

Zeitschrift: Geographica Helvetica : schweizerische Zeitschrift für Geographie = Swiss journal of geography = revue suisse de géographie = rivista svizzera di geografia

Herausgeber: Verband Geographie Schweiz ; Geographisch-Ethnographische Gesellschaft Zürich

Band: 54 (1999)

Heft: 3: Global change issues = Globaler Wandel = Problématique du changement globale

Artikel: Global change and the decline of coral reefs

Autor: Strasser, André

DOI: <https://doi.org/10.5169/seals-872412>

Nutzungsbedingungen

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften auf E-Periodica. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. Das Veröffentlichen von Bildern in Print- und Online-Publikationen sowie auf Social Media-Kanälen oder Webseiten ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. [Mehr erfahren](#)

Conditions d'utilisation

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. La reproduction d'images dans des publications imprimées ou en ligne ainsi que sur des canaux de médias sociaux ou des sites web n'est autorisée qu'avec l'accord préalable des détenteurs des droits. [En savoir plus](#)

Terms of use

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. Publishing images in print and online publications, as well as on social media channels or websites, is only permitted with the prior consent of the rights holders. [Find out more](#)

Download PDF: 25.01.2026

ETH-Bibliothek Zürich, E-Periodica, <https://www.e-periodica.ch>

Global Change and the Decline of Coral Reefs

André Strasser, Fribourg

1 Reefs in space and time

In the world's oceans, many organisms have the capacity to build up reefs by themselves or to actively participate in reef construction: microbes, algae, foraminifera, bryozoans, sponges, bivalves (such as oysters), gastropods, worms, and corals. All of these organisms secrete skeletons or shells of calcium carbonate, or their tissues calcify after death. This harmonisation between organic growth and mineralisation thus creates a solid framework able to resist wave and storm impact, and withstands millions of years of geological processes.

Reefs composed of microbes and primitive algae exist since 2.5 billion years; the first coral reefs appeared some 450 million years ago. Earth history records several periods of abundant reef growth alternating with phases where reefs were less developed (JAMES & BOURQUE 1992). These phases of reef growth and decline are related to ecological changes driven by climate, sea level, water chemistry, sediment input, and nutrients. Thus, fossil reefs may be considered monitors of past Global Changes (e.g., DUPRAZ & STRASSER 1999).

Organic reefs occur in all types of environments, ranging from the deep ocean to shallow waters, from hypersaline basins to freshwater lakes. In this paper, however, we will concentrate on reefs built up by corals in shallow water. Holocene shallow-water coral reefs took up their position following the sea-level rise resulting from the last deglaciation and during the sea-level highstand 6000 to 5000 years ago (BLOOM 1993). They now form fringing reefs (such as along the coasts of the Red Sea), barrier reefs (as for example in eastern Australia), or atolls (as in the Maldives). They are most important in structuring the tropical and subtropical coastal zones and they are most vulnerable when exposed to today's ecological changes.

2 Coral reef ecology

The main framework of shallow-water reefs is constructed by colonial coral species whose polyps live in symbiosis with unicellular algae (zooxanthellae: *Symbiodinium*). Up to 1 million zooxanthellae may live in one small, millimetre-sized coral polyp. These algae produce sugars, glycerine and amino-acids through photosynthesis and nourish the polyp. Photosynthesis also fixes CO₂ and thus facilitates the precipitation of calcium carbonate (aragonite), which the coral polyp then

uses to fashion its skeleton (SCHUHMACHER 1988). Due to the symbiosis with photosynthetic algae, the corals are limited to living in the photic zone (in clear water, this zone may be 90 meters deep). The polyps themselves are mostly active at night and feed on zooplankton transported into their range by currents. The spatial distribution of the coral species depends on the availability of light and water energy. Moreover, members of the same species may adapt their morphology to optimize growth potential. For example, encrusting forms grow on the reef crest where wave impact is highest, and platy forms inhabit deeper water as their large surface permits greater light absorption (Fig. 1).

