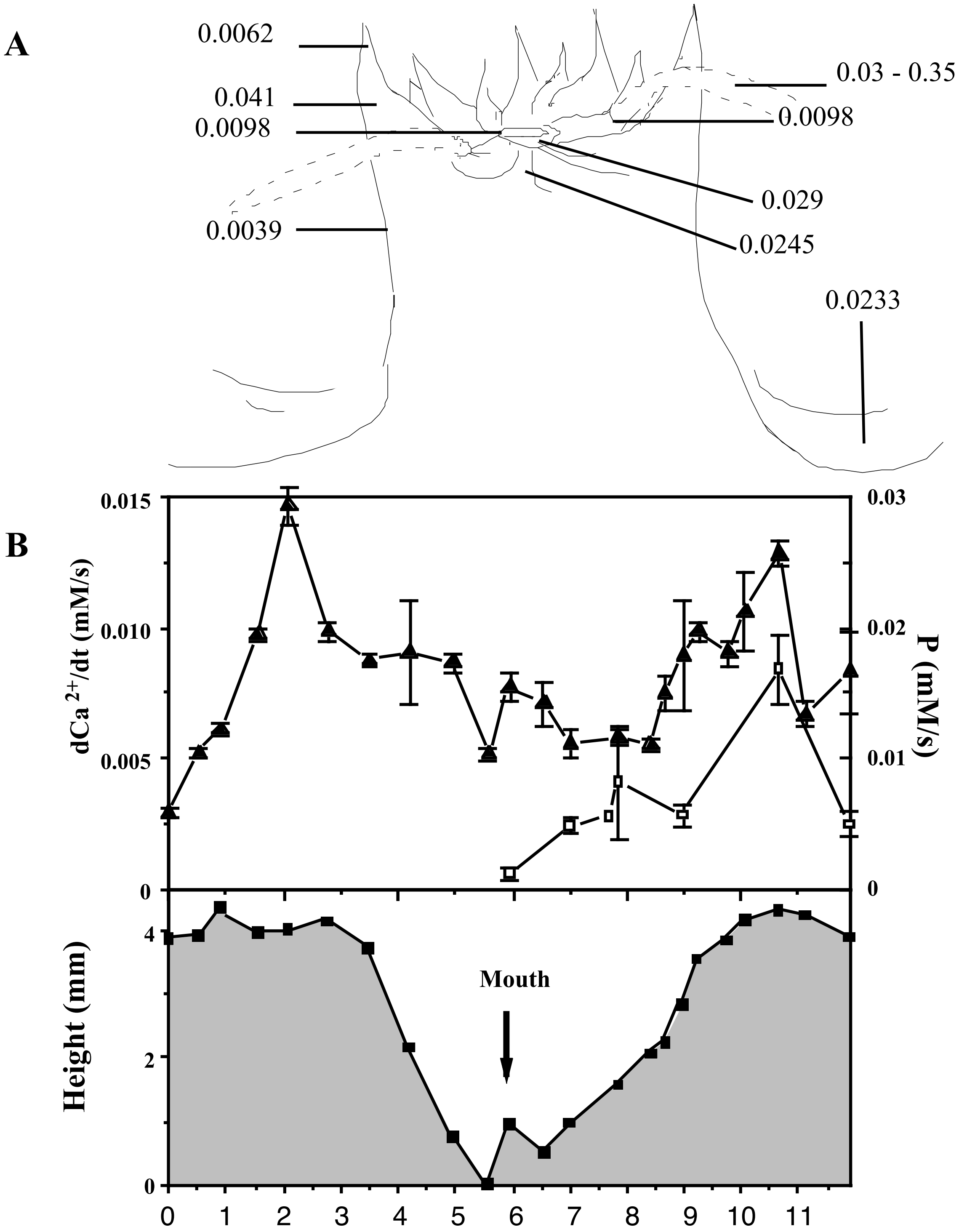

Fig. 3: (A) Schematic diagram of the scleractinian coral *Galaxea fascicularis* polyp showing the position of the microsensor and the rate of gross photosynthesis in (mM/s) over the polyp surface. (B) distribution of gross photosynthesis (□) and Ca^{2+} dynamics (▲) over the polyp surface of the scleractinian coral *Favia* sp.

Distribution of activities

The study of the distribution of gross photosynthesis over the surface of *Galaxea polyps* showed a strong heterogeneity. Relatively high photosynthetic rates were found on the arms and base of the tentacles, the tissue over the middle part of the big septum and to a lower extent in the coenosarc tissue between polyps. This heterogeneity will be investigated more in the future and compared to the distribution of Ca^{2+} uptake. A heterogeneous distribution of photosynthesis was also found in *Favia polyps*, where the highest photosynthesis was found in the rim which is the basis of the tentacles (Fig. 3). This distribution was very similar to the distribution of Ca^{2+} dynamics, suggesting a coupling between Ca^{2+} uptake and photosynthesis.

Coupling calcium uptake and photosynthesis

The suggested coupling between calcification and photosynthesis was investigated in detail. The coupling between CO_2 and Ca^{2+} exchange and photosynthesis by *Favia* sp. was studied with microsensors for Ca^{2+}, O_2, pH and CO_2. The profiles of these compounds, measured perpendicular on the coral surface, were strongly influenced by light. During illumination, the concentration of O_2 and the pH at the polyp surface was higher than in the surrounding seawater, while the concentrations of Ca^{2+} and CO_2 were lower. In the dark the inverse was observed. Furthermore, simultaneous recording of concentration changes at the coral surface, in response to light and inhibitors were performed with pairs of sensors. The concentration changes of CO_2 and pH were slow, while those of Ca^{2+} and O_2 were immediate and fast. The concentration changes of the O_2 and Ca^{2+} concentrations at the coral surface were synchronous in response to changes in light conditions and to inhibition of the photosynthesis. Also, the spatial distribution of photosynthetic activity over a single polyp coincided with the distribution of Ca^{2+} concentration changes (Fig. 3). These results show that Ca^{2+} dynamics at the polyp surface is not an indirect effect of increased $CaCO_3$ precipitation at the skeleton, but indicate the presence of a Ca^{2+} uptake mechanism that is directly correlated to photosynthesis.

Conclusions: Microsensor techniques proved to be highly valuable for coral research. The measurements are direct, and have high spatial and temporal resolution. The technique allowed new observations on the temperature dependence of gross photosynthesis and calcification, and on the mechanism of coupling calcification and photosynthesis.

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High resolution climatic records of corals from the northern Red Sea

Saber Al-Rousan[1,2] Salim M. Al-Moghrabi[2], Jürgen Pätzold[1], Yossi Loya[3] and Gerold Wefer[1]

1) Geowissenschaften (Fachbereich 5) Universität Bremen, Bremen
2) Marine Science Station, Aqaba
3) Department of Zoology, Tel Aviv University, Tel Aviv

The Gulf of Aqaba is characterized by a high diversity of coral reef communities. Coral reefs in the Gulf of Aqaba represent the northern limit (29°32'N) for reef corals in the western Indo-Pacific region (Schuhmacher et al. 1995). Coral reef structure is known to be better developed and the diversity to be higher on the eastern side compared to the western side of the Gulf. Loya and Slobodkin (1971) reported the presence of 97 scleractinian coral species on the western side while 157 species were found on the eastern one (Al-Moghrabi, in preparation). However, no study has yet been carried out to compare the environmental factors that affect the different coral reef development between the eastern and western parts.

Massive hermatypic coral skeletons are excellent monitors of tropical water environments. Corals of this type live in the surface-ocean mixed layer, grow continuously at rates of several millimeters to centimeters per year, and during growth they incorporate isotopic species into their skeleton. The stable oxygen isotopic composition ($\delta^{18}O$) of hermatypic corals has been utilized in numerous reconstructions of past sea surface temperatures and salinities (e.g. Charles et al. 1997, Gagan et al. 2000). Coral $\delta^{18}O$ reflects a combination of local sea surface temperature (SST) and the $\delta^{18}O$ value of ambient seawater (Epstein et al. 1953, Wefer and Berger 1991). The gradient of 0.18 ‰/1°C (Gagan et al. 1994) is widely accepted for the temperature interpretation of *Porites* $\delta^{18}O$ records in the Red Sea (Felis et al. 1998, Moustafa 2000).

Seawater $\delta^{18}O$ is related to changes in salinity as a response to changes in evaporation, precipitation and mixing of waters from different sources. This relation between $\delta^{18}O_{w}$ and salinity is different from ocean to ocean. In the Red Sea a change of 1 ‰ salinity causes a change of 0.29 ‰ in $\delta^{18}O_{w}$ according to Craig (1966) and Andrié and Merlivat (1989). At the northern end of the Gulf of Aqaba the salinity of the surface waters is close to 40.5 and varies by less than 0.5 ‰ throughout the year (Wolf-Vecht et al. 1992; 0.225 ‰ reported by Rasheed 1998). These minor variations in the surface seawater salinity throughout the year are considered to have little effect on the seasonal variation of the seawater $\delta^{18}O$ (0.225 ‰ salinity correspond to 0.06 5‰ $\delta^{18}O$, Craig 1966).

A *Porites* colony was collected in front of the Interuniversity Institute in Eilat at a depth of 15 m in April 1996, while another colony of the same genus was collected in front of the Marine

Science Station in Aqaba at a depth of 18 m in April 1999. Both corals were sectioned along their longitudinal axes to obtain slabs of about 4 mm thickness. X-radiographs were prepared to reveal the annual density bands for determining sampling profiles. Aragonite sub-samples were collected by low-speed drilling using a dentist drill with a 0.6 mm diameter bit. A range of 7 to 12 samples (in average 9) per year were obtained along the maximum growth axis. The isotopic composition of the samples was measured with a Finnigan MAT 251 mass spectrometer at Bremen University.

A 9-year stable oxygen isotope record of the two colonies was generated to investigate similarities and differences between the two sites at the northern end of the Golf of Aqaba. Monthly measurements of the sea surface temperature from Eilat between 1988-2000 were used for comparison (A. Genin, personal communication), while a monthly temperature record from Aqaba was obtained between 1997-2000 (Riyad Manasreh, personal communication). The oxygen isotope time series of corals in both locations show well organized cyclic variations and correspond remarkably well to the monthly SST measurements in Eilat and Aqaba (Fig. 1a, b; correlation coefficient of r = -0.84 for Eilat coral and r = -0.82 for Aqaba coral).

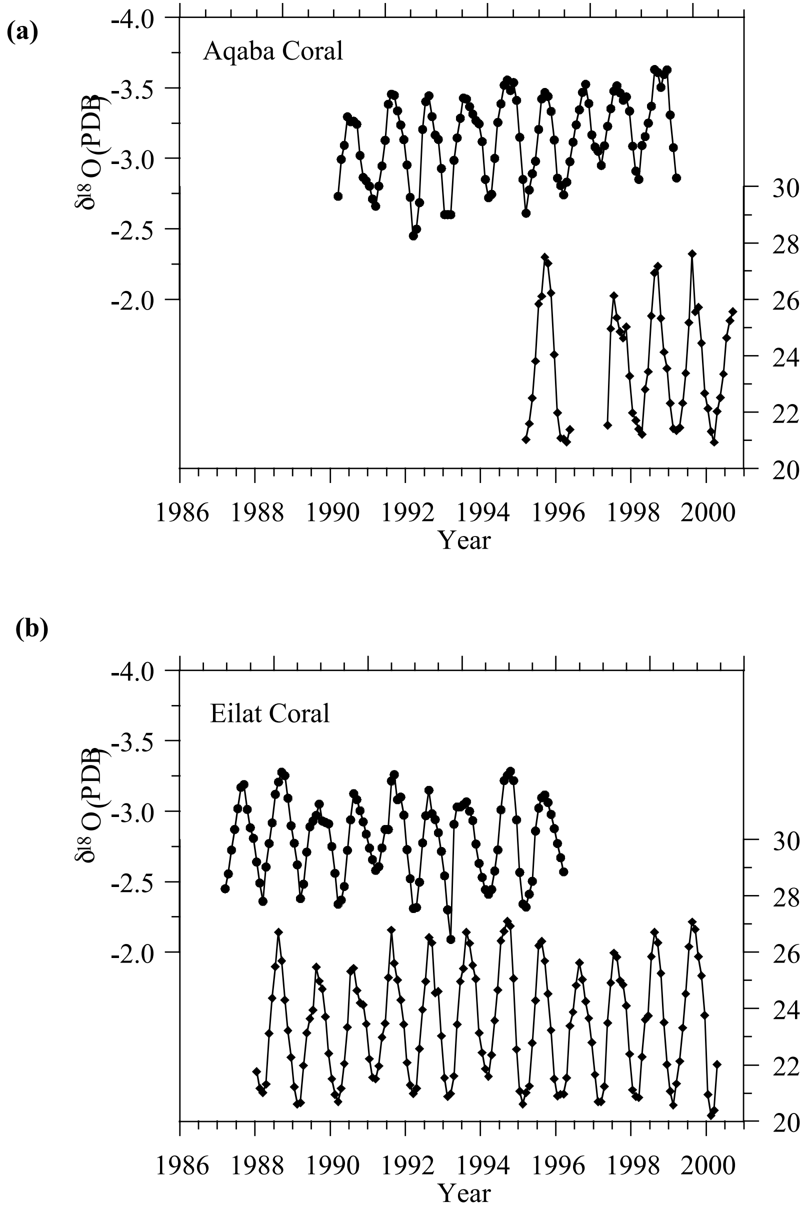

Fig. 1:
Time series of coral $\delta^{18}O$ (PDB) and recorded sea surface temperatures in (a) Aqaba and (b) Eilat.

The measured SST in Eilat reveals an average annual cycle of about 5.4° C. Using the gradient of 0.18 ‰/°C for coral $\delta^{18}O$-temperature dependence (Gagan et al. 1994) the average seasonal coral $\delta^{18}O$ amplitude of 0.83 ‰ reflects a temperature change of about 4.6° C, which is about 86 % of the average seasonal SST amplitude. The expected variation of 0.065 ‰ $\delta^{18}O$ of seawater (related to 0.225 ‰ change in salinity) has a magnitude of 7.8 % of the average seasonal coral $\delta^{18}O$ variation. This indicates that a large majority of the variations in coral oxygen isotope data can be explained by the sea surface temperature variations, and only a small fraction can be attributed to $\delta^{18}O$ variations of surface water.

Comparing the $\delta^{18}O$ records from Aqaba and Eilat in the period 1990-1995, the results show that the $\delta^{18}O$ in Aqaba coral is relatively lighter than that of Eilat in both summer and winter (Fig. 2a). It has been suggested that this is due to high coral growth rates in Aqaba compared to Eilat (12 to 21 mm/year average 16 mm/year and 7 to 12 mm/year average 10.5 mm/year respectively). However, sea surface temperature records (Fig. 2b) showed a consistent temperature difference, with Eilat SST being colder than Aqaba waters by a few tenths of a degree. All these variations are most probably due to variability of the different microenvironments in which the coral grew. These results strongly confirm the reliability of using *Porites* corals in this area to study the past environmental changes.

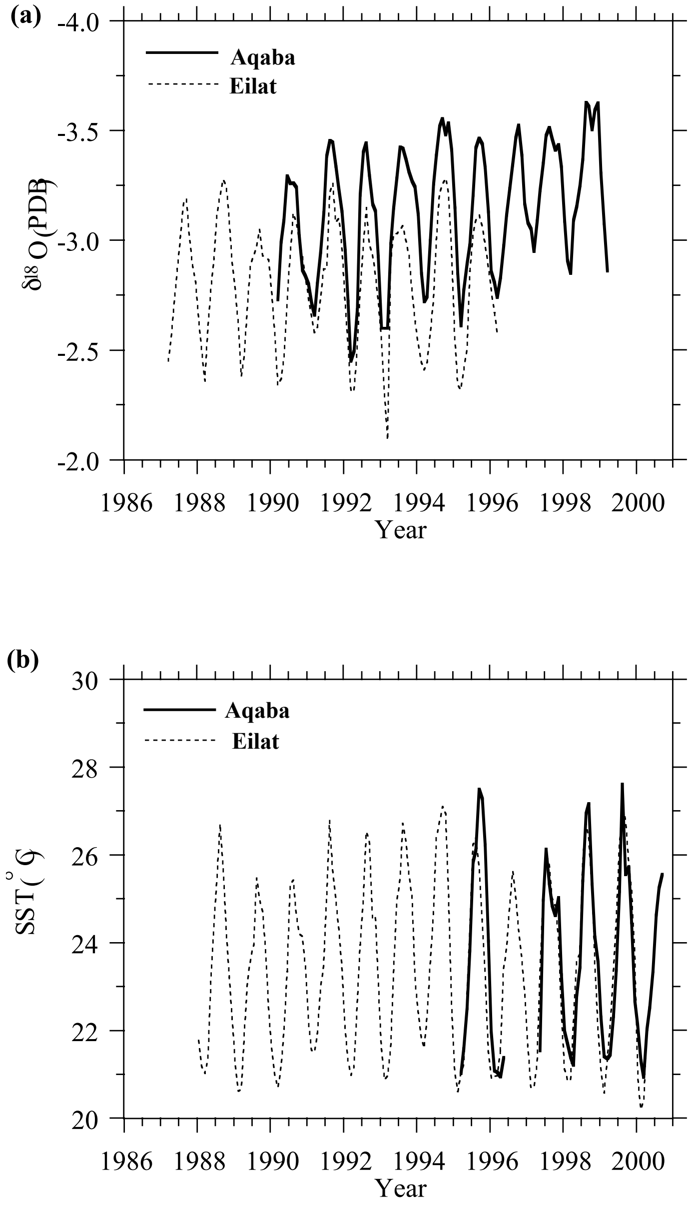

Fig. 2.:
(a) Stable oxygen isotope record of *Porites* corals from Aqaba and Eilat between 1987 and 1999.
(b) Sea surface temperature recorded in Aqaba and Eilat.

An *in situ* calibration study for the use of coral skeletons in climatic research also has been started. Four temperature loggers were deployed for one year (April 1999 till June 2000) on a depth profile at 7, 19, 29 and 42 m in front of the Marine Science Station at Aqaba/Jordan. The loggers recorded the temperature by hourly resolution. Figure 3 shows time series record of weekly and monthly averaged temperatures recorded on the depth profile. One degree difference in temperature between 7 and 42 m was recorded in summer (July-October) due to water stratification, while this difference disappeared during winter due to water mixing. Monthly water samples from the four depths were also collected by scuba diving over the annual cycle for stable oxygen and carbon isotope analysis. To study the diurnal variations of water stable isotope composition water samples were collected for five days from a fixed station and at different times during the day. Two small coral colonies of Porites sp. (20-30 cm in diameter) from each depth along the depth profile were collected in June 2000. The stable isotope composition of coral skeletons will be calibrated against seasonal variables ($\delta^{18}O_{w}$, $\delta^{13}O_{w}$, sea surface temperature). This calibration of coral proxies will be used for further climatic reconstructions with fossil corals collected from the area.

Fig. 3: Time series record of (a) weekly and (b) monthly temperatures measured along a depth profile in front of the Aqaba Marine Science Station during the period April 1999 to June 2000.

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Marine calcification: From molecular - cellular levels to global CO_2 control

Jonathan Erez

The Interuniversity Institute, H. Steinitz Marine Biological Laboratory, Eilat and The Institute of Earth Sciences, Hebrew University, Jerusalem

Foraminifera are unicellular calcifying organisms thriving in the open ocean. Their numerous $CaCO_3$ shells, together with those of the unicellular calcareous algae - the coccolithophores, accumulate to form the oceanic calcareous sediments. Together with the vast amounts of $CaCO_3$ deposited by corals and calcareous algae in shallow coastal reef environments these calcifying groups form a major component of the global carbon cycle. All these calcifying groups have a n essential connection to photosynthesis (directly or via symbiosis), thus coupling the two major processes involved in the oceanic carbon cycle. Global changes and particularly the atmospheric CO_2 increase are bound to have major direct and indirect effects on the physiology of these groups. The goal of this project was to investigate the calcification processes of foraminifera and corals and to assess the potential effects of CO_2 increase on their calcification physiology.

This report is composed of 3 short papers (Bentov and Erez, Meidani et al., Schneider and Erez, this volume) representing the main scientific results obtained during this project. Scientific publications are being prepared now based on these studies and they will be submitted before the end of the year 2000.

The mechanism of calcification in perforate foraminifera

Shmuel Bentov and Jonathan Erez

The Interuniversity Institute, H. Steinitz Marine Biological Laboratory, Eilat and The Institute of Earth Sciences, Hebrew University, Jerusalem

Introduction

Foraminifera are unicellular calcifying organisms thriving in the open ocean. Their numerous $CaCO_3$ shells, together with those of the coccolithophores, accumulate on the sea floor forming the oceanic calcareous sediments which is a major component of the global carbon cycle (Broecker and Peng 1982). As part of the oceanic sedimentary record, foraminifera provide unique stratigraphic and paleoceanographic information. Trace elements and stable isotopes in fossil foraminifera shells are the best tools for deciphering the paleochemistry and paleoceanography of the coupled ocean-atmosphere system. Calcification in foraminifera is a complex energy-demanding process. The mineral phase (low-Mg-calcite, high-Mg calcite or rarely aragonite) is deposited under tight genetic control, mediated by an organic matrix (Weiner and Erez 1984). Calcification processes in foraminifera are not well known because of methodological difficulties in culturing and observing these organisms. While test structure and texture have been studied in detail, the thick calcite skeleton obscured the physiology of biomineralization process. Light microscopy of the endoplasm was virtually impossible under polarized light, and artifacts caused by decalcification of the shell limited TEM studies.

An important breakthrough in calcification research was achieved in our laboratory in 1995. During decalcification experiments with live foraminifera we obtained viable "naked" ameboid cells. These shell-less foraminifera contain symbionts, remain alive and functioning for several weeks, show intensive pseudopodial activity and precipitate skeletal $CaCO_3$. They were first produced from *A. lobifera* and later from other species including planktonic foraminifera. These ameboids allow direct polarized light microscopy of the endoplasm, which is essential in order to identify the initiation of the biomineralization process. Furthermore, these ameboids allow studies using advanced fluorescence imaging microscopy during the calcification process as well as TEM studies that do not require the decalcification step.

The most important observation is that many ameboids freshly isolated from their mother foraminifera contain small-mineralized polarizing granules usually of 0.5-1.0 μm (Fig. 1). These granules cycle with the endoplasm stream and show typical yellow interference color. With time small (1-5 μm) spherulithic $CaCO_3$ crystalline units appear, followed by a wide spectrum of elongated bone-like spherulites which grow to form large round spherulites of 20-60 μm in diameter (Fig. 1). These spherulites show typical extinction cross under polarized light indicating radial crystal arrangement. Often the larger spherical crystal units are left behind, outside the ameboids, while they move from one position to another. Within a few days after separation of the ameboids from the mother individual, the density of the granules increase, small spherulites appear and are actively growing. The ameboids are often surrounded by a layer of seawater vacuoles formed by the anastomosing pseudopods. TEM observations and now also light microscopy suggest that the polarizing granules are membrane-bound and may be produced in special vacuoles within the endoplasm. The birefringent granules were also observed in the cytoplasm of small non-calcified offspring of *A. lobifera* produced in during asexual reproduction, and in the cytoplasm of adult individuals that were crashed physically without any chemical treatment. These phenomena were also observed in the benthic *Amphistegina lessoni* and *Hetetostigina depressa*, and the planktonic *Globigerinoides sacculifer, Globigerinoides ruber* and *Orbulina universa*.

The composition of biomineralized phases in the ameboids

The composition of the mineralized phases found in the ameboids was studied using the Electron Probe Micro Analyzer (EPMA). This is a semi-quantitative information because the target sample may be heterogeneous and small relative to the background mass and because it is difficult to obtain standards for such non-conventional samples. Nevertheless, the compositions reported here provide for the first time analyses of the cellular and initially deposited biomineralized phases of lamellar foraminifera.

Composition of the $CaCO_3$ spherulites

The spherulites are formed actively by the ameboids. They show a wide range of sizes shapes and composition. The microspherulites (1-5 μm) are intracellular and can be observed moving within the endoplasm. They are made of concentric crystals as shown by the extinction cross. In the SEM they show calcite platelets and seem to be similar to the skeletal elements which compose the two dimensional wall of a newly formed chamber in association with the organic matrix. The larger spherulites can be divided into bone-shaped elements (5-15 μm) and large spherical ones 10-60 μm). These spherulites are attached to glass below the ameboid and therefore seem to be extracellular. In reality they are precipitated in the realm of the ectoplasm as was later found using the recovering individuals. They are precipitated by the ameboid and only those, which are covered by the cell, are growing. Often the ameboids are moving and leaving behind a "trail" of spherulites, which are not growing. Twelve spherulites of different sizes and shapes were studied. They were all made of $CaCO_3$ and compositions are shown in Fig. 12. It is clear from these data that the composition changes with size. The small spherulites (1-10 μm) are enriched in Mg (average of 18 % and up to 25 %) and are very low in Sr (below detection when smaller then 10 μm). The spherulites larger then 10 μm are low Mg calcite (~ 3 %) and have roughly 1 % Sr. It is important to note that in normally growing *A. lobifera* the skeleton is composed of alternations of Mg rich and Mg low layers that have been described in our previous reports. An X-ray analysis of powdered *A. lobifera* reveals that indeed the skeleton is composed of two phases (Fig. 12). The rare phase is Mg rich and is probably composed of the microspherulites while the common phase is low Mg calcite which forms the bulk of the calcitic radial test.

Composition of the polarizing granules

The intracellular polarizing granules turned out to be very difficult for chemical analyses. Attempts to dissolve or remove the cell organic matter with NaOCl, or other oxidizing agents caused immediate dissolution of the granules. Even distilled water treatment caused their dissolution in about half an hour. We were able to observe their birefringence in specimens fixed in alcohol or acetone, but these fixatives retain most of the organic matter. Furthermore, since the granules are so small (~ 1μm) the electron beam often activated a volume of sample which was larger then the granule. In addition the SEM image did not resolve the granules from its background mass and the only technique to locate them was the backscatter image which was also uncertain. Therefore, high variability was observed in the composition of the granules. Four elements are dominating in the composition of the granules: Ca, Mg, P, and possibly S. After background subtraction the granules were divided into dense granules and light (low-density) granules. The dense granules, are either Ca rich (Ca:Mg > 4) with only trace amounts of S and P, or Mg rich ones (Mg:Ca ~2) which also contain appreciable amounts of S and P. The major anion in the dense granules is probably CO_3^{2-} and they may actually be very small microspherulites as described above. The light granules have roughly equal amounts of Ca and Mg and equivalent amounts of P and some S. They seem to be a different phase (not $CaCO_3$) and may be divided into Ca rich, Mg rich and P rich (Fig. 12). There is a clear positive correlation between the Mg and S content of the light granules. During the last year of our work we were able to observe and obtain for the first time clear and relatively large polarizing granules (Fig. 8-10). They were large enough to make light microscopic observations and to isolate them for SEM and EPMA analysis. These granules are clearly bundles of needle-like crystals sometimes in a cross like arrangement. The EPMA showed that they contain Mg, Ca, and P at an approximate ratio of 2:1:3, respectively. They are similar to granules described in *Crustacea* and in other unicellular organisms (Brown 1982, Taylor and Simkis 1989). The fact that these granules are so soluble suggests that they may serve as a temporary cellular storage for Ca.

