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Scleractinian assemblages under sediment input: their characteristics and relation to the nutrient input concept

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Abstract

In the geological record, scleractinian-dominated “turbid-water” bioconstructions that accumulated under substantial terrigenous input, along with shallow neritic marls rich in well-preserved corals are common. These occurrences indicate that beyond some threshold, the ecologic and taphonomic effects of sedimentation prevail over the effects of nitrification. Field data and experiments on recent corals show that some taxa cope well with terrigenous turbidity and sedimentation, and acclimate to increased heterotrophy. Colonial corals resilient to sediment input commonly are massive to platy forms of high skeletal plasticity and with large polypars, to effectively reject sediment, or are branched species providing a very small sedimentation area cleaned by feeble currents, or small-polyped massive taxa that tolerate intermittent veneering by sediment. These corals may comprise “siltation assemblages” of recent turbid-water reefs and level-bottoms, in siliciclastic environments. Conversely, excess input of even low amounts of dissolved inorganic nutrients into clear waters adversely affects many coral species. Fossil turbid-water bioconstructions (TWB) were situated in inner shelf to shore zone settings or near storm wave base on shelves or ramps, did not stack into reef complexes, mostly show a cluster to segment fabric, are scarce in or devoid of frame pores with marine cement, and lacked a high carbonate slope. Relative to fossil “clear-water” buildups preserved in pure limestone successions, fossil TWB contain (moderately) diverse coral assemblages, with an increased proportion of sediment-resistant forms. Aside from coral behaviour that is elusive in fossils, the sediment resistance of corals was mainly determined by colony shape and polypar size, but small-polyped, sediment-tolerant corals became common since the Early Cretaceous. Late Jurassic to Cretaceous turbid-water coral assemblages are dominated by plocoid or thamnasterioid forms; corresponding Cainozoic assemblages consist mainly of cerioid and plocoid taxa. In fossil TWB, bioerosion and encrustation are similar or higher than in contemporaneous clear-water buildups. Under higher sediment input, accumulation of discrete TWB was quenched, and level-bottoms of both corals and soft-substrate biota formed. In the resulting “coral marls”, depending on turbidity, sedimentation and substrate stability, the coral fauna consists largely of both solitary corals and (mainly) sediment-resistant pseudocolonial/colonial forms, or is dominated by solitary corals. Many corals show growth “anomalies” resulting from partial mortality due to episodic, rapid sedimentation and unstable substrate. In coral marl environments, because of terrigenous input, nutrient levels

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probably were elevated, yet macroboring and encrustation are very scarce. Beyond some threshold of terrigenous sediment input and accumulation, the ecologic and taphonomic effects of sedimentation and unstable substrate prevail over the effects of nutrient enrichment.

During the Meso-Cainozoic evolution of scleractinians, increasing photoautotrophy and progressive invasion of oligotrophic environments is in contrast to a Late Cretaceous to Cainozoic increase in the relative number of reefs in marginal-marine/siliciclastic settings. This trend may be explained by second-order sea-level fall and shrinking of epicontinental carbonate seas and isolated platforms, driving corals to more narrow, attached shelves, and by a wider total trophic range in which distinct coral assemblages can thrive, as a result of coral evolution and diversification.

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1. Introduction

Most autochthonous coral faunas described in “classic” monographs are from marls to marly limestones rather than pure limestones (e.g. Goldfuss, 1833; Angelis d’Ossat, 1894; Felix, 1903; Oppenheim, 1930). Since the papers of Schlager (1981) and Hallock and Schlager (1986) that underscored the sensitivity of corals to input of nutrients and sediment, there has been, however, an inclination to view corals and siliciclastics as mutually exclusive. Indeed, on mixed siliciclastic–carbonate shelves, reef distribution is mainly controlled by sediment input and dispersal (e.g. Schlager, 1981; Roberts, 1987; Larcombe and Carter, 2004), but there is also a wide overlap between corals and siliciclastics (e.g. Done, 1982; Roberts, 1987; Renema and Troelstra, 2001). Phenomena of stress by nutrients and sediment in recent reefs compel that corals are sensitive to these factors, but by far most records of stressed reefs are from areas affected directly or indirectly by human activity (e.g. Fishelson, 1973; Dodge and Vaisnys, 1977; Dryer and Logan, 1978; Done, 1992; Sammarco, 1996; Rawlins et al., 1998; Souter and Lindén, 2000; Hughes et al., 2003). Anthropogenic stress is more deleterious than most natural stresses, since it is (1) in many cases chronic, (2) intense, with the magnitude of a stress factor often far exceeding the magnitude of that same factor in nature, (3) occurs in combinations that may not be realized in nature, or not in that magnitude, and (4) in many cases is superposed with natural stress events (see, e.g. Done, 1992; Sammarco, 1996; Rawlins et al., 1998; Souter and Lindén, 2000; Gardner et al., 2003; Hughes et al., 2003; McCulloch et al., 2003; Pandolfi et al., 2003).

Since the appearance of scleractinians in the Middle Triassic (e.g. Stanley, 2003), level-bottoms and reefs rich in corals are common in mixed siliciclastic–carbonate lithologies and in siliciclastic/volcaniclastic rocks (Frost and Langenheim, 1974; Frost, 1981; Frost et al., 1983; Martin et al., 1989; Baron-Szabo, 1997, 2002; Sanders and Baron-Szabo, 1997, in press; Gong et al., 1998; Sanders and Pons, 2001; Mitchell, 2002; Wilson, 2002). It is well-known that some coral taxa are more resilient to turbidity and sedimentation than others (Mayer, 1918; Yonge, 1930; Marshall and Orr, 1931; Riegl, 1995; Wesseling et al., 1999, among others), and corals growing in waters of moderate to intermittently high turbidity are not automatically more stressed than their clear-water counterparts (Roy and Smith, 1971; Done, 1982; Johnson and Risk, 1987; Acker and Stearn, 1990; Riegl, 1995; Kleypas, 1996; McClanahan and Obura, 1997; Woolfe and Larcombe, 1998; Larcombe et al., 2001). Holocene turbid-water coral buildups may be considered as “alternative states of development rather than as disturbed or restricted versions” of clear-water reefs (Perry and Larcombe, 2003, p. 430). This view is supported by the numerous turbid-water coral assemblages from the geological record. Coral assemblages may be considered either sensitive or resilient to ecostress, depending on the types, magnitudes and frequency of stress exerted, and the considered scales in space and time (Grigg and Dollar, 1990; Done, 1992; Sammarco, 1996). According to the concepts of Hallock (1987, 1988) and Edinger et al. (2000) on the relation between coral growth and nutrient level (Fig. 1), nutrification leads to increased bioerosion and encrustation of corals, enhanced phytoplankton production lowers water

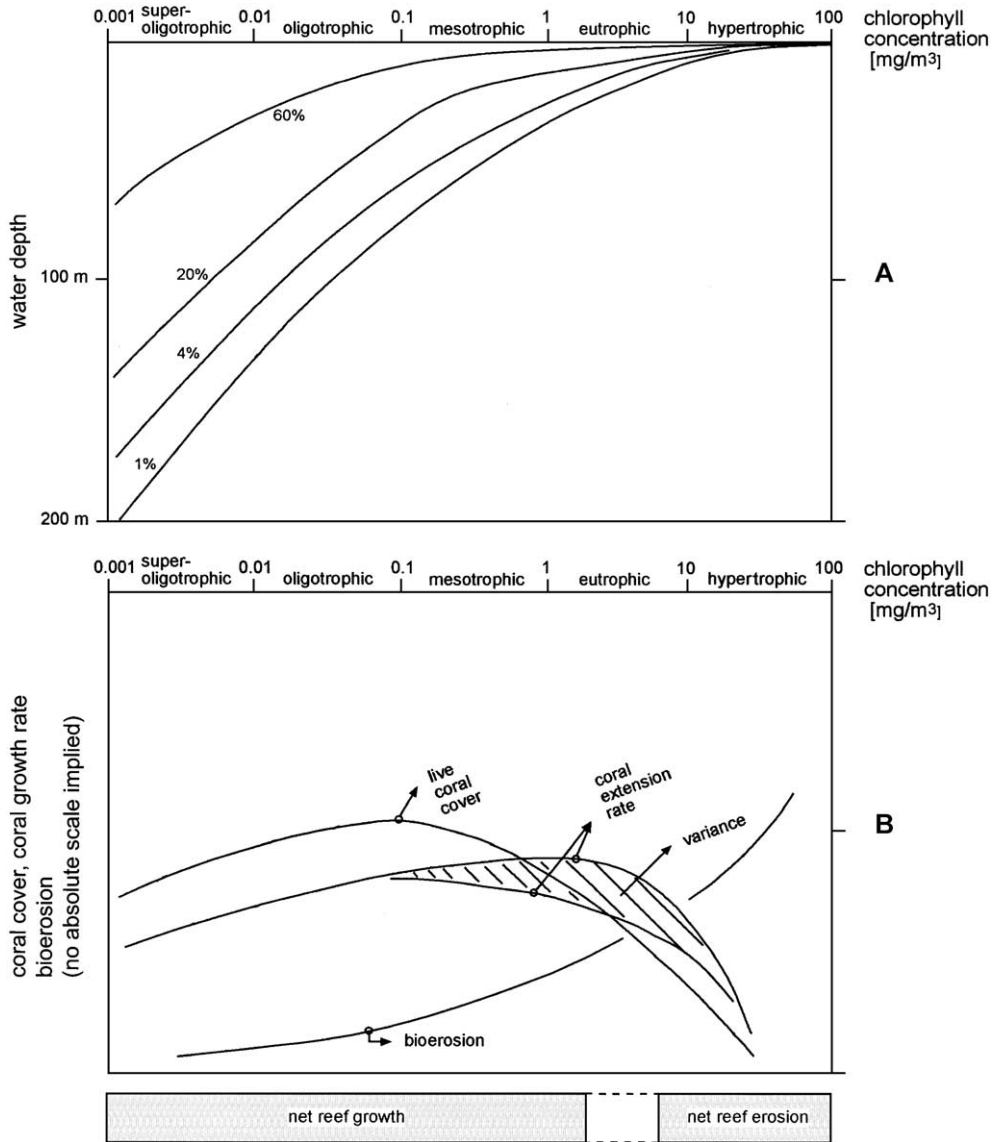


Fig. 1. (A) Trophic resource continuum versus reduction of illumination and growth of recent corals with water depth (from Hallock, 1987, 1988). At any given trophic level, light intensity decreases exponentially with depth. 60%: lower illumination limit for optimum development of branched corals; 20%: lower illumination limit for optimum development of massive corals; 4%: lower illumination limit for coral reef growth; 1%: lower limit of euphotic zone. (B) Trophic resource continuum relative to characteristic variations of live coral cover, coral extension rates (cross-hatched area indicates typical variance of growth rates), trend in intensity of bioerosion, and regime of net reef growth and net reef erosion, for recent reefs subject to different degrees of nutrification (without scale; from Edinger et al., 2000). Note that the trophic regime is shown as a lumped parameter for both water turbidity (=reduction of illumination with depth) and trophic level.

translucence, and corals shift to shallower depths to compensate for lowered illumination. In these concepts, water turbidity is implicitly treated as a parameter for both suspended inorganic sediment

and suspended organic matter, based on the observation that in areas of terrigenous input, increased sedimentation and nutrification in many cases covary, to some degree (e.g. Renema and Troelstra,

2001). As will be outlined in the present paper, however, under prevalent and significant terrigenous sediment input, important palaeoecological and taphonomic characteristics such as intensity of bioerosion and encrustation develop in contrast to the nutrient-input concept. In assemblages subject to sediment input, well before the corals are dying and recruits are eked out or smothered, both the individuals and the community show a set of geologically reconcilable features. During the Cainozoic, increased photoautotrophy of zooxanthellate corals (cf. Stanley and Swart, 1995; Kiessling, 2002) and the appearance of grazing fish were important for invasion of oceanic oligotrophic settings (Wood, 1995). At the same time, Alpine–Himalayan orogenesis, uplift of Tibet, second-order sea-level fall, climatic cooling and onset of glacio-eustasy increased sediment–nutrient input to the seas (Martin, 1996). Indeed, the PaleoReef database (Kiessling and Flügel, 2002) indicates, with fluctuations, a Late Cretaceous to Cainozoic increase in the relative percentage of reefs in marginal marine or siliciclastic settings (Fig. 2) (Kiessling, 2002). Thus, an apparent contradiction emerges: while many corals increased their capacity to build reefs in oligotrophic clear-water areas, the number of reefs in marginal-marine and siliciclastic settings also increased.

This paper presents a concept, mainly from and for a geological–palaeontological point of view, on the relation of corals to terrigenous sediment input. We shall first examine nutrition and growth of extant zooxanthellate corals (z-corals), their reaction to turbidity and sedimentation as documented by experiments and field work from recent “turbid-water” reefs, and evaluate which features of recent turbid-water assemblages can be placed into a sediment input concept applicable to the geological record. Coral assemblages thriving under substantial terrigenous input were and are widespread, consistent with the physiology and skeletal plasticity of many z-corals. We explain the apparent contradiction between increasing photoautotrophy and increasing number of reefs in marginal marine and siliciclastic settings mainly as a result of coral evolution and diversification, that is, by a widening of the total environmental range covered by clear- and turbid-water assemblages together.

2. Definitions

In this paper, the term “coral assemblage” denotes all types of coral communities ranging from rigid bioherms to level-bottoms on unconsolidated substrate. In

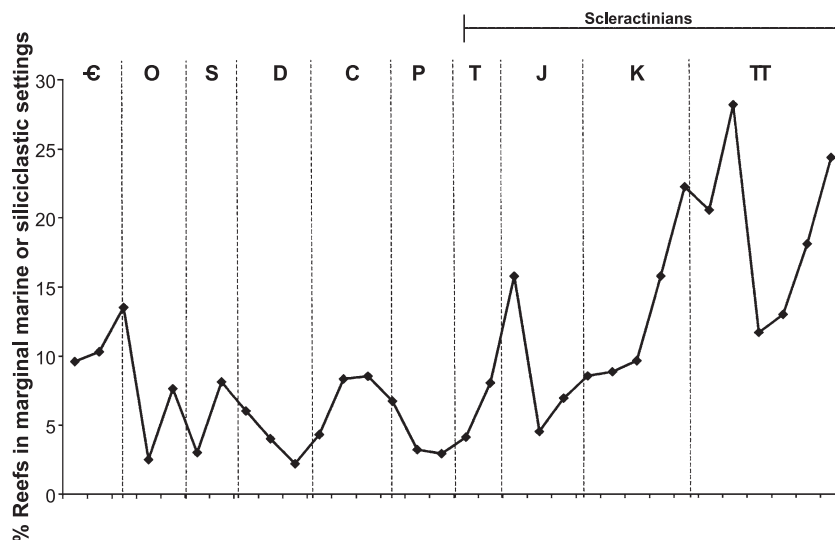


Fig. 2. Relative percentage of reefs that grew in marginal-marine or siliciclastic settings (simplified from Kiessling, 2002, his Fig. 14). Note the generally high Late Cretaceous to Neogene percentage of reefs in such settings.

the literature, an extremely wide meaning of “reef” exists. To denote any lithosome of tabular to biohermal to knoll-like shape that is rich in autochthonous corals, we use the term “coral construction”. From this definition, we exclude lithosomes that originated from level-bottoms of corals in which coral skeletons are spaced more than two times the diameter of the skeletons apart. We therefore follow the classification of bioconstructions (frame reefs, cluster reefs, segment reefs) and level-bottoms by [Riding \(2002\)](#). “Turbid-water bioconstructions” (TWB) denotes discrete lithosomes with recognizable boundaries, whereas “coral marls” accumulated from level-bottoms on soft substrata and lack discrete boundaries.

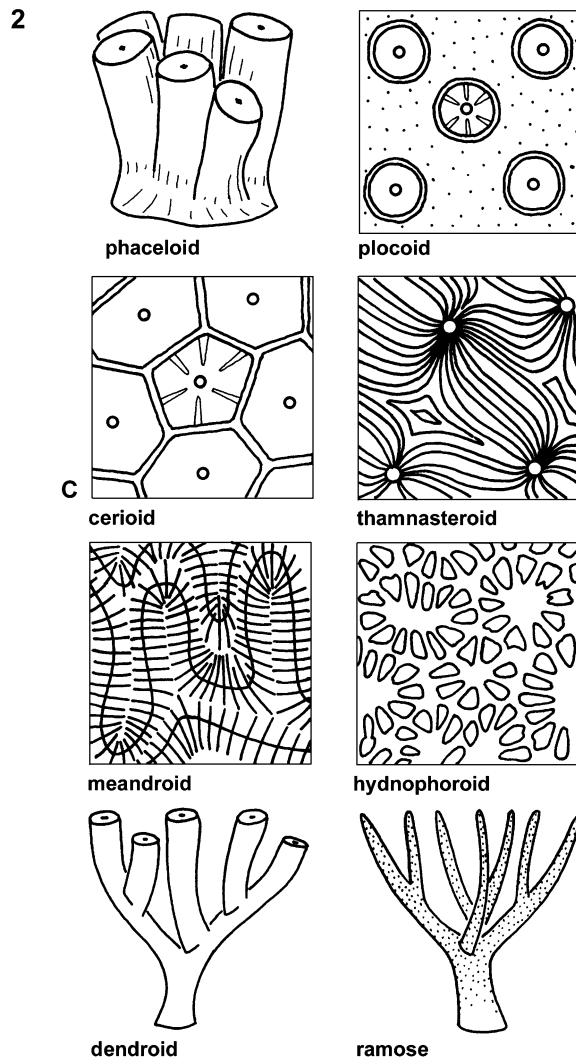
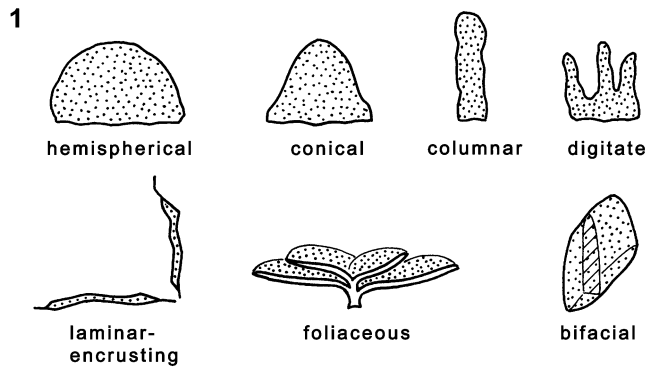
We follow the definition of ecostress by [Rosen \(1982\)](#) as a “gradient between ideal conditions and the ultimate limits of survival”. At the community level, ideal conditions may include intermittent stressful events to maintain high diversity (cf. [Connell, 1978](#); [Tanner et al., 1994](#); [Tanner, 1997](#)). Herein, we distinguish between clear-water coral assemblages in oligotrophic environments and turbid-water assemblages in settings of increased turbidity and siliciclastic deposition caused by terrigenous input, in high-oligotrophic to eutrophic waters ([Fig. 1](#)). We do not deal with turbid-water environments resulting mainly from dissolved nutrient input with little or no siliciclastic input, such as in upwelling zones; for these, the nutrient input concept fully applies (cf. [Hallock, 1987, 1988](#)). In the geological record, a succession with buildups rich in corals and that consists of pure limestones and with no record of elevated nutrient level (e.g. intervals rich in suspension-feeding biota, phosphorite nodules, encrusted hardgrounds, negative $\delta^{13}\text{C}$ excursion) is considered as a record of clear and, by inference, oligotrophic waters (relative to present nutrient levels; see [Martin, 1996](#)). We concede that our distinction of clear- and turbid-water environments is an oversimplification, since in recent settings that would classify as clear-water by the above criteria, sizeable differences in natural nutrient level and water transparency may exist ([D’Elia and Wiebe, 1990](#); [Yentsch et al., 2002](#)). However, because ancient levels of water turbidity (and of short-term sediment accumulation) are as yet impossible to quantify rigidly, we have to use the terms clear water and turbid water in the above defined, wider sense.