Coral physiology and the biochemical formation of calcium carbonate depend on the water temperature, 25 to 27°C being optimal. The geographical distribution of shallow-water reefs between the northern and southern 20°C isochryme (water temperature in winter) reflects this ecological constraint (Fig. 2). Dependent on warm ocean currents, the northernmost coral reefs are today situated in Bermuda (32°30'N) and in Okinawa (30°N), the southernmost along the east-coast (31°30'S) and the west-coast (29°S) of Australia. Individual coral branches can grow up to 20cm per year (*Acropora* sp.), where as massive coral heads grow only 0.5cm per year (SOROKIN 1995). Up to 10kg of calcium carbonate can thus be produced per year and square-metre. Corals are the most important frame-builders, yet organisms living inside, on top of, and around the corals equally contribute to calcium carbonate production.

Reef growth is continuously counterbalanced by reef destruction: fish eat the coral polyps and thereby destroy the limestone skeletons, boring sponges and worms weaken the bases of the coral bushes and make them tumble, and storm waves break the more delicate coral branches. The resulting sediment is transported by gravity flows into deeper realms, or washed into back-reef lagoons and onto the beach by waves and currents. Once the coral fragments have accumulated on the coast, they partly dissolve on contact with the freshwater lens. The dissolved carbonate then precipitates as cement to form solid beachrock that stabilizes the coastal zone (e.g., GISCHLER & LOMANDO 1997).

Coral reefs thus are delicately balanced ecosystems hosting not only a large number of organisms (e.g., up to 200 species of fish were recorded in a single patch-reef; SOROKIN 1995), but also actively structure the coastal zone. Coral reefs form barriers against storm impact and protect the coast from erosion and they define seagrass and mangrove habitats which in themselves constitute complex ecosystems (Fig. 1).

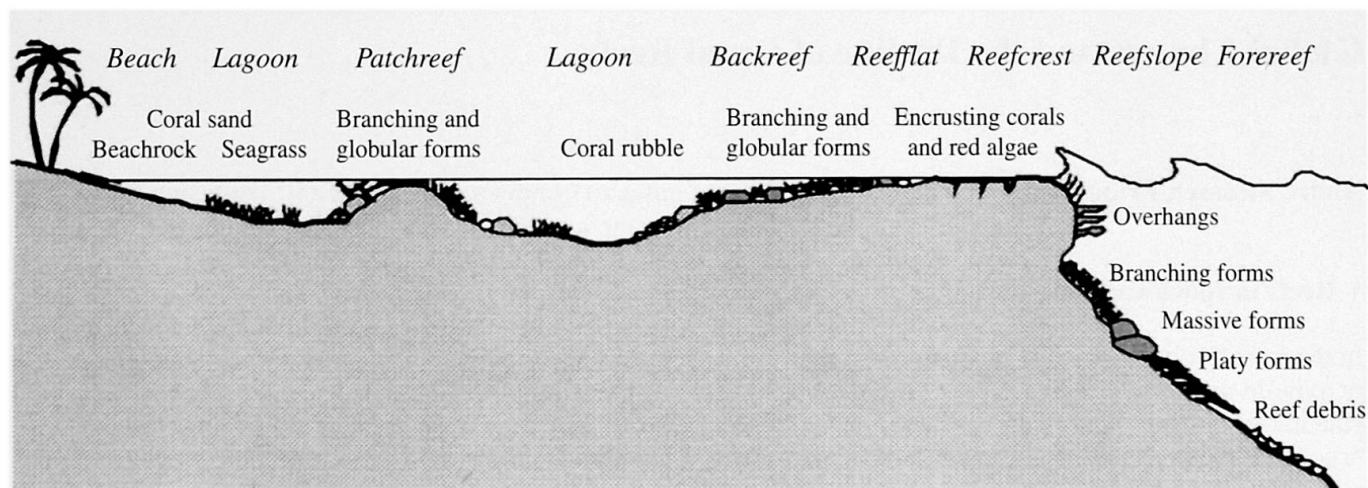


Fig. 1: General coral reef zones. The distribution of coral genera and shape depends mainly on water transparency and water energy; the distribution of sand, rubble, and seagrass on water energy and seafloor morphology (adapted from STRASSER 1997)

Generelle Zonierung eines Korallenriffes. Die Verteilung der Korallen-Genera und deren Form werden vor allem durch Transparenz und Energie des Wassers bestimmt. Die Verteilung von Sand, Geröll und Seegrass hängt von Wasserenergie und Morphologie des Meeresbodens ab (nach STRASSER 1997)