Experiments with Ca -uptake of *A. lobifera* and its ameboid cells

The purpose of these experiments was to follow the kinetics of Ca uptake by intact shells of *A. lobifera*, in comparison with ameboid cells prepared from the same specimens. The radiotracer ^{45}Ca was used to follow Ca uptake and recycling between the cytoplasm and the $CaCO_3$ deposited. A significant lag of ^{45}Ca behind the true calcification rates was observed. The amount of ^{45}Ca taken by the cytoplasm was similar to that of the skeleton on a dry weight basis, suggesting a very large internal Ca pool in these organisms. The ameboid cells produced from the foraminifera pulsed with ^{45}Ca deposited appreciable amounts of ^{45}Ca a-labeled $CaCO_3$ during the non-radioactive chase period. Furthermore, only the ameboids that showed abundance of birefringent granules accumulated ^{45}Ca and eventually deposited $CaCO_3$ spherulites. A quantitative transfer of ^{45}Ca (more then 30 %) was observed from the cytoplasm to the spherulites. These experiments demonstrate that a Ca-pool is a major player in skeletogenesis of radial-lamellar foraminifera. The total internal Ca concentration in the ameboids is at least 50 mM, at least 5 orders of magnitude higher then free Ca^{2+} in normal cells. Uptake of Ca in foraminifera therefore must be an active process where by Ca is concentrated within the cells, stored as an bound phase (possibly the polarizing granules) or a cell compartment (vesicles, Golgi or other) and eventually is precipitated as $CaCO_3$ in the shell. The kinetics of ^{45}Ca uptake and release suggest that in addition to the Ca pool described earlier, most of the Ca precipitated in the shell is acquired via a fast turn-over pool that is not well known at this stage.

Recovering individuals

During the last 2 years of our project we concentrated on another newly developed preparation which tie together the observations made on ameboids with those made on normal live foraminifera. This preparation is made again of the foraminiferan *A. lobibera*, treated with EDTA but instead of the ameboids that are released from the mother individual, we started to make observations on the mother individual while it recovers from its partial dissolution process. Usually the central part of the organism (the knob area) remains intact, but the peripheral region is dissolved. When these organisms are transferred to normal seawater they continue to calcify and grow. But instead of making normal chambers, over the pre-existing skeleton, they precipitate their newly formed chambers flat on the glass slide (Figs. 2-7). Some of these individuals made several chambers and allowed detailed observations on the calcification process that were totally obscure before. Unlike the ameboids these individuals retained the ability to form the chambers including the primary matrix mediated calcification, the lobes of each chamber, the pores and the precipitation of secondary calcite (e.g. Fig. 2-4). The initial calcite deposition is on the organic template marking the external outline of the newly formed chamber (Fig. 2). In *A. lobibera* the external structure of the newly formed chamber appear as elongated lobes, which separate the endoplasm from the ectoplasm (Fig. 5). It is possible that the polarizing granules (which are found only in the endoplasm) provide the Ca and possibly organic matrix for this process and hence the primary calcite is enriched in Mg. This being the case, the granules may exocytose their soluble mineral content just at the boundary between the endoplasm and the ectoplasm. The initially precipitated skeleton may be in the form of amorphous $CaCO_3$ as has been demonstrated recently (Raz et al. 2000). The next stage is the precipitation of the secondary calcite. This occurs in the realm of the ectoplasm by a mechanism that is not clear yet. The process is shown in Figures 7 and 8. Initially a line of spherulites is precipitated (Fig. 7A) and later the entire space between the lobes and this perimeter is calcified (Fig. 7C). The biomineralization process is fast and the mineral precipitated is low-Mg calcite. Possible mechanisms for this process may involve seawater vacuolization as well as activation of Ca-pumps and Ca channels. A schematic presentation of the entire process is given in Fig. 11.

In addition to the many details of the calcification process that we were able to observe, these individuals provided also the framework for understanding the calcification processes in the ameboids. In the following section we provide an integrated scheme of calcification in foraminifera based on our previous observations and the newly acquired data during the last 2 years.

Summary

We present an overall scheme describing the calcification process in perforate foraminifera, based on "naked" foraminiferal ameboids and recovering individuals prepared from symbiont bearing foraminiferan *Amphistegina lobifera*. Calcium is concentrated in the endoplasm in highly soluble, birefringent mineral phase within membrane-bound granules. These granules are composed of Ca, Mg, P possibly S, and may contain organic matrix or some of its components. The turnover time of Ca in this compartment is long, (ca. days). The granules provide Ca for the first $CaCO_3$ crystals that precipitate over the newly formed organic matrix (the "Anlage"). At this stage the chamber consists of a two-dimensional primary wall made of Mg-rich calcitic microspherulites embedded within the organic matrix. Perforations in the primary wall mark the future pores. The second stage of the calcification process involves massive deposition of low-Mg calcite wall. This secondary calcite is made of variable size bone-shaped spherulites that are precipitated in an interwoven structure leaving empty spaces for the pores. The spherulites are layered crystal aggregates with their C-axis perpendicular to the test wall. In the ameboids these units form large (sometime hollow) spherulites. In the intact foraminifera these units form the secondary lamination and are responsible for the bulk of the skeleton deposition. The biomineralization process forming the spherulites is not known at this stage. Most probably this calcite is precipitated in an enclosed vacuolated compartment formed by the ectoplasm. Our observations as well as reports by earlier investigators confirm that calcification is intracellular. Vacuolization of seawater and their modification within the endoplasm to reduce the Mg:Ca ratio and to elevate the pH is probably the main mechanism responsible for the secondary calcification (see also: Meidani et al. 2000). Diffusion of CO_2 into the basic vacuoles or CO_3^{2-} ion transport across the membrane is responsible for the carbon pool that has been described in earlier studies (ter Kuile et al. 1988, 1989). The photosynthesis of symbiotic algae during daytime helps to elevate the pH in the boundary layer where the vacuoles are formed (Jørgensen et al. 1985). It can also be assumed that the turnover of Ca during process is relatively short (perhaps hours) as indicated by radioactive Ca uptake experiments and by imaging observations (Meidani et al. 2000). It is not clear however how these vacuoles are moving from the endoplasm to the site of biomineralization at the ectoplasm pseudopodia network. We suspect that this may be done by numerous very small pinocytotic vesicles that are formed from the large seawater vacuoles and are highly abundant on the axopodia. Our earlier electron probe measurements demonstrated alternations of Mg and S rich and low layers in secondary calcite of perforate foraminifera are in good agreement with this scheme. The trace element distribution coefficients of Sr, Ba, and Cd in foraminifera shells suggest that roughly 90 % of the Ca in the seawater vacuoles is precipitated during the process. Since the $Ca:C_T$ ratio in seawater is roughly 5:1, this may explain why foraminifera must concentrate carbon for calcification. This scheme of calcification helps to explain some of the deviations from thermodynamic equilibrium observed in carbon isotopes and in trace elements in foraminifera shells and thus obtain better paleoceanographic information.

Fig. 1:
Ameboid containing polarizing granules and calcitic spherulites.

Fig. 2:
Polaraized light image showing the first calcite microspherulites which fuse later on to form the thin primary wall of the developing test.

Fig. 3:
SEM micrograph of a newly formed chamber at the end of the primary calcification, showing the calcite microspherulites which form the primary wall.

Fig. 4:
A general view of the first chamber deposited during recalcification, in polarized light. The newly formed chamber is relatively transparent, showing the typical lobes of the species *A. lobifera*. In the vicinity of the extending lobes, aggregates of spherulites are formed which designates the beginning of the secondary calcification.

Fig. 5:
The same specimen as in Fig. 4 in phase contrast showing a highly vacuolated ectoplasm covering the entire area where secondary calcification is in progress.

Fig. 6:
The same specimen as in Figs. 4 and 5 a few hours later. The secondary calcification is almost complete: a layer of spherulites (10-20 mm) was deposited around the new chamber and filled the gaps between the lobes. Note also the pores in the walls of the lobes.

Fig. 7 A:
Pseudopodial network of recovering individual depositing spherulites at the margin of the network

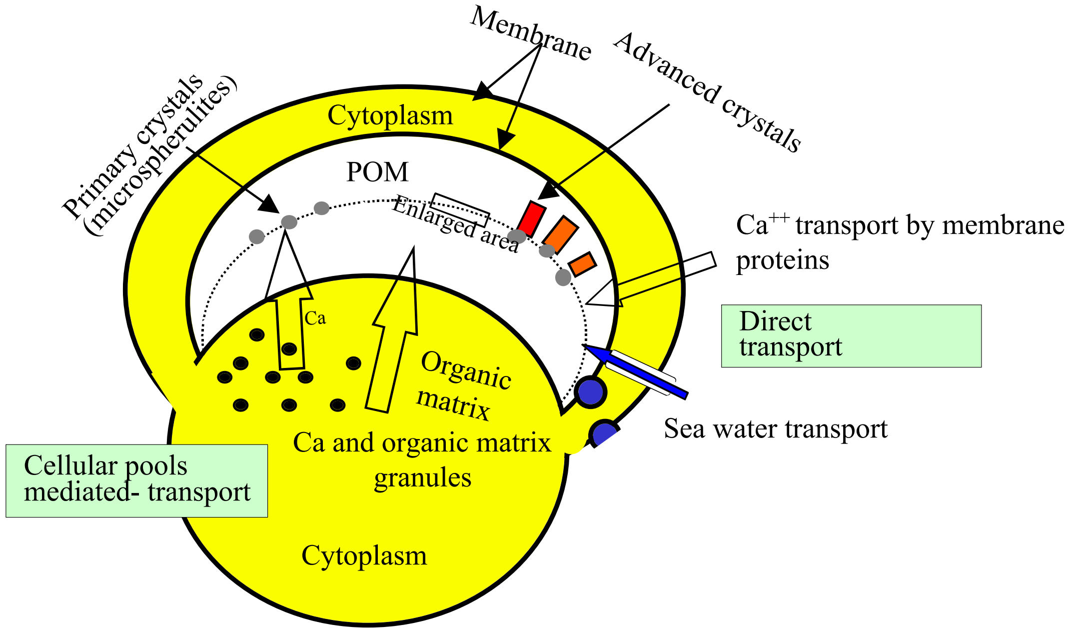
Fig. 7 B:
Polarized light of spherulites deposited at the margin of the pseudopods of Fig. 7A.

Fig. 7 C:
The same individual as in Figs. 7A and B roughly one day later. Spherulites are deposited in the "marked space".

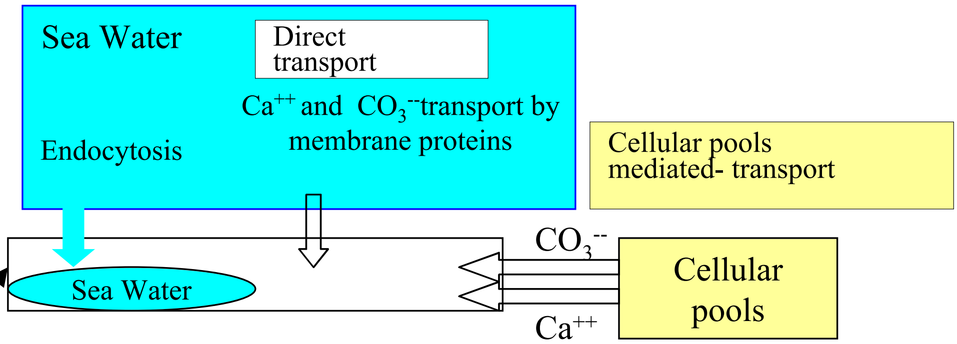
Fig. 8:
In this ameboid the birefringet granules are exceptionally large. It can be seen that each granule is located in a vacuole and that they have a bone like shape

Figs. 9-10:
The large birefringent granules were isolated from the above specimen and were taken for observation by SEM. The SEM micrographs show that the granules are made of bundles of elongated micro-crystals.

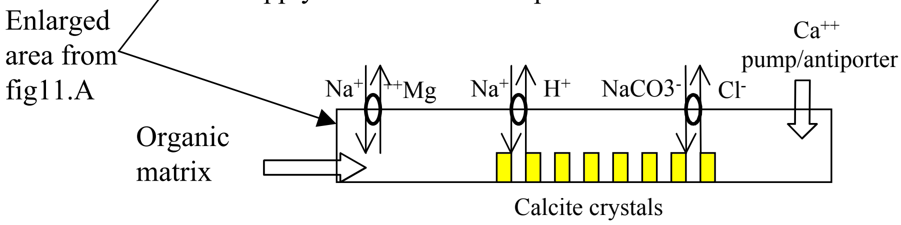
Fig. 11



A. A possible mechanism for space delineation

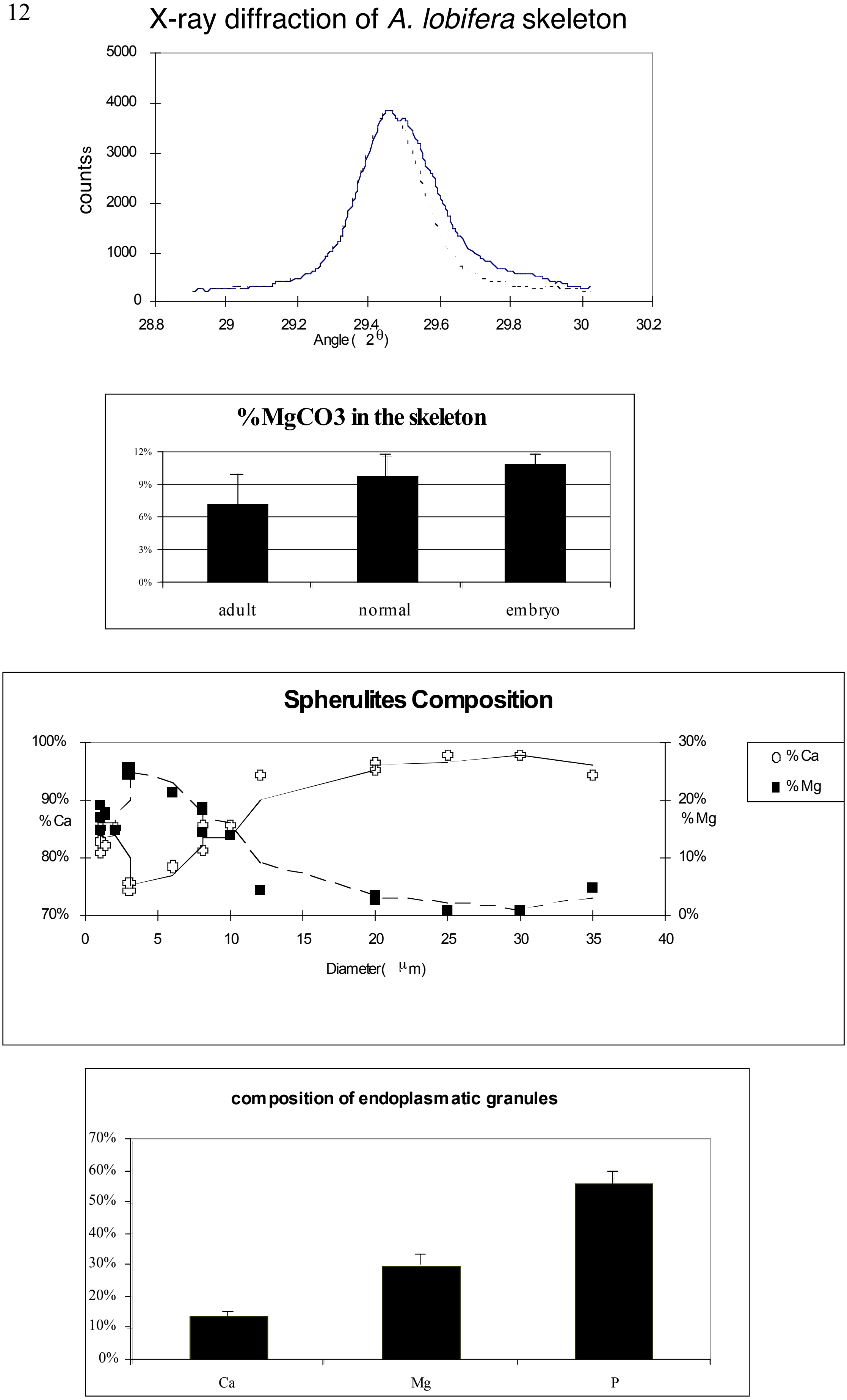


B. step 1: possible mechanisms of ions supply to the delineated space.



C. step 2: possible mechanisms of Calcite deposition within the delineated space.(Ca^{++} and CO$_3^{--}$ concentrating, Rise of pH., Removal of crystal growth inhibitor, Adding of organic matrix.)

Fig. 12


X-ray diffraction of *A. lobifera* skeleton
countss
5000
4000
3000
2000
1000
0
28.8
29
29.2
29.4
29.6
29.8
30
30.2
Angle (2θ)
%MgCO3 in the skeleton
12%
9%
6%
3%
0%
adult
normal
embryo
Spherulites Composition
100%
90%
%Ca
80%
70%
30%
20%
%Mg
10%
0%
0
5
10
15
20
25
30
35
40
Diameter(μm)
○ %Ca
■ %Mg
composition of endoplasmatic granules
70%
60%
50%
40%
30%
20%
10%
0%
Ca
Mg
P

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On the drinking habits of foraminifera: Foraminifera ameboids membrane cycling, calcium and magnesium metabolism

Inbal Meidani, A. Weise, Jonathan Erez and Micha E. Spira

The Interuniversity Institute, H. Steinitz Marine Biological Laboratory, Eilat and
Institute of Earth Sciences, The Hebrew University of Jerusalem

Introduction

Planktonic and benthic foraminifera contribute significantly to the overall calcification processes in the ocean and thus contribute to the ocean capacity to absorb or release atmospheric CO_2 (Lee and Anderson 1991). While various aspects of foraminifera calcification have been described (Angel 1980, Simikiss 1986, Hemleben et al. 1986, ter Kuile et al. 1989), the cellular and molecular mechanisms that underlie the process are largely unknown.

In the present study, we examined the hypothesis that the uptake of calcium by foraminifera and its subsequent concentration and deposition involve the formation of endocytotic vesicles that take up extracellular fluid in a non selective manner - pinocytosis and that the pinocytotic vesicles participate in the process leading to the concentration and subsequent deposition of skeletal calcium carbonate. The experiments were carried out using a cellular preparation of foraminifera ameboids developed by the laboratory of J. Erez (see Bentov and Erez, this volume).

Results

Confocal imaging of foraminifera ameboids revealed that the functional surface area of the ameboids is increased by membrane invagination and pinocytosis.

Membrane invaginations

Membrane invaginations in the form of long tubules extend from the glass substratum into the ameboid's cytoplasm. These tubules maintain continuous access to the external bathing solution, as indicated by the rapid (15-45 sec) loading and clearance of extracellular membrane impermeable fluorescent markers (FITC and sulforhodamine 101) (N=5).

Membrane retrieval -Pinocytosis -

Constitutive pinocytosis of vesicles with a diameter of ~1 µm or less was imaged using a Biorad MRC-1024 confocal scanhead coupled to a Zeiss Axiovert 135 inverted microscope. To that end, ameboids were placed in artificial sea water (ASW; in mM: 457 NaCl, 10 KCl, 10

$CaCl_2$, 55 $MgCl_2$, 2 $NaHCO_3$ and 2 HEPES) containing 50 µM fluorescein isothiocyanate (FITC Sigma) or Sulforhodamine-101 (SR-101, Kodak, laser grade) for 20-30 min. Confocal images (~1 µm optical sections) were acquired every 15 sec. The rate of constitutive membrane retrieval in ASW was estimated to be 240 vesicles/min (N=4). The average number of pinocytotic vesicles at steady state in an ameboid was estimated to be 190000 (N=4). This leads to an estimated effective increase in the ameboid's surface area by ~30 % (estimated surface area of the ameboid/estimated surface area of the population of pinocytotic vesicles). The rate of membrane retrieval was enhanced by incubation of ameboids in low calcium ASW. For example, in 0.4 mM Ca^{2+} ASW, the rate of membrane retrieval increased by a factor of 8.6 (N=4). Under these conditions, the steady state number of pinocytotic vesicles within the ameboids cytoplasm was 540000, leading to an estimated increase in the functional ameboid's surface area by 860 % (n=6). The regulation of the rate of pinocytotic activity by the extracellular calcium concentration may operate to regulate the total levels of the intracellular calcium or additional dissolved elements.

Fusion of pinocytotic vesicles within the cytoplasm

Fusion of retrieved vesicles to endosomes is characteristic of eukariotic cells and serves as a step in the processing of the vesicular content and its subsequent targeting. Estimation of the retrieved vesicles surface area using digital image processing revealed a gradual increase in the surface perimeter of the fluorescently labeled vesicles from an average of 4.5 µm (diameter= 1.19 µm) to 9.5 µm (diameter=1.73 µm) within a period of ~20 min. This increase corresponds to the averaged fusion of two vesicles with an estimated diameter of 1.19 µm. In foraminifera, the fusion of pinocytosed vesicles may serve as a step in the sequence of alterations in the content of the retrieved vesicles.

Exocytosis of the retrieved membrane

The total surface area of the isolated ameboids appears to remain constant. This steady state is achieved by constitutive exocytosis of the retrieved membrane.

The rate of exocytosis of pinocytotic vesicles was estimated by counting the number of remaining fluorescent vesicles after washing away the fluorescent indicator from the bathing medium. In normal ASW, we estimated the rate of fusion of pinocytotic vesicles with the plasma membrane to be 190 vesicles/min (N=2). Given the fact that a fraction of the exocytosed vesicles are formed by the fusion of two pinocytotic vesicles (or a pinocytotic vesicle with a newly synthesized one), the smaller estimated rate of exocytosis with respect to endocytosis (240/190 respectively) may account for the steady state dimensions of the plasma membrane surface area.

Alteration in the concentration of the Mg^{2+} and Ca^{2+} within the pinocytotic vesicles during cycling within the ameboids cytosol

We next attempted to examine possible alterations in the divalent ion composition within the retrieved vesicles while they cycle within the cytoplasm. Initially the composition and ion concentrations of the newly internalized pinocytotic vesicles is identical to that of the ASW in which the experiments were carried out. We imaged the free intravesicular magnesium and calcium concentrations ([Mg^{2+}] and [Ca^{2+}] respectively) in the population of the retrieved vesicles. To image the [Mg^{2+}], the ameboid was incubated in 65 mM Mg^{2+}, 100 µM mag-fura-2, and 10-100 µM Ca^{2+} ASW for a period of ~20 min (in the presence of 10 µM Ca^{2+} the indicator reports only the [Mg^{2+}], Ziv and Spira 1995). The external mag-fura-2 solutions were then thoroughly washed away with normal ASW, and sequential ratio images of the [Mg^{2+}] were acquired (at a rate of one image every 5 sec for 10-30 min) from the population of the retrieved vesicles. Under these conditions, the [Mg^{2+}] rapidly decreased within a period of ~2 min. from ~50mM to an estimated concentration of 2mM .Thereafter, the [Mg2+] remained constant for over a period of 15 min (N=5).

Consecutive ratio images of the [Ca^{2+}] in the retrieved vesicles were obtained following incubation of the ameboids in 2 mM Mg^{2+}, 10 mM Ca^{2+}, ASW (at 2 mM Mg^{2+} mag-fura-2 is insensitive to the [Mg^{2+}] and serves as a [Ca^{2+}] indicator, Ziv and Spira 1995). Under these conditions, the [Ca^{2+}] decreased from 10 mM to the range of 0.1 mM (99 %) within 25 min. The kinetics of the decrease in the [Ca^{2+}] was best fit by two time constants (N=7).

In conclusion, the free intravesicular calcium and magnesium concentration are down regulated. The averaged free magnesium concentration is reduced to a steady state level of 2 mM within two minutes, while the averaged free intravesicular calcium concentration is reduced to >0.1 µM at a significantly slower rate. The reduction in the free ionic concentrations does not necessarily imply that the ions are extruded from the vesicular lumen, but rather that the concentration of the free forms of the ions are reduced. In that respect, it should be noted that attempts to examine the pinocytotic vesicles with polarized light failed and thus we could not establish spatial linkage between crystals and vesicles.

Discussion

Based on the above observation we propose the following model to account for the observations:

1) The ameboid's plasmalema undergoes constitutive pinocytosis which increases the functional surface area of the ameboids by a factor of 1.3 in ASW. Nevertheless, the rate of pinocytosis can be regulated by the external calcium concentration such that a decrease in the external concentration increases rate of pinocytosis. Under the extreme experimental conditions of 0.1 mM Ca^{2+} ASW, the pinocytotic rate increased by a factor of 8.6. While such extreme alterations in the calcium concentration cannot take place in nature, we wish to emphasize that alterations in the cytosolic pH can modulate the rate of endocytosis. Such changes may be related to light dark cycles and photosynthesis by the symbiotic algae residing in large quantities within the cytoplasm.

2) Fusion of internalized vesicles. Our observations suggest that at least a fraction of the pinocytotic vesicles fuse. The increase in the vesicles' cross sectional area is associated with a decrease in the fluorescence intensity signal. Therefore, it is reasonable to assume that fusion occurs with newly synthesized vesicles. These newly synthesized vesicles may contain matrix molecules which facilitate calcium precipitation.

3) During the cycling of the pinocytotic vesicles, the free intravesicular Ca^{2+} and Mg^{2+} concentrations are reduced. The mechanism underlying this reduction was not examined. Nevertheless, it is interesting that the original polarity of calcium pumps and antiporters on the retrieved plasma membrane is such that it should increase rather then decrease the $[Ca^{2+}]$ and the $[Mg^{2+}]$.

It is possible to account for the observed decrease in the $[Ca^{2+}]$ and $[Mg^{2+}]$ by two principal mechanisms:

a) permiabilization of the vesicular plasma membrane and passive diffusion of the divalent ions from the lumen of the vesicular membrane into the cytosol. Under these conditions, the total amount of the calcium and magnesium in the vesicle is reduced;

b) precipitation of the Ca^{2+} within the lumen of the pinocytotic vesicle (as a Ca^{2+} Mg phosphore complex; see Bentov and Erez, this volume) due to reduction in the $[Mg^{2+}]$. This reduction could be caused by passive leakage of Mg^{2+} out of the vesicular lumen into the cytosol.

We have not performed experiments to differentiate between these possibilities. Based on our electron microscope observations (not discussed here), which show that calcium crystals surrounded by lipid membrane are found in the cytosol of the ameboids, we favor the second hypothesis which assumes that the calcium is not removed from the pinocytotic vesicles but rather is trapped within the vesicular lumen, probably as crystals of calcium-magnesium - phosphate (Erez, pers. comm.).

4) The pinocytotic cycle is completed when the internalized membrane fuses with the plasmalema. As we have not been able to co-localize the fluorescent indicators and calcium crystals, we do not know whether the exocytosis is associated with the deposition of calcium granules onto the surface of the ameboid. Electron microscopic observations in the presence of wheat germ agglutinin horseraddish peroxidase revealed that the amoeboid is encapsulated by a thick structureless layer which may serve as the matrix on top of which the foraminifera calcium carbonate skeleton is deposited.

Photosynthesis and calcification in hermatypic corals under variable seawater carbonate chemistry expected from atmospheric CO_2 increase

Kenneth Schneider and Jonathan Erez

The Interuniversity Institute, H. Steinitz Marine Biological Laboratory, Eilat and
Institute of Earth Sciences, The Hebrew University of Jerusalem

Colonies of the coral *Acropora* sp. were collected off the Interuniversity Institute at Eilat, and were incubated for 1-2 hours in the laboratory. Dissolved oxygen, total alkalinity, total inorganic carbon (CT) and its $\delta^{13}C$ were determined at the beginning and end of light and dark incubations. The seawater used were treated to keep either CT, pH or CO_2(aq) constant while changing all other parameters of carbonate chemistry according to changes expected from atmospheric CO_2 increase.