3. Recent corals: some aspects of nutrition, growth and growth form

3.1. Nutrition

Colonial corals are characterized by high nutrient demand (e.g. [Bilger and Atkinson, 1992](#); [Atkinson et al., 1995](#); [Basillais, 1998](#)), and their rate of nutrient uptake correlates positively with both bottom shear stress and current speed ([Charpy, 2001](#); [Hearn et al., 2001](#)). In present-day reef waters, the level of inorganic+organic nutrients varies by a factor of at least 10 ([D’Elia and Wiebe, 1990](#)). Coral nutrition is influenced by coral growth form and polyp integration ([Fig. 3](#)). Polyp integration relates to the degree of connection among polyps, ranging from discrete polyps (solitary and pseudocolonial corals) to polyps that are laterally connected by tissue (high-integrated corals). Recent z-coral faunas are dominated by high-integrated species with calyces 1–5 mm (most common) and 5–10 mm in width; larger calyces and low-integrated corals are less common ([Coates and Jackson, 1987](#)). Z-corals are mixotrophs feeding on (1) storage compounds (lipids) and compounds translocated from their zooxanthellae (photoautotrophic source 1), (2) compounds released by cyanobacteria and unicellular endolithic green algae (photoautotrophic source 2), (3) dissolved organic matter (amino acids, fatty acids, sugars) and dissolved inorganic nutrients, and (4) particulate organic matter, either living or dead, by macro- or microphagy (e.g. [Muscatine, 1973, 1990](#); [Porter, 1976](#); [Tomascik and Sander, 1985](#); [Sorokin, 1990](#); [Schlichter and Brendelberger, 1998](#)). The relative contribution of each food source depends on coral species and on environment ([Foster, 1980](#); [Tomascik and Sander, 1985](#); [Anthony, 1999](#); [Anthony and Fabricius, 2000](#)). Many reef corals cover a large part of their nutrition by heterotrophy (e.g. [Lewis and Price, 1975](#); [Lewis, 1976](#)). All z-corals must feed heterotrophically to some extent, to sustain calcification, their photosymbionts, ATP synthesis, tissue growth, and development of propagules ([Barnes and Chalker, 1990](#); [Dubinsky and Jokiel, 1994](#); [McConnaughey and Whelan, 1997](#); [Anthony, 1999](#)).

Small-polyped z-corals typically are ramose to foliaceous ([Fig. 3](#)), have a thin tissue, a high ratio of living surface S to volume V , a tissue ratio of animal/



plant protein of about 1, face high fluxes of dissolved and fine-particulate nutrients, and cover up to 90% of their nutrition by photosymbiosis. Conversely, large-polyped corals commonly are massive to platy, with a low S/V ratio, have a ratio of animal/plant protein of >1 , face comparatively low fluxes of dissolved nutrients, and cover a large part of their nutrition by heterotrophy (Porter, 1976; Jokiel, 1978; Muscatine et al., 1989; Abelson et al., 1993); these latter corals thus are more akin to animals (Barnes and Hughes, 1988). Large-polyped massive, platy and foliaceous corals are more abundant in lower-lit (deeper) parts of reefs (e.g. Huston, 1985).

3.2. Skeletal growth

Calcification of the coral skeleton is speeded by symbiosis with zooxanthellae, but also proceeds in the dark, at rates about 50% to 5% of light-enhanced calcification (e.g. Huston, 1985; Barnes and Chalker, 1990). Although photosynthetically active radiation decreases exponentially with depth (cf. Fig. 1A), due to photo-acclimation, the rate of photosynthesis is held constant over a wide range (tens of percent) of light intensity. Because of photo-acclimation, many z-corals are light-saturated and calcify at a similar rate over a depth range of tens of meters (e.g. Barnes and Chalker, 1990). Under persistently reduced irradiation, the shape of corals may change to maximize light catchment (e.g. Titlyanov et al., 1996). As a result of the combined effects of photo-acclimation, acclimation to different nutrient sources, and modification of skeletal shape with depth (see also below), many common reef-building corals thrive in depths of a few meters down to more than 70 m (e.g. Goreau and Wells, 1967). Many “submerged” Holocene shelf-edge reefs with their crests in waters more than 10 m deep, and extending down to more than 50 m deep, are thick reefs with vigorous growth and diversified coral assemblages (e.g. Baker and Weber, 1975; Hughes and Jackson, 1985; Macintyre, 1988; Blan-

chon and Jones, 1997). Beyond a lower threshold of irradiation, however, light saturation is not attained, and coral calcification slows down. Slowed growth due to light reduction may perhaps encompass a large part of the total irradiance range wherein a coral can thrive (Barnes and Chalker, 1990).

3.3. Growth form

The growth form of recent colonial corals (Fig. 3) is controlled by both genetic and environmental factors, with the influence of each control variable between species. With respect to environmental factors, the shape of colonial corals is “plastic” mainly in response to (1) light level (turbidity), (2) water energy, (3) abundance and types of nutrients, (4) sediment accumulation, and (5) substrate (Weber, 1974; Graus and Macintyre, 1976; Foster, 1980; Geister, 1983; Falkowski et al., 1990; Roberts et al., 1992). Light level influences the shape of corals that feed mainly phototrophically (Baker and Weber, 1975; Graus and Macintyre, 1976; Huston, 1985; Barnes and Hughes, 1988). On many recent clear-water reefs, fast-growing branched taxa and hemispherical forms prevail down to 10–15 m depth, corresponding to a lower illumination limit of about 40% PAR (cf. Fig. 1A). Within a coral species, to optimize light catchment, platy–foliose forms with the plates oriented subhorizontal tend to develop at and below 4% of surface irradiation (Graus and Macintyre, 1976; Barnes and Hughes, 1988). The change from hemispherical to platy shape occurs over a depth range of about 10–15 m, but at different absolute depths for different species (Hughes and Jackson, 1985). Below about 15–30 m water depth and/or in low-lit habitats such as groove walls, the assemblage is dominated by platy morphs (Goreau, 1959; Geister, 1983; Huston, 1985; Barnes and Hughes, 1988; Blanchon and Jones, 1997).

The influence of water energy on coral growth form depends, among other factors, on the style of feeding.

Fig. 3. (1) Common growth forms in massive to foliaceous, colonial corals. Growth forms are in part genetically determined, but to a variable proportion (depending on species) are also ecomorphs. (2) Most common styles of scleractinian polyp integration. Phaceloid forms are pseudocolonial. For colonial massive forms, the degree of skeletal and physiological integration of coral polyps increases from “low-integrated”, plocoid forms (discrete polypars separated by coenosteum) to cerioid forms (discrete polypars separated by a wall) to “high-integrated” thamnasterioid, meandroid and hydnochoroid forms with polypars fused laterally. Dendroid forms are characterized by one polypar at the end of each branch. In ramose forms, polypars are distributed over the entire colony surface. Most present ramose forms are of cerioid or plocoid integration.

For example, in shallow water, *Agaricia agaricites*, a Caribbean coral feeding mainly by mucus trapment (Lewis and Price, 1975) grows in laminar-encrusting form on steep substrata, and as a unifacial, flat “mesa” with stout pedestal. In deeper waters, this coral grows mainly as a bifacial, vertical plate subperpendicular to prevalent currents, to optimize catchment of food particles and oxygen uptake (Helmuth and Sebens, 1993). Bifacial coral shape is fairly common in poorly lit, deeper reef environments, as an adaptation to heterotrophic feeding (e.g. Schlichter and Brendelberger, 1998). This vertical trend of shape and orientation contrasts with that of other common hermatypes such as *Montastrea annularis*, which becomes platy–foliaceous with depth to optimize light capture (e.g. Graus and Macintyre, 1976). Not all common reef corals, however, change their shape with depth. *Leptoseris cucullata* and *Agaricia lamarcki*, for instance, grow in a platy morphology in depths of a few meters down to more than 70 m (cf. Goreau and Wells, 1967; Hughes and Jackson, 1985). On recent clear-water reefs, sedimentation and unstable substrate exert a significant influence mainly on the smaller-scale distribution of corals (e.g. Bak and Luckhurst, 1980; Hubbard, 1986). Under terrigenous input, with increased areas of unstable substrate, the entire coral assemblage becomes shifted towards sediment-resistant morphs and taxa, and many corals show characteristic features of partial mortality related to sedimentation or unstable substrate (see below). In fossil reefs, the interpretation of growth forms in terms of influence exerted by turbidity and sedimentation therefore is not straightforward, since many fossil coral assemblages consist of a mix of taxa and/or of morphs. Possible exceptions occur where a stratigraphic interval that relates to a specific palaeobathymetric range is strongly dominated by a single or a few coral taxa of constant growth form (e.g. Insalaco, 1996).

4. Sediment resistance of recent corals

Sedimentation is a common influence on scleractinians both in clear-water (James and Ginsburg, 1979) and turbid-water reefs (Hubbard, 1986). Following Stafford-Smith (1993), we distinguish *sediment rejection* as active removal of sediment by a coral, and *sediment tolerance*, as the potential to “hold

out” under a sediment veneer. *Sediment clearance* may be facilitated by active rejection, by growth forms and growth orientations precluding sedimentation, and by passive sediment removal by currents (Table 1). *Sediment resistance* denotes the degree to which a coral withstands prolonged sedimentation, by any of the above means. Biologists experimenting with recent corals arrive at partly different conclusions on the parameters most favourable for sediment clearance. Overall, however, consensus seems to exist that the efficiency of sediment clearance is determined by (1) size and shape of the entire colony, (2) colony surface (rugged, smooth) including morphology of the calyx, (3) a coral’s behaviour, and (4) grain size distribution of the sediment, with mud being more deleterious than sand. The significance of other parameters such as (5) polyp size and/or meander width, and (6) the style of polyp integration (Table 1) is under debate (compare Stafford-Smith, 1993 with Riegl, 1995). Also, the significance of coral behaviour in sediment clearance has been stressed by some authors (Bak and Elgershuizen, 1976; Riegl, 1995). Of the above parameters, coral behaviour is elusive to a palaeontologist, whereas the others relate to features of the skeleton or the sediment, and may be used to estimate ecostress exerted by sedimentation (see below).

4.1. Sediment rejection

Colonial corals reject sediment by four mechanisms: (1) polyp expansion (up to 300–400% volume increase) by water uptake and expulsion (“pumping”), (2) tentacle movement, (3) ciliary action, and (4) mucus secretion (Hubbard and Pocock, 1972; Bak and Elgershuizen, 1976; Stafford-Smith, 1993; Riegl and Branch, 1995). In recent colonial corals, calyx width varies from less than 1 mm to more than 20 mm (Coates and Jackson, 1987; Stafford-Smith, 1993). Large-polyped species effectively reject sediment up to fine gravel size; small-polyped species (e.g. *Porites*) can be effective in rejection of clay to silt (Bak and Elgershuizen, 1976). The most widespread mechanisms of sediment rejection are pumping and tentacle movement. Their efficiency depends on the verve of muscular movement which, in part, is related to the construction of the coral skeleton (Table 1) (Hubbard and Pocock, 1972; Rogers, 1983; Stafford-

Table 1

Types of sediment resistance of recent scleractinians, determined by experiments both in the laboratory and in the field

Type of sediment resistance	Features	Reference	Remarks
Sediment rejection (=active reaction of the coral to offshed sediment)	(1) Calyces long and wide. Polyps mobile. Deep, U- or V-shaped calyces. Septae numerous, fenestrate, ornamentate. Rejection efficiency correlates with polypar size. (2) Branched growth form	(Ad 1) Hubbard and Pocock (1972), Rogers (1983), Stafford-Smith (1993) (Ad 2) Dodge and Vaisnys (1977), Stafford-Smith (1993)	Behaviour is more important than skeletal construction (Bak and Elgershuizen, 1976; Riegl, 1995). Correlation of rejection efficiency with polypar size does not hold for branched corals (Stafford-Smith, 1993, Fig. 7).
Sediment tolerance (=ability of coral to tolerate a sediment veneer)	Poorly known physiological ability of soft tissue.	Bak and Elgershuizen (1976), Rogers (1983), Hodgson (1990), Stafford-Smith (1993), Wesseling et al. (1999)	High sediment tolerance observed in small-polyped taxa, e.g. <i>Porites</i> , <i>Montipora</i> .
Sediment clearance (=all mechanisms or features that favour clearance of sediment from a coral, active and passive)	(1) Effectiveness: Branched, columnar, vertical platy forms>Small domal (highly convex) forms>horizontal-tabular and horizontal-encrusting forms. (2) Settlement and growth on inclined to vertical surfaces	(Ad 1) Bak and Elgershuizen (1976), Dodge and Vaisnys (1977), Lasker (1980), Stafford-Smith (1993), Riegl (1995) (Ad 2) Dodge and Vaisnys (1977)	Clearance rate increases with inclination or convexity of surface. Clearance rate increases with water turbulence. Clearance rate increases with increasing inclination of substrate.
Active movement and buoyancy of coral	(1) Conical colonial corals: e.g. <i>Trachyphyllia</i> , <i>Manicina</i> (soft-bottom forms) (2) Solitary corals: fungiids, and others	(Ad 1), e.g. Hubbard and Pocock (1972), Gill and Coates (1977) (Ad 2), e.g. Goreau and Yonge (1968), Gill and Coates (1977), Chadwick-Furman et al. (2000)	

Smith, 1993). Bak and Elgershuizen (1976) concluded that, for sediment rejection, coral behaviour is more important than skeletal construction. Most experiments and field observations, however, indicate that in massive corals increased calyx or meander width correlate positively with efficiency of sediment rejection (Stafford-Smith, 1993; Philipp and Fabricius, 2003). Riegl (1995, p. 521) found a correlation of calyx size with polypar width (for plocoid forms) or meandrization index only for very fine and fine sand, or if rejection rates were averaged for sediment size classes.

Most meandroid corals are effective sediment rejectors (Bak and Elgershuizen, 1976; Rogers, 1983; Stafford-Smith, 1993). This is supported both by the distribution of some meandroids (e.g. *Diploria*) in environments subject to sediment stress (see below), and by fossil turbid-water assemblages with meandroids as typical elements (Baron-Szabo, 2003; Mitchell, 2002). Stafford-Smith (1993) noted that deep, cerioid calyces and deep, meandroid rows tend

to trap sediment. To persist under sedimentation, such corals may have the polyps continuously expanded, or they have large polyps that easily dump sediment by pumping (cf. Stafford-Smith, 1993). When covered by sediment, in most coral species, rejection starts immediately or after a few hours, or not at all; the latter is the case mainly in corals without tentacles and that feed by ciliary action (e.g. *Porites*, *Acropora*) (Hubbard and Pocock, 1972; Bak and Elgershuizen, 1976; Rogers, 1983; Stafford-Smith, 1993). Sediment rejection by any of the means mentioned above costs metabolic energy (Riegl and Branch, 1995); hence, under high, chronic or frequently repeated sedimentation, the activity of sediment rejection declines (Stafford-Smith, 1993; Riegl, 1995). Under rapid sedimentation, enhanced mucus production is a common (often auxiliary) method of sediment rejection (Bak and Elgershuizen, 1976; Stafford-Smith, 1993) that is costly in terms of metabolic energy and that may also increase the inclination for infection and disease (Hodgson, 1990; Riegl and Branch, 1995).

A comparison of coral assemblages before and after heavy, prolonged stress from siltation and turbidity indicates that the assemblage became dominated by massive meandroids (Dodge and Vaisnys, 1977, p. 728), and by the branched forms *Madracis* and *Oculina* (Dryer and Logan, 1978). Due to their high convexity, small-sized coral heads probably reject sediment more effectively than large specimens of lower convexity (Dodge and Vaisnys, 1977, p. 716; Lasker, 1980; Rogers, 1990; Kleypas, 1996; Riegl, 1995). For all corals, it is more difficult to reject sediment from a horizontal surface than from an inclined or vertical surface (e.g. Bak and Elgershuizen, 1976); on flat surfaces, sediment may be pushed to “dump areas” on the corallum (Riegl, 1995). For branched corals, no correlation between sediment clearance and calyx size was found under field-condition experiments (Stafford-Smith, 1993). Stafford-Smith (1993) showed that, in massive colonial corals, sediment rejection efficiency is quite variable among congeneric species. For fossil coral assemblages, this implies that the response of a coral species to sedimentation will depend, among other factors, on the specific size and construction of the corallum, as well as the active clearance mechanisms used and the duration of polyp expansion (cf. Bak and Elgershuizen, 1976; Riegl, 1995). In addition, corals may acclimate to some degree to turbid-water environments. Experiments (Anthony, 1999) and field measurements (Anthony, 2000) indicate that corals from turbid-water reefs have a background rate of sediment rejection two to four times higher than their conspecifics in clear-water reefs (Anthony and Fabricius, 2000).

4.2. Sediment tolerance

A veneer of sediment can partly or completely choke a coral (Bak and Elgershuizen, 1976; Rogers, 1983; Stafford-Smith, 1993; Wesseling et al., 1999), induce tissue infections (Hodgson, 1990), and reduce a coral's energy budget by cutting off light, reducing food capture and consuming energy for sediment rejection (Stafford-Smith, 1993; Riegl and Branch, 1995). The sediment tolerance of recent *z*-corals differs markedly, ranging from inexorable death to localized necrosis to survival without signs of damage or stress (Hodgson, 1990; Wesseling et al., 1999). If not cleared by currents, *Acropora* is intolerant of

sediment-veneering or burial, and suffers immutable mortality under veneered portions (cf. Hubbard and Pocock, 1972; Rogers, 1983; Wesseling et al., 1999). For some massive corals, tissue necrosis remained confined to flat and concave surfaces veneered by sediment, whereas unveneered short columns and convex knobs commonly stayed healthy (Hodgson, 1990). The acroporid *Montipora* is quite sediment-tolerant, and may be veneered for weeks without signs of physiological damage (Hodgson, 1990). *Montipora* is common to prevalent in many Indo-Pacific turbid-water assemblages, and can also adapt to turbidity and sedimentation by acquiring growth forms ranging from encrusting to foliaceous to branched (Bull, 1982; Stafford-Smith, 1993). Similarly, *Porites* is highly tolerant of being sediment-veneered (Stafford-Smith, 1993) and may largely recover even after complete burial over nearly 3 days (Wesseling et al., 1999). These observations are consistent with the presence, often nearly exclusively, of *Montipora* and/or *Porites* in turbid-water habitats such as carbonate shore zones, lagoons and siliciclastic inner shelf to shore zones (e.g. James and Macintyre, 1985, p. 7; Potts et al., 1985; Fisk and Harriott, 1990; Tudhope and Scoffin, 1994). In coastal turbid zone reefs of South Thailand and eastern Australia, on level-bottoms of muddy siliciclastic sand, *Porites* heads up to a few meters in size are present (Tudhope and Scoffin, 1994; Larcombe et al., 2001). Because inter-taxon competition may sizeably reduce both fitness and abundance of coral taxa (Tanner, 1997), the siliciclastic environment favours the digestively low-ranking, but sediment-tolerant *Porites*. Sediment tolerance probably is related to as yet little-documented physiological features of the tissue (Hodgson, 1990; Stafford-Smith, 1993). Whereas sediment-rejection efficiency can, in part, be related to palaeontologically reconcilable features (calyx width, septation, etc.), at present no criteria to estimate sediment tolerance from a coral's skeleton are at hand.

4.3. Sediment clearance

For sediment clearance, the growth form of a coral is crucial. Among colonial corals, at least under natural conditions where currents are practically always present to sweep off sediment, branched and erect-foliaceous forms are by far the most effective in

clearance of sediment of silt to coarse sand size (Stafford-Smith, 1993). The role of currents (swells, waves, tides) for sediment clearance in natural coral assemblages has been stressed by Woolfe and Larcombe (1999) and Larcombe et al. (2001). In nature, corals promote sediment clearance by attaining growth orientations and shapes favourable for passive removal. For instance, on horizontal surfaces covered with sand or carborundum powder, in standing water, *Agaricia agaricites* has moderate to low rejection efficiency; on vertical surfaces, rejection efficiency is very high (Bak and Elgershuizen, 1976). In natural turbid-water habitats, *A. agaricites* grows with the plates steeply inclined to subvertical (Goreau, 1959; Acevedo et al., 1989). In heavily silted areas of the Caribbean, *A. agaricites* is among the most sediment-resistant corals (e.g. Acevedo et al., 1989). In turbid-water areas, another strategy of corals to enhance sediment clearance by passive removal is to settle on inclined to vertical surfaces (Dodge and Vaisnys, 1977). Corals of domal or high-conical shapes are more effective in clearance than subhorizontal-tabular or subhorizontal-encrusting forms. Moreover, corals with relatively smooth surfaces and of domal to high-conical shape are cleared by feeble currents; conversely, the more “rugged” a corals surface, the larger the tendency for sediment trapment (Stafford-Smith, 1993). Even for small-polyped corals, long and mobile polyps combined with branched form (e.g. *Madracis mirabilis*) result in immediate, combined rejection and passive clearance of all sediment at least up to 3 mm grain size (Bak and Elgershuizen, 1976). Unattached, mobile corals (including mainly solitary and a few colonial forms) prefer substrata of muddy sand to sand, and are highly efficient in sediment clearance; because of their loaf-like shape, fungiform mobile corals tend to keep afloat on the substrate (Goreau and Yonge, 1968; Hubbard and Pocock, 1972; Gill and Coates, 1977; Logan, 1988; Stafford-Smith, 1993; Yamashiro and Nishihira, 1998; Chadwick-Furman et al., 2000).