Zonation générale d'un récif corallien. La distribution des genres de coraux et leur forme sont contrôlées surtout par la transparence et l'énergie de l'eau, tandis que la répartition de sable, gravier et herbier dépend de l'énergie de l'eau et de la morphologie du fond de la mer (d'après STRASSER 1997)

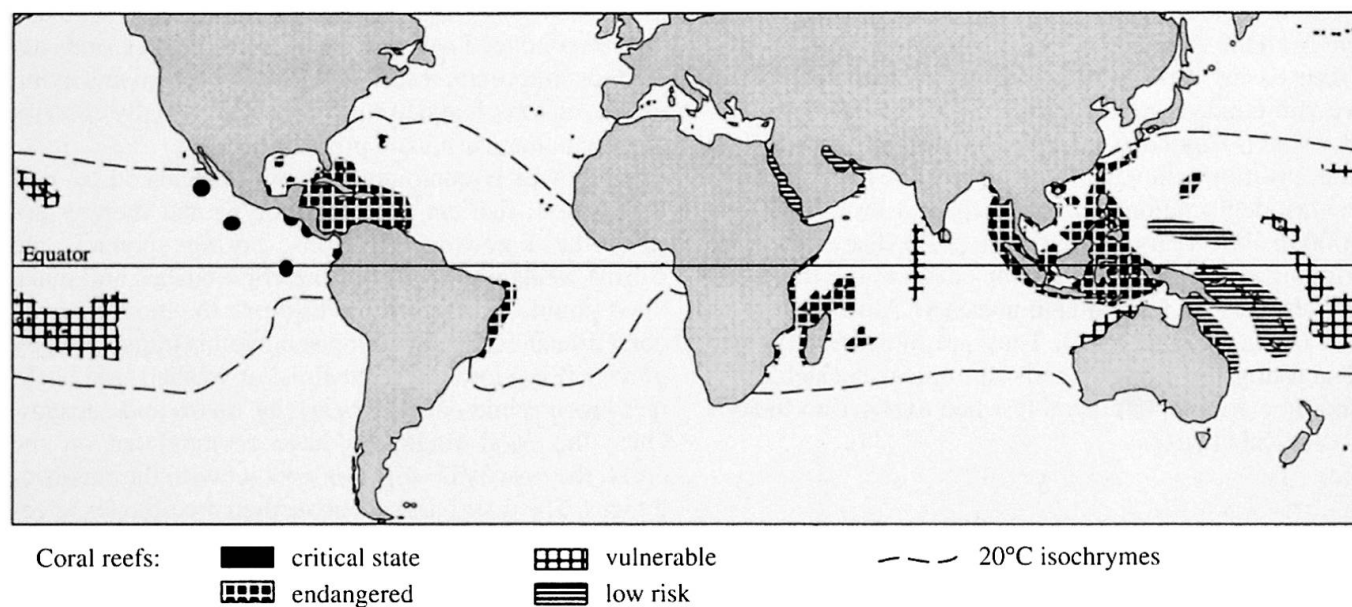


Fig. 2: Distribution and state-of-health of young shallow-water coral reefs. Isochrymes according to SCHUHMACHER (1988), degrees of vulnerability according to JAMESON et al. (1995)

Verteilung und Gesundheitszustand rezenter Flachwasser-Korallenriffe. Isochrymen nach SCHUHMACHER (1988), Bedrohungsgrade nach JAMESON et al. (1995)

Distribution et état de santé des récifs coralliens en eau peu profonde. Isochrymes d'après SCHUHMACHER (1988), degrés de menace d'après JAMESON et al. (1995)