Rates of calcification (light and dark) displayed positive linear slopes with pH of ≈25 % increase for 0.1 pH unit, a value much higher than previously reported by Gattuso et al. (1998, 1999), but similar to those of Langdon et al. (2000). The light to dark calcification ratio decreased as pH rose mainly because dark rates became very low (and even negative) below pH of 8.06. Since the slopes of light and dark calcification as a function of pH (or CO_3^{2-}) are parallel, we suggest that the constant difference between these curves should be the relevant parameter for comparison between light and dark calcification rather then the ratio. Light enhanced calcification may be explained by an internal pH increase of ~ 0.35 units caused by photosynthesis, in accord with earlier microelectrode observations (Kuhl et al. 1995). Atmospheric CO_2 increase may have reduced coral calcification by 25 % and future CO_2 doubling may reduce it by additional 35 %. This may change the balance between growth and erosion of coral reefs towards net erosion. Our data showed that the carbonate ion (CO_3^{2-}) and not necessarily aragonite saturation level (Ω), controls coral calcification rate. Unlike calcification, photosynthesis did not show any trend with pH, $CO_{2(aq)}$ or CT, however, the overall data set (including light and temperature experiments) showed a clear positive correlation between the two processes. We suggest that $CO_{2(aq)}$ for photosynthesis may be provided internally from respiration and indirectly via calcification, which produces protons that combine with HCO_3^- to form $CO_{2(aq)}$ (McConnaughey and Whelan 1997). This latter source may become important at high pH values when $CO_{2(aq)}$ was low, but calcification rates increased. Independent supports for such mechanisms come from our observations on the isotopic fractionations during photosynthesis. Isotopic fractionations relative to $\delta^{13}C$ of CT were very low (Av.: –8 ‰; range: -4 ‰ to -15 ‰), and negatively correlated with $CO_{2(aq)}$ and pH. These may be the lowest isotopic fractionations for any unicellular algae observed in the ocean. At low $CO_{2(aq)}$ the substrate for photosynthetic may be HCO_3^- which combines with protons produced during calcification and forms 13C enriched CO2(aq). Direct $\delta^{13}C$

measurements of the isolated symbionts showed average values of –14 ‰ (ranging from –17 to –11 ‰), suggesting that up to 50 % of the CO_2 utilized by the symbionts may be of respiratory origin (with $\delta^{13}C = -16$ ‰).

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Climate and ocean variability of the northern Red Sea since 1750 reconstructed from coral stable isotopes

Thomas Felis[1], Jürgen Pätzold[1], Yossi Loya[2], Maoz Fine[2], Ahmed H. Nawar[3] and Gerold Wefer[1]

1) Geowissenschaften (Fachbereich 5), Universität Bremen, Bremen
2) Department of Zoology and Porter Super-Center for Ecological and Environmental Studies, Tel Aviv University, Tel Aviv
3) National Institute of Oceanography and Fisheries, Cairo

Introduction

Instrumental climate records are too short to resolve the full range of interannual- to multidecadal-scale natural climate variability. Banded corals, tree rings, ice cores, and varved sediments provide paleoclimatic archives which can be used to reconstruct past climate variability in the pre-instrumental period in annual resolution. These so-called proxy climate indicators provide paleoclimatic records which are important for the assessment of perturbations to the natural climate variability by anthropogenic forcing, for climate predictability and for a better understanding of the different modes of the global climate system, e.g., the El Niño-Southern Oscillation phenomenon, the Asian and African monsoon and the North Atlantic Oscillation. These natural modes have important socio-economic effects owing to their worldwide modulation of droughts, floods, storms, snowfall, or fish stocks at society-relevant timescales (e.g., Mann et al. 1998).

Corals from the modern and fossil reefs of the tropical and subtropical oceans provide an important archive of past climate and ocean variability. The skeleton of reef-building corals carries isotopic tracers that record, e.g., water temperature and salinity (evaporation/rainfall). Massive corals produce annual density bands that can be used for the development of chronologies. Modern corals provide climate records extending back several 100 years from the present. Accurately dated fossil corals provide information on climate variability during time-windows throughout the late Quaternary (e.g., Pätzold and Dullo 2000).

Northern Red Sea corals provide one of the rare opportunities for annual- to seasonal-resolution paleoclimatic reconstructions from the African-Asian desert belt. The subtropical setting provides the opportunity to study the interaction between extratropical and tropical modes of climate variability. Recent coral-based studies as part of the Red Sea Program (RSP) have provided important information on past climate and ocean variability in this region (Felis et al. 1998a, Felis et al. 1998b, Felis 1999, Moustafa et al. 2000, Moustafa 2000, Felis et al. 2000). Here we discuss results from studying two coral stable isotope records. Coral core EILAT-1 was collected at Eilat (Israel) near the northern end of the Gulf of Aqaba and core RUS-95 at Ras Umm Sidd (Egypt) near the southern tip of the Sinai Peninsula in the northern Red Sea (Fig. 1).

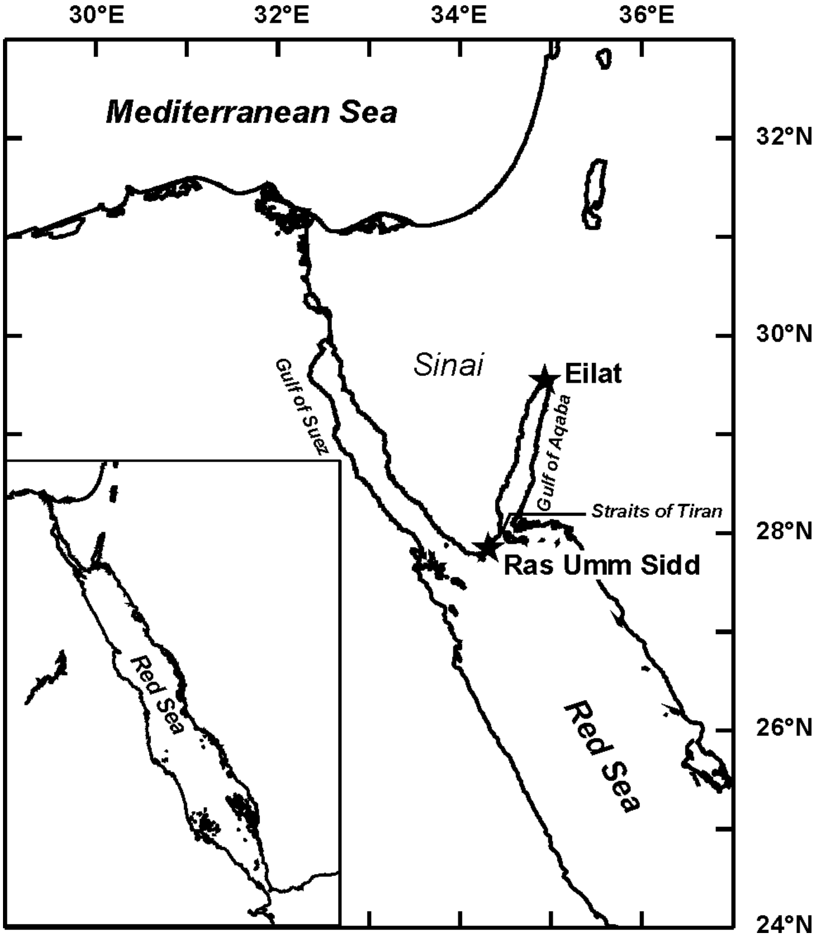

Fig. 1:
Coral-based paleoclimatic research in the northern Red Sea. The sampling locations of the coral cores are indicated by 'star' symbols. Core RUS-95 was collected at Ras Umm Sidd (Ras Mohammed National Park, Egypt), core EILAT-1 was collected at Eilat (Israel).

Vertical water mass mixing and plankton blooms recorded in skeletal stable carbon isotopes of a Gulf of Aqaba coral

The environmental interpretation of the stable carbon isotopic variations in the skeletons of massive corals is still a matter of debate. A 19-year seasonal skeletal $^{13}C/^{12}C$ record of a shallow-water *Porites* sp. coral (EILAT-1) from Eilat (Israel) at the northern end of the Gulf of Aqaba (≈29.5°N) documents interannual events of extraordinarily large plankton blooms, indicated by anomalous 13C depletions in the coral skeleton (Fig. 2) (Felis et al. 1998b). These blooms are caused by deep vertical water mass mixing, convectively driven in colder winters, which results in increased supplies of nutrients to the surface waters. The deep vertical mixings can sometimes be driven by the cooling occurring throughout the Middle East after large tropical volcanic eruptions, a phenomenon first described by Genin et al. (1995). We therefore have evidence in our coral skeletal 13C/12C record for an indirect volcanic signal of the eruptions of El Chichón (Mexico 1982) and Mount Pinatubo (Philippines 1991).

Deep mixing induced $^{13}C/^{12}C$ variations of the dissolved inorganic carbon in the surface waters can be neglected at this location (Shemesh et al. 1994). We therefore suggest that the ^{13}C skeletal depletions can be best explained by changes in the coral's autotrophy-heterotrophy diet, through increased heterotrophic feeding on zooplankton during the blooms. Increased feeding on ^{13}C-depleted zooplankton or increased heterotrophy at the expense of autotrophy can both result in a ^{13}C-depleted coral skeleton.

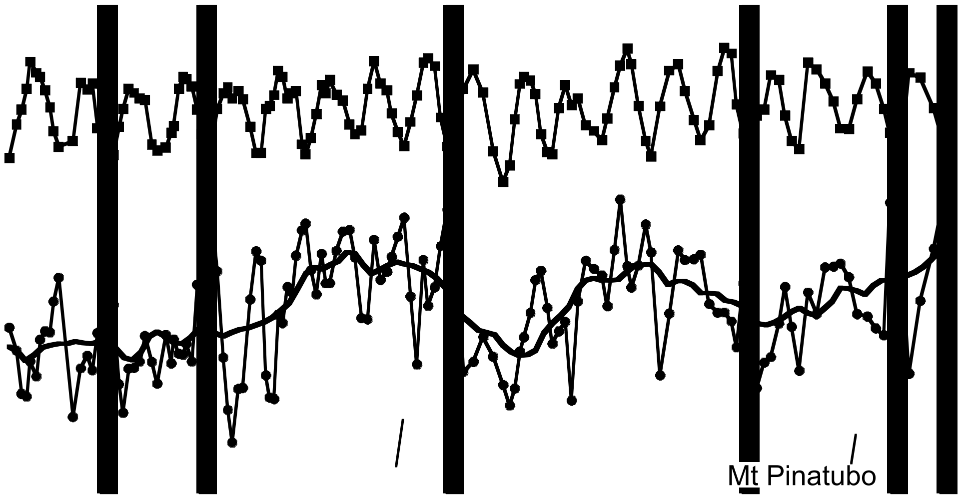

Fig. 2: The Eilat coral stable isotope record (core EILAT-1) from the northern end of the Gulf of Aqaba. The coral oxygen isotope variations (top curve) reflect the seasonal cycle of sea surface temperatures and therefore provide an age model for the coral chronology. The dotted bars indicate winters with deep vertical mixing and increased plankton bloom events, derived from the coral stable carbon isotope record (bottom curve). Vertical dashed lines indicate the two largest tropical volcanic eruptions during the record. Years are from 1974-1993. Modified from Felis et al. (1998b).

However, this suggestion requires more testing. If our conclusions are substantiated, seasonal skeletal $^{13}C/^{12}C$ records of corals which change from autotrophy under normal conditions to increased heterotrophy during bloom events may be used as indicators of ocean paleoproductivity at interannual resolution.

A coral oxygen isotope record from the northern Red Sea documenting Atlantic and Pacific teleconnections on Middle East climate variability since the year 1750

A coral oxygen isotope record from the northern Red Sea provides a bimonthly-resolution time series for the period 1750-1995 (Felis et al. 2000) (Fig. 3). The core (RUS-95) was collected at the end of November 1995 during a RSP-cruise from a 2.6-m-high coral colony (*Porites* sp.) at Ras Umm Sidd (~28°N) in the Ras Mohammed National Park near the southern tip of the Sinai Peninsula (Egypt) (Felis et al. 1998a).

On the seasonal timescale the Ras Umm Sidd coral record primarily reflects information on sea surface temperatures. On interannual timescales seawater isotopic variations probably play a proportionately larger role in the composition of the mean annual coral oxygen isotope signal, which apparently reflects varying proportions of both sea surface temperature and seawater isotopic variability. In conjunction with instrumental observations of climate the coral record suggests for interannual and longer timescales that colder periods are accompanied by more arid conditions in the northern Red Sea but increased rainfall in the southeastern Mediterranean, whereas warmer periods are accompanied by decreased rainfall in the latter and less arid conditions in the northern Red Sea.

One of the prominent modes of Northern Hemisphere climate variability is the North Atlantic Oscillation (NAO). The NAO has a strong influence on large-scale variations in the atmospheric circulation over the North Atlantic and its surrounding continents, controlling regional distributions of surface temperature and precipitation (e.g., Hurrell 1995). The El Niño-Southern Oscillation (ENSO) phenomenon originates in the tropical Pacific Ocean but

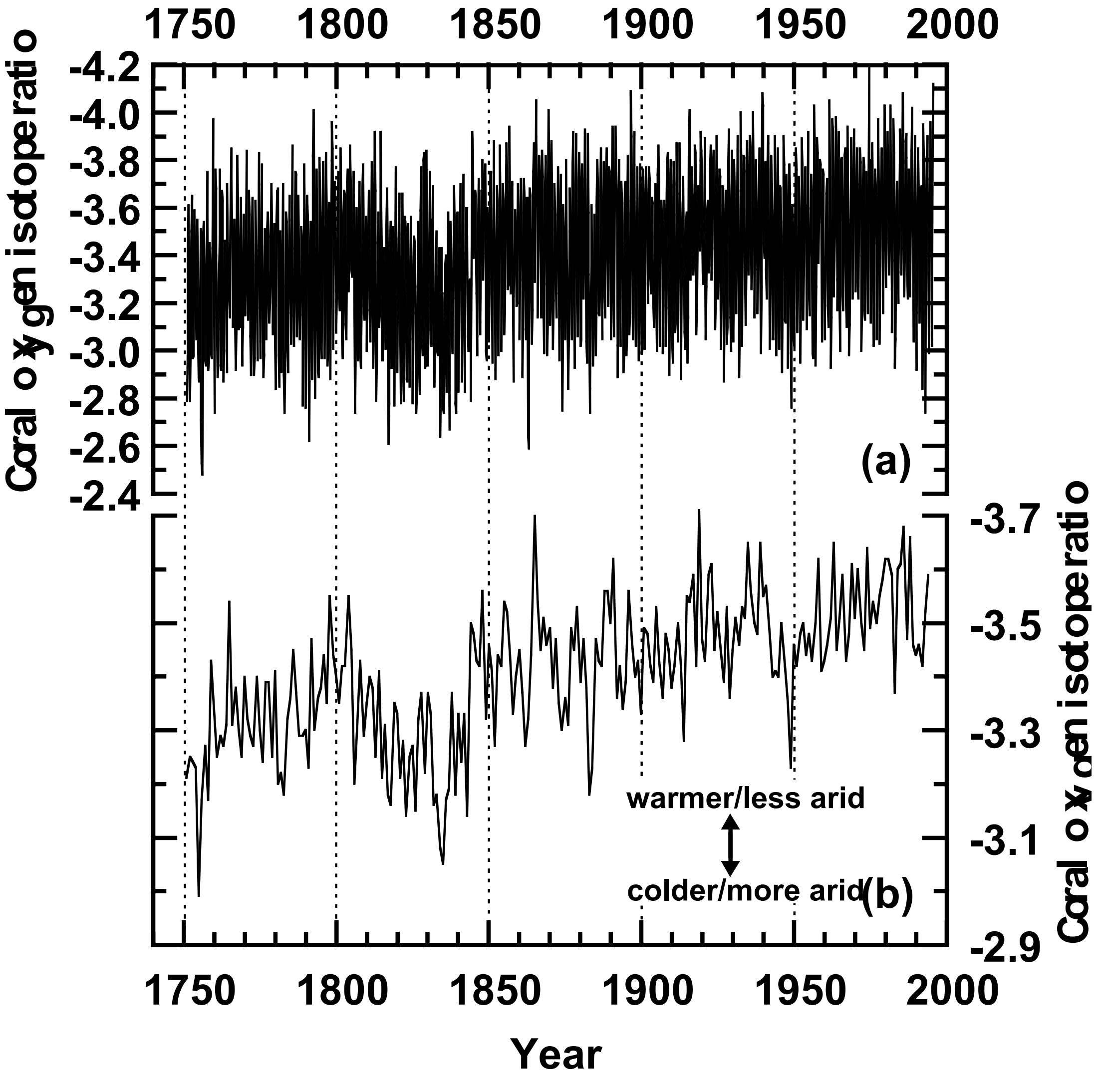

Fig. 3: The Ras Umm Sidd coral oxygen isotope record (core RUS-95) from the northern Red Sea. (a) Bimonthly time series. On the seasonal timescale coral oxygen isotope ratios and sea surface temperatures are strongly correlated. (b) Mean annual time series. The mean annual coral oxygen isotope signal apparently reflects varying proportions of both sea surface temperature and seawater isotopic variability. On interannual and longer timescales, high coral oxygen isotope ratios reflect lower sea surface temperatures but also higher oxygen isotope ratios of the seawater (more arid conditions), whereas low coral oxygen isotope ratios reflect higher sea surface temperatures but also lower oxygen isotope ratios of the seawater (less arid conditions). From Felis et al. (2000).

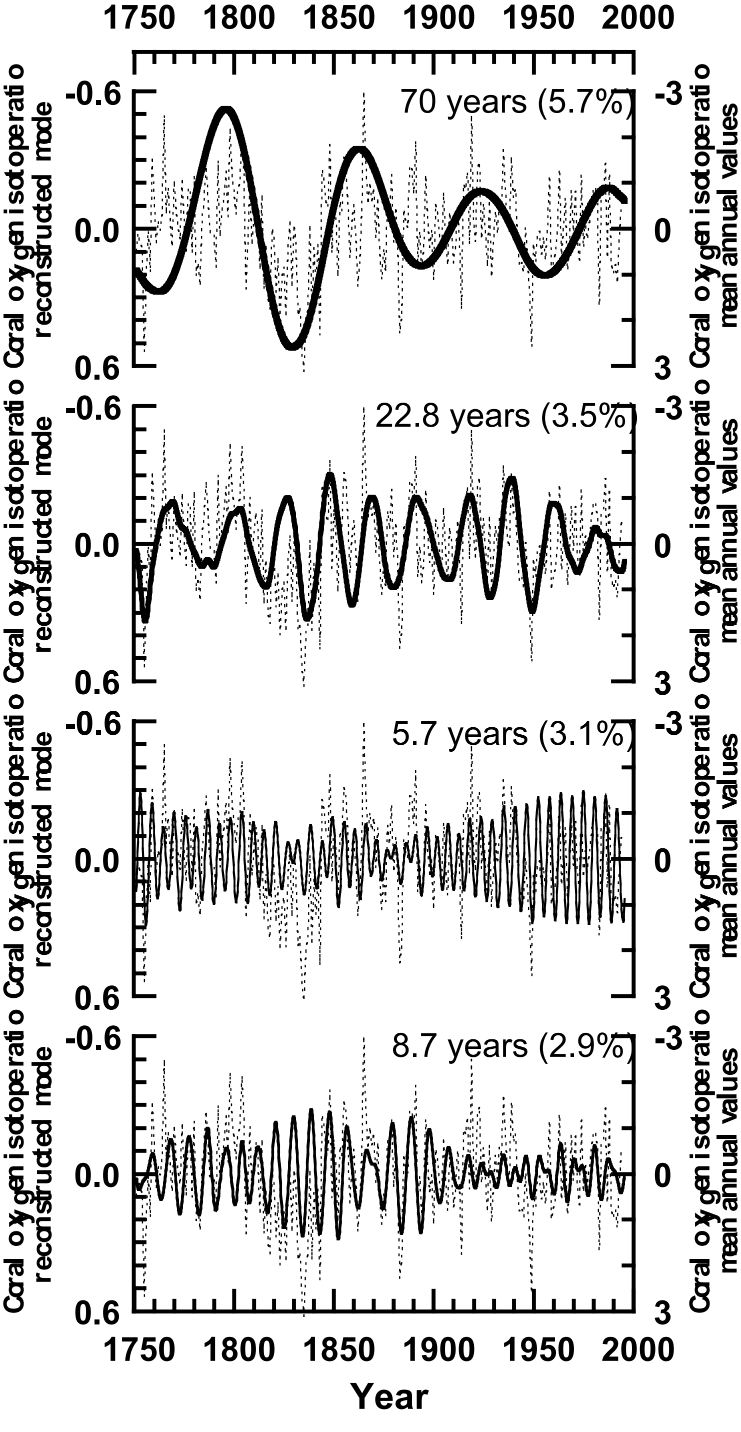

Fig. 4: The results of singular spectrum analysis of the bimonthly Ras Umm Sidd coral oxygen isotope time series with the average seasonal cycle removed. The most prominent oscillatory modes are shown (thick solid lines) with the period and percentage variance (of the detrended seasonal anomaly record) indicated. Also shown is the detrended normalized mean annual coral oxygen isotope time series (thin dotted line) calculated from the seasonal anomaly record. For paleoclimatic interpretation, see Figure 3. From Felis et al. (2000).

influences global climate via atmospheric teleconnection patterns (e.g., Philander 1990). The Ras Umm Sidd coral time series is dominated by a ~70-year oscillation probably of North Atlantic origin (Fig. 4). Interannual to interdecadal variability is correlated with instrumental indices of the NAO, the ENSO, and North Pacific climate variability. The results suggest that these modes contributed consistently to Middle East climate variability during the past ~250 years, preferentially at a period of ≈5.7 years.

This study adds to the present knowledge on the spatial extent of North Atlantic climate variability in the Middle East, where studies usually focus on the northeastern part of the Mediterranean owing to the relatively better coverage with instrumental observations of climate (e.g., Hurrell 1995). Furthermore, North Pacific climate variability seems to play an important role in climate variability in the Middle East. In summary, the Ras Umm Sidd coral record provides evidence that interaction between tropical and extratropical modes of the global climate system had an important control on Middle East climate variability on interannual and longer timescales since at least 1750.

Directions for future research

Moustafa et al. (2000) successfully generated stable isotope records derived from fossil northern Red Sea corals providing time windows of up to 18 years length during the period of the Mid-Holocene (≈5000-6000 years ago). Further work on fossil corals will hopefully provide paleoclimatic information for decade- to century-long time windows during the entire Holocene (the past ≈10000 years) and the last interglacial warm period (≈125000 years ago). Such coral records will enable to study the interaction of the different modes of the global climate system and regional northern Red Sea and Middle East climate variability during these periods.

Acknowledgments

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Geochemical study of trace and major elements in some species of coral reefs, Abu Soma Bay, Red Sea, Egypt

Ahmed H. Nawar and Mohammed Abd El-Wahab

National Institute of Oceanography and Fisheries, Cairo

Summary

Specimens of preserved and recent reef corals have variable concentrations of trace and major elements.

Thirty coral species were subjected to chemical study of their trace and major elements: Cu, Zn, Co, Cd, Ni, Pb, Na, K, Mg, Fe and Sr. Concentrations determined on samples of the preserved and recent corals indicated that a record of skeletal reefs content of toxic metals is preserved.

The pollutants come from oil and heavy metals resulting from oil transport, phosphate ore mining, municipal waste, sewage disposal and other anthropogenic activities associated with tourism activities and consequent mobilization of metals into marine environment, also from runoff (by torrents) and landfilling as a result of tourism buildings.

Paleoclimatic reconstructions of the northern Red Sea during the Holocene inferred from stable isotope records of modern and fossil corals and molluscs

Yaser A. Moustafa[1], Jürgen Pätzold[2], Yossi Loya[3] and Gerold Wefer[2]

1) National Institute of Oceanography and Fisheries, Suez
2) Geowissenschaften (Fachbereich 5), Universität Bremen, Bremen
3) Department of Zoology and Porter Super-Center for Ecological and Environmental Studies, Tel Aviv University, Tel Aviv

Twentieth-century coral oxygen isotope record from the southern Sinai, northern Red Sea

In this study (Moustafa 2000) two high resolution records of $\delta^{18}O$ covering 96 and 50 years of coral growth were extracted from two different Porites colonies (RUS-93a and RUS-93b, respectively). They grew about 250 m apart at Ras Umm Sidd off the southern Sinai coast in the northern Red Sea proper. Two additional $\delta^{18}O$ records were obtained previously from two other colonies (RUS-95, Felis et al. 2000, and RUS-1, Pätzold and Klein, unpublished data), which grew in the same environment about 500 m apart. The correlation coefficients between the four coral $\delta^{18}O$ records from Ras Umm Sidd vary on an annual time scale. The results indicate that local biological effects play a role in individual coral $\delta^{18}O$ records.

We correlated the different coral $\delta^{18}O$ records with the COADS sea-surface temperature (at annual time scales for four time intervals: 1907-1916, 1919-1939, 1946-1966 and 1976-1992) (Fig. 1). The correlation coefficients are also different among the different $\delta^{18}O$ records and COADS SST on annual time scales. Excluding the data gaps, the correlation coefficients varied from -0.45 (RUS-95) to -0.60 (RUS-93a). An average composite $\delta^{18}O$ record of three long chronologies was constructed from 1907-1992. Regression analysis between annual SST and this 3-coral average $\delta^{18}O$ record yields a much better and significant correlation ($r=-0.68$) also excluding the data gaps. Therefore, based on this study, it is advisable to analyze more than one coral from a given locality to obtain a reliable coral $\delta^{18}O$ record that can be used in coral-based paleoclimate studies.

The $\delta^{18}O$/SST gradient varied between 0.15 to 0.18 ‰/°C, with a mean value of 0.165 ‰/°C as in a previous study by Felis et al. (2000). The $\delta^{18}O$ record of RUS-93a indicates a warming in the twentieth century of about 1.1° C. Pronounced cyclicities of 10 and 3.6 years are evident when cross-spectral analysis is applied to the bimonthly $\delta^{18}O$ time series of RUS-93a and RUS-93b. The 3.6-year period is coherent with a similar cyclicity in the Southern Oscillation Index (SOI). Also, a highly coherent 5.8 cyclicity is evident. This period is also present in the $\delta^{18}O$ of RUS-95 (Felis et al. 2000), and happens to be the most prominent period in the co-spectrum of the Northern Atlantic Oscillation (NAO) and El-Niño Southern Oscillation (ENSO).

Fig. 1: Comparison between annual COADS sea surface temperature (SST) and the various coral $\delta^{18}O$ of cores from Ras Umm Sidd (northern Red Sea). a) SST and coral $\delta^{18}O$ from RUS-95 (Felis et al. 2000). b) SST and coral $\delta^{18}O$ from RUS-1 (Pätzold and Klein, unpublished data). c) SST and coral $\delta^{18}O$ from RUS-93a (this study). d) SST and mean annual coral $\delta^{18}O$ of all three cores.

Fig. 2: (a) Mean $\delta^{18}O$ values of *Tridacna* spp. shell carbonate from Eilat (northern Gulf of Aqaba) plotted versus ages. The Nile level data between about 4500 yr BP and 5000 yr BP is shown after Henfling and Pflaumbaum (1991), between about 2700 yr BP and 4050 yr BP is after Westendorf and Henfling (1989) based on hieroglyphical documents.
(b) The Nile deviation of about the last 1400 years is from Riehl and Meitín (1979) based on Nilometer measurements in southern Cairo (Egypt) records.
(c) Dead Sea levels inferred from radiometric-dated levels relative to mean sea level of the ocean (Neev and Emery 1995).
(d) $\delta^{18}O$ values in *G. ruber* during the last 6000 years BP, diameter: 315-400 mm, 20 specimens (Sirocko et al. 1993).