5. Stress by sediment and nutrients

5.1. Sedimentation, turbidity

Sedimentation and turbidity affect coral communities both on the level of individuals and of the entire

assemblage, mainly by (a) increasing soft-substrate areas unfavourable to recruitment and juvenile growth of corals and of some grazers, (b) reducing light penetration and the depth range in which corals can thrive, (c) increasing the amount of metabolic energy needed for sediment rejection, (d) physically disturbing and abrading coral polyps, (e) partially to completely killing corals by sediment veneering or burial, and (f) rendering corals more vulnerable to disease (Dodge et al., 1974; Loya, 1976; Dodge and Vaisnys, 1977; Dryer and Logan, 1978; Lasker, 1980; Rogers, 1983; Hodgson, 1990; Babcock and Davies, 1991; Wittenberg and Hunte, 1992; Stafford-Smith, 1993; Riegl and Branch, 1995; Wesseling et al., 1999; Yentsch et al., 2002). Sedimentation and turbidity exert different effects on coral assemblages, as a result of variations in duration, magnitude and frequency of stressful events.

To illustrate potential effects of different styles of sedimentation–turbidity stress, we may consider the following cases (Fig. 4): (1) a short phase of very high sediment stress, smothering many or all of the corals (case 1 in Fig. 4) (e.g. Dodge and Vaisnys, 1977; Dryer and Logan, 1978), (2) a short phase of high stress, triggering short, intense sediment rejection by corals, but with no obvious longer-term effects (case 2 in Fig. 4) (Tomascik and Sander, 1985, p. 152; Wesseling et al., 1999; Philipp and Fabricius, 2003), (3) a short phase of high turbidity and siltation stress causing sediment rejection and a transient reduction of calcification (case 3 in Fig. 4) (Bak, 1978; see also Dallmeyer et al., 1982), potentially leading to stress bands (cf. Roberts and Harriott, 2003), (4) prolonged, high or moderate stress that may affect a single or a few species hard or fatal, whereas others recover (case 4 in Fig. 4) (cf. Cortés and Risk, 1985; Wesseling et al., 1999), and (5) a low, but frequent or prolonged stress that may shift the coral assemblage towards prevalence of sediment-resistant taxa (see Section 7), and/or that affects the vital state of corals (case 5 in Fig. 4) (e.g. a persistent, moderate reduction of calcification; Dodge et al., 1974). For recent z-corals, except under variations of sediment input ranging over orders of magnitude (Cortés and Risk, 1985), and except severe or chronic sedimentation (Dodge et al., 1974; Dodge and Vaisnys, 1977; Bak, 1978), the skeletal growth rate of corals is not tightly coupled with sediment input (Loya, 1976; Miller and Cruise,

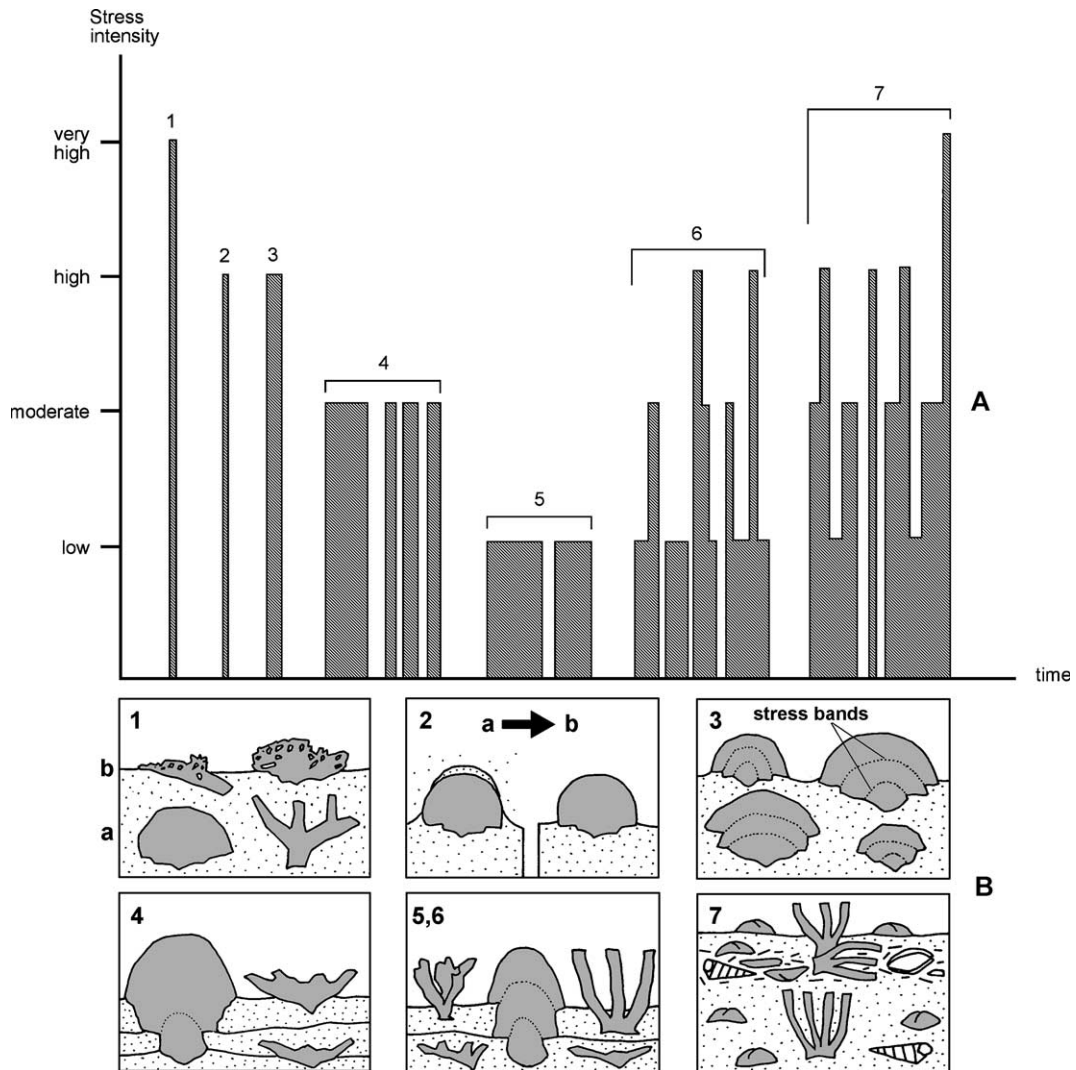


Fig. 4. (A) Conceptual diagram to visualize different stress intensities and durations of stress by sedimentation. Bars or bar groups labelled by numbers 1 to 7 refer to different types of sedimentation stress. (B) Potential impact of stress types as shown above, based on examples described from recent coral assemblages (see text). (1) Complete, permanent burial of corals during an event of rapid sedimentation (a), or smothering followed by re-exposure of dead corals on the sea floor (b). (2) A pulse of sediment fallout (a) is rejected without lasting signs of stress (b). (3) Pulses of sedimentation lead to stress bands and to overgrowth margins, but without shifting the coral assemblage. (4) Pulses of sedimentation may stress sediment-resistant corals and smother others, but the assemblage can restore without major shift. (5, 6) Prolonged and/or frequent sedimentation events may produce a shifted coral assemblage dominated by sediment-resistant forms. (7) Near-chronic sedimentation and turbidity result in a coral assemblage dominated by branched (low-integrated, pseudocolonial) and solitary corals. See text for further description and discussion.

1995; Anthony and Fabricius, 2000). Cases 4 and 5 may include high-diversity coral assemblages that develop in areas of near-chronic or frequent, moderate to low sedimentation stress and low to moderate turbidity (cf. McClanahan and Obura, 1997). Different styles of sedimentation–turbidity stress may be super-

posed. Thus, (6) an area subject to low sediment–turbidity stress may be punctuated by short stress events of moderate or high magnitude, such as diurnal or semidiurnal fallout of sediment resuspended by tides, sediment resuspended by storms, or seasonal river plumes (case 6 in Fig. 4) (Kleypas, 1996;

Larcombe et al., 2001). In this case, the effect of sediment–turbidity stress on a coral assemblage is not easy to estimate, since the ultimate result depends, to a large part, on the ratio of sedimentation to turbidity (cf. Loya, 1976; Woolfe and Larcombe, 1999); this style of stress perhaps includes fairly diverse to low-diversity “siltation assemblages” (see also Section 7). Finally, (7) an assemblage may be subject to near-chronic, moderate sediment–turbidity stress that is punctuated by high-stress events (case 7 in Fig. 4). The resulting coral assemblage is impoverished and dominated by solitary and uniserial, low-integrated or pseudocolonial (phaceloid, dendroid, oculinid) forms that are highly resistant to sedimentation, and that feed largely or entirely heterotrophically (Dryer and Logan, 1978). The above, *conceptual* styles of “stress spectra” serve to illustrate that the geological effect of sedimentation–turbidity stress on a coral assemblage depends, to a large part, on the magnitude–time distribution of stress and on the processes of sedimentation. The local impact of a stress event also depends on the morphology of a reef. For instance, if a steep reef slope is developed, rare events of clastic input may smother the reef flat, whereas on the slope, where little sediment accumulates, the coral assemblage may suffer comparatively little stress, or may recover from the slope (Maniwavie et al., 2001).

Water turbidity and sedimentation correlate only in part, and exert different effects on corals (McClanahan and Obura, 1997; Woolfe and Larcombe, 1998, 1999; Larcombe et al., 2001; Nugues and Roberts, 2003). Around some Australian turbid-water reefs, high concentrations (>200 mg/l) of suspended particulate matter are stirred by swells and waves, and concentrations of >40 mg/l locally prevail over more than 24 h (Larcombe et al., 2001). Tidal currents, although causing resuspension of bottom sediments (Kleypas, 1996), however, prevent sedimentation on the reefs (Larcombe et al., 2001). Diversified coral assemblages thus may persist in siliciclastic environments, at moderate to intermittently high terrigenous turbidity but low sediment accumulation (Done, 1982; Woolfe and Larcombe, 1998, 1999; Nugues and Roberts, 2003). In some Australian turbid-water reefs, many horizontal coral settlement plates were veneered by 3–5 mm of “fine sediment” (presumably silt to mud) after 6 months (Fisk and Harriott, 1990, p. 488), corresponding to a short-term accumulation rate of

6000–10,000 Bubnoff (mm/ka), which the standing stock of corals can easily cope with. Pulses of sedimentation orders of magnitude more rapid, such as caused by dredging, are nearly immediately cleared by most colonial corals (Bak, 1978). On the southern shelf of Puerto Rico, around turbid-water reefs, a layer 65–70 cm thick of terrigenous mud drapes Holocene bioclastic sand; this indicates a rapid increase of terrigenous input, with a mean rate of 4000 Bubnoff over the last 125–150 years, when deforestation and harbour dredging started (cf. Acevedo et al., 1989, p. 95). At present, an impoverished assemblage of sediment-resistant corals thrives on the reefs that once flourished more vigorously (Acevedo et al., 1989). In turbid-water settings, the effects of sedimentation and turbidity on the growth of individual corals are difficult to separate quantitatively (Dodge et al., 1974; Loya, 1976). On heavily polluted nearshore reefs in the Java Sea, at 3 m depth, light level is less than 15%, limiting significant coral growth to shallower depths (cf. Fig. 1A) (Edinger et al., 2000; Endean, 1976, p. 222; Hallock, 1987).

Overall, moderate turbidity and short phases of high turbidity seem less detrimental than sedimentation. Pulses of a few hours to days of rapid sediment fallout exert less of a lasting influence than frequent or chronic sedimentation at lower rates. In the GBR province, in nearshore siliciclastic settings, no reefs are present where medium-term sedimentation rates (since the Holocene shelf flooding about 6 ka B.P.; Kleypas, 1996) exceed 0.3 mm/year (Woolfe and Larcombe, 1999, p. 337). This rate limit is distinctly below the net calcification of reefs in these areas (0.7–5 mm/year; Woolfe and Larcombe, 1999, p. 337), an order of magnitude below growth rates of individual corals (cf. Sanders, 2003, Fig. 21), and is at the lower end of medium-term accumulation rates (thousands of years to 10 ka) of Holocene terrigenous shelves (cf. Enos, 1991, p. 69). The rate of 0.3 mm/year, however, includes rapid, intermittent accumulation as well as non-deposition and erosion, hence pulses of transient sediment settling are included (cf. Sadler, 1981).

5.2. *Nutrition*

With increasing nutrient level, mainly because of increased phytoplankton production and particulate non-living organic matter, sea water becomes less

translucent (Fig. 1). Natural nutrient input producing elevated trophic levels may result from (1) upwelling, (2) suspended matter from rivers or bottom sediments, (3) groundwater discharge, and (4) other factors such as suboxic waters produced by phytoplankton blooms in poorly flushed lagoons, storm eddies with enhanced plankton production, internal waves, and geothermal endo-upwelling (Fishelson, 1973; Johannes, 1980; Schlager, 1981; Hallock and Schlager, 1986; Lewis, 1987; D'Elia and Wiebe, 1990; Done, 1992; Naim, 1993; Rougerie and Fagerstrom, 1994; Dufour and Berland, 1999). For recent reefs, no comparative study exists on the different effects of loading by dissolved nutrients in a clear-water environment versus natural input of terrigenous sediment and non-living particulate organic matter (POM). Geological evidence from turbid-water assemblages (see Section 7 below) suggests that the ecological effects of clear-water, dissolved nutrient loading and sediment–POM loading are broadly similar up to the low- or mid-mesotrophic range, but beyond, the effects increasingly depart and produce distinct fossil records.

In clear-water settings, dissolved nutrient loading hits coral assemblages mainly by impeding coral reproduction and recruitment, increasing mortality, reducing illumination by increasing the concentration of suspended organic matter (phytoplankton, plankton debris, marine snow), increasing bioerosion and encrustation, promoting overgrowth of corals by macroalgae, favouring predator outbreaks, and by disturbing the balance between herbivores, macroalgae and corals (Fishelson, 1973; Banner, 1974; Birkeland, 1977; Kinsey and Davies, 1979; Schlager, 1981; Pastorak and Bilyard, 1985; Rose and Risk, 1985; Hallock, 1988; Hunte and Wittenberg, 1992; Wittenberg and Hunte, 1992; Smith and Buddemeier, 1992; Dubinsky and Jokiel, 1994; Hughes, 1994; Tanner, 1995; McCook, 1999; Edinger et al., 2000; Koop et al., 2001; McCook et al., 2001; River and Edmunds, 2001; Thacker et al., 2001). Although results from long-term experiments with dissolved nutrient input are quite variable with respect to their impact on different coral species, there is little doubt that dissolved nutrient input first impedes coral reproduction (Koop et al., 2001; Cox and Ward, 2002). Along trophic gradients (Tomascik and Sander, 1985), decreased gonad size, and decreased larval output and larval recruitment of common reef-build-

ing corals correlate inversely with dissolved nutrient level (Tomascik and Sander, 1987b; Hunte and Wittenberg, 1992; Wittenberg and Hunte, 1992). Macroalgae disturb corals by shading, physical stress and abrasion, by overgrowth, by occupying substrate potentially available for coral settlement, by reduction of water flow, and by increasing the number of grazers that inadvertently infest juvenile corals (Naim, 1993; Tanner, 1995; River and Edmunds, 2001).

Relative to dissolved nutrient input, coral assemblages seem to be more tolerant to natural input of POM. For some common taxa of massive and platy corals, the degree of heterotrophy is related to polyp size (Porter, 1976). Hence, in turbid-water settings with elevated levels of POM, large-polyped corals are in advantage at least with respect to sediment rejection and aspects of feeding. In areas of siliciclastic input, nutrient elements stored in bottom sediments become available to zooxanthellae only after the buried POM has been processed into dissolved constituents by microbes (Rawlins et al., 1998). In turbid-water environments produced by river input or resuspension, the largest portion of POM is refractory to corals (Anthony, 1999). For suspended, lithic silt to clay, an organic content of commonly a few percent results mainly from overgrowth by microbes (Anthony, 1999). Compared to zooplankton, silt to clay-sized suspended matter is low-quality food, but is locally abundant (Anthony and Fabricius, 2000). Corals from turbid-water settings show both phototrophic and heterotrophic acclimation to turbidity and SPM (Foster, 1980; Tomascik and Sander, 1985, 1987a). Experiments indicate that turbid-water reef corals feed 10–20 times more on SPM than conspecifics in clear-water settings (Anthony, 2000). At least some species of small-polyped, branched reef corals can acclimate to SPM levels identical to peak turbidities in some turbid-water reefs (16 and 30 mg/l), without attaining satiation (Anthony, 1999). With increasing SPM level, nutrient elements are less effectively assimilated. For massive or encrusting, large-polyped reef corals, particle capture rate decreases with increasing SPM, thus widening the tolerance to elevated SPM levels (Anthony, 1999). Corals well-adapted to feeding on SPM are mainly characterized by (1) a high tentacle cleaning rate, (2) large polypars, and (3) high resilience to particle stress (cf. Anthony, 1999). The same features are important in sediment resistance

(see Section 5). Although, in experiments, different coral species react differently to turbidity and SPM, there is evidence suggesting that in natural turbid-water areas, feeding on SPM may be important for sustainment of some coral taxa (Anthony and Fabricius, 2000). Beyond a coral's satiation, however, POM is stressful due to physical disturbance and increased metabolic energy needed for clearance and egestion, while increased mucus production may cause partial to complete mortality by bacterial infestation, disease and suffocation (Hallock and Schlager, 1986; Hallock, 1988; Anthony and Fabricius, 2000). Because many recent reefs and coral level-bottoms thrive in siliciclastic environments, in waters of moderate to intermittently high SPM turbidity, it appears that under natural conditions, overabundance of POM is not readily attained.

6. Recent turbid-water assemblages

6.1. General features

Although water turbidity and sedimentation rate are coupled only in part, turbidity and percentage of terrigenous silt–mud of the bottom sediment correlate fairly closely with each other (Done, 1982; Beach, 1983). Coral assemblages of high to moderate total diversity can thrive under mesotrophic to low-eutrophic conditions, at moderate to high short-term sedimentation rates, and individual corals may grow at lower to higher rates than their clear-water conspecifics (Fig. 1B; Tables 2 and 3) (McClanahan and Obura, 1997; Edinger et al., 2000; Larcombe et al., 2001). With respect to gross biotic composition and diversity, however, in different sedimentation–turbidity regimes, coral assemblages show characteristic differences.