3 Decline of coral reefs

In the course of Earth history, dramatically changing ecological conditions have brought numerous coral genera and species to extinction. However, the reef ecosystems as a whole always were capable to flourish again by replacing the more sensitive species by better adapted ones. For example, the Pleistocene sea-level fluctuations with over 100m amplitudes have periodically dried out reefs, but with each sea-level rise the corals installed themselves again on fossilised relics of their predecessors (e.g., STRASSER & STROHMENGER 1997). As the branching corals, *Acropora palmata* and *A. cervicornis*, in many reefs of the Caribbean are weakened by diseases, they are gradually being replaced by *Agaricia tenuifolia* (ARONSON & PRECHT 1997; ARONSON et al. 1998). Another example are coral branches broken by a storm which serve as substrate for a new generation of corals of the same or another species (BLANCHON et al. 1997). Single causes hindering coral development can commonly be compensated within the reef ecosystem through adaption, and the reef continues to play its role as morphological barrier and diversified habitat. However, with decreasing biodiversity, the vulnerability of the system to further environmental changes increases (ROGERS 1993). If environmental stresses cumulate the ecosystem will collapse and a rapid recolonisation by corals will not be possible. Many environmental factors causing coral-reef decline have existed since the earliest coral reefs. Today, however, several of these factors are enhanced directly or indirectly by human activity, and new stress factors are introduced (Table 1). Thus, the state of a coral-reef ecosystem also reflects the impact of anthropogenically induced Global Change (Fig. 2).

4 Major anthropogenically induced stress factors

4.1 Increase in water temperature and UV-radiation

The anthropogenically enhanced greenhouse effect causes a slow temperature rise of the ocean water to which corals potentially could adapt if given enough time. However, in situations such as the El-Niño phenomenon, the rapid temperature increase to over 30°C causes the corals to expulse their zooxanthellae and bleach, becoming vulnerable to other stress factors (e.g., ANTONIUS 1995; BERKELMANS & OLIVER 1999). Healthy coral polyps can protect themselves against overgrowth or grazing by other organisms by secreting chemical substances (SOROKIN 1995). When they are weakened, however, they are open to bacterial infections and other diseases (ANTONIUS 1995). Further, increased UV-radiation due to thinning of the ozone layer also leads to bleaching and a weakening of the corals (REAKA-KUDLA et al. 1993; COLES & SEAPY 1998).

4.2 Increased sediment and nutrient input

Deforestation, river corrections and agricultural activity lead to increased sediment run-off from the continent into the ocean. Reefs situated off-shore of such areas risk suffocation by sediment. Healthy coral polyps can use their tentacles to clean off sediment grains (SOROKIN 1995), but too much sediment will cover and kill them. Nutrients (in particular phosphorous and nitrogen) are commonly associated with terrigenous input, and they are introduced by sewage and aquaculture. Coral reefs are oligotrophic systems where nutrients are mainly recycled within the reef community. They thus suffer strongly from eutrophication; fast-growing filamentous and fleshy algae will outcompete the corals, especially if these are already weakened by other factors (e.g., LAPOINTE et al. 1993). Increased sediment and nutrient input also decrease water transparency, thus limiting the photosynthetic activity of the zooxanthellae.

4.3 Disturbed ecological equilibrium

Overfishing in reefs, locally with dynamite and poisons, will disturb the natural balance between reef organisms which has taken thousands of years to establish. For example, excessive harvesting of the triton shell (*Charonia tritonis*) for the tourist trade causes an invasion of the starfish *Acanthaster planci*, a predator of coral polyps. This starfish is capable of destroying large areas of coral reefs. The devastated reefs take 10 to 40 years to regenerate (SOROKIN 1995). Although *A. planci* invasions may also be seen in natural ecological cycles, the human impact appears to increase their frequency and magnitude. Another example is that of the *Diadema* sp., a starfish grazing on green algae. The rapid water temperature increase during El-Niño periods leads to their mass-death. The green algae are thus free to overwhelm the corals.

4.4 Physical destruction and pollution

Mining of reefs for limestone, ship traffic through coral-reef passes, anchoring, construction in the coastal zone close to fringing reefs, as well as diving and snorkeling tourists cause physical damage to the corals ranging from breaking off branches to the total destruction of a reef. Even if a nature-loving diver inadvertently touches a coral, a few square-centimetres of tissue will die. Oil spills damage the entire ecosystem. Plastic bags thrown overboard or blown into the ocean from open-air garbage dumps float in the water and (if not eaten by sea turtles and thus killing them) may cover coral heads and lead to their suffocation. Physical destruction by storms is not directly related to anthropogenic factors, but storm tracks may be changed and storm frequency and intensity may increase due to the enhanced greenhouse effect.