Modern and fossil Holocene marine climate record in molluscs (*Tridacna* spp.) from the northern Red Sea

This study focused on the isotopic composition of oxygen in fossil *Tridacna* spp. from an exposed Holocene reef terrace at about 2 m above the present sea-level from the northern Gulf of Aqaba (Red Sea), covering the late- and mid-Holocene periods from 5460 to 1400 ^{14}C years BP (Moustafa 2000).

A recent *Tridacna* sp. was collected alive in June 1996 and analyzed for comparison with the fossil samples. The high-resolution δ^{18}O profile of this recent *Tridacna* sp. shows a range of 1.17 ‰ in δ^{18}O, which is consistent with today sea-surface temperature (SST) range of about 5.3° C. The fossil *Tridacna* spp. δ^{18}O records encompass a range between 1.27 ‰ and 1.00 ‰, which is equivalent to seasonal temperature variations between 6° C and 4.5° C. Mean δ^{18}O values of various fossil *Tridacna* spp. range between 1.20 ‰ and 2.29 ‰ (Fig. 2). These variations in δ^{18}O (about 1.1 ‰) are mainly due to changes in the isotopic composition of sea water.

A likely climatic cause of these mean δ^{18}O variations in the *Tridacna* spp. might consist in an enhancement or a reduction of the Indian and African monsoons, leading to either a greater or scarce rainfall in the highland of east Africa and the Red Sea region, and then to the respective salinity changes in the surface layer of the northern Red Sea. The results presented corroborate hieroglyphical and historical documents of high/low Nile levels during the last about 6000 years BP and also the thickness of varved sediment cores from the northeastern Arabian Sea, which were affected by the intensity change of the African/Asian monsoon (Fig. 2).

Changes in mid-Holocene climate seasonality in the northern Red Sea inferred from coral stable isotopes

Fossil corals from elevated and submerged reefs of the northern Red Sea document climate variability during the Holocene, while significant oceanographic and climatic changes occurred in this region. The stable oxygen and carbon isotopic composition of massive fossil corals like *Porites* sp. can be used to reconstruct these past environmental changes.

During the mid-Holocene near-monthly δ^{18}O records of five fossil corals (*Porites* spp.) from the northern Gulf of Aqaba (Red Sea) show changes in climate seasonality from 5750 – 4450 ^{14}C-years before present (BP) (Moustafa et al. 2000). The average seasonal amplitudes of δ^{18}O in these five coral records are higher (1.5- to 2-fold) compared to modern corals (Fig. 3). This is most probably due to a larger seasonal temperature contrast and a reduction of salinity during the summer seasons in mid-Holocene times. Moreover, mid-Holocene δ^{18}O records reveal a reduced average growth rate (up to 45 %) as compared to modern corals. The reduction of coral growth during the mid-Holocene is probably triggered by an increased input and resuspension of terrestrial sediments.

All these results support the hypothesis of summer monsoon rains reaching the northern Red Sea in mid-Holocene times when seasonal solar radiation was enhanced. Enhanced

Fig. 3: Stable oxygen isotope time series from fossil (4450 - 5750 ^{14}C yr BP) and modern corals. The fossil corals show a considerably higher seasonal δ^{18}O amplitude (about 1.7 times) as well as heavier mean δ^{18}O values (about 0.5‰) compared to modern corals from the same location. Data of modern corals from Klein et al. (1992) and Felis et al. (1998). From Moustafa et al. (2000).

seasonalities can be reconstructed at least from 5750 to 4450 ^{14}C-years BP. A decrease in the mean δ^{18}O values of the fossil corals occurs at about 5000 years BP. This date coincides with a period of rapid decline in the levels of north African lakes and the Nile river indicating a reduced moisture transport from the Atlantic and Indian oceans. Hence, the δ^{18}O signal of the different corals during the mid-Holocene could be controlled by variations in the intensity of the African/Asian monsoon.

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Variations in sclerochronological parameters and stable isotopes with depth in *Porites* spp. corals from the Gulf of Aqaba (Eilat), Red-Sea

Micha Rosenfeld[1], Jürgen Pätzold[2], Gerold Wefer[2], Maoz Fine[1], Ramy Klein[1] and Yossi Loya[1]

1) Department of Zoology and Porter Super-Center for Ecological and Environmental Studies, Tel Aviv University, Tel Aviv
2) Geowissenschaften (Fachbereich 5), Universität Bremen, Bremen

Many reef corals have skeletal density variations with annual periodicity. These bands are prominent in hermatypic massive corals, composed of alternating high-density (HD) and low-density (LD) sub-bands. This banding pattern of hermatypic massive corals together with stable isotope composition ($\delta^{13}C$ and ($\delta^{18}O$), has been used in environmental studies in both recent reefs and in palaeocommunities. Nevertheless, the effects of certain environmental factors such as geographical location and habitat on these skeletal parameters still have some degree of uncertainty. Here we review and summarize the results of a study carried out over the past few years aimed at detecting the effect of water depth on sclerochronological characteristics of the massive coral *Porites* spp. In addition, we present the results of sclerochronological and isotopic analysis of a *Porites* sp. coral collected from 46 m depth in Eilat, Red Sea. Seventy-one annual bands were detected in both the X-radiograph and $\delta^{18}O$ time series. Average growth rate was calculated from the $\delta^{18}O$ variation along the major growth axis and found to be 6.56 (0.92 mm yr^{-1}, with a trend of decreasing growth rates with age. Skeletal isotopic compositions of oxygen and carbon were depleted in both $\delta^{18}O$ and ^{13}C compared to those previously reported for *Porites* spp. from Eilat reefs. The positive correlation with a phase shift we detected between stable carbon and oxygen isotopic ratios also differs from previous observations. These results imply that the interpretation of sclerochronological data from deeper colonies may be problematic and there is need for further research concerning the link between those coral sclerochronological records and environmental data.

Studies in Microbiology and Toxicology

Low molecular weight neurotoxic compounds from marine and fresh water organisms

M. Nabil Aboul-Enein, Khayria M. Naguib, Mohamed N. Gomaa

National Institute of Oceanography and Fisheries, Cairo

Natural products are attractive for use in pharmaceutical and agricultural applications due to their low environmental impact. Moreover, newly isolated compounds may lead to novel prototypes displaying useful biological activity and unique modes of action.

Terrestrial natural products have extensively been used as a source for active and novel molecules. Marine organism, however, are prone to produce totally new metabolites, many of which have proven to be neuroactive. Neurotoxins (e.g. Saxitoxins, Tetrodotoxins, and Conotoxins) have been used extensively as pharmacological tools.

The Red Sea environment is a unique habitat which has not been extensively explored for its potential of harboring bioactive compounds. Here we present several examples of bioactive compounds obtained under the auspices of the Red Sea Project. These naturally occurring, low molecular-weight substances are new lead compounds whose derivatives can be easily synthesized and consequently used as pharmaceutical tools.

Sea anemone toxins

The toxicity of some nematocysts from Cnidaria (Coelenterata) has been known for a long time. Mathias et al. (1960) have established that the lethal component of *Actinia equina* is found in its protein fraction, but they were unable to isolate the toxin. They also reported that the most potent coelenterate toxins are proteins.

The interest in coelenterate toxins increased considerably when Shapiro (1968) published his results on the purification of the first toxic polypeptide isolated from a sea anemone *Condylactis gigantea*, and when the specific action of this toxin on the sodium channel was demonstrated.

Lane (1968) paid much attention to low molecular weight lethal substances isolated from different coelenterate nematocysts. Attempts to isolate toxic proteins from *Anemonia sulcata* have been reported by Beress and Beress (1971) who isolated two polypeptides, of molecular weight in the range, 5000-10,000 Dalton, having a paralyzing effect on crabs and mammals.

Mebs et al. (1983) stated that lethality in mice could not be detected after i.p. injection of the acetone precipitate of the aqueous extracts of the three common occurring sea anemone species *Gyrostoma helianthus, Radianthus koseirensis*, and *Radianthus rhodostoma* collected from the Gulf of Aqaba, Red Sea. However, hemolysins and proteinase inhibitors were found in these sea anemone extracts.

Ichthyotoxicity (less than 0.5 µg/ml water) of the cytolytic sea anemone *Gyrostoma helianthus* toxins was reported by Mebs (1983) and the effects of the sea anemone toxin on clown fish was later studied by Mebs (1994). However, crustaceans (e.g. brine shrimp *Artemia salina*, shore crabs *Metopograpsus oceanicus, Mithraculus* sp.) were reported by Giese et al. (1996) to be resistant to sea anemone cytolytic toxins extracted from *Heteractis magnifica* (from the reefs of Papua, New Guinea), *Entacmaea quadricolor* (Red Sea), and *Condylactis gigantea* (Caribbean Sea). Cytolysins from *Entacmaea quadricolor* were compared to other sea anemone cytolysin and high degree of similarity of the effects was observed (Samejima et al. 2000).

Results

The scientific names of the collected sea anemone samples were confirmed as *Entacmaea quadricolor* (Rueppellx Leuckant 1828) or *Gyrostoma helianthus* (Hemprich and Ehrenberg 1834). The collected samples were obtained from the Red Sea in the vicinity of Hurghada. The crude aqueous ethanolic extract of the collected sea anemone was freeze-dried in order to determine the Dose Response Curve (DRC) in mice.

Neurotoxicity to mice was observed after i.p. injection and the profile of the DRC (Fig. 1) showed that the threshold was at 20 mg/ml with a plateau at 28 mg/ml. The estimated LD$_{50}$ values of the sea anemone crude extract were 19.3 and 27.3 µg/insect for *Musca domestica,* and *Spodopetra littoralis* respectively while it was 732.8 mg/kg for mice when i.p. injected.

Crude extract at a dose of 1/8 LD$_{50}$ when i.p. injected in mice (20 g) showed potent inhibitory effect on *in vivo* AchE activity (Fig. 2). Maximum inhibition was observed after 30 min. of

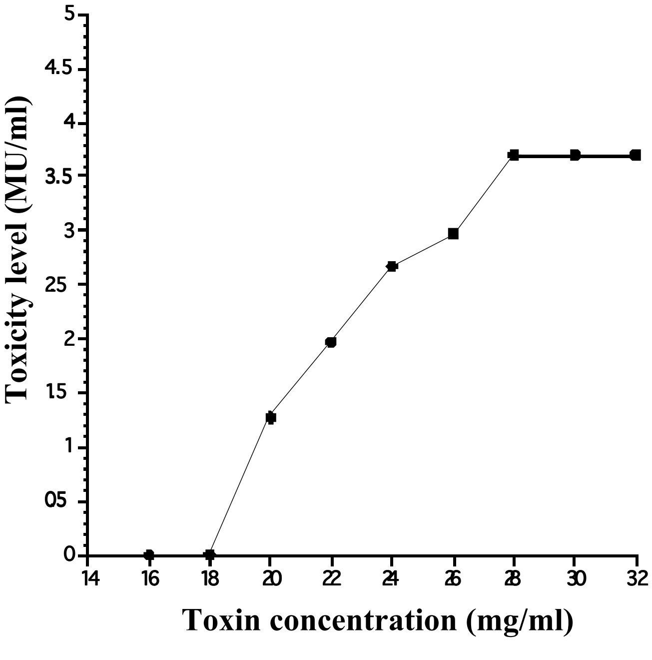

Fig. 1:
Dose response curve in mice after i.p. injection of crude sea anemon extract.

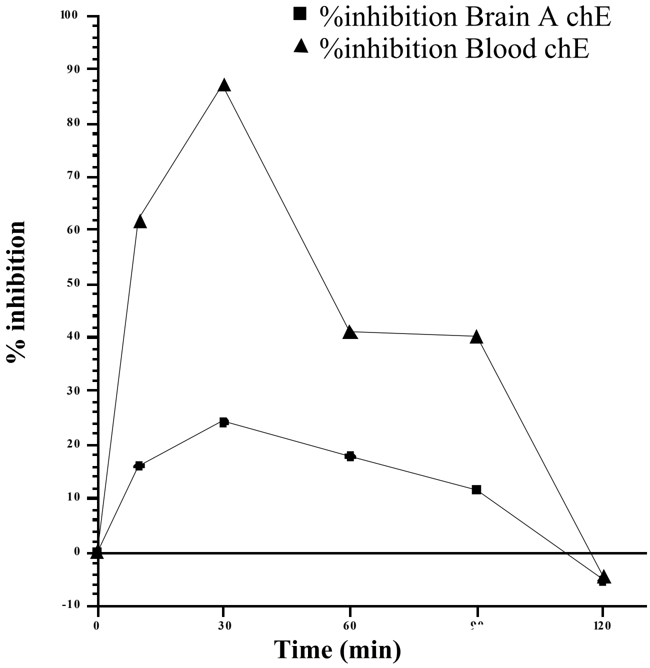

Fig. 2:
Brain and blood chE% inhibition following 1/8 LD i.p. administration in mice of sea anemone crude extract.

treatment. Throughout the tested period the enzyme activity showed tendency to restore its original value indicating its reversibility. Crude extract (using 20 µl of a 10 mg/ml) showed *in vitro* AchE activity. No AchE activity was detected in the tested bacterial, fungal species and brine shrimp.

The freeze-dried crude extract was purified by ultrafiltration through a membrane filter with molecular weight exclusion cut-off 10, 5, 3, 1 and 0.5 k Dalton. A Mouse bioassay was used to follow the toxicity of the different filtrates, which was detected until the 500 Dalton cut-off. Table 1 shows the toxicity level in Mouse Units for each filtrate along with their dry weight per 100 ml filtrate. The toxicity level decreased by 14 % from the crude to the 10 KD and by 35 % from the crude to the 5-1 KD filtrates and by 46 % from the crude to the 0.5 K Dalton filtrates. The dry weight decreased by the same ratio as the toxicity level from the crude to the 10 KD (14 %) and from the 5-KD to the 500-D (17 %). Higher decrease in toxicity level than in dried material at the step from 10 KD to 5 KD may be due to a synergistic effect. The low-molecular-weight-500-D filtrate showed 54 % of the total toxicity of the crude extract after removing 37 % of the dry weight contained in the crude extract.

Tab. 1: Toxicity level of different filtrate of sea anemone aqueous extract after i.p. injection into 20 g male mice.

Toxic fraction	Dry weight of 100 ml extract (g)	Toxicity level of 100 ml extract (MU) Mean±SE	Toxicity (%)	Toxicity level of dry material (MU/g)	Toxicity (%)
Crude	41.77	198±5.9	100	47.4	100
<10 KD	36.16	171±6.8	86.4	47.3	99.6
< 5 KD	31.25	130±4.7	65.7	41.6	87.6
< 3 KD	31.60	132±9.0	66.7	41.8	88.0
< 1 KD	31.60	105±13.3	53.0	33.2	69.9
<0.5 KD	26.45	107±9.6	54.0	40.5	85.3

The mouse assay was also used to follow the toxicity of the freeze-dried filtrate (less than 500 Dalton) after fractionation on Biogel P2. The toxic fractions were detected in the first bed volume of the water elution. Two groups of toxic fractions were observed, the first started at 65 % bed volume and ended at 70 % while the second less toxic fractions came at 91 % and lasted until the 95 % bed volume. Buckley spot test showed that the toxic fractions have two different colors with ninhydrin, purple to brown for the highly toxic first group and yellow color for the second toxic group. These two toxic fractions proved to have different mode of actions.

An HPLC method was adopted to detect the HPLC peak responsible for toxicity in order to trace the toxic compound(s) in further purification steps and to determine percent purity of the isolated toxic compound(s) as a preparation for attempting to elucidate the structure of the responsible active compound(s).

Solar Lake cyanobacterial toxin

The Solar Lake is a hypersaline small pond on the northeast of the Sinai coast at the Gulf of Aqaba. The depth of the lake ranges from 4 to 6 m, depending on the time of year (Por 1968). A period of holomixing is observed in the Solar Lake during the summer where temperature, salinity, and oxygen distribution are homogenous. In fall, stratification of the lake starts to build up and lasts for 9-11 months. The surface salinity of the lake is 35 ppt where the hypersaline water reaches 180 ppt. The lake has an inverse temperature profile where surface water temperature is 16°-20° C, thermocline up to 60.2° C, and bottom around 45° C (Cohen et al. 1977a).

The cyanobacterial mat of the Solar Lake were classified and defined according to their location of the lake water surface to "shallow flat mat" (develops under few centimeters of water) "deep flat mat" (develops under about 30 cm of water) and "gelatinous mats" at the deep bottom water of the lake (Jørgensen et al. 1983). *Oscillatoria limnetica* bloom at the bottom of the lake during stratification is responsible for the facultative anoxygenic photosynthesis (Cohen et al. 1977b). Toxic *Oscillatoria* has been reported in both marine and fresh water habitats (Skulberg et al. 1992, Carmichael 1997).

Neurotoxicity and hepatotoxicity were reported in the toxic bloom of blue-green algae. Neurotoxins are produced primarily by species of *Anabaena flos-aquae* and *Aphanizomenon flos-aquae*. Hepatotoxins were first reported to be produced by *Microcystis aeruginosa* and are, therefore, referred to as microcystins. Other species of blue-green algae however, such as *Anabaena* sp. and *Oscillatoria* sp. also produce microcystins. Microcystins are small proteins that cause extensive liver hemorrhage when ingested. A lethal dose of microcystin will cause liver damage and death in 2-24 hours (Carmichael 1992).

Cyanobacterial toxins still constitute a major source of natural product toxins, "biotoxins", found in surface supplies of freshwater. Known neurotoxin producers are still found only within species and strains of *Anabaena, Aphanizomenon, Oscillatoria* and *Trichodesmium*. Hepatotoxin microcystins and nodularin are produced by strains and species within the genera

Microcystis, Anabaena, Hapalosiphon, Nodularia, Nostoc and *Oscillatoria* (Carmichael 1997). Guanidine alkaloid hepatotoxin, cylindrospermopsin is produced by *Cylindrospermopsis raciborskii* (Hawkins et al., 1985).

Individual cases of poisoning and survey reports over the last few years continue to show that a significant number of blooms are toxic in any given area. In the majority of cases, however, the same type of toxin has been found to be responsible. This includes the hepatotoxic microcystins and nodularins and the neurotoxic anatoxins and saxitoxins (Falconer 1993).

The mouse bioassay which was typically the first test for toxicity in screening algal toxins is rapidly being replaced by other bioassays, chemical and immunological methods (Carmichael 1997). Bacterial assay (*Staphylococcus aureus* and *Candida albicans*) has been used to test the production of bioactive material from thermotolerant *Phormidium* (Fish and Codd 1994). Brine shrimp (*Artemia salina*) was used to detect toxicity of microcystin from *Microcystis* (Campbell et al. 1994).

Toxic *Oscillatoria* has been reported in both marine and fresh water habitat. Toxicity was found in *Oscillatoria nigroviridis* (Mynderse et al. 1977), in *Oscillatoria acutissima* (Barchi et al. 1984), in *Oscillatoria vaucher* sp. (Sivonen et al. 1989), in *Oscillatoria agardhii* (Oestensvik et al. 1981, Sano and Kaya 1995, Shin et al. 1995), in benthic *Oscillatoria* sp. (Edwards et al. 1992), and in *Oscillatoria formosa* (Skulberg et al. 1992, Hemscheidt et al. 1995b). The structure and site of action of *Oscillatoria late-virens* metabolite was studied and its use as an algicide (herbicide) has been documented (Bagchi 1995).

Results

Toxic cyanobacterial samples of *Oscillatoria limnetica* collected from the Solar Lake, Taba, Sinai was extracted and purified. Both the crude and semi pure extracts of the toxic cyanobacteria were subjected to different bioassays to test their toxic effect on mammals, insects, and some selected microorganisms.

The LD_{50} of *Oscillatoria limnetica* crude extract against *Musca domestica, Spodopetra littoralis* and *Agrotis ipsilon* larvae were 1.9, 7.6, and 9.1 µg/insect respectively while the LC_{50} of *Culex pipens* was 233 ppm.

No activity was detected in crustacean brine shrimp (*Artemia salina*) with concentrations reaching 2000 ppm. Also, no activity was detected in 10 species of phytopathogenic fungi after exposure to different concentrations that reached up to 1600 ppm.

Purification of the *Oscillatoria limnetica* crude extract on molecular weight exclusion filters decreased the LD_{50} against mice from 2891 to 2010 mg/kg (30.5 %) and against *Musca domestica* from 1.9 to 1.1 µg/insect (42 %). The highest decrease in LD_{50} due to the application of the purified material was observed in the case of *Spodopetra littoralis* where the LD_{50} decreased from 7.6 to 1.6 µg/insect (79 %).

The calculated LD_{50} of the crude extract for *Musca domestica* was 100 mg/kg indicating a

Tab. 2: Toxicity level of cyanobacterial mat crude extract and different filtrates after 1 ml i.p. injection in 20 g male mice of 150 mg/ml.

Toxic filtrates	Toxicity level (MU) Mean±S.E.	Dry weight (mg/ml)
Crude	1.35 ± 0.08	11.0
less than 10,000 Dalton	1.67 ± 0.08	82.4
less than 5,000 Dalton	1.66 ± 0.22	78.2
less than 3,000 Dalton	1.66 ± 0.09	74.9
less than 1,000 Dalton	2.25 ± 0.12	68.2
less than 500 Dalton	2.11 ± 0.07	69.8

higher susceptibility (~29 fold) of insects compared with mice to the *Oscillatoria limnetica* toxic extract suggesting the safety of using such toxins as a pesticide.

Table 2 showed the dry weight and toxicity level in Mouse Units per ml filtrate after freeze drying of 100 ml of the crude extract and from each filtrate. The toxicity was detected until the filtrate of less than 500 Dalton, and no toxicity was detected in the retained material. No significant differences were found among the toxicity of the 10, 5, and 3 K Dalton filtrates and among the 1000 and 500 Dalton filtrates. The toxicity level of the 500 D filtrates increased to 2.11 MU compared to the crude extract which recorded 1.35 MU. The dry weight of the crude extract decreased from 110 mg/ml to 69.8 mg/ml for the 500-Dalton filtrate. Toxic filtrate (less than 1000 Dalton) was freeze-dried and its toxicity profile (Fig. 3) showed that the threshold was at 100 mg/ml with a plateau at 200 mg/ml.

Aqueous toxic extract was further purified using gel filtration column chromatography. A reverse phase HPLC technique (isocratic elution with 2 % acetonitrile aqueous solution adjusted to pH 2.5 with phosphoric acid and UV detection at 254 nm) was used to detect the toxic compound in the crude cyanobacterial extracts of the Solar Lake. Toxic and non-toxic fractions of the gel filtration were used to identify the responsible peak for toxicity by HPLC. The isolated toxin from the HPLC was freeze-dried and checked for channel blocking activity. The pure material is under investigation for structure elucidation.

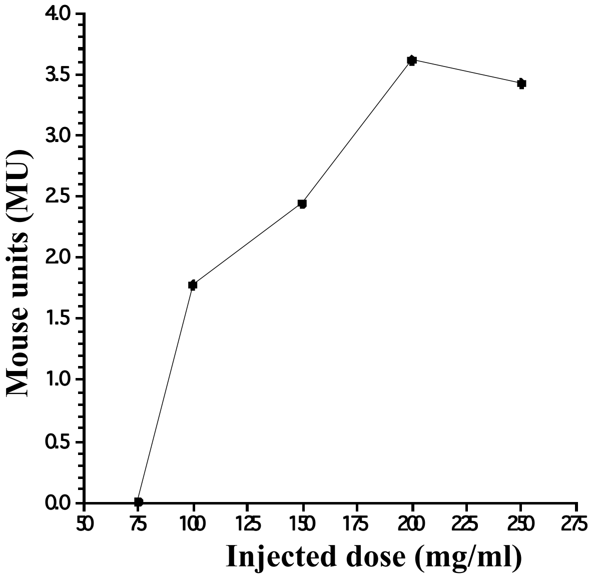

Fig. 3:
Dose response curve of semi pure filtrate (<1000 D) of cyanobacterial mat collected from the Solar Lake.

Fresh water cyanobacterial toxin(s)

Neurotoxicity was detected in the cyanobacterial samples collected from cyanobacterial winter bloom of the Egyptian fresh water environment. Aqueous extraction of the cyanobacterial samples was performed using ultrasonication to disrupt the algal cells. Ultrafiltration showed that the toxic compound(s) was observed in the fraction below 500 Dalton. The responsible organism for toxin production proved to be *Lyngbya limnetica*. Toxic filtrate (less than 500 Dalton) was freeze-dried and its toxicity profile showed that the threshold was at 7.5 mg/ml. No toxicity was detected at 5 mg/ml and a plateau was found at 20 mg/ml where no significant differences were detected between 20, 22.5, and 25 mg/ml (Fig. 4). The toxin was found to be a sodium channel blocker and completely reversible.

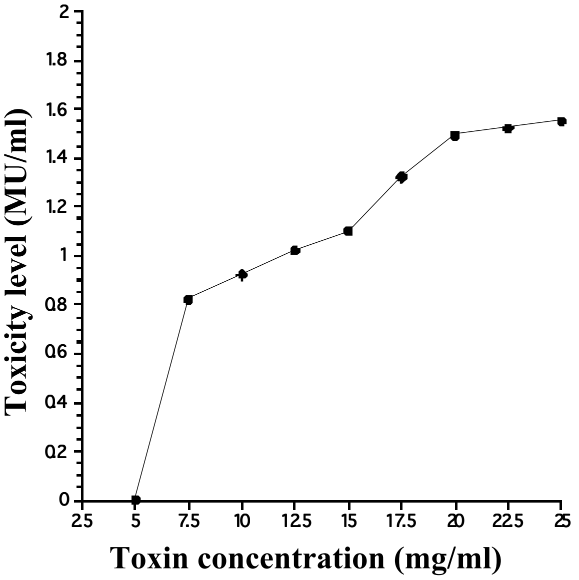

Fig. 4:
Dose responce curve in mice after i.p. injection of less than 500 Dalton filtrate of the fresh water cyanobacteria *Lyngbya limnetica.*

Electrophysiological analysis of neurotoxic peptides from cone snails

Arik Hasson, Yana Shtern and Micha E. Spira

Department of Neurobiology, The Hebrew University of Jerusalem and
The Interuniversity Institut, H. Steinitz Marine Biological Laboratory, Eilat

Introduction

Venoms are used by animals for prey capture or as a defense mechanism. They consist of a mixture of substances which are produced in specialized glandular tissues or within single cells and are introduced into the prey by a specialized apparatus. The majority of venomous animals are static or slow in respect to their prey. The inferior locomotory abilities of the venomous predator are compensated for by specialized behavioral adaptations such as ambush hunting and by the development of immobilizing venoms and apparatus to transfer the venom. The most efficient paralyzing venoms consist of compounds that interfere with the functions of neurons, muscles and synapses. These compounds are collectively referred to as neurotoxins.

Neurotoxins are usually classified according to their pharmacological functions and sites of action:

(A) Modulators of action potential generation and propagation,

(B) Presynaptically active neurotoxins that interfere with neurotransmitter release,

(C) Toxins that block ligand-gated channels.

The majority of the well characterized and commonly utilized neurotoxins are neurotoxins directed toward vertebrates. A significantly smaller number of neurotoxins directed toward invertebrate have been identified. Because of small chemical and structural differences between vertebrate and invertebrates neurotoxins binding sites, “vertebrate neurotoxins” do not recognize functional targets of invertebrate nervous systems. For example, the concentrations of tetrodotoxin (TTX), required to block the neuronal sodium channels of the marine mollusc *Aplysia* are three orders of magnitude greater than those required to block sodium channels of vertebrates. Another example is w-conotoxin-GVIA, a well known blocker of the vertebrate's presynaptic calcium channels, which does not block voltage gated calcium channels of *Aplysia*.