(1) At prevalently low turbidity (visibility about 10–15 m), assemblages show no major shift of composition, but the relative abundance of coral taxa may be changed compared to clear-water counterparts (e.g. McClanahan and Obura, 1997). (2) At intermediate levels of terrigenous turbidity (visibility about 5–10 m), *Acropora* disappears, or becomes minor in abundance (Loya, 1976; Done, 1982; Acevedo et al., 1989; Tudhope and Scoffin, 1994; Perry, 2003; see also Wesseling et al., 1999). Moreover, the diversity

of both *Acropora* and non-*Acropora* assemblages may range from less to higher than their clear-water counterparts, and the relative abundance of coral taxa in some cases is more evenly distributed than on clear-water reefs (Bull, 1982; Done, 1982; Acevedo et al., 1989; McClanahan and Obura, 1997). The similar to higher diversity of such turbid-water assemblages may result from several factors, such as reduced interspecific competition due to reduced coral cover, preference of suspension-feeding and sediment-resistant coral taxa without disappearance of taxa feeding more on photosynthate, and acclimation of corals to increased suspension feeding and lowered light level (see Sections 3–6). By introducing disturbance (e.g. larger areas of unstable substrate, increased mortality) and releasing interspecific competition, moderately elevated levels of turbidity and sedimentation exert a diversifying effect (cf. Huston, 1985; McClanahan and Obura, 1997; Tanner, 1997; see also Connell, 1978; Woodley, 1992; Tanner et al., 1994). There is evidence that coral cover correlates with water transparency (Yentsch et al., 2002), but for both clear- and turbid-water reefs, there is little correlation between coral cover and diversity; highest, or high, diversities were recorded in areas with coverage of 25–95% (e.g. Huston, 1985, p. 158; Larcombe et al., 2001; Nugues and Roberts, 2003).

(3) In settings of prevalently high turbidity (visibility less than about 5 m), a distinct change of the coral assemblage occurs. The lower limit of coral growth is shifted to very shallow depth (cf. Fig. 1A), both total diversity and total coral cover are reduced, with the *relative* proportion of cover by sediment-resistant corals increased (in patches with high coverage due to limited settlement substrate; cf. Fisk and Harriott, 1990). Moreover, colony size ranges within wider limits, smaller-sized specimens (typically of coral heads) become more abundant, and “deep-water” morphs able to cope with sedimentation are common to prevalent (Dodge and Vaisnys, 1977; Dryer and Logan, 1978; Riegl, 1995). A reduced ecological zonation, however, is typically developed also at high turbidity (Roy and Smith, 1971; Bull, 1982; Beach, 1983; Cortés and Risk, 1985; Huston, 1985; Pastorak and Bilyard, 1985; Tomascik and Sander, 1985; Johnson and Risk, 1987; Hallock, 1988; Acevedo et al., 1989; Acker and Stearn, 1990; Hunte and Wittenberg, 1992; Wittenberg and Hunte,

Table 2

Water transparency and trophic regimes (see Fig. 1) of selected turbid-water coral assemblages

Water transparency (Secchi disk)	Designation	Other features	Location	Remarks	Reference
Up to 2 m	very turbid	turbidity caused by carbonate mud	Lagoon of Fanning atoll, Pacific	Coral patch reefs rising from 4 to 5 m in depth	Roy and Smith (1971)
10–15 m	low-turbid	(as above)	Lagoon of Fanning atoll, Pacific	Coral patch reefs rising from 10 to 15 m in depth	Roy and Smith (1971)
5–15 m	turbid to low-turbid	–	Peruvian upwelling zone	–	Hallock (1987, p. 461, and refs. therein)
0.2–2 m	very turbid	Turbidity caused by terrigenous input	Man Bay, southern Phuket island, Thailand	Tabular fringing reef similar to that of Tang Khen Bay (see below)	Tudhope and Scoffin (1994)
0.2–4 m	very turbid visibility of 1–2 m corresponded to 15–20 mg/l suspended sediment	(as above)	Tang Khen Bay, southern Phuket island, Thailand	Tabular fringing reef 2–3 m thick, with extensive intertidal reef flat, reef dominated by large <i>Porites</i> heads, low reef front made up by the relief of single <i>Porites</i> colonies, muddy foreereef at 2–5 m depth	Tudhope and Scoffin (1994)
3–10 m	very turbid to turbid	(as above)	Hi island, Southern Thailand	Fringing reef dominated by large <i>Porites</i> heads, reef front down to about 10 m depth	Tudhope and Scoffin (1994)
More than 10 m	low-turbid	(as above)	Racha Yai island, Southern Thailand	Fringing reef with patches of massive corals (<i>Porites</i>) and branched corals; substrate is bioclastic sand to gravel; reef front slopes down to about 14 m depth	Tudhope and Scoffin (1994)
0.5–5 m	very turbid	low- to mid-eutrophic regime	Mixed clastic–carbonate shelf of SW Sulawesi; shore zone	Solitary fungiids and impoverished assemblage of colonial corals on substrata of sandy mud to muddy sand	Renema and Troelstra (2001, p. 128–129)
1–5 m (wet season)	very turbid (wet season)	low- to mid-mesotrophic regime	Mixed clastic–carbonate shelf of SW Sulawesi; inner to middle shelf	Mixed colonial–solitary coral assemblage, small coral reef islands topped by bioclastic beaches	Renema and Troelstra (2001, p. 128–129)
10–17 m (dry season)	low-turbid to clear (dry season)	(dry season)			
7.5–20 m (wet season)	turbid to clear (wet season)	high-mesotrophic to low-eutrophic regime	Mixed clastic–carbonate shelf of SW Sulawesi; outer shelf	Shallow-water banks up to >5 km in length, with diversified coral assemblage	Renema and Troelstra (2001, p. 128–129)
10–30 m (dry season)	low-turbid to clear (dry season)	(dry season)			
15 m and more	Clear	–	“Muertos shelf tract” of Puerto Rico	Substrate of pure skeletal sand to skeletal gravel (IR 0–5%)	Beach (1983, Figs. 4–7), Acevedo et al. (1989)
5–10 m	Turbid	–	“Muertos shelf tract” of Puerto Rico	Mainly substrata of marly line mud (IR 20–35%) to terrigenous mud (IR 75–100%)	Beach (1983, Figs. 4–7)
2.5–5 m	very turbid	–	“Muertos shelf tract” of Puerto Rico	Substrate of terrigenous mud (IR 75–100%)	Beach (1983, Figs. 4–7)
– (not provided)	SPM peaks: >100–90 mg/l SPM: 2–10 mg/l	–	Inner shelf and coastal turbid zone reefs, GBR province	High-diverse, shifted, non- <i>Acropora</i> siltation assemblages	Kleypas (1996)
14.55–16.55 m	low-turbid to clear	–	eastern shore of Kenya	Watamu “control reef” site	McClanahan and Obura (1997)

Table 2 (continued)

Water transparency (Secchi disk)	Designation	Other features	Location	Remarks	Reference
7–9.4 m	Turbid	sedimentation 3–4 mg/cm ² /day	eastern shore of Kenya	Malindi “high-sediment reef” site	McClanahan and Obura (1997)
– (not provided)	SPM peaks: up to >200 mg/l SPM:>40 mg/l locally over more than 24 h	–	Coastal turbid zone reefs, GBR province	High-diverse, shifted, non- <i>Acropora</i> siltation assemblages	Larcombe et al. (2001)

Designations of water transparency (Secchi disk visibility) are ours: very turbid (0.5–5 m visibility), turbid (5–10 m), low-turbid (10–15 m), and clear (15 m and more). IR=Insoluble residue.

1992, Kleypas, 1996; Larcombe et al., 2001; Yentsch et al., 2002). Because of the shift of colonial corals to shallow depths, an increased percentage of soft-substrate areas, and because binders (e.g. red algae, bryozoans, sessile foraminifera) decrease in turbid-water environments of elevated sedimentation, the capacity to reef-building is strongly limited (see below). Even on coral mounds and thickets growing in very shallow, very turbid waters, above the illumination depth limit for most corals, high total diversity may be sustained, although the assemblages are dominated by sediment-resistant taxa (Bull, 1982; Larcombe et al., 2001). (4) Upon still higher turbidity and sedimentation, a level-bottom assemblage is established, massive morphs of high-integrated colonial corals disappear, ramose-colonial and branched low-integrated (dendroid, phaceloid, oculinid) coral taxa persist or appear, and solitary corals (today most of them mobile forms) may become common to abundant (Goreau and Yonge, 1968; Dodge and Vaisnys, 1977; Gill and Coates, 1977; Dryer and Logan, 1978; Renema and Troelstra, 2001). In environments of intermittently rapid sedimentation, very large-polyped, stout-conical to flabellate, mobile meandroid corals (*Manicina*, *Trachiphyllia*) are also common (Gill and Coates, 1977).

6.2. Bioconstructions

Recent turbid-water coral constructions are situated in a mid- to inner shelf position of overall moderate to low mean water energy, or are fringing reefs more-or-less sheltered from waves. For persistence of these turbid-water bioconstructions, local physiography, exposition (windward-leeward), longshore currents, wave/tide regime and presence and width of intertidal

areas all are significant in modulating sediment–nutrient input (Roberts, 1987; Acker and Stearn, 1990; Hubbard, 1986; Tudhope and Scoffin, 1994; Rawlins et al., 1998; Woolfe and Larcombe, 1998; Larcombe et al., 2001; Perry, 2003). On the other hand, an energy regime too low is unfavourable, since clearing of sediment for instance during storms (Hillis and Bythell, 1998) or by tides (Woolfe and Larcombe, 1998; Perry, 2003) is important for persistence of these assemblages.

Many recent turbid-water reefs rise from bottoms a few meters to about 15–20 m in depth (Roy and Smith, 1971; Loya, 1976; Bull, 1982; Johnson and Risk, 1987; Kleypas, 1996; Larcombe et al., 2001; Perry, 2003). Reef flats, if individuated at all (cf. Kleypas, 1996), in many cases are poorly zoned and indistinct, and commonly gradually merge into a gently-dipping slope (Roy and Smith, 1971; Loya, 1976; Bull, 1982; Johnson and Risk, 1987; Kleypas, 1996). Slopes of turbid-water reefs typically consist of a substrate of more-or-less clayey to silty, sandy mud to muddy sand of mixed siliciclastic–bioclastic composition. The slopes commonly bear a coral assemblage distinct from the reef flats, and locally may be scattered with small coral mounds and coral thickets (Bull, 1982; Johnson and Risk, 1987; Kleypas, 1996). Natural turbid-water bioconstructions in waters less than a meter to about 20 m in depth geologically may be biostromes, i.e. they rise less than a meter to a few meters from their substrate and are a few tens to hundreds of meters in lateral extent (Loya, 1976; Tudhope and Scoffin, 1994; Larcombe et al., 2001). Such biostromes may have abrupt, steep lateral terminations (Tudhope and Scoffin, 1994; Larcombe et al., 2001). The bottom sediment adjacent to a coral biostrome may be terrigenous sand to sandy mud with

Table 3

Sediment accumulation rates on recent turbid-water reefs, in mm/year or in mg/cm² day

Location	Sediment accumulation	Effect(s)	Reference	Remarks
Discovery Bay, Jamaica	up to 19 mg/cm ² day	Growth rate of <i>Montastrea annularis</i> statistically slowed	Dodge et al. (1974)	“Carbonate–mud turbidity” caused by daily resuspension. Unshifted backreef assemblage.
Southern shelf of Puerto Rico	4 mm/year=4.000 B (deposited probably since 125–150 years)	Reefs and coral assemblages subject to distinct siltation stress	Beach (1975) in: Acevedo et al. (1989, p. 95)	Shifted siltation assemblage (see Acevedo et al. 1989)
Eastern shelf of Puerto Rico (as above)	150 mg/m ² day (“West reef”) 30 mg/m ² day (“East reef”)	<i>Montastrea cavernosa</i> dominant <i>Agaricia</i> common	Loya (1976)	Shifted, stable siltation assemblage
Turbid-water fringing reefs, GBR province	3–5 mm/6 months=6000–10,000 B (silt to clay-sized sediment)	Coral settlement on horizontal plates impeded	Fisk and Harriott (1990)	Living corals easily cope with this rate of accumulation (cf. Bak, 1978)
–	–	10 mg/cm ² day: threshold accumulation rate between “normal” and “high-sediment” reefs	Rogers (1990)	Deduced from sediment traps
Turbid-water nearshore reefs, GBR province	200 mg/cm ² day, over days to weeks	Reefs strongly dominated by <i>Porites</i> and <i>Montipora</i>	Stafford-Smith (1993, p. 241)	Shifted siltation assemblage
Turbid- to clear-water reefs, E Kenya	3–4 mg/cm ² day on turbid-water reefs	No major shift in coral assemblage	McClanahan and Obura (1997)	High-diverse, low-siltation assemblages
Turbid-water nearshore reefs, GBR province	–	Suggested medium-term (since about 6 ka B.P.) accumulation threshold for turbid-water reefs: 0.3 mm/year=300 B	Woolfe and Larcombe (1999, p. 337)	Medium-term threshold rate includes pulses of transient sedimentation

1 B (Bubnoff)=1 mm/ka.

primary hydrodynamic structures (Larcombe et al., 2001), or a muddy sand to sandy mud of mixed terrigenous–carbonate composition (Loya, 1976; Tudhope and Scoffin, 1994). Age-dated cores indicate that Holocene TW coral buildups commonly are short-lived, and are punctuated by pulses of sedimentation (Tudhope and Scoffin, 1994; Kleypas, 1996; Scoffin et al., 1997; Smithers and Larcombe, 2003). Whereas the total diversity of TW coral communities may be high, a few sediment-resistant taxa typically are dominant (Larcombe et al., 2001; Perry, 2003). Drill cores show that at least most inner shelf to shore zone buildups are mounds to biostromes of poorly sorted, coarse bioclastic “rubble”, whereas coral boundstones comprise a minor portion. Within the buildups, the pore space typically is filled by terrigenous mud to silt, or by mixed bioclastic–siliciclastic sediment (Tudhope and Scoffin, 1994; Kleypas, 1996; Smithers

and Larcombe, 2003). As outlined farther below, the described shape, size and internal features of recent TW coral constructions compare fairly well with the geological record.

On the recent mixed siliciclastic–carbonate shelf of SW Sulawesi (monsoonal climate), from the shore zone to the outer shelf, a gradient in coral assemblages and bioconstructions can be identified (Renema and Troelstra, 2001). In the shore zone with very turbid water, level-bottoms composed of solitary corals and an impoverished assemblage of colonial corals thrive on sandy mud to muddy sand, in a low- to mid-eutrophic regime (Table 2) (Renema and Troelstra, 2001). On the inner to middle shelf, in waters 20–30 m in depth and in a mesotrophic regime, a mixed colonial–solitary coral assemblage thrives; the colonial corals mainly occur in association with small “reefal islands” topped by bioclastic beaches. Water

turbidity varies strongly with the wet/dry monsoonal season (Table 2). The outer shelf ranges from 30 m to generally less than 50 m in depth. Dry season chlorophyll concentrations indicate a high-mesotrophic to low-eutrophic regime, and waters range from turbid to clear with monsoonal season. In this zone, shallow-water banks (top within 5 m water depth) up to more than 5 km in length are present that support a diversified scleractinian assemblage (Renema and Troelstra, 2001).

The western part of the muddy Sunda shelf is scattered by coral buildups a few tens of meters in size to small platforms up to more than 6 km across that rise from 30–40 m in depth (Roberts, 1987). As a result of permanently elevated water turbidity, coral assemblages thrive only in the upper 15–20 m; below, a sharp decrease in coral cover is observed. On the eastern Sunda shelf, another area with small carbonate platforms up to about 10 km in size is present (Roberts, 1987). Again, mainly because of permanently turbid water, dense coral growth does not exceed 12–15 m in depth, and platy to foliose “deep-water” morphs prevail already at 10 m depth. The buildups show relatively steep flanks, and probably grew more vigorously during the Holocene sea-level rise and early highstand, when most siliciclastic sediment accumulated in estuaries and deltas. Upon Holocene sea-level stillstand and persistent terrigenous input, the buildups of the Sunda shelf probably will be encased by siliciclastics (Roberts, 1987).

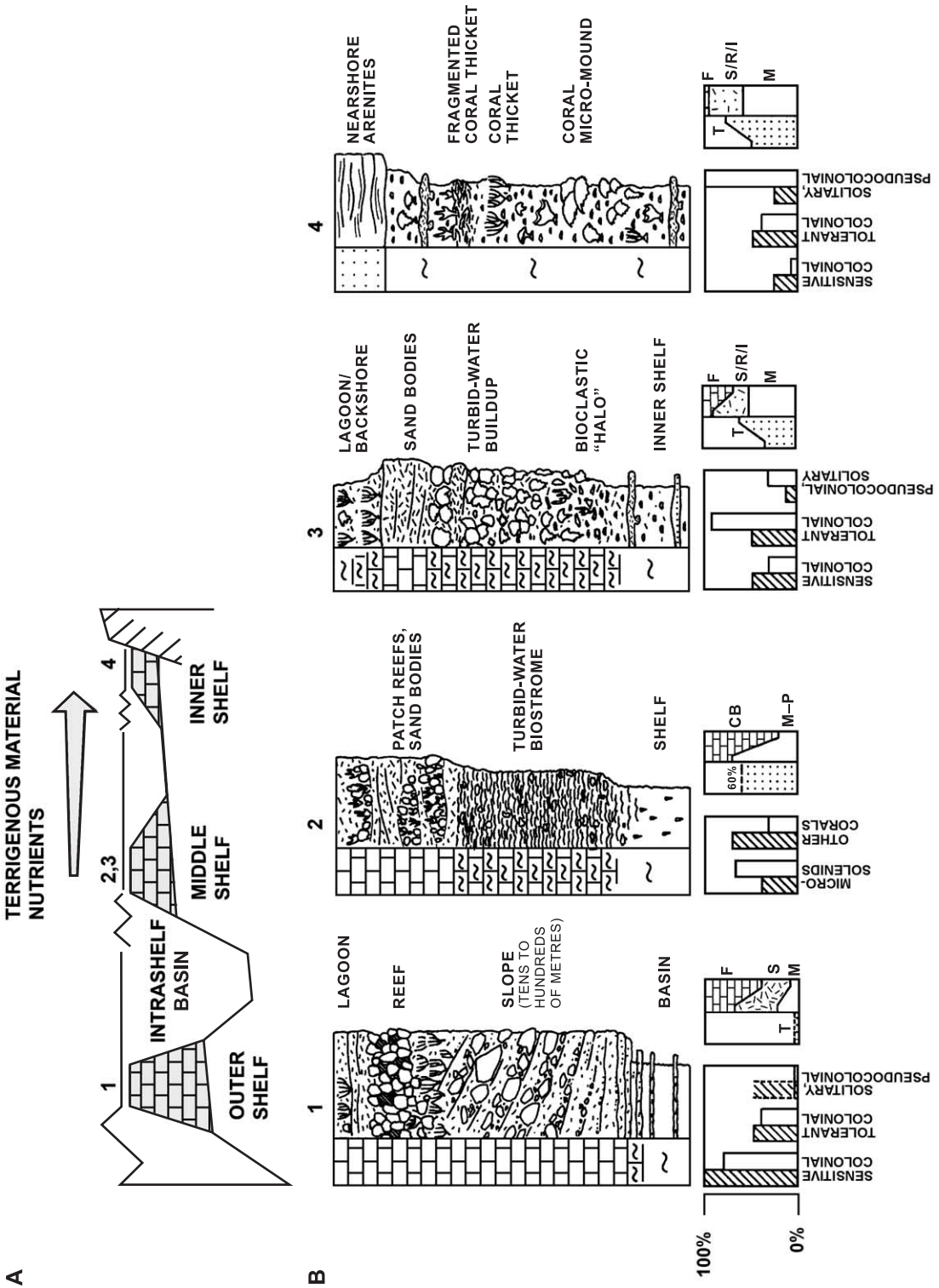
7. Fossil turbid-water assemblages

7.1. Bioconstructions: general features

Fossil TWB developed in any tectonic setting wherever terrigenous input was present (depending on climate, cf. Wilson and Lokier, 2002; Olivier et al., 2004), but most examples are from convergent margins (e.g. Coates, 1977; Polsak, 1981; Sanders and Baron-Szabo, 1997; Gong et al., 1998; Sanders and Höfling, 2000; Sanders and Pons, 2001; Mitchell, 2002; Wilson, 2002), and from settings undergoing extension and strike-slip (e.g. Hayward, 1982; Santisteban and Taberner, 1988; Martin et al., 1989; Braga et al., 1990; Leinfelder et al., 1994; Wilson, 2002).