Factor	Consequence for individual corals and reefs	Natural processes	Anthropogenic processes
Sea-level changes	Drowning or emersion of reefs	Waxing and waning of polar ice-caps, thermal expansion of ocean water	Increased greenhouse effect
Increasing water temperature	Bleaching of corals	Changes in insolation and oceanic circulation	Increased greenhouse effect
Sediment load	Suffocating of coral polyps, reduced water transparency	Increased rainfall in the hinterland, change in vegetation cover	Deforestation, river corrections, mining, agriculture
Nutrients	Eutrophication, increase in algae, perturbation of the ecosystem	Increased river input, changing ocean currents, upwelling	Input through agriculture, sewage, and aquaculture
Infectious diseases	Death of corals	unknown	unknown
UV-radiation	Bleaching, cell damage	Thinning of ozone layer, e.g. after volcanic eruptions	Thinning of ozone layer through CFCs
Ecological imbalance	Coral ecosystem collapse through competing organisms, reduced biodiversity	Changes in water temperature, storms, less herbivores	Increased greenhouse effect, harvesting of marine organisms
Fishing	Disturbance of the ecosystem		Overfishing (locally with dynamite and poison), damage through nets
Mining	Physical destruction		Building activity
Building	Physical destruction, pollution		Building activity
Ship traffic	Physical destruction through grounding and anchoring, spilled freight, oil pollution		Trade, tourism
Hydrocarbon exploration and production	Physical destruction, pollution		Exploitation, transport
Tourism	Physical destruction, pollution		Recreation, thoughtlessness
Souvenirs	Physical destruction, perturbation of the ecosystem		Trade, thoughtlessness

Tab. 1: Natural and anthropogenic threats and stress factors (adapted from STRASSER 1997)

*Natürliche und anthropogene Bedrohungen und Stressfaktoren (nach STRASSER 1997)**Menaces et facteurs de stress naturels et anthropogéniques (d'après STRASSER 1997)*

Action	Global effect	Local effect
Reduction of anthropogenic output of greenhouse gases to slow down temperature increase in tropical and sub-tropical waters	X	
Reduction of sediment and nutrient run-off through better management of forestry, agriculture, and building activity in the hinterland of coral reefs		X
Improved control of waste production and discharge in the coastal zone		X
Improved control of ship traffic close to reefs		X
Improved control of offshore exploration and production of hydrocarbons		X
Improved control of building activity close to reefs		X
Improved control of tourism, especially of recreational diving		X
Improved integrated management of the coastal zone		X
Improved legal protection of coral reefs (e.g., by creating national parks)		X
Prohibition of coral-reef mining		X
Prohibition of fishing with dynamite, poison, and drift-nets		X
Prohibition of collecting and trading souvenirs from living reefs		X
Education of the local population, local policy makers, and tourists	X	
Education on all levels that coral reefs are vital for the future of humankind	X	

Tab. 2: Measures to be taken to mitigate coral reef decline (STRASSER 1997)
Massnahmen zur Verminderung des Niedergangs der Korallenriffe (STRASSER 1997)
Mesures à prendre pour diminuer le déclin des récifs coralliens (STRASSER 1997)

5 Perspectives

According to JAMESON et al. (1995), 10% of the world's shallow-water coral reefs are already destroyed, and the remaining reefs are threatened to various degrees (Fig. 2). Only one third of all reefs can be considered to be in good health. 30% will probably die in the next 10 to 20 years, and the rest will be endangered due to the general increase in water temperature. Global warming also causes sea level to rise (20cm to 1 metre within the next 100 years; IPCC 1996). In healthy coral reefs, the growth potential is high enough to keep pace with such a sea-level rise. Weakened reefs, however, will be outpaced and lose their function as protective barriers of the coastal zone. Direct impact by physical destruction, pollution, eutrophication, and sediment input are likely to increase especially along the coasts of developing countries with rapid industrialisation. The consequences of all of the above are enhanced flooding during spring tides and storms, coastal erosion, loss of habitat for marine organisms (including economically important ones), and loss of attractivity for tourism.