In the present study we identified, isolated and characterized novel neurotoxins that can be utilized as research tools and provide useful lead compounds for the development of new biocides and pharmacological agents for clinical use.

We based our study on the assumption that the feeding specificity of cone snails is expressed by the unique pharmacological properties of the venom's neuropeptides.

Cone snails and conotoxins

The Conidae are a large family of approximately 500 species of marine snails which are venomous predators (Gray et al. 1988, Olivera et al. 1990, Olivera et al. 1991b). To capture prey, the victim is mechanically harpooned by the cone snail with a disposable hollow tooth through which the venom is injected (Olivera et al. 1990).

On the basis of their feeding and hunting behavior *Conus* snails are subdivided into fish eaters (piscivorous), mollusc eaters (molluscivorous) and worm eaters (vermivorous) (Olivera et al. 1990).

Cone snails have developed a unique biochemical hunting strategy. The venom of each species contains over 20 small neurotoxic peptides, called conotoxins. These peptides bind with high selectivity to neuronal and muscular receptors and thereby alter their activity. The pharmacological diversity and specificity of conotoxins is among the highest of venomous animals (Olivera et al. 1990, Olivera et al. 1991b). These peptides are among the smallest and most stable toxins that are encoded by nucleic acids (Gray et al. 1988. Olivera et al. 1990, Olivera et al. 1991b). The stability of conotoxins is achieved mainly through high disulfide bonding. In the majority of known toxins, other than conotoxins, the disulfide bonding is composed of cysteine residues that are evenly distributed throughout the length of the peptide. This "even" distribution requires the formation of fairly long peptides to enable the correct folding of the peptide. *Conus* peptides, on the other hand, are assembled from intermediate-sized propeptide molecules (Olivera et al. 1990, Olivera et al. 1991b). The cysteines that contribute to the disulfide bonding of these propeptides are present only at the COOH-terminal. After the secretion and folding of these molecules, the disulfide-rich C-terminal end of these propeptides is proteolytically cleaved to form small rigid toxins that are highly cross-linked by disulfide bridges. Therefore, the amino acids that are important for the interaction of the mature toxin with its target are those required for the correct folding of the propeptide (Olivera et al. 1990, Olivera et al. 1991b). This mode of biosynthesis leads to formation of small peptides (12-34 amino acids) that are well defined in their three dimensional structures (Gray et al. 1988, Olivera et al. 1990, Olivera et al. 1991b).

Although a great diversity exists among peptides of *Conus* venoms, their major peptidic contents, the conotoxins, display in most cases one of three characteristic arrangements of cysteine residues: A “2-loop” scaffold (CC---C---C); a “3-loop” scaffold (CC---C---C---CC) and a “4-loop” scaffold (C--C---CC---C---C) (Olivera et al. 1991b). The 4-loop framework has been shown to exist in over 29 *Conus* peptides. This group forms what is known now as the O-super family of conotoxins. These conotoxins have a wide range of pharmacological activities (Olivera et al. 1995, Olivera et al. 1994).

The biochemical targets strategy of piscivorous cone snails

The "main concern" of the piscivorous cone snails in hunting fish is the superior speed of the fish escape response. Accordingly, the piscivorous cone snails evolved two hunting adaptations: The first, a behavioral adaptation in the form of ambush or web-hunting (a physical net that facilitates the capture of prey) and the second, a neurotoxic adaptation, the development of toxins that almost instantaneously paralyze the envenomated fish.

The rapid fish paralysis is achieved by the blockade of the neuromuscular apparatus at three critical sites by three classes of polypeptide conotoxins:

(a) The w-conotoxins that block voltage gated calcium currents at the presynaptic terminals, thus preventing the release of acetylcholine,

(b) The a-conotoxins which block the postsynaptic acetylcholine receptor,

(c) The m-conotoxins that block the generation of muscle membrane action potentials (Cruz et al. 1976, Cruz et al. 1978, Olivera et al. 1985a, Olivera et al. 1984, Olivera et al. 1990; Olivera et al. 1991b).

In contrast to the very large body of knowledge accumulated on conotoxins derived from piscivorous cone snails, only a very small number of studies was devoted to the characterization of conotoxins derived from molluscivorous and vermivorus Conidae. The studies performed in our laboratory (Fainzilber et al. 1991; Hasson, MSc thesis 1991) were the first studies in which an analysis of a purified neurotoxin of a molluscivorous cone snail were provided.

The "neuropharmacological strategy" of molluscivorous cone snails

The neuropharmacology of molluscan muscle membrane and neuromuscular junctions differs from that of vertebrates. Unlike vertebrates, the majority of molluscan muscles are non spiking and the contraction is controlled by the graded amplitude and summation of post junctional potentials. Accordingly, muscle contraction or neuronal sodium channels of molluscs are not blocked by m-conotoxin derived from piscivorous Conidae.

The neurotransmitter of molluscan neuromuscular junctions is glutamatergic. Thus, a-conotoxins derived from fish hunting cone snails are inefficient in molluscs. The acetylcholine (ACh) receptors in the mollusc central nervous system (CNS) are relatively insensitive to vertebrate ACh receptors antagonists and are not blocked by a-conotoxins derived from fish hunting cone snails (Fainzilber et al., 1994a).

Finally, voltage gated presynaptic calcium channels of molluscs are not blocked by w-conotoxins derived from fish-eating cone snails' venoms. These observations suggested that the molluscivorous cone snails had to develop a set of specialized neurotoxins that recognize the relevant physiological target molecules in molluscs.

The present study undertook to isolate and characterize the mechanism of action of major neurotoxic components in molluscivorous and vermivorous cone snails' venoms directed toward their natural prey. For the study we used *Aplysia* neurons in primary cultures and intentionally focused our investigation on the isolation, identification and characterization of neuropeptide directed toward:

(a) voltage gated neuronal sodium channels,

(b) voltage gated calcium channels and

(c) neuronal acetylcholine receptors.

Because of the limited amounts of cone snails collected within the RSP the research was conducted using *Penaceous* toxins collected prior to the establishment of the RSP in the Gulf of Aqaba and conotoxin provided by B. M. Olivera and J. M. McIntosh.

Summary of the main observations

(A) In collaboration with Prof. W. Stühmer we identified INa blocking activity in the venom of *C. arenatus.*

(B) 7 novel neuroactive peptide fractions and 17 potentially active fractions isolated from 3 species of molluscivorous cone snails were identified. Out of these fractions we characterized the mode of action of 4 major novel conotoxins: d-conotoxin-GmVlA, μ-conotoxin-PnIVB, μO-conotoxin-MrVIA/μO-conotoxin-MrVIB and a-conotoxin-PnIA isolated from *Conus gloriamaris, C. pennaceus, C. marmoreus*, and *C. pennaceus,* respectively. The study led to the identification of a new conotoxin super-family that is now termed the O-super family (Fainzilber et al. 1991, Hasson et al. 1993, Spira et al. 1993, Fainzilber et al. 1994a, Shon et al. 1994, Shon et al. 1995, Hasson et al. 1995a, Hasson et al. 1995b).

Two neuropharmacological target strategies are utilized by the molluscivorous species:

(A) Induction of epileptic like movements of the envenomed snail prey into and out of its shell enabling its consumption. These epileptic like movements are the outcome of increased excitability resulted from delayed inactivation rates of the macroscopic voltage-gated sodium currents.

(B) Induction of flaccid paralysis which is due to decreased excitability and blockade of action potential formation. These effects are the outcome of blockade of the voltage-gated sodium channels. In addition we found that within this category nic-AChRs, Ca^{2+} channels or both are also blocked.

<u>d-GmVlA</u>

The novel conotoxin d-GmVlA derived from the venom of *Conus gloriamaris* increases action potential duration by slowing down the inactivation rate of the macroscopic voltage-gated sodium current.

(A) The toxin modifies the sodium current inactivation kinetics from a single exponential to a slower decay which can be described by two time constants. At high toxin concentrations it is difficult to differentiate between the two time constants. The changes in the inactivation time constants may account for the typical alterations in the action potential shape induced by d-GmVlA.

(B) The toxin shifts the steady-state inactivation (H_∞) curve to the positive potential direction and the steady-state activation m_∞) curve to the negative potentials.

(C) d-GmVlA binds to the external side of *Aplysia* sodium channels in a 1:1 ratio.

(D) At d-GmVlA concentrations > 1.5 µM the peak I_{Na^+} is increased to 120 % of the current amplitude in control runs. The E.C.$_{50}$ for this effect was 0.62±0.114 µM.

(E) The effects of d-GmVlA are completely reversed by depolarizing prepulse.

m-PnIVA

The novel conotoxin m-PnIVA derived from the venom of *Conus pennaceus* blocks the generation and propagation of action potentials by blocking voltage-gated sodium channels without any effect on other ionic current.

(A) Partial blockade of the sodium current by the toxin, is not associated with alterations in either the current voltage relations of the current and its reversal potential or the H_∞ and m_∞ curves of the sodium current.

(B) µ-PnIVB binds to the external side of *Aplysia* sodium channel in a 1:1 ratio.

(C) Complete I_{Na^+} blockade by µ-PnIVB occurred at 90±9.95 nM the I.C.$_{50}$ was at 15.2±1.82 nM and nH (Hill coefficient) was 1±0.175.

mO-MrVIA

The novel conotoxin mO-MrVIA derived from the venom of *Conus marmoreus* blocks the generation and propagation of action potentials by blocking voltage-gated sodium channels without any effect on potassium currents.

(A) Blockade of the sodium current by the toxin is not associated with alterations of either current-voltage relationships and their reversal potential or the m_∞ curve of the sodium current.

(B) Blockade of the sodium current is associated with a negative shift of the steady-state inactivation curve.

(C) In addition to the blockade of sodium channel of *Aplysia*, mO-MrVIA also blocks the inactivating calcium current in that preparation. Complete I_{Na^+} blockade by mO-MrVIA occurred at 180±27.95 nM, I.C.$_{50}$ was at 69±4.34 nM and nH was 1.6±0.32 (n=6). Complete $I_{Ca^{2+}}$ blockade occurred at 98±6.98 mM, I.C.$_{50}$ was at 2.6±0.216 mM and nH was 0.79±0.11.

(D) The ability of mO-MrVIA to block the voltage-gated I_{Na^+} is almost completely reversed by long depolarizing conditioning prepulses. However, the blockade of $I_{Ca^{2+}}$ is not affected by depolarization.

(E) Dose response measurements of I_{Na^+}/[µO-MrVIA] in the presence of d-GmVlA revealed negative cooperativity between the binding sites of these toxins that share cysteinic scaffold and additional homologies.

mO-MrVIA and mO-MrVIB are 30 aminoacid isotoxins. MrVIA and MrVIB have a common cysteine framework but differ from each other by three amino acids. We assume that the substitution of arginine at position 3 by Serine reduces the positive charge of MrVIB in respect to MrVIA. This substitution may be sufficient to cause the significant reduction in the calcium current blocking efficiency of MrVIB while the other neuropharmacological characteristics of the two isotoxins remain similar.

The differences and similarities in the functions of the two isoforms are summarized below.

(A) The effectiveness of the two isoforms as calcium current inhibitors of cultured *Aplysia* neurons is significantly different. The $I.C._{50}$ of MrVIA is 2.5 µM and that of MrVIB is ~ 40 µM. We cannot compare the concentration that induces complete blockade of the calcium current as we never reached this value for MrVIB. The $I.C._{50}$ of MrVIA for the sodium current is ~70 nM and that of MrVIB ~90 nM. Complete blockade of the sodium current by MrVIA is observed at ~0.2 µM, while at ~1 µM by MrVIB.

(B) The peak values and reversal potentials of the sodium and calcium currents are not altered by the isotoxins.

(C) While MrVIA shifts the values of the sodium current steady state inactivation curve toward negative values by approximately 6 mV (from-28.5 mV to -22 mV), MrVIB does not alter this parameter. The slope value of the sodium inactivation curve is not altered by either MrVIA or MrVIB (s=5.2±0.2).

(D) The Ca^{2+} current inactivation or activation curves are unaffected by both isotoxins.

(E) The decrease charge of MrVIB does not eliminate the dependence of sodium current blocking action on the trans membrane voltage.

(F) While the $I.C._{50}$ of the two isotoxins toward the sodium channels is similar, the slopes of their dose response relationship curves are different. That of MrVIA is 1.6 while that of MrVIB is 2.4. This values suggests two binding sites of MrVIB and MrVIA to a sodium channel. Nevertheless, the suggestion of positive cooperativity confirmed by the sigmoidal form of the dose response curve may account for the good fit between the experimental data (MrVIB: $I.C._{50}$= 90 nM) and the linear regression equation (MrVIB: K_d=100 nM).

By comparison of the neuropharmacological properties of the two isotoxins MrVIA and MrVIB, we showed that the substitution of a single aminoacid may underlie significant alterations in the affinity of the conotoxin to the calcium channels.

a-PnIVA

The novel conotoxin a-PnIVA derived from the venom of *Conus pennaceus* blocks the acetylcholine receptors of *Aplysia*. This is the first a-conotoxin shown to affect ACh receptors of molluscs.

The main observations that were made within the sponsorship of the RSP are summarized in the PhD thesis of Dr. Arik Hasson and the MSc thesis of Mrs. Yana Shtern.

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Oxygen, sulfur and carbon cycling in Solar Lake microbial mats

Henk M. Jonkers, Andrea Wieland and Dirk de Beer

Max-Planck-Institut für Marine Mikrobiologie, Bremen

Solar Lake microbial mats were chosen as a model ecosystem to study the microbial cycling of oxygen, sulfur and carbon into detail. These hypersaline mats are characterized by high rates of primary productivity, but a low yearly biomass accretion. The latter phenomenon is probably due to high rates of organic carbon remineralization (Cohen and Krumbein 1977). These mats are dominated, in terms of biomass, by unicellular and filamentous cyanobacteria, the main primary producers in this system (Krumbein et al. 1977). The cyanobacteria produce, in addition to oxygen, organic metabolites which can be mineralized by aerobic and anaerobic heterotrophic bacteria. Carbon dioxide, a major substrate for cyanobacteria, is regenerated in this way. CO_2 is probably a rate limiting substrate for photosynthesis due to diffusion limitations in these dense mats as is indicated by strong pH increases in the top layer of the sediment during the photosynthetic period (Jørgensen et al. 1983). In this two-fold study, research focused on:

1) the effect of the environmental parameters temperature and light on the regulation of oxygen and sulfur cycling and

2) the (in)organic carbon cycling in Solar Lake mats. Microsensor-, nuclear magnetic resonance-imaging, radiotracer-, molecular- and culturing techniques were used to elucidate the respective phenomena.

Microsensor measurements in Solar Lake mats revealed that temperature strongly affected gross- and net photosynthesis as well as oxygen consumption and sulfide production (Wieland and Kühl 2000). Areal rates of gross and net photosynthesis were maximal at 30° C, i.e. close to the *in situ* temperature of the natural habitat (Fig. 1). Sulfide production increased strongly with temperature leading to saturation of sulfide oxidation capacity and even sulfide efflux out of the mat (Fig. 1). It was thus concluded that a temperature increase above the *in situ* conditions results in an increase in the ratio respiration/photosynthesis, i.e. decreased primary production.

Nuclear Magnetic Resonance (NMR) imaging was used to investigate the diffusive properties of microbial mats in two dimensions (Wieland et al., accepted). Pulsed Field Gradient NMR revealed changes in the H_2O diffusion coefficient (D_S), while multi-echo imaging NMR yielded images of the water density in Solar Lake mats (Fig. 2). Both water density and diffusion coefficient were found to correlate with the laminated and heterogeneous distribution of microbial cells and exopolymers within the mat. It was shown that for correct analysis of

Fig. 1: Temperature depence of oxygen-, photosynthesis-, pH- and sulfide profiles.

oxygen profiles with a diffusion-reaction model the variations in diffusivity must be taken into account.

The tight coupling between organic and inorganic carbon pools was demonstrated in mixed culture incubation experiments using isolates of various microorganisms obtained from Solar Lake microbial mats. Cyanobacteria excrete glycolate during periods of high photosynthetic activity as a consequence of the oxygenase reaction of the CO_2-fixing enzyme ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco) due to a high ratio of oxygen and CO_2. We hypothesized that a mutual beneficial relationship exists between cyanobacteria and aerobic

Fig. 2: Effect of diffusivity on the analysis of O_2 profiles (A) and profile of the average diffusivity in a microbial mat (B)

heterotrophs in these CO_2 diffusion-limited ecosystems: Organic carbon released by cyanobacteria is directly mineralized by aerobic heterotrophs resulting in regeneration of photosynthesis-limiting CO_2. The activity and growth characteristics of mixed cultures of the cyanobacterium *Dactylococcopsis salina* and aerobic heterotrophic glycolate-using strains were compared with axenic cultures of *Dactylococcopsis salina*. No additional organic carbon source was provided to the cultures. In these experiments it was demonstrated that specific

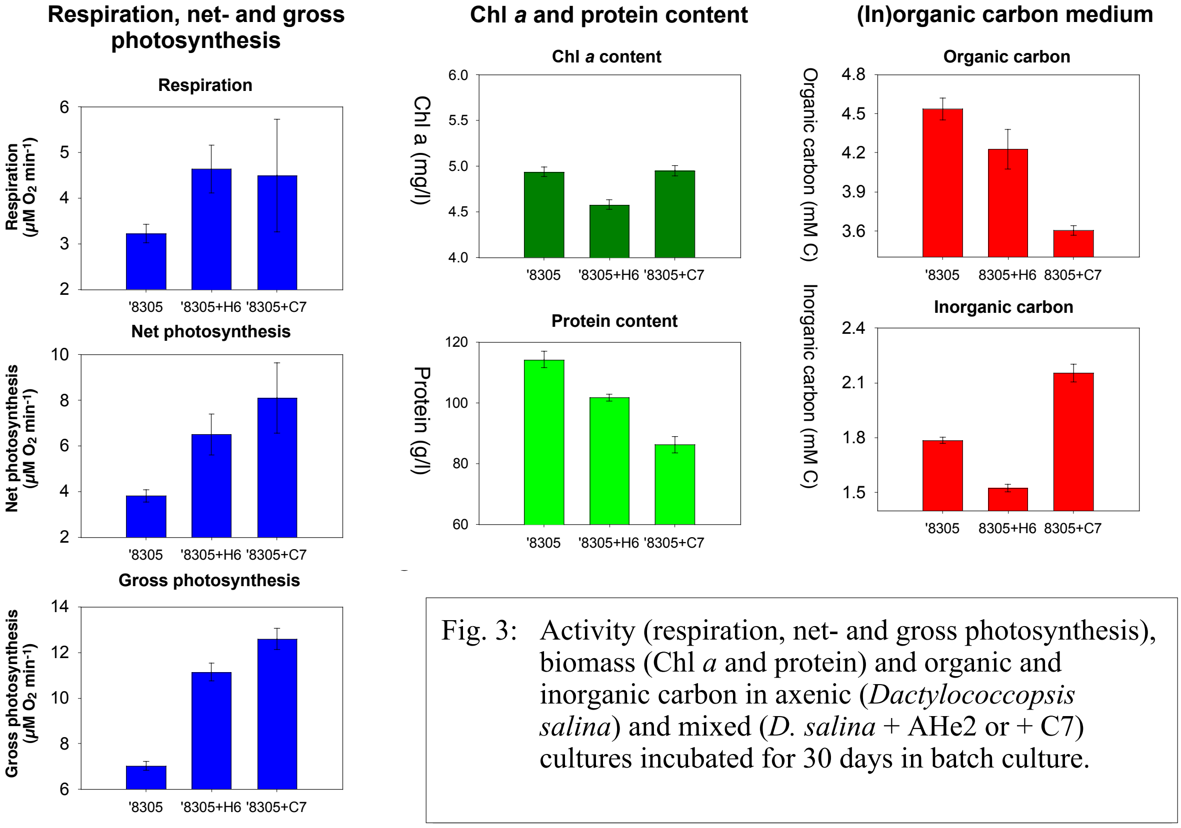

Fig. 3: Activity (respiration, net- and gross photosynthesis), biomass (Chl *a* and protein) and organic and inorganic carbon in axenic (*Dactylococcopsis salina*) and mixed (*D. salina* + AHe2 or + C7) cultures incubated for 30 days in batch culture.

respiration, net- and gross photosynthetic rates were significantly higher in mixed cultures and, moreover, that mixed cultures contained less organic but more inorganic carbon what suggests that excreted organic carbon was converted to inorganic carbon. However, protein and chlorophyll *a* measurements revealed that axenic cyanobacterial cultures produced significantly more biomass than mixed cultures (Fig. 3). Thus, in mixed cultures a tight coupling exists between organic carbon production and consumption, but simultaneously competition occurs for growth-limiting nutrients. The isolated aerobic heterotrophic glycolate-using strains could be classified in two major groups with respect to substrate utilization patterns. One group consisted of strains specialized in utilization of low weight fatty acids and alcohols, typically C-1 to C-4 compounds, while the other group consisted of strains which could degrade higher molecular weight carbohydrates (glucose and related compounds). The substrate utilization patterns of both groups suggest that they may play an important role in the mineralization of cyanobacterial metabolites such as low molecular weight fermentation and photo-oxidation products, and high molecular weight extracellular polymeric substances respectively. Sequencing of the 16S rRNA genes of all isolates revealed that they all cluster phylogenetically in the alpha-proteobacteria. Present research tries to elucidate the spatial organization of these heterotrophs and cyanobacteria in microbial mats using species specific fluorescent labeled 16S rRNA gene probes.

Radio-tracer experiments were performed with mixed cultures of dominant Solar Lake microbial mat organisms to demonstrate organic carbon flow from cyanobacteria to heterotrophic microorganisms. Two unicellular strains and one filamentous strain of cyanobacteria (*Aphanothece halophytica* PCC 7418, *Synechococcus* PCC 7003 and *Microcoleus chthonoplastes* PCC 7420) were pre-incubated in the light with $H^{14}CO_3^-$, enabling them to produce labeled organic storage compounds. These cultures were subsequently washed and incubated together with the aerobic heterotrophic bacteria strain AHe and AHe7, and the purple sulfur bacterium *Halochromatium glycolicum*, and the sulfate-reducing bacteria *Desulfovibrio oxyclinae* and *Dv. halophilus*. These mixed cultures were incubated under oxic/light and anoxic/dark conditions, mimicking the day and night situation in a microbial mat. In a parallel experiment mixed cultures were incubated with ^{14}C-labeled pyruvate. The respective transfer and uptake of labeled compounds by the non-cyanobacterial species could be demonstrated using MAR-FISH (Micro-Auto Radiography Fluorescent In Situ Hybridization) technique. Interestingly, under aerobic conditions significant uptake of organic compounds by both sulfate-reducing bacteria and aerobic heterotrophs was observed. These results demonstrate that during photosynthesis sulfate-reducing bacteria may successfully compete with aerobic heterotrophic bacteria for cyanobacterial metabolites in microbial mats.

Our multi-disciplinary approach contributed to fundamental understanding of the oxygen, sulfur and carbon cycles in microbial benthic ecosystems.

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Molecular mechanisms underlying microbial ecology in the Red Sea: Niche adaptation in marine unicellular and filamentous Cyanobacteria

Debbie Lindell[1], Quingfeng Wang[1], Hong Li[1], Rudi Gottlieb[1], Hanne Frøhlich[2], Ulrich Sommer[2] and Anton F. Post[1]

1) The Interuniversity Institute, H. Steinitz Marine Biological Laboratory, Eilat
2) Institut für Meereskunde an der Universität Kiel, Kiel

Introduction

Phytoplankton communities in oligotrophic seas often thrive under nutrient deplete conditions and nitrogen, phosphorus and iron may each become the limiting factor for primary productivity. The northern Red Sea and the Gulf of Aqaba are examples of such oligotrophic systems. Their open waters are populated with phytoplankton communities dominated by picophytoplankton (unicellular algae <2µm). The picophytoplankton community structure responds strongly to changes in nutrient availability. In winter-mixed, nutrient-replete waters one observes a dominance of eukaryotic algae, whereas prokaryotic phytoplankton dominates the stratified surface layers in summer (Lindell and Post 1995). High desert dust levels over the Gulf of Aqaba likely avoid the occurrence of iron limitation, but picophytoplankton may become limited by phosphorus (Li et al. 1998). Likewise the nitrogen-fixing cyanobacterium *Trichodesmium* may become P limited during its bloom season (Stihl et al. in press). However, in general nitrogen is believed to be the limiting nutrient for primary production in these waters.

Assessment of the productivity or growth limiting factor is an issue of much debate. There is no “easy way” of determining the limiting nutrient along depth profiles or over a given span of time. Our aim is to develop molecular probes (based on DNA, RNA, antibodies) which report on nutrient stress responses in unicellular phytoplankton species. Our main effort has focused on the *ntcA* gene, which encodes a regulatory gene required for the early steps of response to nitrogen stress in the marine cyanobacteria *Synechococcus* WH7803 (Lindell et al. 1998) and *Trichodesmium* WH9601 (Wang et al., in prep.). *NtcA* is a DNA binding protein involved in the transcriptional regulation of nitrogen acquisition and metabolism genes in cyanobacteria. The expression of *ntcA* in *Synechococcus* WH7803, present as a single copy gene, is down-regulated in the presence of ammonium, and is essential for adaptation to nitrate-nitrite utilization as well as other N-sources (Lindell et al. 1998, 1999). Specifically, *ntcA* transcription occurred when cells were supplied with MSX and azaserine, inhibitors of ammonium metabolism, glutamine synthetase and glutamate amino-transferase. This finding indicates that ammonium mediates the repression of *ntcA*, but is not the effector molecule. RNA analyses revealed the presence of two transcript populations of which the larger transcript was identified as a constitutive message and the smaller transcript as the induced message. The constitutive message was always found at a constant, basal level. The induced message is found only when ammonium has been deprived, regardless of whether an alternative N source is present or not. We have demonstrated that *ntcA* is expressed under environmentally relevant conditions and that it is an informative probe for use in field studies (Lindell et al., submitted). The gene is transcribed when ammonium concentrations drop below 1 μM. No transcript accumulated when cultures were deprived of phosphorus or iron, showing that *ntcA* responded to nitrogen stress specifically. Its transcription occurs as a rapid response (less than 2 hours for maximal expression) to ammonium limitation and upon addition of ammonium transcript levels decline with a half time of 2-3 minutes (Lindell et al. 1998). *ntcA* was specifically amplified from marine cyanobacterial species, but not from heterotrophic bacteria, phototrophic bacteria and eukaryotic algae. A gene tree based on *ntcA* sequences of PCR products from a number of *Prochlorococcus* and *Synechococcus* strains was markedly similar to a tree based on 16S rDNA sequences. This tree allowed to distinguish different clades of *Synechococcus* and *Prochlorococcus*, some of which had representatives in Gulf of Aqaba phytoplankton communities (Lindell et al., unpubl. res.). All these findings together provide a firm basis for studies of differential *ntcA* expression among natural phytoplankton of the Gulf of Aqaba and the northern Red Sea. A protocol for *in situ ntcA* expression studies has been developed and allows to distinguish ammonium sufficiency (basal expression) from the utilization of alternative N sources (intermediate expression) and N deprivation (maximal expression).