Most TWB accumulated in an on-shelf/on-ramp to nearshore position (Fig. 5), or in low-energy shelf/ramp settings, or as fringing reefs. In some cases, TWB developed along the margins of and within shallow intra-shelf basins with siliciclastic input (see Fig. 5A). The more-or-less sheltered, lower-energy position of many TWB kept nutrient flux lower (cf. Jokieli, 1978; Abelson et al., 1993; Bilger and Atkinson, 1995; Hearn et al., 2001), allowed for the necessary upward shift of corals closer to sea-level, to compensate lowered light incidence (cf. Hallock, 1988; Yentsch et al., 2002), and allowed more delicate, low-light level forms to grow in shallow waters. An alternative lower-energy habitat is provided by a position deeper on the shelf; such a position may have pertained mainly to Middle Triassic to Late Jurassic assemblages with lower levels of photoautotrophy (cf. Flügel, 2002; Leinfelder et al., 2002; see Section 10).

With respect to thickness, prevalent lithologies, depositional systems and aspects of bioconstructed fabrics, fossil clear-water buildups differ from turbid-water bioconstructions. Because of their preferred position near shelf margins, many clear-water buildups were associated with a carbonate slope depositional system. The slope succession is distinct with respect to thickness, depositional processes and products (e.g. isolated boulders spalled off by rock-fall, deposits of debris flows and turbidites) from the underlying basinal and overlying reefal to peri-reefal intervals (Fig. 5B/1). From the Middle Triassic to recent, many bioconstructors other than corals comprised a subordinate to major portion of clear-water reefs (Kiessling et al., 1999). Although the ultimate fabric of a bioconstruction is also influenced by energy exposure and by the frequency of destructive events, clear-water buildups in many cases tend to have a frame fabric with pores containing marine cement. Upon increased terrigenous input, individual bioconstructions did not merge and aggrade into larger reef complexes, but tended to stay as smaller turbid-water buildups, encased by mixed siliciclastic–carbonate lithologies, in a position deeper on the shelf (e.g. Leinfelder, 1994; Nose, 1995). Alternatively, buildups nucleated in relatively shallow waters in an on-shelf position, where individuation of a carbonate slope was largely or totally precluded by low depositional relief (Fig. 5B/2) (Olivier et al., 2004).



Coral boundstones with a marly matrix may form at comparatively low water energy and/or in slightly greater depths in the lower part of the buildups (cf. Insalaco, 1996) whereas up-section, corresponding to more shallow waters, limestones deposited from coral patch reefs and interspersed carbonate sand bodies are present (Bertling and Insalaco, 1998). At higher terrigenous input, bioconstructions became confined to the inner shelf to shore zone. The resulting TWB lacked a carbonate slope, or were fringed by a bioclastic “halo” (Fig. 5B/3) (e.g. Hayward, 1982; Martin et al., 1989; Sanders and Höfling, 2000). The buildups developed by coral colonization from substrata of shelly mud to shelly, muddy sand, or overlie a basal interval of bioclastic rubble. Intervals deposited from such TWB consist mainly of floatstone and small patches of boundstone (segment reefs to cluster reefs), and are rarely more than 10 m in thickness (e.g. Pfister, 1985; Höfling, 1997; Sanders and Baron-Szabo, 1997); buildups with a higher content of boundstone (frame reefs) are comparatively rare in this category (e.g. Martin et al., 1989). The bioconstructions commonly are topped by more-or-less pure packstones to grainstones that accumulated from bioclastic sand bodies (e.g. Polsak, 1981; Sanders and Höfling, 2000). Alternatively, depending on terrigenous input and sea-level changes, TWB are overlain by marls or by siliciclastic/volcaniclastic lithologies (Frost and Weiss, 1979; Frost, 1981; Frost et al., 1983; Gong et al., 1998; Sanders and Pons, 1999; Olivier et al., 2004). Interparticle frame porosity is scarce to absent, as is interparticle marine cement (e.g. Hayward, 1982; Martin et al., 1989;

Braga et al., 1990; Sanders and Höfling, 2000). As a result of the vagaries of smothering by sediment, re-exposure of dead corals or rapid, permanent burial by sediment, macroboring and encrustation are highly variable, both within and among such bioconstructions. Although a quantitative statement is impossible to provide as yet, it is roughly at this level of terrigenous input (probably corresponding to the low-turbid to turbid range of water transparency, compare Table 2) and in these types of coral buildups where the effects of sedimentation start to compete with and override effects of nutrient input. In recent coral assemblages, enhanced microbialite development is characteristic of nitrification and elevated alkalinity (Camoin and Montaggioni, 1994; Camoin et al., 1999; Sprachta et al., 2001). Massive microbialites were also observed in fossil coral constructions that were subject to low or moderate levels of terrigenous input, i.e. in the range where effects of sedimentation and nitrification may overlap (cf. Reitner, 1986; Sanders and Pons, 1999; Dupraz and Strasser, 2004; Olivier et al., 2004). Upon still-increased terrigenous input and/or upon frequently unstable substrate, intervals of “coral marls” accumulated in an inner shelf to shore zone setting (Fig. 5B/4). In these marls, due to an overall high sediment accumulation rate, corals commonly show growth features related to partial mortality by sedimentation and unstable substrate. Moreover, because of intermittent pulses of rapid sediment accumulation, the corals are very well-preserved, and boring and encrustation are scarce to absent (see below for further description).

Fig. 5. Major geological features of fossil clear- and turbid-water coral assemblages. Not to scale. (A) On a shelf with terrigenous input, clear-water buildups (1) typically grew in the high-energy zone near the shelfbreak. Turbid-water buildups (2, 3) were situated along the margins of or within intrashelf basins. On the inner shelf and in the shore zone, thin turbid-water buildups (4) or coral marls accumulated. (B, 1) Clear-water buildups commonly were frame reefs, with pores filled by marine cement. The coral fauna is dominated by ecologically sensitive taxa. In many cases, clear-water buildups grew in front of and prograded over a carbonate slope. Together, the slope-to-reef succession may be tens of meters to hundreds of meters thick. (2, 3) Turbid-water buildups may occur in “upward-cleaning” packages from siltstones to marls below to limestones above. These buildups lack a carbonate slope, in many cases are segment reefs to cluster reefs, and are poor in or devoid of cement-filled frame pores. The colonial coral fauna is dominated by forms comparatively resistant to sedimentation and turbidity. Intervals deposited by such buildups typically are a few meters to a few tens of meters thick. (4) Coral marls accumulated under the highest relative rate of terrigenous input, in an inner shelf to shore zone setting. In these marls, by far most corals occur isolated, but locally mounds composed of a few stacked corals or (reworked) coral thickets are present. The colonial coral fauna is dominated by sediment-resistant forms, and solitary corals are abundant. Intervals of coral marls typically range in thickness from a few decimeters to a few tens of meters. Cross-hatched bars: coral diversity. White bars: coral abundance. CB=coral boundstone. T=terrigenous material (stippled bar). F=frame fabric. S=Bioclastic sand. M=mudstone texture (undifferentiated, terrigenous and/or carbonate). M–P=mudstone to packstone. S/R/I=Sand (bioclastic), Rubble (bioclastic), Insoluble terrigenous silt and sand.

7.2. Fossil turbid-water bioconstructions: aspects of dynamics

Depending on sedimentation versus turbidity, substrata of mud to muddy sand were colonized in a different fashion. By broad analogy to recent turbid-water assemblages (Table 2), probably at low sediment accumulation but at low to moderate turbidity, soft muddy substrata were colonized by platy to laminar-encrusting to vasiform growth forms of stress-resistant coral taxa (see also Section 7.3 below) (e.g. Frost and Weiss, 1977; Wilson and Lokier, 2002). These corals, in turn, provided the base for massive growth forms and taxa. Alternatively, the base of buildups was provided by massive corals that show a wide range of features related to partial mortality due to sedimentation and unstable substrate (Fig. 6), or by small patches of coral boundstones (Sanders and Baron-Szabo, 1997). Substrata of clean, terrigenous sand were colonized by large-polyped corals effective in sediment rejection, or by sediment-

tolerant taxa (Crame, 1980). At high rates of sediment accumulation, branched corals prevailed, and grew up along with sedimentation (e.g. Bailey and Tedesco, 1986; Leinfelder, 1994). Branched corals settled on small patches of hard substrata, such as mollusc shells, solitary corals or on small, massive corals that suffered early death. As long as high sediment accumulation prevailed, however, massive corals remained scarce, or were absent.

During accumulation of TWB, episodic smothering of the assemblage by sediment was comparatively common and, due to repeated re-colonization by corals, may give rise to vertically repetitive stacks of peculiar coral taxa (Martin et al., 1989). In many cases, however, the sediment veneer that killed the corals may not be preserved, because the sediment subsequently was wiped off by currents (cf. Dodge and Vaisnys, 1977). If the recurrence interval of disturbances, including pulses of sedimentation, is shorter than the time needed for community recovery, the assemblage may remain “quenched” at a lower

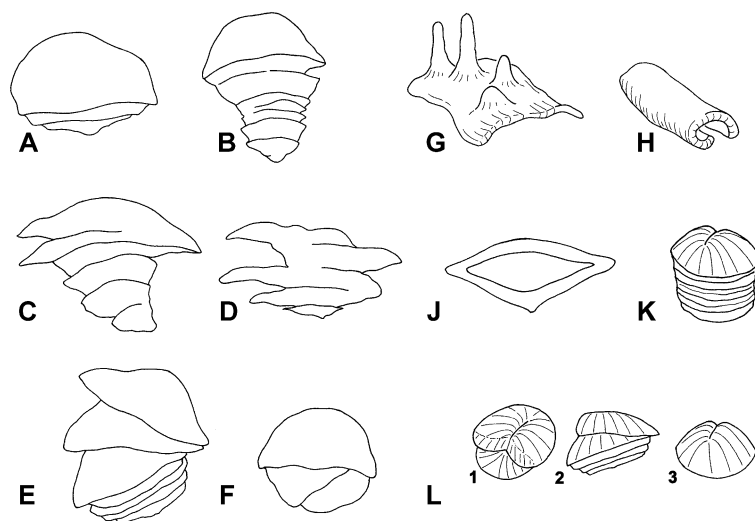


Fig. 6. Common shapes of corals in soft-substrate environments with sedimentation and/or unstable substrate. (A) Normal-grown, hemispherical coral head, with a few overgrowth margins at the base. (B) Head coral, grown in columnar shape, with constrictions and overgrowth margins due to sedimentation and slight tilting. (C) Massive coral of pseudo-ceratoid to mushroom-like shape, due to tilting and episodic sedimentation. (E) Coral of “lumpy” to laminar-interconnected shape. (E) Coral head, subject to three events of marked tilting. (F) Circumrotatory coral, resulting from frequent overturn on unstable substrate. (G) Laminar-encrusting morph, with protruding knobs and columns. (H) “Roll-up” laminar-encrusting morph. (J) Laminar morph, with a “Pizza calzone” cross-section resulting from infill of the central depression with sediment, followed by overgrowth. (K) Extinct solitary coral *Cunnolites*, grown in columnar shape with small overgrowth margins, to keep pace with sedimentation. (L) *Cunnolites*, with overgrowth “bulge” and constriction, resulting from tilting and partial mortality, followed by growth of surviving part of coral. (L1) Oblique view from above. (L2) Side view (see also Fig. 7D). (L3) Shape of *Cunnolites* in absence of tilting and/or sedimentation.

structural level. Such frequently disturbed communities are common in recent clear-water areas, too (Done, 1992; Riegl, 2001) and in turbid-water assemblages, giving rise to “rubble piles” instead of reefs (Kleypas, 1996). In the rock record, many TWB show no or only an indistinct, simple vertical succession and zonation, and appear as mounds to sheets of rudstone to floatstone composed of disoriented and more-or-less fragmented corals and other fossils (e.g. Sanders and Baron-Szabo, 1997; Sanders, 1998). Conversely, both vertically and laterally, other fossil TWB show a succession with respect to prevalent coral growth forms and taxa (Frost and Weiss, 1977; Masse and Philip, 1981; Pomar, 1991; Insalaco, 1996; Bertling and Insalaco, 1998), associated framebuilders (e.g. skeletal sponges), and fossils that dominate in the crestal part of the buildup (stromatoporoids, rudists). Successions of this larger-scale type are at least prevalently of allogenic origin (Gili et al., 1995). In upward-shoaling/“cleaning” successions, turbid-water assemblages rich in or composed entirely of, either, taxa resistant to sedimentation, and/or of platy to foliaceous forms to optimize light catchment are present in the lower part of the succession, whereas the upper part is dominated by massive and/or branched forms (Fig. 5B/2) (Insalaco, 1996; Bertling and Insalaco, 1998; Bosellini, 1998; Wilson and Lokier, 2002).

Fossil coral assemblages that grew under frequent disturbance may lack evidence for autogenic succession, and even distinct coral assemblages may not represent zones (e.g. Budd et al., 1989). In frequently disturbed, recent assemblages, local communities are determined more by recruitment than by competition (Bak and Luckhurst, 1980; Riegl, 2001); recruitment, in turn, in part results from random distribution of settlement substrates, such that the small-scale distribution of coral taxa can be identical to random distributions (Bradbury and Young, 1983). Even if time is available for complete recovery, the site-specific histories of disturbance and recolonization may completely or largely determine the composition of the final “climax” community (Tanner et al., 1994, 1996). In fossil coral bioconstructions, thus, the small-scale (decimeters to a few meters) distribution of coral taxa, growth forms and polyp integrations is probably determined by both allogenic and autogenic processes, but these are difficult to separate unambigu-

ously in the geological record. In this respect, a less-detailed data set obtained from a larger number of buildups over a larger area may be more informative than a detailed study performed on a smaller scale, since the larger-scale data set may reveal an overall prevalence of some morphs and taxa (cf. Pandolfi, 2002).

In summary, typical features of the dynamics of fossil TWB are (1) direct or indirect evidence for intermittent smothering by sediment, and (2) the local presence of vertical successions of coral taxa and morphs that may be interpreted as controlled mainly by the sediment resistance of these taxa. Because of the characteristics of many turbid-water assemblages, such as a lower percentage of frame fabrics and increased proportion of areas of soft substrate, the same types of disturbance (e.g. a storm) that act on both clear- and turbid-water assemblages result in different depositional characteristics in the rock record.

7.3. Coral marls

In Meso-Cainozoic neritic successions, intervals of silty to sandy marls rich in both potentially reef-building organisms (e.g. colonial corals, skeletal sponges) and a diversified level-bottom biota (e.g. solitary corals, bivalves, gastropods, brachiopods, echinoids, bryozoans, larger benthic foraminifera) are fairly common. Such coral marls accumulated where sufficient illumination and patches of hard substrate (e.g. solitary corals, shell fragments) were present, in settings of episodically or permanently elevated turbidity and intermittently rapid sedimentation. Depositional conditions for coral marls were met in the palaeobathymetrically deeper, seaward continuation of coral-dominated buildups (e.g. Sanders and Pons, 2001), in lagoonal/bay areas with siliciclastic input (e.g. Frost, 1981; Bosellini and Trevisani, 1992; Simo, 1993; Bosellini and Stemann, 1996; Sanders and Pons, 1999), or on low-energy sectors of shelves (e.g. Gili, 1993; Sanders et al., 1997; Rehfeld and Ernst, 1998; Sanders and Pons, 2001). Intervals of coral marl typically range in thickness from a few decimeters to a few tens of meters. Thicker intervals may be interspersed with other lithologies, or with shallow neritic marls that are comparatively poor in corals.

In the marls, most of the colonial corals occur as isolated specimens. Depending on depositional conditions, colonial corals may be abundant but only a few centimeters in size, or the coral fauna is a mix of a few large-sized specimens and much more numerous small ones (Baron-Szabo, 1997, 2003), or the fauna consists of a few relatively large specimens in growth position (e.g. Gili, 1993; Sanders and Pons, 2001). Many specimens of both non-mobile solitary corals and massive colonial corals show growth features related to partial mortality because of intermittent sedimentation and/or of tilting on unstable substrate (Fig. 6). For massive corals, a widespread growth feature is a columnar to club shape with more-or-less numerous, distinct constrictions of diameter (Figs. 6

and 7A) (Kühn, 1925; Höfling, 1989; Sanders and Pons, 1999). The retreats in the coral skeleton result from mortality of the marginal portion of the colony due to incomplete clearance after sedimentation (Lasker, 1980; Cortés and Risk, 1985; MacDonald and Perry, 2003, Fig. 7D). After death of the marginal fringe, upon recovery, the coral grew over the substrate again, and an “overgrowth margin” formed. Other typical shapes of colonies grown under high, episodic sediment accumulation include a highly irregular, “knobby to lumpy” shape, “interconnected platy to laminar growth”, and laminar-encrusting shape with scattered, protruding “knobs” and columns, as a result of partial mortality by sedimentation (Fig. 6) (Kühn, 1925; Martin et al., 1989, p. 278;

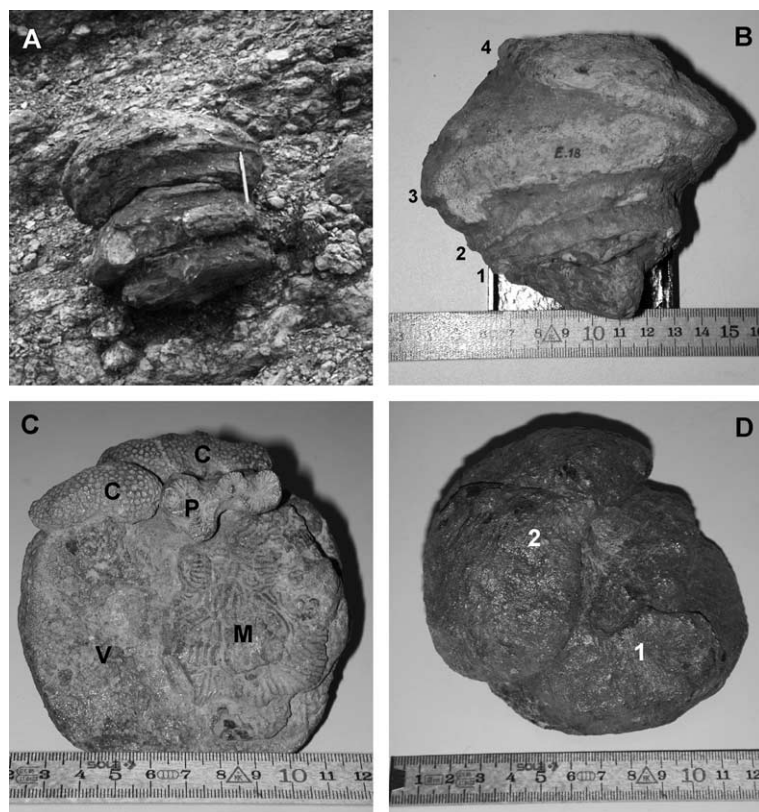


Fig. 7. (A) Shallow neritic marls with large, massive corals. The corals are preserved upright in the sediment, and show a columnar growth form with distinct constrictions of diameter, and overgrowth margins. Santonian, southern Pyrenees. Pen for scale is 14 cm. (B) Thamnasterioid coral with overgrowth margins (labelled 1 to 4) that change their orientation due to tilting of the colony during growth. Upper Santonian, Austria. Scale in centimeters. (C) Plan view onto upper valve of rudist *Vaccinites* (V). The upper valve has been overgrown by a laminar-encrusting meandroid coral (M), a small *Pachygyra* (P), and two small specimens of the cerioid form *Actinacis* (C). Upper Santonian, Austria. Scale in centimeters. (D) Solitary coral *Cunnolites* with distinct overgrowth rim. Following partial mortality from tilting into the substrate (1), the coral recovered and regrew from the surviving portion (2). Upper Santonian, Austria. Scale in centimeters.