Many scientists and politicians are well aware of these problems, and several international programs monitor the state of coral reefs (e.g., EAKIN et al. 1997; <http://cord.aoml.noaa.gov>; [http://www.ust.hk/\(webrc/reefcheck/reef.html\)](http://www.ust.hk/(webrc/reefcheck/reef.html)) and co-ordinate research (e.g., the Land-Ocean Interaction in the Coastal Zone, LOICZ, program of the International Biosphere-Geosphere Program, IGBP). Efforts to mitigate environmental impact on these delicate ecosystems are increasing, and even coral-reef restoration is attempted locally (PRECHT 1998). The most important task, however, will be to make people aware of the ecological and economic importance of coral reefs. As in other terrestrial and aquatic ecosystems, the sound health of coral reefs is vital to local fishermen and to the inhabitants of coastal cities, to dive-tour operators and to the pharmaceutical industry (who may discover as yet unknown therapeutic substances in reef organisms). Thus, it is not enough to simply use coral reefs as indicators of Global Change; active measures have to be taken to slow down or stop the world-wide decline of coral reefs (Table 2).

Earth history has shown that even small modifications of an environmental factor may cause complex feedback loops that eventually affect the whole biosphere of which the human being is part. It is thus in our own interest to care for coral reefs as we should care for rain forests, tundra, or alpine meadows. From the perspective of geological time-scales, these ecosystems are resilient enough and will adapt to environmental changes, even if in the process some species become extinct and are replaced by new ones. Within the next decades and centuries, however, the decline of coral reefs is irreversible and will certainly be strongly felt.

Acknowledgement

I wish to thank Prof. ROBERT N. GINSBURG (University of Miami) for having initiated the International Year of the Reef in 1997, which has greatly helped to increase public awareness of coral reef ecosystems.

Literature Cited

- ANTONIUS, A. (1995): Pathologic syndromes on reef corals: a review. – In: Proc. 2nd Europ. Reg. Meeting ISRS, Luxemburg, Publ. Serv. Géol. Lux. 24: 161-169.
- ARONSON, R.B. & W.F. PRECHT (1997): Stasis, biological disturbance, and community structure of a Holocene coral reef. – In: *Paleobiology* 23: 326-346.
- ARONSON, R.B., PRECHT, W.F. & I.G. MACINTYRE (1998): Extrinsic control of species replacement on a Holocene reef in Belize: the role of coral disease. – In: *Coral Reefs* 17: 223-230.
- BERKELMANS, R. & J.K. OLIVER (1999): Large-scale bleaching of corals on the Great Barrier Reef. – In: *Coral Reefs* 18: 55-60.
- BLANCHON, P., JONES, B. & W. KALBFLEISCH (1997): Anatomy of a fringing reef around Grand Cayman: storm rubble, not coral framework. – In: *Journal of Sedimentary Research* 67: 1-16.
- BLOOM, A.L. (1993): The coral record of late glacial sea level rise. – In: Proc. Coll. Global Aspects of Coral Reefs, Miami: 1-6.
- COLES, S.L. & D.G. SEAPY (1998): Ultra-violet absorbing compounds and tumorous growths on acroporid corals from Bandar Khayran, Gulf of Oman, Indian Ocean. – In: *Coral Reefs* 17: 195-198.
- DUPRAZ, C. & A. STRASSER (1999): Microbialites and micro-encrusters in shallow coral bioherms (Middle to Late Oxfordian, Swiss Jura Mountains). – In: *Facies* 40: 101-130.
- EAKIN, C.M., McMANUS, J.W., SPALDING, M.D. & S.C. JAMESON (1997): Coral reef status around the world: where are we and where do we go from here? – In: Proc. 8th Int. Coral Reef Symp. 1, Panama: 277-282.
- GISCHLER, E. & A.J. LOMANDO (1997): Holocene cemented beach deposits in Belize. – In: *Sed. Geol.* 110: 277-297.
- IPCC (INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE) (1996): *Climate Change 1995, the Science of Climate Change*. – Cambridge: Cambridge Univ. Press.
- JAMES, N.P. & P.-A. BOURQUE (1992): *Reefs and Mounds*. – In: WALKER, R.G. & N.P. JAMES (eds): *Facies Models, Response to Sea Level Change*. – Geological Association, Canada: 323-347.
- JAMESON, S.C., McMANUS, J.W. & M.D. SPALDING (1995): State of the reefs, regional and global perspectives. – Int. Coral Reef Initiative Executive Secretariat, Silver Spring, MD, U.S.A., Background Paper.
- LAPOINTE, B.E., MATZIE, W.R. & M.W. CLARK (1993): Phosphorus inputs and eutrophication on the Florida reef tract. – In: Proc. Coll. Global Aspects of Coral Reefs, Miami: 106-112.
- PRECHT, W.F. (1998): The art and science of reef restoration. – In: *Geotimes* Jan. 1998, Alexandria, VA, U.S.A.: 16-20.
- REAKA-KUDLA, M.L., O'CONNELL, D.S., REGAN, J.D. & R.I. WICKLUND (1993): Effects of temperature and UV-B on different components of coral reef communities from the Bahamas. – In: Proc. Coll. Global Aspects of Coral Reefs, Miami: 126-131.
- ROGERS, C.S. (1993): Hurricanes and coral reefs: the intermediate disturbance hypothesis revisited. – In: *Coral Reefs* 12: 127-137.
- SCHUHMACHER, H. (1988): *Korallenriffe; Verbreitung, Tierwelt, Ökologie*. – München: BLV.
- SOROKIN, Y.I. (1995): *Coral Reef Ecology*. – Berlin: Springer.
- STRASSER, A. (1997): *Korallenriffe: von der Vergangenheit in die Zukunft*. – In: *Bulletin Société Fribourgeoise des Sciences Naturelles* 86: 39-53.
- STRASSER, A. & C. STROHMENGER (1997): Early diagenesis in Pleistocene coral reefs, southern Sinai, Egypt: response to tectonics, sea-level and climate. – In: *Sedimentology* 44: 537-558.