Whereas *Synechococcus* forms an omnipresent component of phytoplankton, one finds the filamentous cyanobacterium *Trichodesmium* only during summer. This colony-forming, nitrogen-fixing species may populate the N-deplete surface layers with blooms in excess of 100,000 colonies per m^3 (Gottlieb et al., unpubl. res.). *Trichodesmium* blooms contribute an approximate 10 % of annual primary production in the Gulf of Aqaba and form a significant influx of new nitrogen. Based on the observations on *Synechococcus* spp. one would expect *ntcA* to be required for adaptation to N-deplete conditions and development of a nitrogen-fixation potential. True as this might be, *ntcA* displays a different mode of action in *Trichodesmium*. *NtcA* was identified in three *Trichodesmium* sp. cultures, cloned for the axenic strain WH9601 as a 9.0 kb DNA fragment and sequenced with its flanking regions (Wang et al., unpubl. res.). RT-PCR analysis of *ntcA* expression in *Trichodesmium* sp. strain WH9601 revealed that *ntcA* was not repressed by ammonium at concentrations up to 2 mM. However, transcription of a nitrogenase gene and a nitrate transporter gene was largely repressed when cells were exposed to elevated ammonium concentrations. Expression of these genes was upregulated in an indiscriminate manner once ammonium was absent from the medium and cells were dependent on either nitrogen fixation or nitrate utilization to meet their N-demands. *ntcA* message levels declined under these conditions. These findings suggest that *ntcA* is involved in the regulation of N-metabolism of *Trichodesmium*, but acts as a repressor of transcription rather than as an activator, which was the case for the non nitrogen-fixing *Synechococcus*. *NtcA* is thus not suited as a probe for assessing the N-status of *Trichodesmium* populations.

Lastly, as part of our RSP activities, we have identified a novel cyanobacterial nitrate transporter encoded by *napA*, present in the marine *Trichodesmium* but not in freshwater cyanobacteria (Wang et al. 2000). Cloning of the gene and its subsequent expression in a mutant strain of *Bacillus subtilis*, impaired in nitrate uptake, proved its function as a cyanobacterial nitrate transporter. The gene was then identified in marine *Synechococcus* strains and present efforts are directed to identifying this gene in *Prochlorococcus* as well. Related research has provided genomic sequence information along with phenotypic properties of a *napA*$^-$ mutant of *Synechococcus* sp. WH7803 indicating that nitrite utilization can be uncoupled from nitrate uptake and reduction in this species. The nitrite and nitrate utilization potential are co-expressed in all known freshwater cyanobacteria as well as in the marine *Trichodesmium* sp.

Our findings show that marine cyanobacteria are a group of photosynthetic prokaryotes with a similar genetic make-up for adaptation to N-limiting environments. However, to fine-tune this adaptation potential and meet the requirements of their ecological niche they employ additional genetic tools: 1) genomic rearrangements, allowing genes to be expressed as operons or as individual genes, and 2) different transcriptional regulation, like *NtcA* mediated activation vs. repression of N-gene expression.

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Distribution and diversity of *Archaea* corresponding to the limnological cycle of a hypersaline stratified lake (Solar Lake, Sinai, Egypt)

Eddie Cytryn[1], Dror Minz[1], Ronald S. Oremland[2] and Yehuda Cohen[1]

1) Division of Microbial and Molecular Ecology and The Moshe Shilo Minerva Center for Marine Biogeochemistry, Institute of Life Sciences, Hebrew University of Jerusalem, Jerusalem
2) U.S. Geological Survey, Menlo Park, California

Abstract

The vertical and seasonal distribution and diversity of archaeal sequences was investigated in a hypersaline, stratified, monomictic lake, Solar Lake, Sinai, Egypt, during the limnological development of stratification and mixing. Archaeal sequences were studied via phylogenetic analysis of 16S rDNA sequences as well as denaturing gradient gel electrophoresis analysis. The 165 clones studied were grouped into four phylogenetically different clusters. Most of the clones isolated from both the aerobic epilimnion and the sulfide-rich hypolimnion were defined as cluster I, belonging to the Halobacteriaceae family. The three additional clusters were all isolat-ed from the anaerobic hypolimnion. Cluster II is phylogenetically located between the genera *Methanobacterium* and *Methanococcus*. Clusters III and IV relate to two previously documented groups of uncultured euryarchaeota, remotely related to the genus *Thermoplasma*. No crenarchaeota were found in the water column of the Solar Lake. The archaeal community in the Solar Lake under both stratified and mixed conditions was dominated by halobacteria in salinities higher than 10 %. During stratification, additional clusters, some of which may pos-sibly relate to uncultured halophilic methanogens, were found in the sulfide- and methane-rich hypolimnion.

(full text in "Appl. Environ. Microbiol. 66, 3269-3276")

Unexpected population distribution in a microbial mat community: Sulfate-reducing bacteria localized to the highly oxic chemocline in contrast to a eukaryotic preference for anoxia

Dror Minz[1], Susan Fishbain[1], Stefan J. Green[1], Gerard Muyzer[2], Yehuda Cohen[3], Bruce E. Rittmann[1] and David A. Stahl[1]

1) Department of Civil Engineering, Northwestern University, Evanston, Illinois
2) Max-Planck-Institut für Marine Mikrobiologie, Bremen
3) The Moshe Shilo Center for Marine Biogeochemistry, Alexander Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Jerusalem

Abstract

The distribution and abundance of sulfate-reducing bacteria (SRB) and eukaryotes within the upper 4 mm of a hypersaline cyanobacterial mat community were characterized at high resolution with group-specific hybridization probes to quantify 16S rRNA extracted from 100-µm depth intervals. This revealed a preferential localization of SRB within the region defined by the oxygen chemocline. Among the different groups of SRB quantified, including members of the provisional families “Desulfovibrionaceae” and “Desulfobacteriaceae,” *Desulfonema*-like populations dominated and accounted for up to 30 % of total rRNA extracted from certain depth intervals of the chemocline. These data suggest that recognized genera of SRB are not necessarily restricted by high levels of oxygen in this mat community and the possibility of significant sulfur cycling within the chemocline. In marked contrast, eukaryotic populations in this community demonstrated a preference for regions of anoxia.

(full text in "Appl. Environ. Microbiol. 65(10), 4659-4665")

Diversity of sulfate-reducing bacteria in oxic and anoxic regions of a microbial mat characterized by comparative analysis of dissimilatory sulfite reductase genes

Dror Minz[1], Jodi L. Flax[1], Stefan J. Green[1], Gerard Muyzer[2], Yehuda Cohen[3], Michael Wagner[4], Bruce E. Rittmann[1] and David A. Stahl[1]

1) Department of Civil Engineering, Northwestern University, Evanston, Illinois
2) Max-Planck-Institut für Marine Mikrobiologie, Bremen
3) The Moshe Shilo Center for Marine Biogeochemistry, Alexander Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Jerusalem
4) Technische Universität München, Lehrstuhl für Mikrobiologie, München

Abstract

Sequence analysis of genes encoding dissimilatory sulfite reductase (DSR) was used to identify sulfate-reducing bacteria in a hypersaline microbial mat and to evaluate their distribution in relation to levels of oxygen. The most highly diverse DSR sequences, most related to those of the *Desulfonema*-like organisms within the ∂-proteobacteria, were recovered from oxic regions of the mat. This observation extends those of previous studies by us and others associating *Desulfonema*-like organisms with oxic habitats.

(full text in "Appl. Environ. Microbiol. 65(10), 4666-4671")

Transition from anaerobic to aerobic growth conditions for the sulfate-reducing bacterium *Desulfovibrio oxyclinae* results in flocculation

Pavel Sigalevich, Eran Meshorer, Yael Helman and Yehuda Cohen

Division of Microbial and Molecular Ecology, Moshe Shilo Minerva Center for Marine Biogeochemistry,
Institute of Life Sciences, Hebrew University of Jerusalem, Jerusalem

Abstract

A chemostat culture of the sulfate-reducing bacterium *Desulfovibrio oxyclinae* isolated from the oxic layer of a hypersaline cyanobacterial mat was grown anaerobically and then subjected to gassing with 1 % oxygen, both at a dilution rate of 0.05 h^{-1}. The sulfate reduction rate under anaerobic conditions was 370 nmol of SO_4^{2-} mg of $protein^{-1}$ min^{-1}. At the onset of aerobic gassing, sulfate reduction decreased by 40 %, although viable cell numbers did not decrease. After 42 h, the sulfate reduction rate returned to the level observed in the anaerobic culture. At this stage the growth yield increased by 180 % compared to the anaerobic culture to 4.4 g of protein per mol of sulfate reduced. Protein content per cell increased at the same time by 40 %. The oxygen consumption rate per milligram of protein measured in washed cell suspensions increased by 80 %, and the thiosulfate reduction rate of the same samples increased by 29 % with lactate as the electron donor. These findings indicated possible oxygen-dependent enhancement of growth. After 140 h of growth under oxygen flux, formation of cell aggregates 0.1 to 3 mm in diameter was observed. Micrometer-sized aggregates were found to form earlier, during the first hours of exposure to oxygen. The respiration rate of *D. oxyclinae* was sufficient to create anoxia inside clumps larger than 3 µm, while the levels of dissolved oxygen in the growth vessel were 0.7±0.5 µM. Aggregation of sulfate-reducing bacteria was observed within a *Microcoleus chthonoplastes*-dominated layer of a cyanobacterial mat under daily exposure to oxygen concentrations of up to 900 µM. *Desulfonema*-like sulfate-reducing bacteria were also common in this environment along with other nonaggregated sulfate-reducing bacteria. Two-dimensional mapping of sulfate reduction showed heterogeneity of sulfate reduction activity in this oxic zone.

(full text in "Appl. Environ. Microbiol. 66(11), 5005-5012")

Sulfate reduction and possible aerobic metabolism of the sulfate-reducing bacterium *Desulfovibrio oxyclinae* in a chemostat coculture with *Marinobacter* sp. strain MB under exposure to increasing oxygen concentrations

Pavel Sigalevich[1], Mark V. Baev[1], Andreas Teske[2] and Yehuda Cohen[1]

1) Division of Microbial and Molecular Ecology, Moshe Shilo Minerva Center for Marine Biogeochemistry,
Institute of Life Sciences, Hebrew University of Jerusalem, Jerusalem
2) Woods Hole Oceanographic Institution, Woods Hole

Abstract

A chemostat coculture of the sulfate-reducing bacterium *Desulfovibrio oxyclinae* together with a facultative aerobe heterotroph tentatively identified as *Marinobacter* sp. strain MB was grown under anaerobic conditions and then exposed to a stepwise-increasing oxygen influx (0 to 20 % O_2 in the incoming gas phase). The coculture consumed oxygen efficiently, and no residual oxygen was detected with an oxygen supply of up to 5 %. Sulfate reduction persisted at all levels of oxygen input, even at the maximal level, when residual oxygen in the growth vessel was 87 µM. The portion of *D. oxyclinae* cells in the coculture decreased gradually from 92 % under anaerobic conditions to 27 % under aeration. Both absolute cell numbers and viable cell counts of the organism were the same as or even higher than those observed in the absence of oxygen input. The patterns of consumption of electron donors and acceptors suggest that aerobic incomplete oxidation of lactate to acetate is performed by *D. oxyclinae* under high oxygen input. Both organisms were isolated from the same oxic zone of a cyanobacterial mat where they have to adapt to daily shifts from oxic to anoxic conditions. This type of syntrophic association may occur in natural habitats, enabling sulfate-reducing bacteria to cope with periodic exposure to oxygen.

(full text in "Appl. Environ. Microbiol. 66(11), 5013-5018")

Oxygen-dependent growth of the sulfate-reducing bacterium *Desulfovibrio oxyclinae* in coculture with *Marinobacter* sp. strain MB in an aerated sulfate-depleted chemostat

Pavel Sigalevich and Yehuda Cohen

Division of Microbial and Molecular Ecology, The Moshe Shilo Minerva Center for Marine Biogeochemistry,
The Institute of Life Sciences, The Hebrew University of Jerusalem, Jerusalem

Abstract

A chemostat coculture of the sulfate-reducing bacterium *Desulfovibrio oxyclinae* and the facultatively aerobic heterotroph *Marinobacter* sp. strain MB was grown for 1 week under anaerobic conditions at a dilution rate of 0.05 h^{-1}. It was then exposed to an oxygen flux of 223 µmol min^{-1} by gassing the growth vessel with 5 % O_2 . Sulfate reduction persisted under these conditions, though the amount of sulfate reduced decreased by 45 % compared to the amount reduced during the initial anaerobic mode. After 1 week of growth under these conditions, sulfate was excluded from the incoming medium. The sulfate concentration in the growth vessel decreased exponentially from 4.1 mM to 2.5 µM. The coculture consumed oxygen effectively, and no residual oxygen was detected during either growth mode in which oxygen was supplied. The proportion of *D. oxyclinae* cells in the coculture as determined by *in situ* hybridization decreased from 86 % under anaerobic conditions to 70 % in the microaerobic sulfate-reducing mode and 34 % in the microaerobic sulfate-depleted mode. As determined by the most-probable-number (MPN) method, the numbers of viable *D. oxyclinae* cells during the two microaerobic growth modes decreased compared to the numbers during the anaerobic growth mode. However, there was no significant difference between the MPN values for the two modes when oxygen was supplied. The patterns of consumption of electron donors and acceptors suggested that when oxygen was supplied in the absence of sulfate and thiosulfate, *D. oxyclinae* performed incomplete aerobic oxidation of lactate to acetate. This is the first observation of oxygen-dependent growth of a sulfate-reducing bacterium in the absence of either sulfate or thiosulfate. Cells harvested during the microaerobic sulfate-depleted stage and exposed to sulfate and thiosulfate in a respiration chamber were capable of anaerobic sulfate and thiosulfate reduction.

(full text in "Appl. Environ. Microbiol. 66(11), 5019-5023")

Annex

Annex 1

Research Participants of RSP

	Name		**Affiliation**	**Institution**
Egyptian	Abass Madkor	Mr. Hashem	PhD student (F)	NIOF, Hurghada
	Ali	G. H.	PhD student	NIOF
	Ali Yousef	Mr. Emad	PhD student (E)	NRC, Cairo
	Abd El Kreem	Mr. S.	PhD student (A)	NIOF, Barrag
	Abd El-Monem	Dr. Ahmed	scientist (A, Theme I)	NIOF, Cairo
	Abd El Radi	Mr. Mohammed	PhD student (F)	NIOF, Hurghada
	Aboul-Enein	Prof. Dr. Nabil	PI (G, Theme IV)	NIOF, Cairo
	Amin	Prof. Dr. Ekram	President	NIOF, Cairo
	Awad	Mr. Mohammed H. H.	PhD student (B)	NIOF, Suez
	Badawi	Prof. Hussein	former President	NIOF, Cairo
	Badawi	Miss Ama Fawzi	PhD student (D)	NIOF, Alexandria
	Beltagy	Prof. Ali	PI (D)	NIOF, Alexandria
	Dowidar	Dr. Magdy	scientist (Theme I)	NIOF, Alexandria
	El Absawi	Mr. Mohammed	PhD student (C)	NIOF, Alexandria
	El Azoni	Dr. Aida	scientist (E)	NRC, Cairo
	El-Bishbishi	Dr. Mohammed	scientist	NIOF, Alexandria
	El-Gharabawi	Dr. M.	PI (C)	NIOF, Alexandria
	El-Ibiary	Ahmed I.	SSC	NIOF, Cairo
	El Naggar	Mr. Atef	PhD student (C)	NIOF, Alexandria
	El-Samra	Prof. Dr. Mohammed	PI (B)	NIOF, Suez
	El-Wahab	Mr. Mohamed	student (F)	NIOF
	Geneid	Mr. Yasser A. H.	PhD student (B)	NIOF, Suez
	Gomaa	Dr. Mohamed Nasr	PI (E/G)	NIOF, Cairo
	Hamdi	Mr. Emad	PhD student (A)	NIOF, Barrag
	Hussein	Dr. Khamis A.	Vice President	NIOF, Cairo
	Ibrahim	Prof. Dr. Ezzat	PI (A)	NIOF, Cairo
	Maiyza	Dr. Ibrahim	PI (Theme I)	NIOF, Alexandria
	Moneer Hilal	Mr. Amro	PhD student (A)	NIOF, Barrag
	Moustafa	Dr. Yaser	scientist (F, Theme III)	GeoB, NIOF
	Naguib	Prof. Khayria M.	PI (E)	NIOF, Cairo
	Naguib	Prof. Mohammed	PI (E)	NRC, Cairo
	Nawar	Prof. Dr. Ahmed H.	PI (F)	NIOF, Hurghada
	Rahman	Dr. Nasser Saber A.	scientist (A, Theme I)	NIOF, Suez
	Shabana	Mr. E. F.	scientist (Theme IV)	
	Shokry Amar	Dr. Mohammed	scientist (F)	NIOF, Suez
	Taha	Dr. Ola El-Din	scientist (A, Theme I)	NIOF, Cairo
	Wahb Allah	Mr. Ahmed	PhD student (F)	NIOF, Hurghada
	(El-Saadani	Mrs. Rawia	financial officer	NIOF, Cairo)

Annex 1 (cont.)

	Name		Affiliation	Institution
German	de Beer	Dr. Dirk	scientist (Theme IV)	MPIMM
	Felis	Dr. Thomas	PhD stud. (F, Theme III)	GeoB
	Frøhlich	Mrs. Hanne	PhD student (C)	IfM
	Häse	Dr. Clivia	PostDoc (A, Theme I)	IUI/ZMT/DLR
	Hempel	Prof. Dr. Gotthilf	Internat. Coord./ SSC/ PI	ZMT
	Hüttel	Dr. Markus	Theme IV	MPIMM
	Jørgensen	Prof. Dr. Bo Barker	PI (E, Theme IV)	MPIMM
	Jonkers	Dr. Henk	scientist (Theme IV)	MPIMM
	Kappner	Mrs. Isabella	MSc stud. (Aqaba Proj.)	ZMT
	Kochzius	Mr. Mark	PhD stud. (Aqaba Proj.)	ZMT
	Kötter	Mrs. Iris	PhD stud. (NEBROC)	ZMT
	Kühl	Dr. Michael	scientist (E)	MPIMM
	Kumbartzky	Mr. Guido	MSc stud. (Aqaba Proj.)	ZMT
	Maack	Mr. Thilo	MSc stud. (Aqaba Proj.)	ZMT
	Munkes	Mrs. Britta	MSc stud. (Aqaba Proj.)	ZMT
	Pasenau	Mrs. Ilka	MSc stud. (Aqaba Proj.)	ZMT
	Pätzold	Dr. Jürgen	PI (F, Theme III)	GeoB
	Penner	Dr. Reinhold	PI (D)	MPIBC
	Richter	Dr. Claudio	PI (B; II; Aqaba) / Secr.	ZMT
	Sommer	Prof. Dr. Ulrich	PI (C, Theme I)	IfM
	Sinschek	Mrs. Kathrin	MSc stud. (Aqaba Proj.)	ZMT
	Stihl	Mrs. Andrea	PhD student (C)	IfM
	Stühmer	Prof. Dr. Walter	PI (G)	MPIEM
	Tilzer	Prof. Dr. Max	PI (A, Theme I)	Univ. Konstanz
	Thomas	Dr. David	PostDoc (A)	AWI
	Vesper	Mrs. Heike	MSc stud. (Aqaba Proj.)	ZMT
	Voigt	Mr. Alexander	MSc stud. (Aqaba Proj.)	ZMT
	Wefer	Prof. Dr. Gerold	PI (F, Theme III)	GeoB
	Wieland	Dr. Andrea	PhD stud. (E, Theme IV)	MPIMM
	Wunsch	Dr. Mark	PhD stud. (Aqaba Proj.)	ZMT
	Zopfi	Dr. Jacob	PhD stud. (E, Theme IV)	MPIMM
Israeli	Baranes	Dr. Avi	SSC	IUI
	Belousov	Mr. Vladimir	PhD stud. (A, Theme I)	Bar Ilan Univ.
	Bentov	Mr. Shmuel	MSc student (D)	Hebrew Univ.
	Berkovitch	Mr. A.	MSc student (D)	Hebrew Univ.
	Berman-Frank	Dr. I.	scientist (D)	IUI
	Brokovich	Mr. Eran	PhD stud. (B, Theme II)	IUI
	Cohen	Prof. Dr. Yehuda	PI (E, Theme IV)	Hebrew Univ.
	Cytryn	Mr. Eddie	MSc stud. (E, Theme IV)	Hebrew Univ.
	Dubinsky	Prof. Dr. Zvy	PI (Theme I)	Bar Ilan Univ.
	Erez	Prof. Dr. Jonathan	PI (D, Theme III)	IUI

Annex 1 (cont.)

	Name		Affiliation	Institution
Israeli	Feldstein	Mr. Tamar	MSc student (B)	IUI
	Fine	Mr. Maoz	student (F)	IUI
	Genin	Dr. Amatzia	PI (B, Theme I)	IUI
	Gottlieb	Mr. Rudi	MSc student (C)	Tel Aviv Univ.
	Hasson	Dr. Arik	PhD student (G)	Hebrew Univ.
	Helman	Mr. Yahel	MSc (E)	IUI
	Iluz	Dr. David	PhD student (A)	Bar Ilan Univ.
	Kamenir	Dr. Yury	(Theme I)	IUI
	Kaplan	Dr. A.	(Theme I)	IUI
	Kimor	Prof. Dr. Baruch	(Theme I)	Technion
	Kizner	Dr. Zvy	(Theme I)	
	Klein	Dr. Ramy	PostDoc (F)	IUI
	Laor	Mr. Ronit	MSc student (E)	Hebrew Univ.
	Lazar	Dr. Boaz	PI (A)	Hebrew Univ.
	Li	Dr. Hong	scientist (C)	IUI
	Lindell	Dr. Debbie	scientist (C)	IUI
	Loya	Prof. Dr. Yossi	PI (F)	Tel Aviv Univ.
	Mamdjanov	Mrs. Irena	MSc stud. (Theme IV)	Hebrew Univ.
	Meidani	Mrs. Inbal	MSc student (D)	Hebrew Univ.
	Meshorer	Mr. Eran	MSc student (E)	IUI
	Minz	Dr. Dror	scientist (Theme IV)	Hebrew Univ.
	Nahari	Mr. Ronen	MSc student (E)	Hebrew Univ.
	Post	Dr. Anton	PI (C)	IUI
	Raz	Mr. Michal	MSc student (D)	Hebrew Univ.
	Rosenfeld	Mr. Micha	PhD student (F)	Tel Aviv Univ.
	Schneider	Mr. Kenneth	MSc student (D)	Hebrew Univ.
	Shtern	Mrs. Yana	MSc student (G)	Hebrew Univ.
	Sigalevich	Dr. Pavel	PhD student (E)	Hebrew Univ.
	Silverman	Mr. Jack	PhD student (A)	
	Sokoletsky	Mr. Leonid	PhD stud. (A, Theme I)	Bar Ilan Univ.
	Spira	Prof. Dr. Micha	PI (G)/ SSC	Hebrew Univ.
	Stambler	Dr. Noga	PI (A, Theme I)	Bar Ilan Univ.
	Wang	Dr. Quingfeng	PostDoc (C)	Hebrew Univ.
	Yahel	Mr. Gitai	PhD stud. (B, Theme II)	Hebrew Univ.
	Yahel	Mrs. Ruthi	PhD stud. (B, Theme II)	Hebrew Univ.
	Yaari	Mr. G.	MSc student (E)	Hebrew Univ.
	Zask	Mr. Alon	MSc student (E)	Hebrew Univ.

Annex 1 (cont.)

	Name		**Affiliation**	**Institution**
Palestinian	Abdeen	Prof. Dr. Ziad	PI(G) / SSC	Al Quds Univ.
	Al-Barghuthy	Mr. Fikry	student	Al Quds Univ.
	Al-Qutob	Dr. Mutaz	PhD / PI (A, Theme I)	Al Quds Univ.
	Farrah	Mr. Karim	MSc (A)	Al-Najah Univ., Al Quds Univ.
	Ghrayeb	Mr. Raed	MSc (A)	Al-Najah Univ., Al Quds Univ.
	Khater	Dr. Issa	PI (A) / SSC	PCG
Jordanian	Abu-Hilal	Prof. Dr. Ahmad	PI (Aqaba Project)	MSS
	Al-Horani	Mr. Fuad	PhD stud. (AqabaProj.)	MSS/MPIMM
	Al-Moghrabi	Dr. Salim	PI (Aqaba Project)	MSS
	Al-Najjar	Dr. Tariq	PhD stud. (Aqaba Proj.)	MSS/IfM
	Al-Rousan	Mr. Saber	PhD stud. (Aqaba Proj.)	MSS
	Al-Sabi	Mr. Ahmed	MSc stud. (Aqaba Proj.)	MSS
	Al-Sokhny	Mr. Khaled	MSc stud. (Aqaba Proj.)	MSS
	Al-Zereini	Wael	MSc stud. (Aqaba Proj.)	MSS/MPIMM
	Badran	Dr. Mohammad I.	PI (Aqaba Project)	MSS
	El-Zibdeh	Dr. Mohammad	PI (Aqaba Project)	MSS
	Froukh	Mr. Tawfiq	MSc stud. (Aqaba Proj.)	MSS
	Kanaan	Mrs. Nemeh	MSc stud. (Aqaba Proj.)	MSS
	Khalaf	Dr. Maroof	PI (Aqaba Project)	MSS
	Manasreh	Mr. Riyad	PhD student	MSS
	Odat	Mr. Nidal	MSc stud. (Aqaba Proj.)	MSS
	Rasheed	Mr. Mohammad	PhD student	MSS/MPIMM

Annex 2
Publications during RSP I and RSP II

I. Oceanic system of the Gulf of Aqaba

Al-Najjar, T. (2000): The seasonal dynamics and grazing control of phyto- and mesozooplankton in the northern Gulf of Aqaba. Dissertation, Universität Bremen, Germany, 121pp

Al-Qutob, M., Lazar, B., and Häse, C.: Does phytoplankton drive nitrite dynamics in the Gulf of Aqaba, Red Sea? (submitted to the ASLO Aquatic Sciences Meeting, 2001, Albuquerque, USA)

Badran, M. I.: Evidence from long term records on high summer new primary production in the oligitrophic waters of the Gulf of Aqaba, Red Sea. (submitted to the ASLO Aquatic Sciences Meeting, 2001, Albuquerque, USA)

Belousov, V., Dubinsky, Z., and Stambler, N.: High frequency fluctuations of the underwater light field in the Gulf of Eilat. (manuscript)

Dowidar, M., and Richter, C.: Mesozooplankton communities in the Gulf of Aqaba and northern Red Sea. (manuscript)

Farstey, V., B. Lazar, and Genin, A.: Homogeneous vertical distribution of oceanic zooplankton in a deep mixed layer. (in revision)

Genin, A., McGehee, D., and Jaffe, J.S.: On the anisotropic nature of zooplankton swimming: *in situ* observations using a three-dimensional acoustic imaging system. (submitted)

Genin, A.: Vertical motions of water and zooplankton in coastal waters. (in prep.)

Genin, A., Jaffe, J., Richter, C., Ahmed, A. A., Ayalon, I., Ohevia, M., and McGehee, D.: The behavioral response of zooplankton to downwelling: Sir Alister's plankton wheel revisited. (submitted to the ASLO Aquatic Sciences Meeting 2001, Albuquerque, USA)

Gottlieb, R. (1998): Seasonal abundance, primary productivity and nitrogen fixation in *Trichodesmium* populations in the Gulf of Eilat. MSc thesis, Tel Aviv University, Israel, 72pp

Häse, C.: Phytoplankton productivity during the mixing season in the Gulf of Aqaba. (submitted to the ASLO Aquatic Sciences Meeting, 2001, Albuquerque, USA)

Häse, C., Dubinsky, Z., Erez, J., Iluz, D., Al-Qutob, M., Lazar, B., Stambler, N., and Tilzer, M. M.: Seasonal and vertical patterns of the primary production in the Gulf of Aqaba Red Sea. (in prep.)

Häse, C., Al-Qutob, M., Lazar, B., Dubinsky, Z., Stambler, N., and Tilzer, M. M.: Co-limitation of phytoplankton productivity by nitrogen and phosphorus in the Gulf of Aqaba, Red Sea. (in prep.)