Bosellini, 1998; MacDonald and Perry, 2003, Fig. 8D). On soft substrata, the buried portion of toppled corals is choked. Growth anomalies indicative of toppling include re-orientation of growth direction of the entire colony (Fig. 7B), often combined with a mortality rim. Other growth anomalies that result from toppling include a continuous curvature or a sharp kink of coral branches (Bailey and Tedesco, 1986) and subspherical colonies with polypars over all the corallum (circum-

rotatory shape; e.g. Abbott, 1975; Höfling, 1989). In the marls, the corals typically are well-preserved, and macroboring and encrustation commonly are scarce to absent. This suggests that the corals were smothered by sediment and, during the same or a closely following depositional event, ultimately buried. In recent coral assemblages killed by sedimentation, re-exposed dead corals typically are densely riddled by macroborings (Dodge and Vaisnys, 1977). In coral marls, although no

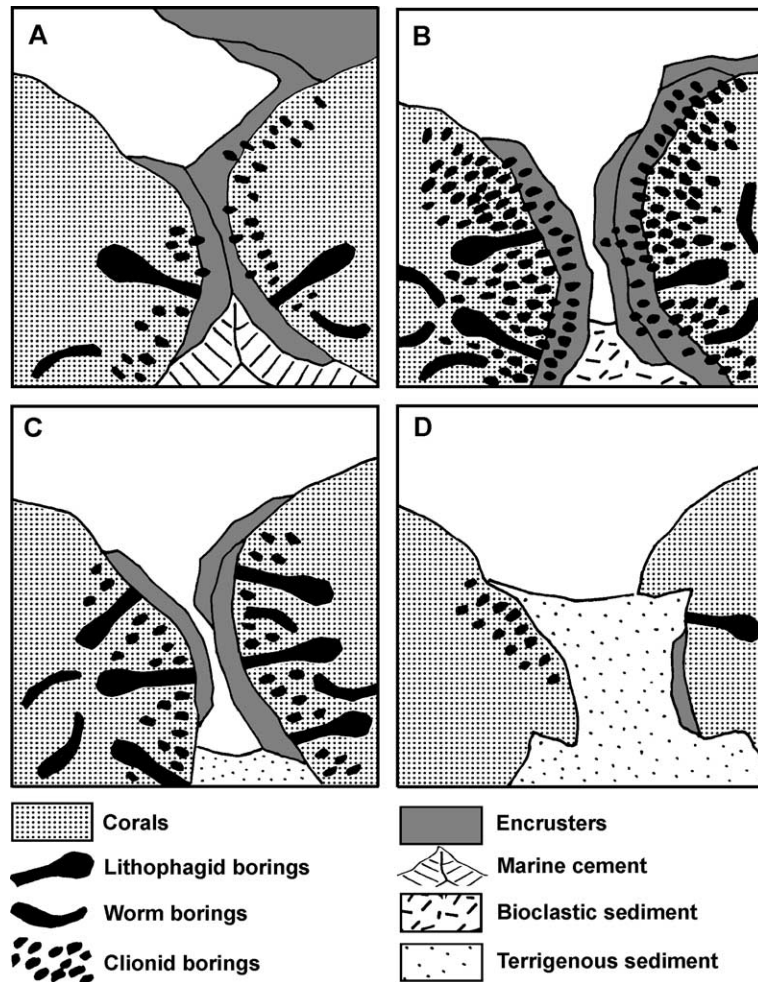


Fig. 8. Scheme of coral taphonomy relative to nutrient input, turbidity, and sedimentation. (A) In clear-water reefs, encrustation and macroboring tend to be kept at low to moderate levels, allowing for reef framework construction. (B) Under elevated nutrient input, both bioerosion and, up to some limit, encrustation are intensified. The capacity for reef frame construction is lowered, or quenched. (C) If water turbidity from terrigenous input prevails over sediment accumulation, bioerosion may be intensified, and macroboring communities are shifted (e.g. from clionid dominance to prevalence of lithophagids and worms). (D) If sedimentation of terrigenous material prevails, both macroboring and encrustation overall are low. Capacity to framebuilding is lowered or quenched by sedimentation. Many corals show growth features related to sedimentation and unstable substrate (see Fig. 6).

detailed study has been performed on microboring in bioclasts, as far as seen (by thin section petrography) by the present authors, intensity of microboring is similar or not significantly above the levels observed in pure bioclastic limestones from clear-water environments (although microboring assemblages may differ from that of contemporaneous clear-water reefs; cf. Perry and Macdonald, 2002).

Besides corals and level-bottom biota, depending on geological period, other potential bioconstructors such as skeletal sponges and rudists may be present. Also these other bioconstructors may show features related to sedimentation and/or unstable substrate (see, e.g. Johnson et al., 2002), and may have provided a settlement substrate for corals (Fig. 7C). Solitary corals typically are common to abundant, and are most characteristic for coral marls of Jurassic to Miocene age (Coates and Jackson, 1987; Leinfelder et al., 1994; McCall et al., 1994; Sanders et al., 1997; Baron-Szabo, 2003). Relative to their maximum possible size, and despite their abundance, for at least some extinct, non-mobile solitary corals (e.g. *Cunnolites*), the overwhelming number of specimens may be an order of magnitude below their maximum observed size. Furthermore, the abundant small specimens only rarely show features related to unstable substrate and sedimentation, whereas such features are fairly common on large specimens (Figs. 6K, L and 7D). In coral marls, thickets composed of massive and/or branched corals and other bioconstructors (e.g. rudists, skeletal sponges) are locally present. In addition, small buildups composed of just a few larger corals grown upon each other and, depending on the geological period, other bioconstructors may be present (Fig. 5B/4) (e.g. Sanders and Pons, 2001). These buildups range in shape from inverted cones composed of a few stacked corals to mounds and biostromes, range in thickness from a few decimeters to a few meters, and in lateral dimension typically are a few decimeters to a few meters (mounds) to a few tens of meters (biostromes). Again, depending on depositional conditions, the corals of the individual, small buildups may be small-sized, but buildups that consist of a few, large corals also formed (Sanders and Pons, 2001).

The marls may contain a wide spectrum of coral taxa. With respect to relative abundance of taxa, however, the spectrum is shifted relative to both

coeval turbid-water and clear-water bioconstructions by being dominated by low-integrated colonial taxa (e.g. phaceloid, dendroid) and/or by solitary corals (e.g. Coates and Jackson, 1987, their Fig. 5; Baron-Szabo, 1999, 2003). The judgement of both the relative percentage of solitary/colonial corals and the integration style of colonial corals must take into account that integration overall became higher during the Meso-Cainozoic (see also Section 9; Coates and Jackson, 1987; Wood, 1995), and that solitary corals are less widespread in post-Miocene assemblages (McCall et al., 1994).

7.4. Taphonomy

In recent clear-water reefs, the most common macroborers are clionid sponges (typically >80%), followed by lithophagid bivalves and by worms. Other macroborers, such as barnacles and shrimps, are accessory (e.g. Bromley, 1996; Perry, 1998). Widespread encrusters are red algae, bryozoans and sessile foraminifera (Hallock and Schlager, 1986). In clear-water reefs, macroboring and encrustation of corals remain at a level resulting in a positive net carbonate budget, and allowing for reef accretion and frame construction (Fig. 8A). At elevated nutrient input, macroboring, microboring, microbialite development, and abundance of grazers each tend to be enhanced (Fig. 8B) (Hallock, 1988; Camoin and Montaggioni, 1994; Edinger et al., 2000). Depending on both magnitude and duration of nutrient input, increased bioerosion may quench development of coral framework, and may lead to reef erosion (e.g. Hallock and Schlager, 1986; Sammarco, 1996). In addition, nutrient-enhanced growth of both fleshy algae and encrusting calcareous algae outcompetes living corals (see Section 5.2). In recent turbid-water reefs subject to comparatively low sediment accumulation, at least in some cases, the macroboring assemblage shows a shift from clionid dominance to dominance of lithophagids and worms (Fig. 8C) (Sammarco and Risk, 1990; Risk et al., 1995; Perry, 1999; MacDonald and Perry, 2003). No quantitative investigation exists on the types and amounts of encrustation in recent turbid-water reefs compared to adjacent clear-water reefs. Coral assemblages subject to high rates of terrigenous sediment accumulation are characterized by low levels of encrustation and

macroboring (Fig. 8D) (Scoffin, 1992). In such areas, development of reef framework is kept low or quenched, and the corals may show features of partial mortality related to sedimentation and unstable substrate (see Section 7.3 above).

The above conceptual trends of taphonomy as a function of nutrient input, terrigenous turbidity and sedimentation are subject to substantial local variation. For instance, on recent reefs, the fore-reef macroboring community typically is dominated by clionids, while in back-reef, lagoonal and nearshore areas, bivalves and worms are significant (e.g. Perry, 1998). With much scatter, the infestation by macroborers tends to be highest both in shallow-water (back-reef, lagoonal) areas and on the deeper fore-reef, but this not necessarily correlates with the rate of macroboring (Perry, 1998). Both reef type and the style of reef preservation are not only functions of bioerosion, but also are strongly influenced by energy exposure (e.g. Zankl and Schroeder, 1972; Ginsburg and Schroeder, 1973; Hubbard et al., 1990; Blanchon et al., 1997). Moreover, different coral taxa are of variable susceptibility to different macroborers (Perry, 1996, 1998).

For fossil coral reefs, a few semi-quantitative data and many qualitative observations indicate that macroboring assemblages were dominated by clionids at least since and including the Jurassic (Perry and Bertling, 2000). Fossil coral assemblages that were subject to stress by prevalent nutrient input show a relatively increased density of macroborings, but there is marked variation among sites both with respect to density of infestation and to prevalent types of macroborers (e.g. Leinfelder et al., 2002). Both from recent and fossil TW coral assemblages, there is some evidence that under low to moderate terrigenous input, boring by clionids decreases while lithophagid boring intensifies (MacDonald and Perry, 2003; Dupraz and Strasser, 2004). Conversely, fossil coral assemblages subject to substantial clastic sedimentation commonly show low levels of encrustation and macroboring (Leinfelder et al., 2002; Sanders and Baron-Szabo, in press). Whereas it may be assumed that a fossil coral assemblage was subject to sediment stress, for turbid-water communities able to cope with siltation, this is not necessarily the case (see Section 6), but has to be independently checked.

8. Estimate of stress by turbidity and sedimentation

To estimate the extent to which sediment input may have determined the composition of a fossil coral assemblage (Table 4), clear-water (pure carbonate) and turbid-water assemblages including their host lithologies must be compared (Fig. 9) (Frost, 1981; Pfister, 1985; Edinger and Risk, 1994; Baron-Szabo, 1997; Dupraz and Strasser, 2004; Sanders and Baron-Szabo, in press). Wide ecotolerance of a coral taxon is indicated if it is present in a wide range of lithologies from a variety of environments. This comparative approach allows to sort out small-polyped colonial corals that probably were of high sediment tolerance. For some Cretaceous and Tertiary turbid-water coral assemblages, a relatively high diversity is indicated (Frost, 1981; Masse and Philip, 1981; Bosellini and Trevisani, 1992; Baron-Szabo, 1997; Baron-Szabo, 2002, 2003). Even in Late Triassic coral-sponge mounds that accumulated under substantial terrigenous input, 39 species of corals are present (Fürsich and Wendt, 1977). Due to the presence of both hard- and soft-substrate patches, however, total diversity as shown by a tabellaric list anyhow tends to be high (Fig. 9). In recent turbid-water assemblages subject to substantial siltation stress, very low coral cover may correlate with high total diversity (Dryer and Logan, 1978). Diversity indices considering both species and their abundance, however, yield low values, correctly reflecting a shifted assemblage dominated by a few sediment-resistant taxa (Dryer and Logan, 1978). In fossil assemblages, abundance–diversity data are only significant if a similar data set from both a fossil clear-water and a turbid-water assemblage of similar age is available. Unfortunately, in nearly all investigations of fossil coral faunas, neither the numeric nor a semi-quantitative indication of abundance is given, or for a few taxa only. The scale of fossil collecting also is important. In recent clear-water coral communities, diversity on a scale of a few meters to tens of meters may be down to about 50% the diversity on a scale of hundreds of meters (Done, 1992). A few meters to a few tens of meters, however, is a typical scale of many exposures and/or of more detailed sampling in larger outcrops.

Similar to many recent turbid-water communities, fossil assemblages indicate that with increasing terrestrial input (marly limestones to marls or silt-

Table 4

Parameters to estimate sediment stress on a fossil coral assemblage

Parameter	Significance	Remarks
Comparison of CW/TW assemblages	Recognition of sediment-resistant coral taxa	Factors unrelated to turbidity and sedimentation also influence assemblage differences Should be compared to coeval CW buildups
Prevalent texture, lithologies (limestone, marl), and shape of bioconstructions	Qualitative estimate of sediment input and control by terrigenous sedimentation and unstable substrate	
Abundance-diversity data of CW/TW assemblages	(Semi-)Quantitative recognition of shift in assemblage due to sediment input	Rarely available. Significance increases with increasing no. of locations investigated
Coral size frequency distribution	To estimate influence of sediment accumulation on the assemblage	In friable marls, small specimens are more conspicuous than in limestones
Number of coral growth increments	Age when corals died	Growth bands often not preserved
Coral growth features resulting from sediment-related partial mortality and unstable substrate	To estimate influence of episodic sediment accumulation and unstable substrate on the assemblage	Should be observed on a significant number of specimens
Increased abundance or dominance of corals with medium to very large polyps	To estimate influence of sediment input on assemblage composition	Must be compared to CW assemblage, must take into account coral evolution
Increased abundance or dominance of high-integrated corals of a peculiar integration type	To estimate influence of sediment input on assemblage composition	as above
Increased abundance or dominance of low-integrated and solitary corals	To estimate influence of sediment input on assemblage composition	as above
Degree of macroboring and encrustation	Macroboring and encrustation correlate inversely with sediment accumulation	Under low sediment input similar to CW assemblages
Total diversity	Recognition of taxa that perhaps were precluded by turbidity-sedimentation stress	Limited significance as an estimator of sediment stress
Growth form(s) of entire coral colonies (not related to partial mortality by sedimentation and unstable substrate)	Control over growth form exerted by water turbidity	Interpretation difficult in many cases, rests on personal experience of observer with other coeval coral assemblages

The parameters are best used in combination. See text for discussion. CW=clear water; TW=turbid water. Polypar widths were delimited as follows: small, up to 3 mm; medium, 3–8 mm; large, 8–15 mm; very large, >15 mm.

stones), the coral size frequency distribution tends to be skewed towards small specimens; typically, a few large specimens also are present. Ecostress related to a turbid-water setting may also be estimated from the number of growth increments. Where low growth increment numbers suggest that most corals died young, increased mortality by sediment–turbidity stress may be inferred (e.g. [Insalaco, 1996](#)). If photosymbiosis is relevant to calcification, however, the width of growth increments should change over geological time. For fossil scleractinians, no comparative study exists on the relative difference in growth increment width of the same species under clear- and turbid-water conditions (see also Section 5.1). In TWB of the type shown in [Fig. 5B/3](#), and in coral marls ([Fig. 5B/4](#)), corals showing growth features related to episodic sedimentation and/or tilting are common. The abundance in particular of massive

corals with a more-or-less “normal”, hemispherical to stout-conical shape relative to massive corals with the described growth anomalies provides an estimator to which extent sedimentation and unstable substrate influenced the assemblage.

With much limitation, a prevalence of some types of polyp integration over others may also be considered as an estimator of the control exerted by sedimentation. Similarly, and relative to clear-water assemblages, a common presence or dominance of corals with large to very large-sized polypars (see [Table 4](#)) may be related to increased sediment input, and thus may be used as an estimator of sedimentation control. In both clear- and turbid-water assemblages, however, the prevalent polyp integrations and polypar widths changed significantly during coral evolution, and sediment-tolerant taxa with small polyps existed at least since the Early Cretaceous (see Section 9).

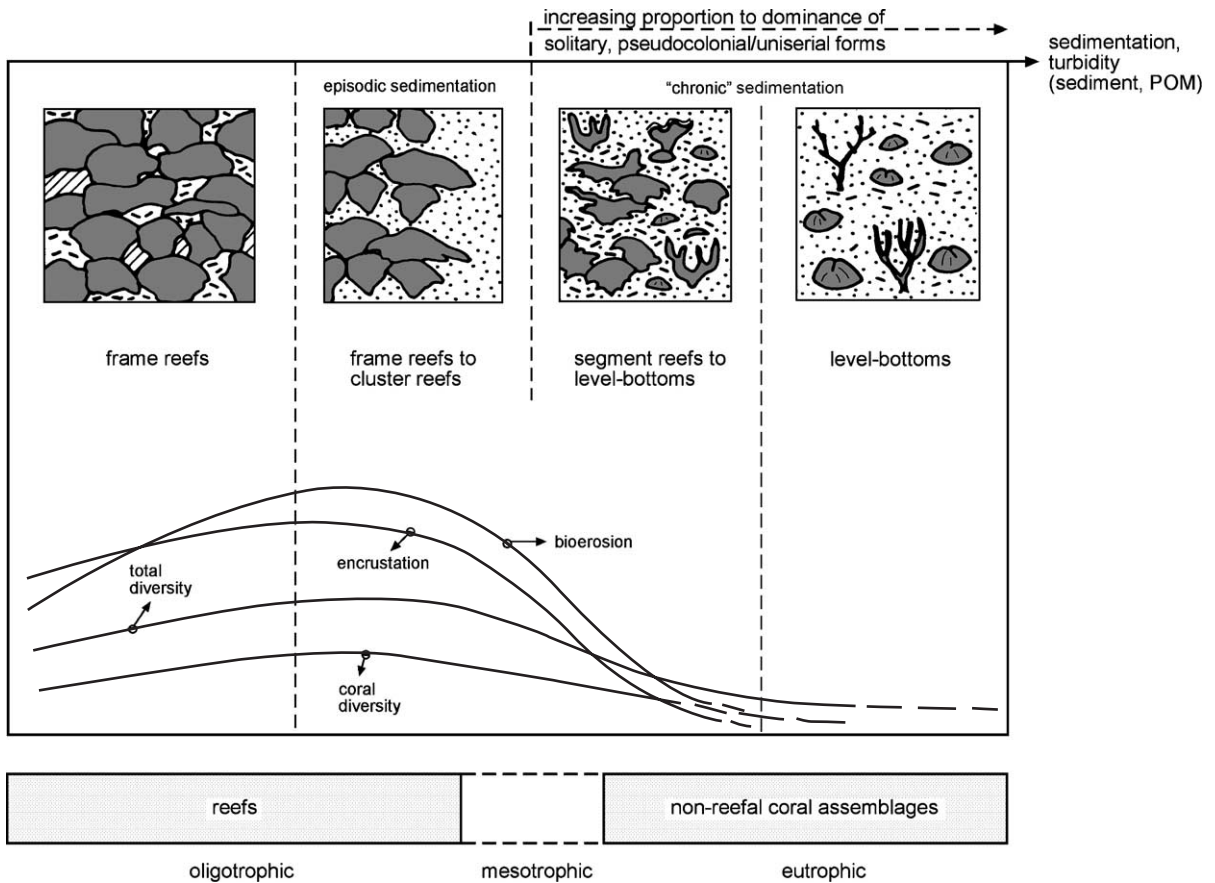


Fig. 9. Conceptual scheme of scleractinian assemblages relative to sediment input. Left half of diagram: Under no or episodic, marked sediment input, frame reefs to cluster reefs with cement-filled pores (cross-hatched) are common. If nutrient input occurs under these conditions, the ecologic and taphonomic effects of nutrient input prevail. Right half of diagram: Under frequent to “chronic” terrigenous sediment input, segment reefs to level-bottom assemblages form, and the ecologic and taphonomic effects of sedimentation predominate. See text for further discussion.

Thus, polyp integration and polypar width are meaningful parameters only if compared to clear-water assemblages of similar age.

In some Eocene turbid-water buildups of northern Spain, coralline algal crusts up to 30 cm thick are present (Taberner and Bosence, 1985), but thick coralline crusts were also described from recent clear-water coral reefs (Zankl and Schroeder, 1972). Overall, however, up to low or moderate amounts of terrigenous sedimentation, giving rise to marly limestones, the extent of both encrustation and boring tends to be similar or somewhat higher relative to coeval clear-water assemblages (Fig. 9) (Leinfelder et al., 1994, p. 40; Sanders and Baron-Szabo, 1997). In turbid-water assemblages that grew under near-

chronic sediment input and/or that were subject to frequent pulses of rapid sediment accumulation or resuspension, epibiontic overgrowth and boring may be scarce to absent and, despite their common growth anomalies, most of the corals are excellently preserved (e.g. Leinfelder et al., 1994, p. 40; Sanders and Baron-Szabo, in press).