Summary:

Global Change and the Decline of Coral Reefs

Ever since coral reefs exist, changing environmental conditions have periodically led to their decline. However, within the perspective of geological time-spans, corals have always managed to re-install themselves. Today, human activity has enhanced stress factors and added new ones that cause a rapid and (on the human time-scale) irreversible decline of many reef ecosystems. The reasons for the disturbance of these complex communities are multiple, but global warming is a key factor. As a result, coral reefs lose their vital role of protecting coastal areas from flooding and storm impact and of creating habitats for numerous marine organisms. In this short article, natural and anthropogenically induced stress factors are discussed, and measures for mitigating or stopping coral-reef decline are proposed.

Zusammenfassung: Global Change und das Absterben der Korallenriffe

Umweltveränderungen haben periodisch zum Absterben von Korallenriffen geführt seit diese existieren, aber jedesmal (allerdings in geologischen Zeiträumen) ist den Korallen gelungen, sich wieder zu installieren. Heute jedoch führt die menschliche Aktivität zur Verstärkung von gewissen Stressfaktoren und zur Hinzufügung von neuen, was zu einem raschen und (innerhalb des menschlichen Zeitmassstabes) irreversiblen Absterben zahlreicher Korallen-Ökosysteme führt. Die Gründe für den Untergang dieser komplexen Lebensgemeinschaften sind vielseitig, aber die globale Erwärmung spielt dabei eine Schlüsselrolle. Die Korallenriffe verlieren so ihre vitale Funktion als Schutzwall der Küsten gegen Überflutungen und Stürme sowie als Habitat für eine grosse Anzahl mariner Organismen. In diesem kurzen Artikel werden die natürlichen und die anthropogenen Stressfaktoren diskutiert und Handlungsmöglichkeiten vorgeschlagen, die das Absterben der Korallenriffe verlangsamen oder verhindern können.

Résumé : Changements globaux et le déclin des récifs coralliens

Des changements environnementaux ont périodiquement amené au déclin de récifs coralliens depuis que ceux-ci existent sur terre. A chaque reprise, mais à des échelles de temps géologique, les coraux ont réussi à se

réinstaller. Aujourd'hui, l'activité humaine augmente certains facteurs de stress et en ajoute d'autres, provoquant le déclin rapide et irréversible (à l'échelle humaine) d'une grande partie des écosystèmes récifaux. Les raisons pour la perturbation de ces communautés complexes sont multiples, mais le réchauffement global en est un facteur clé. Les récifs coralliens perdent ainsi leur fonction protectrice des côtes contre les inondations et l'impact des tempêtes, et leur rôle vital comme habitat pour un grand nombre d'organismes marins. Dans cette note, les facteurs de stress naturels et anthropogéniques sont discutés, et des actions sont proposées pour ralentir ou stopper le déclin des récifs coralliens.

Prof. Dr. **André Strasser**, Institut de Géologie, Université de Fribourg, Pérolles, CH-1700 Fribourg.
e-mail: andreas.strasser@unifr.ch