Häse, C., Dubinsky, Z., Ibrahim, E.A., Lazar, B., Abdel Monem, A., Al-Qutob, M., Iluz, D., Stambler, N., Taha, O.E., Tilzer, M. M.: Nutrient versus energy limitation of phytoplankton productivity in the Gulf of Aqaba during deep winter mixing. (in prep.)

Häse, C., Ibrahim, E. A., Lazar, B., Abdel-Monem, A., Al-Qutob, M., Iluz, D., Stambler, N., Taha, O.E., Tilzer, M. M., and Dubinsky, Z.: The deep chlorophyll maximum in the northern Red Sea: Depth distribution, composition, and photosynthetic potential. (in prep.)

Hamed, A. R. Hassan (1998): Hydrography of the Gulf of Aqaba. MSc thesis, Cairo University, Egypt, 60pp (not directly RSP financed)

Iluz, D. (1997): The light field, phytoplankton pigmentation and productivity in the Gulf of Eilat. PhD thesis, Dept. of Life Sciences, Bar-Ilan University, Ramat-Gan, Israel, 169pp

Iluz, D.: The optical properties of the underwater light field in the Gulf of Aqaba. (submitted to Mar. Ecol. Progr. Ser.)

Iluz, D., Stambler, N., and Dubinsky, Z.: The underwater light field in the Gulf of Elat (Aqaba), Red Sea. (submitted to the ASLO Aquatic Sciences Meeting, 2001, Albuquerque, USA)

Kamenir, Y., Brenner, S., Dubinsky, Z., Häse, C., Iluz, D., Lazar, B., Al-Qutob, M., Sokoletsky, L., and Stambler, N.: Time-spatial structure of Gulf Elat plankton community: A simulation model. (submitted to Ecological Modelling)

Lazar, B., Erez, J., Dadashev, A., Al-Quotob, M., and Luz, B.: Indirect estimation of export production from observed decreases in oxygen concentration within the aphotic zone of the Gulf of Aqaba (manuscript)

Li, H., Veldhuis, M. W. J., and Post, A. F. (1998): Alkaline phosphatase activities among planktonic communities in the northern Red Sea. Mar. Ecol. Prog. Ser., 173:107-115

Lindell D., Padan E., and Post A. F. (1998): Regulation of *ntcA* expression and nitrite uptake in the marine *Synechococcus* sp. strain WH7803. J. Bacteriol. 180 (7), 1878-1886

Manasreh, R. (1998): Water circulation in Jordanian waters of the Gulf of Aqaba, Red Sea. MSc thesis, Yarmouk University, Jordan, 112pp

Post, A. F., Dedej, Z., Gottlieb, R., Li, H., and Sommer, U.: *Trichodesmium* population dynamics in surface waters of the northern Red Sea. (manuscript)

Sokoletsky, L., Dubinsky, Z., Shoshany, M., and Stambler, N.: Modelling of solar flux and atmospheric transmittance in cloudy conditions: Comparison of the Gulf of Aqaba (Eilat) with other sites in Israel and abroad. (submitted to Solar Energy)

Sokoletsky, L., Dubinsky, Z., Shoshany, M., and Stambler, N.: Bio-optical and remote sensing methods of the estimation of phytoplankton concentration in the Gulf of Aqaba (Eilat). (submitted to Deep-Sea Research)

Sommer, U. (2000): The scarcity of medium sized phytoplankton in the northern Red Sea explained by strong bottom-up and weak top-down control. Mar. Ecol. Progr. Ser. 197, 19-25

Stambler, N.: The underwater light field in the Gulf of Aqaba (Eilat), Red Sea: Influence of phytoplankton and non-living substances (1995-2000). (submitted to the ASLO Aquatic Sciences Meeting, 2001, Albuquerque, USA)

Stambler, N., Dubinsky, Z., and Iluz, D.: Photoacclimation of phytoplankton in the Gulf of Aqaba: Evidence from flow cytometry. (in prep.)

Stambler, N., Dubinsky Z., Iluz, D., and Lazar, B.: Influence of phytoplankton and non-living substances on the underwater-light field in the Gulf of Aqaba, Red Sea. (in prep.)

Stihl, A., Sommer, U. and Post, A.: Are natural populations of the marine, diazotrophic cyanobacterium *Trichodesmium* in the Red Sea limited by P-availability? (submitted J. Phycol.)

Tilzer, M. M.: The Gulf of Aqaba: Climatic conditions as main determinants of primary productivity. (submitted to the ASLO Aquatic Sciences Meeting, 2001, Albuquerque, USA)

Wang, Q., Li, H., and Post, A. (2000): Nitrate assimilation genes of the marine diazotrophic, filamentous cyanobacterium *Trichodesmium* sp. strain WH 9601. J. Bacteriol. 182 (6), 1764-1767

II. Ecology of coral reefs

Al-Rousan, S. (1998): Sediment role in nutrient cycle within the coral reefs of the Gulf of Aqaba, Red Sea. MSc thesis, Yarmouk University, Jordan, 133pp

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Zopfi, J. (2000): Speciation and transformation of sulfur intermediates in stratified ecosystems – A comparative study. Dissertation, Universität Bremen, Germany, 131pp

Annex 3

MSc- and PhD- Theses in the Framework of RSP

Proj. Theme	**Name**		**Institute/ University**	**Title** **(completed in...)**
A, I	M. Al-Qutob	(PhD)	Al Quds Univ.	Nutrient distribution and dynamics in the Gulf of Aqaba. **(2000)**
A	M. S. Abd El Kreem	(PhD)	NIOF	
A	H. Hassan	(MSc)	Cairo University	Hydrography of the Gulf of Aqaba. **(1998)**
A	D. Iluz	(PhD)	Bar-Ilan	The light field, phytoplankton pigmentation and productivity in the Gulf of Eilat. **(1997)**
A	Amro Moneer Hilal	(PhD)	NIOF	
A	J. Silverman	(PhD)	Hebrew Univ.	
A, I	L. Sokoletsky	(PhD)	Bar-Ilan	Bio-optical and remote sensing methods for estimation of phytoplankton concentrations in the Gulf of Aqaba (Eilat).
A, I	V. Belousov	(PhD)	Bar-Ilan	The underwater light fields fluctuations in the Gulf of Aqaba.
A	R. Ghrayeb	(MSc)	Al-Najah Univ.	Short-term varaitions in the abundance of phytoplankton near a coral reef.
B	M. H.H. Awad	(PhD)	NIOF	
B, II	E. Brokovich	(MSc)	Tel Aviv Univ.	Reef fish communities and biodiversity in the northern Gulf of Aqaba, Eilat.
B, I	A. K. Farrah	(MSc)	Al-Najah Univ.	Short-term varaitions in the abundance of zooplankton near a coral reef.
B	T. Feldstein	(MSc)	IUI	
B, II	M. Wunsch	(PhD)	ZMT/Bremen	Exploration of structure and trophodynamics of coelobite (cavity-dwelling) communities in Red Sea coral reefs. **(2000)**
B, II	G. Yahel	(PhD)	Hebrew Univ.	Sources and sinks of phytoplankton and dissolved organic carbon in coral reefs: From individual filter feeders to community scales.
B, II	R. Yahel	(PhD)	Hebrew Univ.	Diel dynamics of zooplankton, organic and inorganic particles in waters over coral reefs.
B, II	A. Youssef	(PhD)	Univ. Alexandria	Ichthyology of butterflyfish larvae in the northern Red Sea. (deceased 27.1.99)
C	M. El Absawi	(PhD)	NIOF	
C	A. El Naggar	(PhD)	NIOF	
C	H. Frøhlich	(PhD)	IfM	(left the project Febr. 1997)
C	R.Gottlieb	(MSc)	IUI/Tel Aviv Univ.	Seasonal abundance, primary productivity and nitrogen fixation in *Trichodesmium* populations in the Gulf of Eilat. **(1998)**
C	A. Stihl	(PhD)	IfM/Kiel	Regulation of phosphate acqisition in *Trichodesmium.* (left the project Dec.1998)
D	A. F. Badawi	(PhD)	NIOF	
D	S. Bentov	(MSc)	Hebrew Univ.	Biomineralization processes in foraminifera. **(1998)**

Annex 3 (cont.)

Proj. Theme	Name		Institute/ University	Title (completed in...)
D	I. Meidani	(MSc)	Hebrew Univ.	Ca-metabolism in foraminiferal ameboids using imaging techniques. **(2000)**
D	R. Michal	(MSc)	Hebrew Univ.	
D	H. Schneider	(MSc)	Hebrew Univ.	The effects of pH and CO_2(aq), on the isotopic fractionation of corals. **(2000)**
F	F. Barghuthy	(PhD)	Al Quds Univ.	(left the project)
E	E. Cytryn	(MSc)	Hebrew Univ.	Diversity and distribution of *Archaea* correlated to the limnological conditions in a startified hypersaline lake (Solar Lake, Sinai). **(1999)**
E	E. Hamdi	(PhD)	NIOF	
E	Y. Helman	(MSc)	Hebrew Univ.	Development and application of two dimensional mapping of sulfate reduction activity across O_2 – H_2S. **(1997)**
E	I. Mamadjanov	(MSc)	Hebrew Univ.	Biodegradation of petrolium by cyanobacterial mats. **(1999)**
E	E. Meshorer	(MSc)	Hebrew Univ.	Shifts in community structure of cyanobacteria and sulfate reducing bacteria following exposure to crude oil. **(1999)**
E	R. Laor	(MSc)	Hebrew Univ.	Community structure of sulfate reducing bacteria in the Solar Lake during annual limnological cycle by dsr phylogeny.
E	R. Nahari	(MSc)	Hebrew Univ.	Structure of sulfate reducing bacteria in the chemocline of the Solar Lake.
E	P. Sigalevich	(PhD)	Hebrew Univ.	Physiology of oxygen-tolerant sulfate reducing bacteria in a hypersaline cyanobacterial mat (Solar Lake, Sinai). **(2000)**
E	E. Ali Yousef	(PhD)	NIOF	
E, IV	A. Wieland	(PhD)	MPIMM/Bremen	Microsensor analysis of oxygen and sulfide turnover in hypersaline microbial mats. **(1999)**
E	G. Yaari	(MSc)	Hebrew Univ.	Fluxes of oxygen in Solar Lake cyanobacterial mats following exposure to oil compounds.
E	A. Zask	(MSc)	Hebrew Univ.	Nitrogen species in the Solar Lake-Sinai, sources and fluxes. **(2000)**
E	J. Zopfi	(PhD)	MPIMM/Bremen	Speciation and transformation of sulfur intermediates in stratified ecosystems. **(2000)**
F	H. A. Madkor	(PhD)	NIOF	
F	M.AbdEl Radi	(PhD)	NIOF	
F	T. Felis	(PhD)	GeoB/Bremen	Climate and ocean variability reconstructed from stable isotope records of modern subtropical corals (Northern Red Sea). **(1999)**
F	M. Rosenfeld	(PhD)	IUI/Tel Aviv Univ.	Bleaching effects on *Porites* corals revealed from sclerochronology.
F	A. Wahb Allah	(PhD)	NIOF	
F	Y. Moustafa	(PhD)	GeoB/Bremen, NIOF	Paleoclimatic reconstructions of the northern Red Sea during the holocene inferred from stable isotope records of modern and fossil corals and molluscs. **(2000)**

Annex 3 (cont.)

Proj. Theme	Name		Institute/ University	Title (completed in...)
G	A. Brink	(MSc)	Göttingen/Univ.	Untersuchungen zur Wirkungsweise von Conustoxinen auf spannungsabhängige Ionenkanäle. **(1998)**
G	A. Hasson	(PhD)	Hebrew Univ.	Electrophysiological analysis of neurotoxic peptides from cone snails. **(2000)**
G	Y. Shtern	(MSc)	Hebrew Univ.	Electrophysiological analysis of neurotoxic peptides from cone snails.
Aqaba	T. Al-Najjar	(PhD)	MSS/ IfM, Kiel	The seasonal dynamics and grazing control of phyto- and mesozooplankton in the northern Gulf of Aqaba. **(2000)**
Aqaba	S. Al-Rousan	(MSc)	MSS/Yarmouk	Sediment role in nutrient cycle within the coral reefs of the Gulf of Aqaba, Red Sea. **(1998)**
Aqaba	N. Kanaan	(MSc)	MSS/Yarmouk	Studies on planktivorous fish ecology in the coral reef of the Gulf of Aqaba. **(1998)**
Aqaba	I. Kappner	(MSc)	ZMT/Bremen	Distribution, population structure and feeding ecology of vermetid snails in the northern Gulf of Aqaba. **(1998)**
Aqaba	T. Maack	(MSc)	ZMT/Bremen	Freßverhalten und -aktivität von *Chromis pembae* (Pomacentridae) im nördlichen Golf von Aqaba. Feeding ecology of *Chromis pembae* (Pomacentridae, Pisces). **(1998)**
Aqaba	C. Maier	(MSc)	ZMT/Bremen	Distribution and abundance of internal bioeroders in coral reefs. A field survey in the northern Red Sea. **(1997)**
Aqaba	R. Manasreh	(MSc)	MSS/Yarmouk	Water circulation in Jordanian waters of the Gulf of Aqaba, Red Sea. **(1998)**
Aqaba	B. Munkes	(MSc)	ZMT/Bremen	The role of zooplanktivorous fish in the supply of new (allochthonus) material to the coral reef.
Aqaba	Pasenau, I.	(MSc)	ZMT/Bremen	Raubdruck und Schwarmverhalten verschiedener Altersgruppen bei *Neopomacentrus miryae* (Pomacentridae: Teleostei) und *Pseudanthias squamipinnis* (Serranidae: Teleostei). **(2000)**
Aqaba	M. Rasheed	(MSc)	MSS/Yarmouk	Assessment of trace nutrient and chlorophyll *a* gradient within a coral reef of the Gulf of Aqaba, Red Sea. **(1998)**
Aqaba	K. Sinschek	(MSc)	ZMT/Bremen	Aktivität und Nahrungsaufnahme von *Dendrophyllia* sp. (Cnidaria, Scleractina) im Golf von Aqaba. **(1999)**
Aqaba	H. Vesper	(MSc)	ZMT/Bremen	Abundanz und Verteilung von *Dendrophyllia* sp. (Scleractinia) im Korallenriff von Aqaba, Jordanien. **(1998)**
Aqaba	A. Voigt	(MSc)	ZMT/Bremen	Strömungsinduzierte Zooplanktonverteilung vor einem Korallenriff im nordöstlichen Golf von Aqaba. **(1998)**
Aqaba	S. Al-Rousan	(PhD)	MSS/Yarmouk GeoB/Bremen	High resolution Holocene climate records of corals and foraminifera from the Northern Red Sea.
Aqaba	F. Al-Horani	(PhD)	MSS/Yarmouk MPIMM,Bremen	Photosynthesis and calcification in hermatypic corals
Aqaba	R. Manasreh	(PhD)	MSS/Yarmouk IOW,Warnem.	Modeling of the water circulation in the Gulf of Aqaba, Red Sea.
Aqaba	M. Rasheed	(PhD)	MSS/Yarmouk MPIMM,Bremen	Organic matter remineralization in carbonate and quartz sands of the Gulf of Aqaba, Red Sea, Jordan.

Annex 3 (cont.)

Proj. Theme	Name		Institute/ University	Title (completed in...)
Aqaba	T. Froukh	(MSc)	MSS/Yarmouk	Fish larvae from the Jordanian coast of the Gulf of Aqaba, Red Sea
Aqaba	W. Al-Zereini	(MSc)	MSS/Yarmouk	Octocorallia in the Gulf of Aqaba (Jordan)
Aqaba	K. Al Sokhny	(MSc)	MSS/Yarmouk	Nutrients and chlorophyll *a* in relation to density currents in coral reef waters of the Gulf of Aqaba, Red Sea
Aqaba	N. Odat	(MSc)	MSS/Yarmouk	Assessment of fish stocks with emphasis on Scombridae in the Gulf of Aqaba, Jordan.
Aqaba	A. Al Sabi	(MSc)	MSS/Yarmouk	Sponges in the Gulf of Aqaba (Jordan)
	M. Kochzius	(PhD)	ZMT/Bremen	Gene flow and larval dispersal of coral reef fishes in the Gulf of Aqaba and northern Red Sea.
NEBROC	I. Kötter	(PhD)	ZMT/Bremen	Autecological studies on cryptofauna.

Annex 4

RSP Personnel-Exchange

1996

Month	Date	Name	Sending Institution	Host Institution
January	20-26	Claudio Richter	ZMT Bremen	IUI Eilat, MSS Aqaba
March	1- 9	Gotthilf Hempel	ZMT Bremen	MSS Aqaba, IUI Eilat
July	1-23	Claudio Richter	ZMT Bremen	IUI Eilat, MSS Aqaba
August-October		Conny Maier	ZMT Bremen	Ras Mohammed Nationalpark, Sharm Esh Sheikh
October	5-18	Gotthilf Hempel	ZMT Bremen	NIOF Alexandria; EEAA Alexandria; NIOF Hurghada; NIOF Cairo; MSS Aqaba; University of Jordan Amman; Yarmouk University Irbid; Hebrew University Jerusalem; IUI Eilat; Deutsche Vertretung Jericho; PCG; Al Ashar University; Islamic University

1997

Month	Date	Name	Sending Institution	Host Institution
January	27-30	Gotthilf Hempel	ZMT Bremen	Hebrew University Jerusalem; IUI Eilat
January	7- 8	Clivia Häse	IUI Eilat	NIOF Cairo
January	26-28	Clivia Häse	IUI Eilat	Bar Ilan University
February-May	11-30	Claudio Richter	ZMT Bremen	IUI Eilat; MSS Aqaba
February-July		Alexander Voigt	ZMT Bremen	MSS Aqaba
February-July		Thilo Maak	ZMT Bremen	MSS Aqaba
April-July		Kathrin Sintschek	ZMT Bremen	MSS Aqaba
April-August		Heike Vesper	ZMT Bremen	MSS Aqaba
May-August		Isabella Kappner	ZMT Bremen	MSS Aqaba
May-August		Guido Kumbartzky	ZMT Bremen	MSS Aqaba
June	7-13	Ahmad Abu-Hilal	MSS Aqaba	ZMT Bremen
June-July	15-30	Tariq Al-Najjar	MSS Aqaba	ZMT Bremen; IfM Kiel
July-August	21-24	Claudio Richter	ZMT Bremen	IUI Eilat; MSS Aqaba
August	22-29	Matthias Bödding	MPI Göttingen	Hebrew University Jerusalem
August	22-29	Walter Stühmer	MPI Göttingen	Hebrew University Jerusalem
Nov.-December	10-19	Claudio Richter	ZMT Bremen	IUI Eilat, MSS Aqaba
November		Andrea Stihl	IUI Eilat	NIOF Alexandria
November		Anton Post	IUI Eilat	NIOF Alexandria
December	1- 4	Gotthilf Hempel	ZMT Bremen	State Minister of Environment, NIOF Cairo; EEAA Cairo

Annex 4 (cont.)

1998

Month	Date	Name	Sending Institution	Host Institution
February-March	11- 3	Claudio Richter	ZMT Bremen	MSS Aqaba
February-March	24-15	Tariq Al-Najjar	MSS Aqaba	IfM Bremen
January	24-29	J. Ott	IfZ, Vienna	MSS Aqaba, IOI Eilat, Al Quds Univ., Hebrew Univ., Bar Ilan Univ., Tel Aviv Univ., Solar Lake
January	24-29	J.-O. Strømberg	KMRS, Fiskebäckskil	MSS Aqaba, IOI Eilat, Al Quds Univ., Hebrew Univ., Bar Ilan Univ., Tel Aviv Univ., Solar Lake
January	24-29	M. Türkay	FIS, Frankfurt	MSS Aqaba, IOI Eilat, Al Quds Univ., Hebrew Univ., Bar Ilan Univ., Tel Aviv Univ., Solar Lake
March		Tariq Al-Najjar	MSS Aqaba	NIOF Suez
April	18-28	Tariq Al-Najjar	MSS Aqaba	NIOF Suez
April-May	28- 1	Yehuda Cohen	Hebrew Univ.	NRC Cairo
May	23-25	Gotthilf Hempel	ZMT Bremen	Univ. of Jordan Amman; Yarmouk Univ. Irbid
June	9-13	Ulrich Sommer	IfM Kiel	IUI Eilat; MSS Aqaba
July-October	7-27	Marc Kochzius	ZMT Bremen	MSS Aqaba
July	16-29	Mohammad Badran	MSS Aqaba	ZMT Bremen
November	4- 6	Maroof Khalaf	MSS Aqaba	ZMT Bremen
Nov.-December	21-13	Claudio Richter	ZMT Bremen	MSS Aqaba
Nov.-December	21-20	Heike Möhlig	ZMT Bremen	MSS Aqaba
Nov.-April	17- 1	Mohammed Rasheed	MSS Aqaba	MPI Bremen
Nov.-March	24-?	Saber Al-Rousan	MSS Aqaba	GEO, University Bremen

1999

Month	Date	Name	Sending Institution	Host Institution
March	1-24	Claudio Richter	ZMT Bremen	MSS Aqaba
March-July	1- 4	Colette Wabnitz	ZMT Bremen	MSS Aqaba
April-November	19- 3	Marc Kochzius	ZMT Bremen	MSS Aqaba; IUI Eilat
April-July	22-26	Isabella Kappner	ZMT Bremen	MSS Aqaba
May-June	15-19	Claudio Richter	ZMT Bremen	MSS Aqaba
May-November	16- 3	Ilka Pasenau	ZMT Bremen	MSS Aqaba
May-June	25-20	Iris Kötter	ZMT Bremen	MSS Aqaba
June	2- 9	Gotthilf Hempel	ZMT Bremen	I. Khater and M. Al-Qutob, Jerusalem; IUI Eilat; MSS Aqaba; University of Jordan Amman; Yarmouk University Irbid; NIOF Cairo
July-August	19- 7	Mohammad Badran	MSS Aqaba	ZMT Bremen
July-October	10-18	Yasser Geneid	NIOF Cairo	Wattenmeerstation Sylt; ZMT Bremen
September	1-20	N. Saber Abdel Rahman	NIOF Cairo	MSS Aqaba
October	6-31	Saber Al-Rousan	GEO,Uni Bremen	MSS Aqaba
October	14-22	Thomas Felis	GEO,Uni Bremen	MSS Aqaba
October	23-29	Max Tilzer	Uni Konstanz	IUI Eilat
Oct.-November	31- 3	Yousef Y. Ahmed	MSS Aqaba	IUI Eilat
November	15-21	Wolfgang Fennel	IOW Warnemünde	MSS Aqaba
November	16-25	Claudio Richter	ZMT Bremen	MSS Aqaba
December	12-19	Nedal Al-Ouran	Jordan Royal Ecol. Diving Society	ZMT Bremen

Annex 4 (cont.)

2000

Month	Date	Name	Sending Institution	Host Institution
January	17	Wael Zereini	MSS Aqaba	Senckenberg Institut, Frankfurt, Manfred Grasshoff
February-March	14-26	N. S. Abdel Rahman	NIOF Cairo	IfM Kiel
February-May	16-5	Ahmed Al-Sabi	MSS Aqaba	Centre D'Oceanologie de Marseille, Jean Vacelet
February-March	16-18	Sabine Kadler	ZMT Bremen	MSS Aqaba
February-May	16-16	Iris Kötter	ZMT Bremen	MSS Aqaba
February-May	16-16	Britta Munkes	ZMT Bremen	MSS Aqaba
February-March	22-26	Mark Wunsch	ZMT Bremen	MSS Aqaba
February	22-28	Gotthilf Hempel	ZMT Bremen	MSS Aqaba
February-March	22-25	Claudio Richter	ZMT Bremen	MSS Aqaba
March	13-30	Clivia Häse	IUI Eilat	Univ. Konstanz; Tony Walsby, Bristol; ZMT Bremen
April	5-11	Max Tilzer	Univ. Konstanz	Bar Ilan University Jerusalem
April-May	5-17	Magdy Dowidar	NIOF Alexandria	ZMT Bremen
April	6-20	Nedal Al-Ouran	Jordan Roy. Ecol. Diving Society	ZMT Bremen
April-June	10-9	Nidal Odat	MSS Aqaba	ZMT Bremen
April-May	16-15	Mark Wunsch	ZMT Bremen	MSS Aqaba
April	23-30	Yoav Porat	IUI Eilat	MSS Aqaba
May	27-30	Venugopalan Ittekkot	ZMT Bremen	MSS Aqaba
May-June	27-2	Gotthilf Hempel	ZMT Bremen	MSS Aqaba; IUI Eilat; Al-Quds Univ. Jerusalem
May	28-31	Clivia Häse	IUI Eilat	NIOF Cairo
May-June	24-16	Marc Kochzius	ZMT Bremen	MSS Aqaba
May	6-22	Khayria Naguib Nabil Aboul-Enein	NRC Cairo	MPI für Experimentelle Medizin Göttingen
May	6-29	Mohammed Gomaa	NRC Cairo	MPI für Experimentelle Medizin Göttingen
June	3-11	Mutaz Al-Qutob	PCG Jerusalem	ASLO-Confernce Copenhagen
June-July	9-1	Saber Al-Rousan	GEO,Uni Bremen	MSS Aqaba
June	17-23	Thomas Felis	GEO,Uni Bremen	MSS Aqaba
June-August	16-23	Tawfiq Froukh	MSS Aqaba	ZMT Bremen
June-July	23-16	Mohammad Badran	MSS Aqaba	IOW Warnemünde
June-July	23-10	Mohammad El-Zibdeh	MSS Aqaba	ZMT Bremen
July	21-29	Gotthilf Hempel	ZMT Bremen	Univ. of Jordan Amman; Yarmouk Univ. Irbid
July-August	20-18	Maroof Khalaf	MSS Aqaba	ZMT Bremen, Senckenberg Institut Frankfurt
August	2-29	Salim Al-Moghrabi	MSS Aqaba	ZMT Bremen, Univ. of Nice-Sophia Antipoli, Monaco
August	6-20	Wael Al-Zereini	MSS Aqaba	Tel Aviv University, Benayahu
September	17-22	Yury Kamenir	Bar Ilan Univ. Ramat Gan	European Marine Microbiology Symposium (EMMS7 Netherlands)
August-Sept.	17-25	Magdy Dowidar	NIOF Alexandria	ZMT Bremen
September-October	18-12	Ali Hammad	MSS Aqaba	IfM Kiel, Kortum; Labor für Meßtechnik, Thomas J. Müller
Sept.-Oct.	29-24	Khalid Al-Trabeen	MSS Aqaba	Universität Düsseldorf, Peter Proksch

Annex 4 (cont.)