Whereas sedimentation produces a record, former water turbidity is elusive. Relative to their clear-water counterparts, the commonly smaller thickness of both recent and fossil TWB reflects the upward shift of corals towards light (cf. Fig. 1). As mentioned, in many coral taxa, growth form may vary as a result of light level, sedimentation and water energy. Other common corals, by contrast, show no or very little

variation of shape upon changes of environment (see Sections 3 and 6). Many fossil turbid-water assemblages consist of a more-or-less variegated mix of coral taxa and morphs (e.g. Frost, 1981; Mitchell, 2002; Baron-Szabo, 1997, 2003). Under terrigenous input, light level, sedimentation and water energy (due to the preferred position of TWB in lower-energy settings) all covary, hence the shape of a coral represented a compromise between light catchment, sediment clearance, and local water energy regime. To estimate the extent to which turbidity, sedimentation and water energy determined the shape of a fossil coral taxon, the range of shapes of that taxon under clear-water conditions had to be known, at least. Quantitative data sets of this kind do not exist; it still rests to the observer's experience to environmentally interpret growth forms, and to concede the limits of interpretation (e.g. Pfister, 1977; Frost, 1981).

9. Turbid-water assemblages in time

Scleractinians appeared during the middle Anisian stage of the Middle Triassic (Stanley, 2003), as solitary and phaceloid forms that thrived in both reefal and non-reefal assemblages (Flügel, 2002, p. 398). The earliest coral communities were part of sponge-coral mounds and biostromes that typically accumulated under terrigenous input, in turbid waters around storm wave base (e.g. Senowbari-Daryan et al., 1993). Middle to Late Triassic coral faunas are dominated by phaceloid and phacelo-dendroid forms with medium to large-sized polypars, and by solitary corals with large to very large coralla (Table 5). In Triassic assemblages massive, encrusting and ramose forms (cerioids, thamnasterioids, plocoids, meandroids) with small to large polypars are subordinate, typically both in abundance and diversity. Most Triassic corals thrived from shelf margins to marly slopes and marly, shallow basinal or deep lagoonal environments (Flügel, 2002, pp. 398, 412). Because of the prevalence of medium-large polypars, and because phaceloids and phacelo-dendroids were widespread, Triassic assemblages were highly resistant to both turbidity and sedimentation (cf. Flügel, 2002). Geochemical and biometrical data suggest that photosymbiosis started only during the Late Triassic (Stanley, 1981; Coates and Jackson, 1987; Stanley

and Swart, 1995). Middle to Late Triassic coral assemblages that thrived within or adjacent to siliciclastic environments are common and, in many cases, of higher diversity than their clear-water counterparts (Flügel, 2002).

Following the end-Triassic mass extinction, Early Jurassic coral faunas were dominated by solitary and phaceloid forms that thrived on soft substrata, under moderate siliciclastic input (Leinfelder et al., 2002, p. 474). During the Middle Jurassic, corals radiated, and mounds and reefs rich in high-integrated forms became common (Leinfelder et al., 2002, p. 478 ff.). Coral reefs with a species diversity, per coral association, broadly similar to modern reefs first emerged during Late Jurassic time (Leinfelder et al., 2002, p. 466). Relative to recent reef corals, both linear extension rates and, probably, efficiency of photosymbiosis of Late Jurassic thamnasterioid and meandroid forms was lower (Leinfelder et al., 2002, p. 468 f.). Late Jurassic coral assemblages sustained high diversities at low to moderate terrigenous input (Leinfelder et al., 2002, pp. 468 f, 492 f.; Dupraz and Strasser, 2004; Olivier et al., 2004). Late Jurassic clear-water assemblages are dominated by forms with small to medium polypars, and are typically composed of both branched (phaceloid, ramose, dendroid) and massive forms (Table 5). Among massive and ramose forms thamnasterioids (including microsole-nids), cerioids and plocoids prevail; massive meandroids may also be significant. Bioconstructions of moderately turbid waters are dominated by massive to platy thamnasterioids (e.g. *Microsolena*, *Dimorpharaea*), but massive to knobby to platy cerioids and plocoids may comprise a substantial to prevalent portion. At high turbidity and sedimentation, mono- to paucispecific level-bottoms and thickets were dominated by branched (phaceloid, phacelo-dendroid, ramose) and flabellate forms, and by solitary corals. Most corals of Late Jurassic turbid-water assemblages show small- to medium-sized polypars. Large to very large polypars are present mainly in solitary corals that constituted a substantial part of the assemblage only under marked, frequent or near-chronic siltation. Because of the relatively high diversification of the Late Jurassic coral fauna with respect to integrations and morphs, both the amount and frequency of sedimentation influenced the composition of a turbid-water assemblage with respect to prevalent

Table 5

Schematic summary of differences between clear- and turbid-water scleractinian assemblages in geological time

	Clear-water assemblages	Turbid-water assemblages	Representative references
Middle–Late Triassic	mainly phaceloid–dendroid corals with medium–large corallites, large solitary corals, massive colonial corals subordinate	Similar to clear-water assemblage	Brandner and Resch (1981) Stanton and Flügel (1987) Turnsek (1997)
Late Jurassic	mainly phaceloid, thamnasterioid, plocoid, cerioid forms	Phaceloid–dendroid forms, thamnasterioid (microsolonid) and plocoid forms, solitary corals	Leinfelder (1994) Insalaco (1996) Turnsek (1997) Bertling and Insalaco (1998) Dupraz and Strasser (2004) Olivier et al. (2004)
Cretaceous	massive corals>branched corals; plocoid, cerioid, meandroid, thamnasterioid forms	Thamnasterioid, plocoid, (sub)cerioid, meandroid forms, solitary corals, few branched corals	Polsak (1981) Baron-Szabo (1994, 1997, 1999, 2001, 2002) Baron-Szabo and Fernandez-Mendiola (1997) Turnsek (1997) Stössel (1999) Mitchell (2002) Götz (2003)
Eocene–Oligocene	massive corals>branched corals, mainly plocoid–(sub)cerioid forms	branched (phaceloid, ramose) and columnar cerioid, plocoid, phaceloid corals: all in changing relative abundance; solitary corals	Frost and Langenheim (1974) Frost and Weiss (1979) Frost (1981) Frost et al. (1983) Budd et al. (1989) Edinger and Risk (1994) Bosellini (1998) Bosellini and Trevisani (1992)
Miocene–Recent	massive corals>branched corals (but: since Pliocene: branched acroporids, pocilloporids prevalent in shallow reef environments), plocoid, meandroid, cerioid corals	Ramose to fasciculate, massive and platy–foliaceous corals of cerioid, plocoid and meandroid integration, solitary corals	Beach (1983) Johnson and Risk (1987) Acevedo et al. (1989) Martin et al. (1989) Edinger and Risk (1994) McClanahan and Obura (1997) Larcombe et al. (2001)

Except probably for Middle–Late Triassic coral faunas, relative to their clear-water counterparts, turbid-water assemblages are characterized by an increased proportion of sediment-resistant massive forms, and by branched (phaceloid, dendroid, ramose) corals, columnar and platy–foliaceous forms, and solitary corals. Polypar widths were delimited as follows: small, up to 3 mm; medium, 3–8 mm; large, 8–15 mm; very large, >15 mm. See text for further description.

morphs (branched, massive, encrusting) and integrations (Leinfelder, 1994; Nose, 1995; Olivier et al., 2004).

Cretaceous clear-water assemblages consist mainly of massive forms with small- and small–medium-sized polypars, and are dominated by plocoids, cerioids, meandroids and thamnasterioids; plocoid corals typically are the most diverse. Thamnasterioid corals are subordinate both in abundance and diversity, or are absent. Branched forms (dendroid, phaceloid, ramose) and solitary corals are accessory. Limited data from Early Cretaceous assemblages indicate that at least some coral constructions that

grew in moderately turbid waters and at moderate water energy were dominated by microsolenids. Soft-substrate, turbid-water assemblages may consist of branched low-integrated (phaceloid, dendroid) forms, colonial corals (mainly plocoids and meandroids), and solitary corals. For Late Cretaceous turbid-water assemblages, a relatively good database exists. Two end-member assemblages are distinguished, (A) thamnasterioid–plocoid–cerioid assemblages of biostromes to mounds that accumulated at low to moderate turbidity, and at low to moderate terrigenous sedimentation, and (B) solitary coral–plocoid–meandroid assemblages of level-bottoms in coral marls,

locally with a substantial portion of cerioid–subcerioid and flabellate meandroid taxa. Another feature of Late Cretaceous turbid-water assemblages, both of type A and type B, is scarcity of phaceloid and dendroid forms, both with respect to diversity and abundance; ramose corals, however, may locally be common in thickets and biostromes. In type B assemblages, small-polypar forms with a highly “plastic” skeleton (e.g. *Actinacis*, *Actinastraea*) are common to prevalent; these forms probably were of high sediment tolerance. The Late Cretaceous appears to mark the time when small-polypar, sediment-tolerant colonial forms became a common to prevalent element of turbid-water assemblages.

Geological and palaeontological evidence suggests that the K/T transition was not accompanied by a mass extinction among corals as severe as the end-Triassic one (Flügel and Kiessling, 2002). Middle Eocene to Oligocene clear-water assemblages are dominated by plocoid and/or cerioid corals, whereas meandroids, thamnasterioids, phaceloids and dendroids together commonly make up a small to accessory part (Table 5). In sheltered clear-water areas, branched corals (ramose, phaceloid, dendroid) were common. In the palaeobathymetrically deeper part of bioconstructions, under moderate sedimentation and moderate to low turbidity, the coral assemblage may be dominated by thamnasterioids and/or by small-polyped, stress-resistant plocoids (*Actinacis*). Turbid-water bioconstructions are dominated by plocoid and cerioid corals with small to medium polypars; branched forms (e.g. *Caulastrea*) may locally be common, but overall seem to be of subordinate importance. Oligocene assemblages from turbid-water bioconstructions are dominated by small-corallite plocoids (e.g. *Actinacis*) and cerioids (*Porites*, *Goniopora*) with a porous, highly “plastic” skeleton; these same coral taxa comprise a subordinate portion of clear-water bioconstructions. Ramose forms are common, whereas phaceloids and dendroids are of subordinate importance. A Middle Eocene turbid-water assemblage that accumulated under high, frequent to near-chronic sedimentation (marls to siliciclastic siltstones) contains a substantial amount of solitary corals, and is rich in phaceloid and dendroid forms. During the Oligocene to Pleistocene, in the Caribbean, extinction and restriction versus speciation produced a shift from Oligocene plocoid-

cerioid dominated coral faunas to Pliocene–Recent meandroid–plocoid dominated assemblages (cf. Edinger and Risk, 1994). Data on Miocene and Pliocene turbid-water assemblages are limited. In the Tortonian of southern Spain, numerous turbid-water patch reefs are present that are dominated by *Porites* (cerioid) and *Tarbellastrea* (plocoid), two small-corallite genera that grew in stout branches, with an inverted-cone shape of the entire colony. Other corals, such as *Siderastrea* (cerioid, medium-sized polypars, mainly hemispherical), *Palaeoplesiastrea* (plocoid, small-sized polypars, typically laminar-encrusting) and *Platygyra* (meandroid, medium polypars, laminar-encrusting and inverted cone-shaped forms) are subordinate in abundance. No solitary corals are reported. From the Middle Miocene of East Kalimantan (SE Asia), turbid-water bioconstructions each up to a few meters thick have been described. In their lower part, these consist mainly of sheetstones and platestones with *Pachyseris* (meandroid, medium-sized polypars) and *Leptoseris* (meandroid, medium to large polypars), and the solitary coral *Cycloseris*. Up-section, floatstones and pillarstones with branched *Porites* (cerioid, small polypars) and *Stylophora* (plocoid, small-sized polypars) are present. The top-most interval is represented by domestones and mixstones with branched and massive forms such as *Favia* (cerioid, small–medium polypars), *Porites* (cerioid, small polypars) and *Goniopora* (cerioid, small polypars) (Wilson and Lokier, 2002).

Holocene turbid-water assemblages are dominated by sediment-resistant cerioid and plocoid forms with small to medium polypars, and by meandroids with medium–very large polypars; thamnasterioid forms are rare to absent. Massive and platy growth forms are prevalent. In areas of high sedimentation, branched forms (ramose, dendroid, phaceloid, oculinid, fasciculate) may be common; except in areas subject to frequent, very rapid sedimentation, and except ramose forms, branched corals overall are subordinate to rare in recent turbid-water assemblages. Solitary corals appear to become common to prevalent, relative to the number of colonial corals, only under high and persistent terrigenous input (cf. Renema and Troelstra, 2001).

The above summary does not represent a strictly quantitative evaluation, but allows recognition of a few trends in time. (1) At low to moderate siliciclastic input, in a turbidity–sedimentation regime

where discrete bioconstructions can form, only a minor shift of the coral assemblages occurred relative to contemporaneous clear-water counterparts. (2) *Thamasterioid* corals, common in Late Jurassic to Late Cretaceous turbid-water bioconstructions, are subordinate to absent in younger turbid-water assemblages. (3) At high terrigenous input, except for the Triassic, assemblages became shifted towards branched and solitary forms that thrive in level-bottoms. With the possible exception of the Late Cretaceous, high-clastic assemblages retained a “primitive” character in being dominated by low-integrated, branched corals and solitary corals. (4) At least since and including the Late Cretaceous, many turbid-water assemblages contained a significant amount of or were dominated by small-polypar colonial forms of high skeletal plasticity and, probably, of high sediment tolerance.

10. Discussion

In reefs under sediment input, a host of factors only indirectly related or unrelated to turbidity and sedimentation influence composition and persistence of coral assemblages. Despite advances, the complex interplay of these factors is not yet fully clear even to biologists working with recent corals and reefs under sediment input (Riegl, 1995; McClanahan and Obura, 1997). For fossil coral assemblages, and in view of the evolutionary change of prevalent coral types, this precludes a simple interpretation of sediment stress based on a single criterion. Much more detailed and well-processed data from fossil coral assemblages are needed to test which of the criteria to estimate sediment stress are the most useful, and to what extent sediment input determined a fossil assemblage.

The present-day global distribution and diversity of corals is mainly determined by water temperature and by nutrient input in upwelling zones but, on a large scale, is not obviously controlled by terrigenous input (cf. Stehli and Wells, 1971; Glynn, 1976; Rosen, 1984; Hubbard, 1997). The Indo-Pacific diversity center (IPDC) of corals (Stehli and Wells, 1971; Rosen, 1984) is situated in an area that, by its abundant clastic input from large islands, by its high seismic activity, by occurrence of typhoons, impact of ENSO events, and by the nearly chronic environ-

mental perturbations from Quaternary sea-level changes coupled with siliciclastic input (Potts, 1983, 1984) may be regarded as being unfavourable to corals. In the area of the IPDC, with the exception of Quaternary glacio-eustasy, a similar environment existed at least since the early Oligocene (cf. Fulthorpe and Schlanger, 1989; Wilson and Rosen, 1998; Adams et al., 1990; Perrin, 2002; Wilson, 2002). Yet this area was one of the major global centers of coral reef development and diversity increase since Oligocene time (Wilson and Rosen, 1998; Perrin, 2002, pp. 595–604, 607; McCoy and Heck, 1976). In present reef communities, highest diversities are sustained in settings with a wide trophic range, such as high-island systems (Hallock, 1987). Similarly, the evolution of polytaxic reef biotas may require an expanded trophic continuum over longer intervals of time (Hallock, 1987; Wood, 1993, 1995). Some authors conceded that fossil scleractinian reefs were unlike recent reefs in that many of the ancient reefs thrived on mixed siliciclastic–carbonate shelves (e.g. Flügel, 2002, p. 443). In the geological record, biogenic structures up from a few decimeters to meters in width and a few decimeters to a few meters in height are variously designated as mounds, patch reefs or reefs, depending on the reef definition used (see, e.g. Flügel, 2002; Leinfelder et al., 2002). On recent mixed siliciclastic–carbonate shelves, innumerable coral patches of similar dimensions are present (e.g. Roberts, 1987; Wilson and Lokier, 2002) that would hardly be termed “reefs” by many biologists, yet if fossilized were designated as mounds or patch reefs by many geologists. In the recent, only larger clear-water reefs are “accepted” as individual reef entities, while many smaller turbid-water reefs and coral patches go unregistered (cf. Larcombe et al., 2001). Thus, as also suggested by the PaleoReef database (Fig. 2), coral assemblages growing under terrigenous input in marginal marine and siliciclastic settings are common and, geologically, many of them were classified as reefs or buildups.

During the Phanerozoic, nutrient levels probably increased, with fluctuations, from Cambro-Devonian superoligotrophic seas to higher nutrient levels of Cainozoic time (Martin, 1996). During scleractinian evolution, as a result of increasing photoautotrophy, shallow-water coral faunas became increasingly dominated by high-integrated, small-polyped forms (Coates

and Jackson, 1987; Stanley and Swart, 1995). A gross amount of 25% autotrophy is assumed for Late Triassic and 75% for Cainozoic communities, respectively (Kiessling, 2002, p. 645 f.). Increased photoautotrophy combined with the Eocene appearance of grazing fish probably were crucial for Cainozoic corals to invade oligotrophic intra-oceanic environments (Wood, 1995). During the late Cainozoic, Alpine–Himalayan orogenesis, uplift of Tibet, increasing land areas in equatorial regions, climatic cooling and glacio-eustasy led to increased sediment–nutrient input to the seas (Martin, 1996). During the Cretaceous to Cainozoic, with fluctuations, the relative percentage of reefs in marginal-marine and siliciclastic settings overall increased, to a peak of 28% in the middle Eocene and of 24% in the Miocene (Fig. 2), but many Tertiary turbid-water reefs still remain to be described (cf. Wilson and Lokier, 2002). Thus, while many corals increased their capacity to thrive in clear-water areas,

the relative number of reefs in marginal-marine and siliciclastic settings increased, too. Cainozoic corals, however, probably were driven into marginal-marine and siliciclastic environments by disappearance of Mesozoic epicontinental carbonate seas, narrowing of shelves associated with second-order sea-level fall, and shrinking of isolated carbonate platforms. In this case, the ability of coral faunas of overall increased photoautotrophy to also thrive in siliciclastic environments may be viewed as a general adaptation (within specific limits) of many corals to conditions in marginal-marine or siliciclastic settings. In addition, diversification of high-integrated, small-polyped corals with “plant-like” feeding allowed for invasion of oligotrophic environments, yet small-polyped sediment-tolerant forms evolved, too, and many medium- to large-polyped, high-integrated forms and low-integrated, “primitive” corals retained a comparatively high capacity to cope with sediment–POM input. Evolution and diversifica-

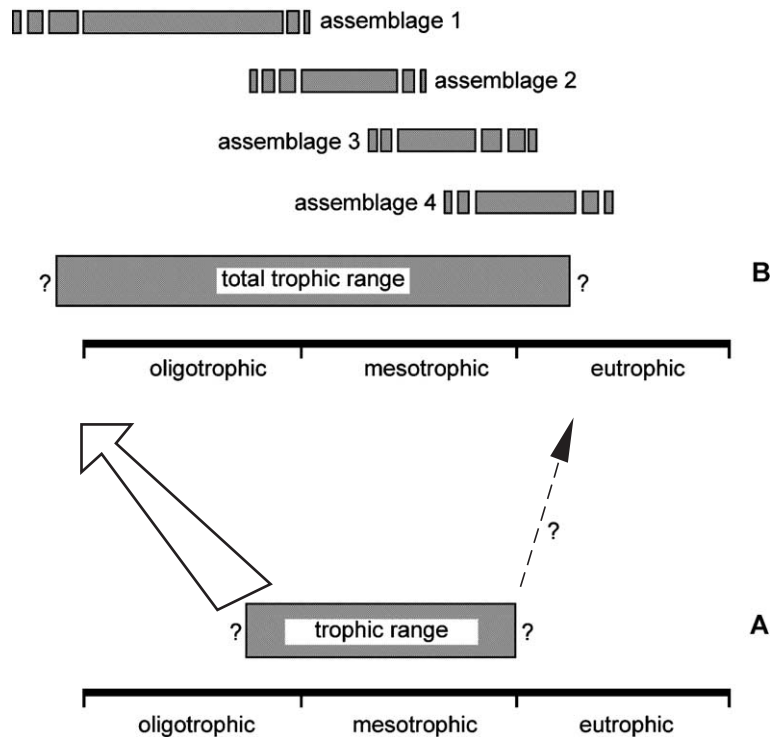


Fig. 10. Hypothesis to explain increasing relative percentage of scleractinian reefs in marginal marine or siliciclastic settings over time (see Fig. 2). (A) Early, low-diverse coral assemblages probably had a comparatively wide, undifferentiated trophic range. (B) During evolution and diversification of corals, oligotrophic environments were invaded. Late Mesozoic to Cainozoic global change (see text) provided an increased area of turbid-water habitats. Because of coral diversification and retainment, to varying degrees, of an ability to cope with sediment–POM input, a wider total trophic range can be covered by distinct coral assemblages.

tion thus widened the total environmental range in which distinct coral assemblages can thrive (Fig. 10). This hypothesis is supported by the observation that early coral assemblages show little distinction with respect to prevalent growth forms and taxa in different settings and under different degrees of terrigenous input (see Section 9), whereas recent clear- and turbid-water assemblages are distinguished by a number of features such as prevalent growth forms and taxonomic composition.