2000

Month	Date	Name	Sending Institution	Host Institution
October		Marc Kochzius, Iris Kötter, Claudio Richer, Mark Wunsch	ZMT Bremen	Bali, Indonesia
October		Maroof Khalaf, Mohammad El-Zibdeh	MSS Aqaba	Bali, Indonesia
November-January 2001	9- 9	Fuad Al-Horani	MPI Bremen	MSS Aqaba
December	3- 6	K. Abdel-Hamid Hussein	NIOF Cairo	Pacem in Maribus 2000, Hamburg
December	6-20	Khaled Al-Sokhny	MSS Aqaba	ZMT Bremen
December-January 2001	19-15	Mohammad Rasheed	MPI Bremen	MSS Aqaba

Annex 5
RSP - Workshops and Meetings

Year	Date	Title	Location	Participants
1994	*27 October*	*1st Meeting of the Scientific Steering Committee*	*Bremen*	*Hussein K. Badawi, Avi Baranes, Ahmed I. El-Ibiary, Amatzia Genin, Joachim Harms, Gotthilf Hempel, Bo B. Jørgensen, Issa Khater, Erwin Neher, Jürgen Pätzold, Reinhold Penner, Claudio Richter, Ulrich Schlüter, Micha Spira, Noga Stambler, Walter Stühmer, Gerold Wefer*
1995	22-25 October	1st General Assembly	Dahab	Abdallah, Ziad Abdeen, Mohammed Abdel Rahman, M. Aly Mohamed, A. A. Ahmed, A. Azran, Hussein K. Badawi, O. A. M. Badawi, Avi Baranes, Fikry Barghuthy, Ahmed Beltagy, Yehuda Cohen, S. Dikvert, Zvy Dubinsky, A. El Azzuny, M. S. El Besbeshy, N. El Din Ibrahim, M. N. El Enein, M. El Gazar, T. A. El Gazar, Ahmed I. El-Ibiary, M. El Rowy, A. El Saadany, M. I. El Samra, O. M. El Shewicky, Jonathan Erez, T. Feldstein, Thomas Felis, Maoz Fine, M. T. Gamal, Amatzia Genin, Raid Ghrayeb, V. K. Gouda, S. Hamed, Joachim Harms, A. Hassan, G. Y. Hazboun, Gotthilf Hempel, Ezzat Ibrahim, Bo B. Jørgensen, J. K. Khalaf, Issa Khater, Kulitz, Boaz Lazar, Debbie Lindell, Yossi Loya, M. A. Mahar, Ibrahim Maiyza, F. Mendez, M. Meyer, M. Moustafa, Khayria Naguib, Ahmed H. Nawar, Erwin Neher, Jürgen Pätzold, Reinhold Penner, Anton Post, Mutaz Al-Qutob, Claudio Richter, M. Saleh, M. Sarwat, S. Sella, K. Sety, Ulrich Sommer, Micha Spira, M. A. Srour, Noga Stambler, Walter Stühmer, D. Thomas, Max Tilzer, M. I. Zaki
1995	23-25 October	2nd Meeting of the Scientific Steering Committee	Dahab	Ziad Abdeen, Hussein K. Badawi, Avi Baranes, Ahmed I. El-Ibiary, Gotthilf Hempel, Erwin Neher, Claudio Richter, Micha Spira
1996	14-15 May	Joint Workshop of Projekt D and F	Sharm Esh Sheikh	cancelled
	2 July	3rd Meeting of the Scientific Steering Committee	Aqaba	Ziad Abdeen, Hussein K. Badawi, Avi Baranes, Ahmed El-Ibiary, Gotthilf Hempel, Claudio Richter, Micha Spira

Annex 5 (cont.)

Year	Date	Title	Location	Participants
1997	29-31 January	1. Joint Workshop of Project A and B	Eilat	cancelled
	16 and 19 March	4th Meeting of the Scientific Steering Committee	Eilat	Ziad Abdeen, Hussein K. Badawi, Avi Baranes, Ahmed I. El-Ibiary, Joachim Harms, Gotthilf Hempel, Claudio Richter, Ulrich Schlüter, Micha Spira, Walter Stühmer
	16-19 March	2nd General Assembly	Eilat	Ziad Abdeen, H. Abd El-Monem, Ahmed Abd El-Monem E. Abd El-Moula, A.M. Abd El-Sala, M. Abd El-Wahab, Ahmad Abu-Hilal, Salim Al-Moghrabi, E. M. Ali, M. I. Atia, A. Azoni, Hussein K. Badawi, Mohammed Badran, Avi Baranes, Fikry Barghuthy, I. Bargil, Ali Beltagy, D. Chernov, Yehuda Cohen, R. K. Diroti, Zvy Dubinsky, M. M. El-Gharabawi, Ahmed El-Ibiary, Atif M. El-Naggar, Mohammed El-Samra, Mohammed El-Zibdeh, M. S. El-Bishbeshy, M. N. Eldin, R. S. Eldin, Jonathan Erez, Maoz Fine, Thomas Felis, Amatzia Genin, Raid Ghrayeb, Clivia Häse, Joachim Harms, A.M. Helal, Gotthilf Hempel, Ezzat Ibrahim, David Iluz, M. A. Khalaf, R. Klein, M. Kobler, Boaz Lazar, Li Hong, Debbie Lindel, Yossi Loya, M. A. Mahar, Ibrahim Maiza, Inbal Meidani, Khayria Naguib, Mohammed Naguib, A. H. Nawar, Jürgen Pätzold, Anton Post, Mutaz Al-Qutob, Claudio Richter, S. Shehata, J. Silberman, Micha Spira, Noga Stambler, WalterStühmer, Max Tilzer, Mark Wunsch, Yaser Moustafa
	6 November	Meeting of German Principal Investigators	Bremen	Gotthilf Hempel, Bo B. Jørgensen, Erwin Neher, Jürgen Pätzold, Claudio Richter, Walter Stühmer, Max Tilzer, Gerold Wefer
	11-13 November	"Molecular Approaches to Marine Sciences" Workshop of Projects C, E and G	Jerusalem	cancelled
	1-4 December	Meeting of the International RSP-Coordinator and the Egyptian Minister of High Education and State Minister for Scientific Research and others	Cairo	Hussein Badawi, Ahmed El-Ibiary, Gotthilf Hempel, Ezzat Ibrahim, Issa Khater, Mofid Shehaba, Egyptian PhD students
	9-10 December	Meeting of Project A	Bar Ilan	Mutaz Al-Qutob, Clivia Häse, Boaz Lazar, Noga Stambler, Max Tilzer
	11-12 December	Joint Plankton Workshop of Projects A, B and C	Eilat	Mutaz Al-Qutob, Zvy Dubinsky, Clivia Häse, Amatzia Genin, Li Hong, Boaz Lazar, Anton Post, Claudio Richter, Andrea Stihl, Max Tilzer, Mark Wunsch Invited Guest Speaker: Baruch Kimor

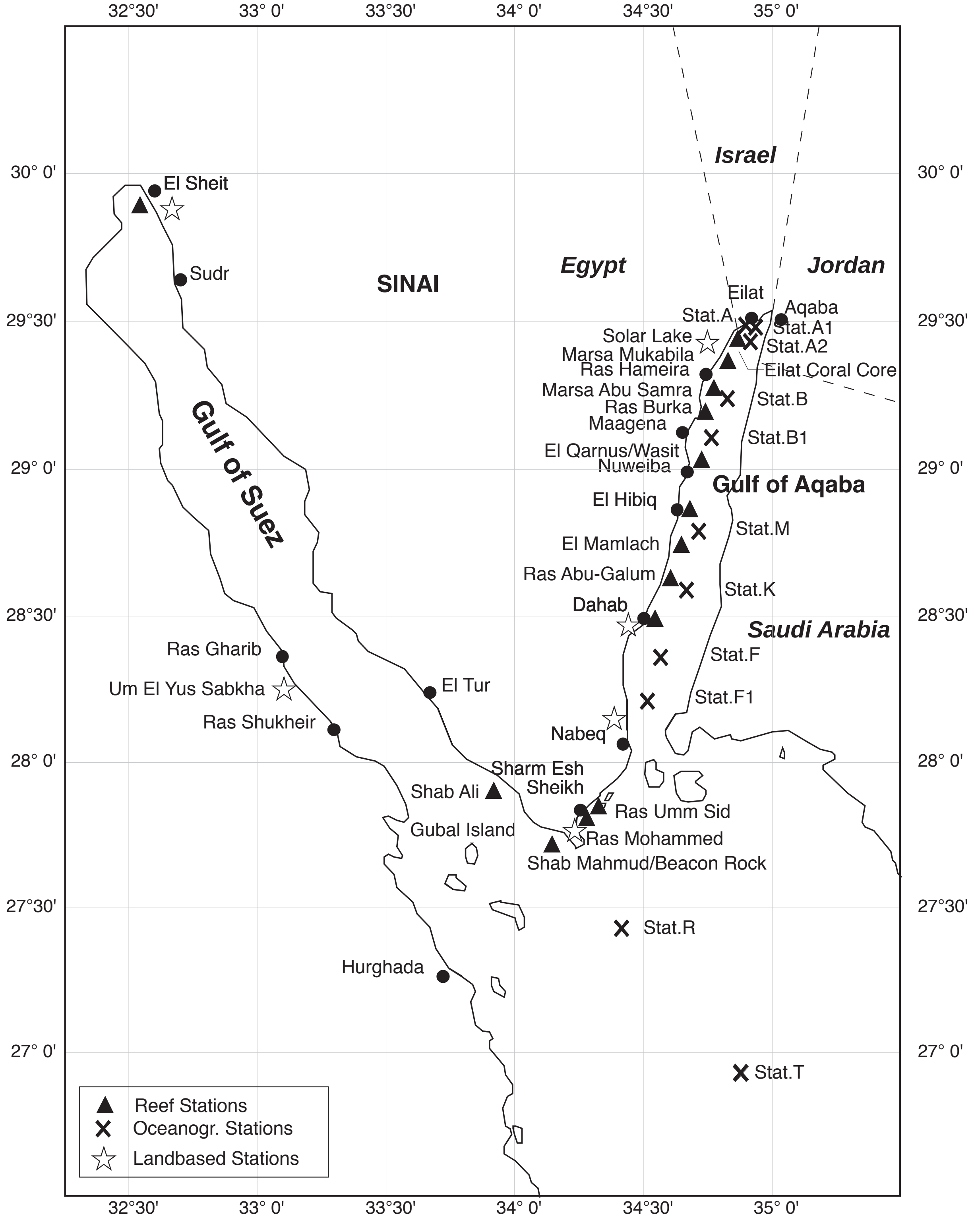
Annex 5 (cont.)

Year	Date	Title	Location	Participants
1998	9-10 March	Meeting of Project A	Bremen	Clivia Häse, David Iluz, Boaz Lazar, Noga Stambler, Max Tilzer
	10-15 March	3rd General Assembly	Bremen	Ziad Abdeen, Ahmed Abd El-Monem, Nabil Aboul-Enein, Ahmad Abu-Hilal, Salim Al-Moghrabi, Tariq Al-Najjar, Mutaz Al-Qutob, Saber Al-Rousan, Hussein Badawi, Mohammad Badran, Avi Baranes, Ali Beltagy, Bodo v. Bodungen, Yehuda Cohen, Ola El-Din Taha, M. El-Ghërarbawi, Ahmed El-Ibiary, Mohammed El-Samra, Mohammed El-Zibdeh, Kai Emeis, Jonathan Erez, Thomas Felis, Maoz Fine, Amatzia Genin, Raid Ghrayeb, Mohammed Gomaa, Joachim Harms, Clivia Häse, Arik Hasson, Gotthilf Hempel, Ezzat Ibrahim, David Iluz, Bo B. Jørgensen, Nemeh Kanaan, Isabella Kappner, Iris Kötter, Boaz Lazar, Yossi Loya, Thilo Maack, Cornelia Maier, Ibrahim Maiyza, Riayd Manasreh, Inbal Meidani, Yaser Moustafa, Kharyia Naguib, Mohammed Naguib, Ahmed Nawar, Erwin Neher, Jörg Ott, Jürgen Pätzold, Anton Post, Mohammed Rasheed, Dietmar Richter, Claudio Richter, Ulrich Schlüter, Ulrich Schöttler, Kathrin Sinschek, Ulrich Sommer, Micha Spira, Noga Stambler, Andrea Stihl, Jarl-Ove Strømberg, Walter Stühmer, Max Tilzer, Michael Türkay, Heike Vesper, Alexander Voigt, Gerold Wefer, Petra Westhaus-Ekau, Andrea Wieland, Mark Wunsch, Amany Youssef, Jakob Zopfi
	11 and 14 March	5th Meeting of the Scientific Steering Committee	Bremen	Ziad Abdeen, Ahmad Abu-Hilal, Hussein K. Badawi, Avi Baranes, Ahmed I. El-Ibiary, Gotthilf Hempel, Erwin Neher, Claudio Richter, Ahmed I. Shehata, Micha Spira
	17-20 May	Project A Paper writing workshop	Barrage	Ahmed Abd El-Monem, Clivia Häse, Ezzat Ibrahim, Boaz Lazar, Noga Stambler
	May	Project E Paper Writing Workshop	Taba	
	9-12 June	Biomineralization Workshop	Jerusalem and Eilat	Denis Allemand, Ahuva Almogi-Labin, Dirk de Beer, Jelle Bijma, Colin Brownlee, Jonathan Erez, Jean-Pierre Gattuso, Ted McConnaughey, Jürgen Pätzold, Stephanie Rink, Howie Spero, Micha Spira, R. Vago, Steve Weiner, Richard Zeebe
	2 July	6th Meeting of the Scientific Steering Committee	Cairo	Ziad Abdeen, Ahmad Abu-Hilal, Hussein Badawi, Avi Baranes, Ahmed El-Ibiary, Gotthilf Hempel, Issa Khater, Claudio Richter, Micha Spira
	11 September	Meeting of Project A	Jerusalem	Boaz Lazar, Zvy Kizner, Noga Stambler, Max Tilzer

Annex 5 (cont.)

Year	Date	Title	Location	Participants
1999	10 March	7th Meeting of the Scientific Steering Committee	Aqaba	Ziad Abdeen, Ahmad Abu-Hilal, Avi Baranes, Gotthilf Hempel, Issa Khater, Erwin Neher, Claudio Richter, Micha Spira
	9-10 May	Meeting of Project A	Jerusalem	Mutaz Al-Qutob, Vladimir Belousov, Zvy Dubinsky, Jonathan Erez, Clivia Häse, David Iluz, Juri Kamenir, Boaz Lazar, Leonid Sokoletsky, Noga Stambler, Max Tilzer
	21 October	8th Meeting of the Scientific Steering Committee	Taba	Ahmad Abu-Hilal, Ekram Amin, Avi Baranes, Osama El-Badawy, Ahmed El-Ibiary, Raoia El-Saadany, Gotthilf Hempel, Khamis A. Hussein, Petra Westhaus-Ekau
	24 October	Meeting of Theme I	Aqaba	Ahmad Abu-Hilal, Salim Al-Moghrabi, Tariq Al-Najjar, Ahmad Al-Sabaa, Khaled Al-Sokhny, Wael Al-Zereini, Mohammad Badran, Zvy Dubinsky, Mohammad El-Zibdeh, Jonathan Erez, Abdel-Karim Farrah, Tawfiq Froukh, Amatzia Genin, Clivia Häse, Maroof Khalaf, Boaz Lazar, Riyad Manasreh, Nidal Odat, Anton Post, Mohammed Rasheed, Noga Stambler, Max Tilzer
	25-28 October	Meeting of Project A	Eilat	Mutaz Al-Qutob, Vladimir Belousov, Zvy Dubinsky, Clivia Häse, David Iluz, Juri Kamenir, Boaz Lazar, Leonid Sokoletsky, Noga Stambler, Max Tilzer
2000	19 January	Meeting of German Principal Investigators	Bremen	Gotthilf Hempel, Bo B. Jørgensen, Erwin Neher, Claudio Richter, Ulrich Sommer, Walter Stühmer, Max Tilzer, Gerold Wefer, Petra Westhaus-Ekau
	22-29 February	Meeting of the International Coordinator with RSP-Partners	Aqaba	Ahmad Abu-Hilal and scientist of MSS, Avi Baranes, Ahmed El-Ibiary and scientists of NIOF, Issa Khater, Claudio Richter, Micha Spira, Mark Wunsch
	6-7 April	Meeting of Project A	Bar Ilan Univerity	Mutaz Al-Qutob, Vladimir Belousov, Zvy Dubinsky, Clivia Häse, David Iluz, Juri Kamenir, Boaz Lazar, Leonid Sokoletsky, Noga Stambler, Max Tilzer
	28 May	Theme II Workshop	Aqaba	Mohamed Abd El-Hamid, Ahmad Abu-Hilal, Salim Al-Moghrabi, Ahmad Al-Sabi, Wael Al-Zereini, Mohamed El-Zibdeh, Tawfiq Froukh, Gotthilf Hempel, Venugopalan Ittekkot, Khaled Jamaan, Maroof Khalaf, Marc Kochzius, Riyad Manasreh, Caitriona McInerney, Ahmed H. Nawar, Helge Niemann, Claudio Richter
	27-30 May / 2 June	Meeting of the International Coordinator and the new Director of ZMT with Jordanian, Palestinian and Israeli RSP-Partners	Aqaba, Eilat, Ost-Jerusalem	Ziad Abdeen, Ahmad Abu-Hilal, Salim Al-Moghrabi, Mutaz Al-Qutob, Mohammad Badran, Avi Baranes, Yehuda Cohen, Zvy Dubinsky, Mohamed El-Zibdeh, Jonathan Erez, Gotthilf Hempel, Venugopalan Ittekkot, Maroof Khalaf, Issa Khater, Boaz Lazar, Anton Post, Micha Spira
	23-24 July	Meeting of the International Coordinator with the Presidents of the University of Jordan and of Yarmouk University (Vice Presidents and Deans are members of the MSS Council)	Amman, Irbid	Gotthilf Hempel, Walid Al-Maani (President University Jordan), Salman Al-bdour (Vice President Administrative Affairs), Fayes Al-Khasawneh (President Yarmouk University), Hisham Gharaibeh (Vice President Academic Affairs), Sami Mahmoud (Dean of Faculty of Science), Zaidan Kafafi (Dean of Scientfic Research and Grauduate Studies)

Annex 6
RSP - Oceanographic, Reef and Landbased Stations



Annex 7
RSP - Expeditions

1995

Month	Date	Project	Station
Nov./Dec.	26- 3	F	Ras Mohammed
December	11-15	B	Eilat, Abu-Galum, Dahab, Nuweiba, Ras Burka

1996

January		E	Hypersaline environments: Um El Yus Sabkha, El Sheit, between Ras Sudr and El Tur, Ras Mohammed, Gavish Sabkha (Nabeq), Dahab, Solar Lake
January	17	E	Solar Lake
January	29-30	A	A1
February	26-27	A	Solar Lake
March	11-12	A	A1
March	12	RSP-Course	A
April	8-16	F	cancelled
April	29	A	A1
April	23	E	Solar Lake
May	20	A	A1
June	2-10	C	A, A1, B, B1, M, R, T
July	14-22	A+D	A, A2, B, F, F1, K, M, Ras Umm Sid, Ras Abu-Galum, Dahab
August	1- 8	B	Eilat Nat.Reserve,Ras Burka,El Hibiq, Ras Abu-Galum,Dahab,Ras Umm Sid, Sharm Esh Sheikh
August	16-24	G	Dahab, El-Hibiq, Ras Burka
August	27-28	A	A
September	12	A	A
December	17	A	A

1997

January	7-14	E	
January	13-20	B	Eilat, Ras Abu-Galum, El Mamlach, El Hibiq, Nuweiba, Ras Burka
March	2- 8	E	Solar Lake
April	6-12	E	Solar Lake
May	1-9	F	cancelled
May	1-9	A	A1, Nabeq, Dahab, Ras Abu-Galum, El Mamlach, El Hibiq, El Qarnus, Wasit, Nuweiba, Ras Burka, Marsa Abu-Samra, Marsa Mukabila, Ras Umm Sid, Shab Mahmud, Beacon Rock, Shab Ali, Ras Mohammed
May	11-17	E	cancelled
May	25-31	C	A1, B1, M, F, R, Ras Abu-Galum, Ras Mohammed
August	12-23	B	Ras Abu-Galum, Hibeq, Ras Burka
November	18-29	B	cancelled

Annex 7 (cont.)

1998

Month	Date	Project	Station
January	30	A	A
February	2	A	A
February	9	A	A
February	18-28	B	cancelled
March	11	A	A
March	23	A	A
May	28	A	A
May	31	A	A
May/June	31- 9	C	A, A1, B1, F, M, R, Ras Abu-Galum
June	15	A	A
July	13	A	A
July	27	A	A
September	7	A	A
November	1- 8	C	A1, F, M, Sharm El-Sheikh, Ras Abu-Galum
Nov./December	30-11	B	Ras Burka

1999

Month	Date	Project/Stat.	Principal Investigator
January	25	Theme I / A	Boaz Lazar
February	1	Theme I / A	Boaz Lazar
March	8	Theme I / A	Boaz Lazar
March	25	Theme I / A	Boaz Lazar
April	19	Theme I / A	Boaz Lazar
May	3	Theme I / A	Boaz Lazar
May	11	Theme I / A	Anton Post
May	24	Theme I / A	Boaz Lazar
May	25	Theme I / A	Boaz Lazar
June	14	Theme I / A	Anton Post
June	28	Theme I / A	Boaz Lazar
July	28	Theme I / A	Boaz Lazar
August	23	Theme I / A	Boaz Lazar
August	24	Theme I / A	Anton Post
September	6 (night)	Theme I / A	Boaz Lazar
October	2	Theme I / A	Boaz Lazar
October	3	Theme I / A	Anton Post
October	4 (night)	Theme I / A	Boaz Lazar
October	21	Theme I / A	Boaz Lazar
October	22	Theme I / A	Boaz Lazar
December	26	Theme I / A	Anton Post
December	27	Theme I / A	Anton Post

Annex 8

RSP - Courses

1995

Date	Title	Loc.	Participants	Lecturers
13-22 December	Introduction to Marine Sciences for PCG Students	Eilat	14 students	Bracha Ben-Ezra, Viriana Farstey, Amatzia Genin, Boaz Lazar, Anton Post

1996

Date	Title	Loc.	Participants	Lecturers
10 - 23 March	Junior Introductory Course on Marine Science	Eilat	Hashem Madkoor Abass, Zeinab Abdel Baki, Mohamed Abd El-Wahab, Ahmed Wahab Allah, Fikry Al-Barghuthy, Mutaz Al-Qutob, Mohamed Shokry A. Ammar, Muneif Mohamed Ayash, Vladimir Belousov, Irina Bushman, Atif M. El-Naggar, Heba Saad El-Sayed, Thomas Felis, Maoz Fine, Hanne Frøhlich, Jawad Ali Hasan, Amir M. Helal, Alaa Khalil Julani, Cornelia Maier, Yasser Moustafa, Emad Hamadi M. Sabhi, Leonid Sokoletsky, Hisham Mohamed Tahan, Michael Taksir	A. Almogi, Avi Baranes, Nanette Chadwick-Furman, Yehuda Cohen, Zvy Dubinsky, Jonathan Erez, Katharina Fabricius, Amatzia Genin, Gotthilf Hempel, Boaz Lazar, Yossi Loya, I. Lubatsch, Anton Post, Claudio Richter, David Thomas

1997

Date	Title	Loc.	Participants	Lecturers
2-7 February	Zoo- and Phytoplankton Course	Eilat	Ahmed Abd El-Monem, Fikry Al-Barghuthy, Mutaz Al-Qutob, A. Boulos, Eran Brokovich, A.K. Fassah, M. R. Fishar, Raid Ghrayeb, A. M. Helal, Guido Kumbartzky, A. Manei, R.J. Merry, A. Pearlman, Micha Rosenfeld, E. H. M. Sobhy, Alexander Voigt, Y. Yehashua, A. H. Zeidan	A. Almogi-Labin, N. Ben-Eliahu, Jonathan Erez, B. Ben-Ezra, Amatzia Genin, N. Gordon, D. Goulet, Clivia Häse, Baruch Kimor, Anton Post, Noga Stambler, L. Zelickman
12-21 March	Junior Introductory Course on Marine Science	Eilat	K. Abaza, M. S. Abdel Karim, O. Abd El Wahab Farha, T. M. Abu-Saleh, Tariq Al-Najjar, M. Biran, N. De Weik, S. Draschba, M.A. Elabaady, S. Fridman, Y. A. H.Gunied, A.M. Helal, A. Z. M. Hamouda, A. K. Julani, S. Karko, H. Kuhnert, A. Leshem, S. F. Moushasha, T. Ricart, Stefanie Rink, A. Ullrich, Andrea Wieland, A. H. Zeidan	Dror Angel, Avi Baranes, Nanette Chadwick-Furman, Yehuda Cohen, Arik Diamant, Zvy Dubinsky, Mohammed El-Samra, Jonathan Erez, B. Farstay, Amatzia Genin, Dennis Goulet, Gotthilf Hempel, Bo B. Jørgensen, Boaz Lazar, Yossi Loya, Khayria M. Naguib, Anton Post, Claudio Richter, Micha Spira, Walter Stühmer, Gerold Wefer

Annex 8 (cont.)

1998

Date	Title	Loc.	Participants	Lecturers
12-16 November	Diving Course	Aqaba	Khaled Al-Sokhny, Ahmad Al-Sabi, Wael Al-Zereini, Tawfiq Froukh, Riyad Manasreh, Nidal Odat	Royal Diving Center, Aqaba

1999

Date	Title	Loc.	Participants	Lecturers
27 Febr. - 8 March	Junior Course	Aqaba	Mahmoud Abd El-Radi, Abdulla Abu-Talib, Mohammed Al-Hawwash, Fuad Al-Horani, O. Al-Momamy, Ahmad Al Sabaa, Mohammad Al-Salahat, Tariq Al-Salman, Jasem Al-Shweiky, Khaled Al Sokhny, M. Abdelgaliel El-Absawi, Osama El-Badawi, Sarah Cohen, Atef M. El-Naggar, Tawfiq Froukh, Yaser Geneid, Noa Hundert, Yousef Jamal, Sabine Kadler, Iris Kötter, Riyad Saleh A. Manasreh, Shira Milo, Britta Munkes, Hytham Nassar, Nir Nesher, Nidal Odat, Yoav Porat, Mohammed Yusef Rasheed, Yaser K. Sangaa, Khalid Tarabin	Khamis Abd El-Hamid Hussein, Ahmad Abu-Hilal, Salim Al-Moghrabi, Mutaz Al-Qutob, Mohammed Skokri A. Amar, Mohammad Badran, Ahmed I. El-Ibiary, Mohamed El-Samra, Mohammad El-Zibdeh, Jonathan Erez, Clivia Häse, Gotthilf Hempel, Maroof Khalaf, Yossi Loya, Ibrahim A. Maiyza, Anton Post, Claudio Richter, Shawki Z. Sabaa, Mark Wunsch
3-12 April	Diving Courses (Open Water, Advance Open Water, First Medic Aid, Rescue, Practice)	Aqaba	Al Adel Jabbar, Khaled Al Sokhny, M. Ammar, Tawfiq Froukh, H. Abbas Madkur, Riyad Saleh A. Manasreh, Nidal Odat, Khalid Tarabin, M. Zaki, Wael Zereini	Royal Diving Center, Aqaba
29 May- 8 June	Identification Course	Aqaba	Abd El-Hamid Abd El-Rahman, Khaled Mohamed Abd El-Salam, Mohamed Abd El-Wahab, Rania Al-Bishtawe, Rania Al-Hamayel, Samah Al-Hilew, Omer Al-Momani, A. Arad, R. Armoza, Magdy El-Khalafawi, Gamal Mohamed El-Shabrawi, Abdul-Karim Farah, Yousef Jamal, Duraid Khrewish, Caitriona McInerny, Helge Niemann, T. Ouzen, Raed Risq, A. Schlesinger, Yosry Abd El-Aziz Soliman, Mohamed Amin Swelam, S. Weiss, Wael Zereini, Afif Ziedan, A. Zvulunic	Ahmed Abu-Hilal, Salim Al-Moghrabi, Ahmed Al-Sabia, Mohammed Badran, Avi Baranes, Y. Benayahu, Nanette Chadwick-Furman, Mohamed Mohamed El-Komi, Mohammad El-Zibdeh, Tawfiq Froukh, D. Golani, M. Goren, Gotthilf Hempel, Maroof Khalaf, Marc Kochzius, Sherif El-Sayed Ramadan

Annex 9
"Meteor" Cruise 44, Leg 2, Station Map