11. Conclusions

- (1) Meso-Cainozoic “clear-water” bioconstructions with corals often stacked into thicker reef complexes, are mainly situated at or near the shelf-break, and most are characterized by a prevalence of frame to cluster fabric with marine cement in frame pores, and by a distinct carbonate slope depositional system. Under terrigenous input, development of reef complexes was suppressed, and buildups with corals were situated in the inner shelf to shore zone, or in a deeper position (near storm wave base) on the shelf. Fossil “turbid-water” bioconstructions are characterized by the absence of a distinct carbonate slope, by prevalence of cluster to segment fabrics, and by a scarcity to absence of cement-filled frame pores. Under substantial, frequent sedimentation or resuspension, level-bottoms rich in solitary corals, colonial corals and other biota (e.g. molluscs, echinoderms) formed.
- (2) Fossil turbid-water bioconstructions contain low-diverse to diverse (relative to coeval clear-water buildups) assemblages dominated by sediment-resistant coral taxa and morphs. Besides a coral’s behaviour (elusive in fossils), the sediment resistance of a coral is mainly determined by growth form and polypar width; polyp integration and the construction of the calyx seem to be less important. Small-polyped corals of high sediment tolerance, however, probably existed at least since the Early Cretaceous.
- (3) Middle–Late Triassic coral faunas showed comparatively little differentiation with respect to sediment input. Late Jurassic to Cretaceous turbid-water, colonial coral faunas of bioconstructions are dominated by plocoid and/or thamnasterioid forms. Cainozoic turbid-water communities consist mainly of cerioid and plocoid corals. In coral marls, level-bottom assemblages are dominated, either by abundance or also by diversity, by solitary corals, but may also be rich in colonial forms.
- (4) For fossil clear-water reefs and for buildups that accumulated under low terrigenous input, nutrient enrichment resulted in increased bioerosion and encrustation (cf. Hallock, 1988; Edinger et al., 2000). For turbid-water bioconstructions and level-bottoms that formed under frequent or near-permanent, moderate to high sediment input, the effects of sedimentation prevail, and macro-boring and encrustation become low to minimal.
- (5) We suggest that a Cretaceous to Cainozoic increase in the relative number of reefs in marginal-marine or siliciclastic settings (Kiesling, 2002), paralleled by increasing efficiency of photosymbiosis (e.g. Stanley, 2003), is explained by coral evolution and diversification, resulting in a widening of the total trophic range in which distinct coral assemblages can thrive.

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References

- Abbott, B.M., 1975. Implications for the fossil record of modern carbonate bank corals. *Geol. Soc. Amer. Bull.* 86, 203–204.
- Abelson, A., Miloh, T., Loya, Y., 1993. Flow patterns induced by substrata and body morphologies of benthic organisms, and their roles in determining availability of food particles. *Limnol. Oceanogr.* 38, 1116–1124.

- Acevedo, R., Morelock, J., Olivieri, R.A., 1989. Modification of coral reef zonation by terrigenous sediment stress. *Palaios* 4, 92–100.
- Acker, K.L., Stearn, C.W., 1990. Carbonate-siliciclastic facies transition and reef growth on the northeast coast of Barbados, West Indies. *J. Sediment. Pet.* 60, 18–25.
- Adams, C.G., Lee, D.E., Rosen, B.R., 1990. Conflicting isotopic and biotic evidence for tropical sea-surface temperature during the Tertiary. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 77, 289–313.
- Angelis d'Ossat, G. de, 1894. I corallari dei terreni Terziari dell'Italia settentrionale. Collezione Michelotti. Museo Geologico R. Università di Roma. *Atti Reale Accad. Lincei, Mem.* 5, Cl. Sci. Fis. Mat. Nat. 1, 164–280 (Università di Roma).
- Anthony, K.R.N., 1999. Coral suspension feeding on fine particulate matter. *J. Exp. Mar. Biol. Ecol.* 232, 85–106.
- Anthony, K.R.N., 2000. Enhanced particle-feeding capacity of corals on turbid reefs (Great Barrier Reef, Australia). *Coral Reefs* 19, 59–67.
- Anthony, K.R.N., Fabricius, K.E., 2000. Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. *J. Exp. Mar. Biol. Ecol.* 252, 221–253.
- Atkinson, M.J., Carlson, B., Crow, G.L., 1995. Coral growth in high-nutrient, low-pH seawater: a case study of corals cultured at the Waikiki Aquarium, Honolulu, Hawaii. *Coral Reefs* 14, 215–223.
- Babcock, R., Davies, P., 1991. Effects of sedimentation on settlement of *Acropora millepora*. *Coral Reefs* 9, 205–208.
- Bailey, R.H., Tedesco, S.A., 1986. Paleoeecology of a Pliocene coral thicket from North Carolina: an example of temporal change in community structure and function. *J. Paleontology* 60, 1159–1176.
- Bak, R.P.M., 1978. Lethal and sublethal effects of dredging on reef corals. *Mar. Poll. Bull.* 9, 14–16.
- Bak, R.P.M., Elgershuizen, J.H.B.W., 1976. Patterns of oil-sediment rejection in corals. *Mar. Biol.* 37, 105–113.
- Bak, R.P.M., Luckhurst, B.E., 1980. Constancy and change in coral reef habitats along depth gradients at Curacao. *Oecologia* 47, 145–155.
- Baker, P.A., Weber, J.N., 1975. Coral growth rate: variation with depth. *Earth Planet. Sci. Lett.* 27, 57–61.
- Banner, A.H., 1974. Kaneohe Bay, Hawaii: urban pollution and a coral reef ecosystem. *Proc. 2nd Int. Symp. Coral Reefs*, 2, Hawaii Institute of Marine Biology, University of Hawaii, Hawaii, pp. 685–702.
- Barnes, D.J., Chalker, B.E., 1990. Calcification and photosynthesis in reef-building corals and algae. In: Dubinsky, Z. (Ed.), *Ecosystems of the World, Coral Reefs*, vol. 25. Elsevier, Amsterdam, pp. 109–131.
- Barnes, R.S.K., Hughes, R.N., 1988. *An Introduction to Marine Ecology*. Blackwell, Oxford (351 pp).
- Baron-Szabo, R.C., 1994. Palökologie von nordspanischen Korallen des Urgon (Playa de Laga, Prov. Guernica, N-Spanien). *Berliner geowiss. Abh. (E)* 13, 441–451.
- Baron-Szabo, R.C., 1997. Zur Korallenfazies der ostalpinen Kreide (Helvetikum: Allgäuer Schrättalkalk; Nördliche Kalkalpen: Brandenberger Gosau). *Taxonomie, Palökologie. Zitteliana* 21, 3–97.
- Baron-Szabo, R.C., 1999. Taxonomy of Upper Cretaceous scleractinian corals of the Gosau Group (Weissenbachalm, Steiermark, Austria). *Abh. geol. B.-A.* 56, 441–464.
- Baron-Szabo, R.C., 2001. Corals of the Theresienstein reef (Upper Turonian-Coniacian, Salzburg, Austria). *Bull. Biolog. Soc. Washington* 10, 257–268.
- Baron-Szabo, R.C., 2002. Scleractinian corals of the Cretaceous. A guide to Cretaceous forms with descriptions, illustrations, and remarks on their systematic position. Baron-Szabo (publ. on own expense), Knoxville (Tennessee) (539 pp).
- Baron-Szabo, R.C., 2003. Taxonomie und Ontogenie von Korallen der ostalpinen Oberkreide (Hochmoos- und Grabenbachschichten, Gosau Gruppe, Santon). *Jb. Geol. B.-A.* 143, 107–201 (Vienna).
- Baron-Szabo, R.C., Fernandez-Mendiola, P.A., 1997. Cretaceous scleractinian corals from the Albian of Cabo de Ajo (Cantabria Province, N-Spain). *Paläont. Z.* 71, 35–50.
- Basillais, E., 1998. Functional role of the fractal morphology of corals: a full model of the nutrient turbulent diffusion fluxes to a coral reef. *C. R. Acad. Sci. Paris, Sci. de la vie* 321, 295–298.
- Beach, D.K., 1983. Oligocene reef tract development, southwestern Puerto Rico. Part II. Holocene analog, modern reef and reef-associated sediments, southern insular shelf of Puerto Rico. *Sedimenta IX*, 108–132.
- Bertling, M., Insalaco, E., 1998. Late Jurassic coral/microbial reefs from the northern Paris Basin-facies, palaeoecology and palaeobiogeography. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 139, 139–175.
- Bilger, R.W., Atkinson, M.J., 1992. Anomalous mass transfer of phosphate on coral reef flats. *Limnol. Oceanogr.* 37, 261–272.
- Bilger, R.W., Atkinson, M.J., 1995. Effects of nutrient loading on nutrient uptake kinetics of coral reef communities. *Limnol. Oceanogr.* 40, 279–289.
- Birkeland, C., 1977. The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. *Proc. 3rd Int. Coral Reef Symp.*, 1, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, pp. 16–21.
- Blanchon, P., Jones, B., 1997. Hurricane control on shelf-edge reef architecture around Grand Cayman. *Sedimentology* 44, 479–506.
- Blanchon, P., Jones, B., Kalbfleisch, W., 1997. Anatomy of a fringing reef around Grand Cayman: storm rubble, not coral framework. *J. Sediment. Res.* 67, 1–16.
- Bosellini, F.R., 1998. Diversity, composition and structure of Late Eocene shelf-edge coral associations (Nago Limestone, northern Italy). *Facies* 39, 203–226.
- Bosellini, F., Stemann, T.A., 1996. Autoecological significance of growth form in the scleractinian *Actinacis rollei* Reuss (Oligocene, Lessini Mountains, Northern Italy). In: Cherchi, A. (Ed.), *Autoecology of selected fossil organisms. Achievements and problems. Boll. Soc. Paleont. It.*, vol. 3, pp. 31–43.
- Bosellini, F., Trevisani, E., 1992. Coral facies and cyclicity in the Castलगomberto Limestone (Early Oligocene, Eastern Lessini Mountains, Northern Italy). *Riv. It. Paleont. Strat.* 98, 339–352.

- Bradbury, R.H., Young, P.C., 1983. Coral interactions and community structure: an analysis of spatial pattern. *Mar. Ecol. Progr. Ser.* 11, 265–271.
- Braga, J.C., Martin, J.M., Riding, R., 1990. Coral reefs in coarse-terrigenous sedimentary environments (Upper Tortonian, Granada Basin, southern Spain). *Sediment. Geol.* 66, 135–150.
- Brandner, R., Resch, W., 1981. Reef development in the Middle Triassic (Ladinian and Cordevolian) of the Northern Limestones Alps near Innsbruck, Austria. In: Toomey, T.F. (Ed.), *European fossil reef models. Soc. Econ. Pal. Min. Spec. Publ.*, vol. 30, pp. 203–231.
- Bromley, R.G., 1996. *Spurenfossilien: Biologie, Taphonomie und Anwendungen*. Springer, Berlin (347 pp).
- Budd, A.F., Johnson, K.G., Edwards, J.C., 1989. Miocene coral assemblages in Anguilla, B.W.I., and their implications for the interpretation of vertical succession in fossil reefs. *Palaios* 4, 264–275.
- Bull, G.D., 1982. Scleractinian coral communities of two inshore high island fringing reefs at Magnetic Island, North Queensland. *Mar. Ecol. Progr. Ser.* 7, 267–272.
- Camoin, G.F., Montaggioni, L.F., 1994. High energy coralgal-stromatolite frameworks from Holocene reefs (Tahiti, French Polynesia). *Sedimentology* 41, 655–676.
- Camoin, G.F., Gautret, P., Montaggioni, L.F., Cabioch, G., 1999. Nature and environmental significance of microbialites in Quaternary reefs: the Tahiti paradox. *Sediment. Geol.* 60, 15–49.
- Chadwick-Furman, N.E., Goffredo, S., Loya, Y., 2000. Growth and population dynamic model of the reef coral *Fungia granulosa* Klunzinger, 1879 at Eilat, northern Red Sea. *J. Exp. Mar. Biol. Ecol.* 249, 199–218.
- Charpy, L., 2001. Phosphorus supply for atoll biological productivity. *Coral Reefs* 20, 357–360.
- Coates, A.G., 1977. Jamaican coral-rudist frameworks and their geologic setting. In: Frost, S.H., Weiss, M.P., Saunders, J.B. (Eds.), *Reefs and Related Carbonates—Ecology and Sedimentology*, Amer. Assoc. Petrol. Geol. Studies in Geology, vol. 4, pp. 83–91.
- Coates, A.G., Jackson, J.B.C., 1987. Clonal growth, algal symbiosis, and reef formation in corals. *Paleobiology* 13, 363–378.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.
- Cortés, J.N., Risk, M.J., 1985. A reef under siltation stress: Cahuita, Costa Rica. *Bull. Mar. Sci.* 36, 339–356.
- Cox, E.F., Ward, S., 2002. Impact of elevated ammonium on reproduction in two Hawaiian scleractinian corals with different life history patterns. *Mar. Poll. Bull.* 44, 1230–1235.
- Crame, J.A., 1980. Succession and diversity in the Pleistocene coral reefs of the Kenya coast. *Palaeontology* 23, 1–37.
- Dallmeyer, D.G., Porter, J.W., Smith, G.J., 1982. Effects of particulate peat on the behavior and physiology of the Jamaican reef-building coral *Montastrea annularis*. *Mar. Biol.* 68, 229–233.
- D’Elia, C.F., Wiebe, W.J., 1990. Biogeochemical nutrient cycles in coral-reef ecosystems. In: Dubinsky, Z. (Ed.), *Ecosystems of the World, Coral Reefs*, vol. 25. Elsevier, Amsterdam, pp. 49–74.
- Dodge, R.E., Aller, R.C., Thomson, J., 1974. Coral growth related to resuspension of bottom sediments. *Nature* 247, 574–577.
- Dodge, R.E., Vaisnys, J.R., 1977. Coral populations and growth patterns: responses to sedimentation and turbidity associated with dredging. *J. Mar. Res.* 35, 715–730.
- Done, T., 1982. Patterns in the distribution of coral communities across the central Great Barrier Reef. *Coral Reefs* 1, 95–107.
- Done, T., 1992. Phase shifts in coral communities and their ecological significance. *Hydrobiologia* 247, 121–132.
- Dryer, S., Logan, A., 1978. Holocene reefs and sediments of Castle Harbour, Bermuda. *J. Mar. Res.* 36, 399–425.
- Dubinsky, Z., Jokiel, P.L., 1994. Ratio of energy and nutrient fluxes regulates symbiosis between zooxanthellae and corals. *Pac. Sci.* 48, 313–324.
- Dufour, P., Berland, B., 1999. Nutrient control of phytoplanktonic biomass in atoll lagoons and Pacific ocean waters: Studies with factorial enrichment bioassays. *J. Exp. Mar. Biol. Ecol.* 234, 147–166.
- Dupraz, C., Strasser, A., 2004. Nutritional modes in coral-microbialite reefs (Jurassic, Oxfordian, Switzerland): evolution of trophic structure as a response to environmental change. *Palaios* 17, 449–471.
- Edinger, E.N., Risk, M.J., 1994. Oligocene-Miocene extinction and geographic restriction of Caribbean corals: roles of turbidity, temperature, and nutrients. *Palaios* 9, 576–598.
- Edinger, E.N., Limmon, G.V., Jompa, J., Widjatmok, W., Heikoop, J.M., Risk, M.J., 2000. Normal coral growth rates on dying reefs: are coral growth rates good indicators of reef health? *Mar. Pollution Bull.* 40, 404–425.
- Endean, R., 1976. Destruction and recovery of coral reef communities. In: Jones, O.A., Endean, R. (Eds.), *Biology and geology of coral reefs*, *Biology* 2, vol. 3. Academic Press, New York, pp. 215–254.
- Enos, P., 1991. Sedimentary parameters for computer modeling. In: Franseen, E.K., Watney, W.L., Kendall, C.G. St. C., Ross, W. (Eds.), *Sedimentary modeling: computer simulations and methods for improved parameter definition*. Kansas Geol. Survey Bull., vol. 233, pp. 63–99.
- Falkowski, P.G., Jokiel, P.I., Kinzie, R.A., 1990. Irradiance and corals. In: Dubinsky, Z. (Ed.), *Ecosystems of the World, Coral Reefs*, vol. 25. Elsevier, Amsterdam, pp. 89–107.
- Felix, J.P., 1903. Studien über die korallenführenden Schichten der oberen Kreideformation in den Alpen und in den Mediterrangebieten. *Palaeontographica* 49. Schweizerbart, Stuttgart, pp. 163–359.
- Fishelson, L., 1973. Ecology of coral reefs in the Gulf of Aqaba (Red Sea) influenced by pollution. *Oecologia* 12, 55–67.
- Fisk, D.A., Harriott, V.S., 1990. Spatial and temporal variation in coral recruitment on the Great Barrier Reef: implications for dispersal hypotheses. *Mar. Biol.* 107, 485–490.
- Flügel, E., 2002. Triassic reef patterns. In: Kiessling, W., Flügel, E., Golonka, J. (Eds.), *Phanerozoic reef patterns*, *Soc. Econ. Pal. Min. Spec. Publ.*, vol. 72, pp. 391–463.
- Flügel, E., Kiessling, W., 2002. Patterns of Phanerozoic reef crises. In: Kiessling, W., Flügel, E., Golonka, J. (Eds.), *Phanerozoic reef patterns*. *Soc. Econ. Pal. Min. Spec. Publ.*, vol. 72, pp. 691–733.

- Foster, A.B., 1980. Environmental variation in skeletal morphology within the Caribbean reef corals *Montastrea annularis* and *Siderastrea siderea*. *Bull. Mar. Sci.* 30, 678–709.
- Frost, S.H., 1981. Oligocene reef coral biofacies of the Vicentin, northeast Italy. In: Toomey, T.F. (Ed.), *European fossil reef models*. Soc. Econ. Pal. Min. Spec. Publ., vol. 30, pp. 483–539.
- Frost, S.H., Langenheim, R.L., 1974. *Cenozoic reef biofacies*. Northern Illinois Press, Dekalb (Illinois) (388 pp).
- Frost, S.H., Weiss, M.P., 1979. Patch-reef communities and succession in the Oligocene of Antigua, West Indies: summary. *Geol. Soc. Am. Bull.* 90, 612–616.
- Frost, S.H., Harbour, J.L., Beach, D.K., Realini, M.J., Harris, P.M., 1983. Oligocene reef tract development, southwestern Puerto Rico. *Sedimenta IX*, 1–107.
- Fulthorpe, C.S., Schlanger, S.O., 1989. Paleo-oceanographic and tectonic setting of early Miocene reefs and associated carbonates of offshore southeast Asia. *Amer. Assoc. Petrol. Geol. Bull.* 73, 729–756.
- Fürsich, F.T., Wendt, J., 1977. Biostratigraphy and palaeoecology of the Cassian Formation (Triassic) of the southern Alps. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 22, 257–323.
- Gardner, T.A., Cotre, I.M., Gill, J.A., Grant, A., Watkinson, A.R., 2003. Long-term region-wide declines in Caribbean corals. *Science* 301, 958–960.
- Geister, J., 1983. Holozäne westindische Korallenriffe: geomorphologie, ökologie und fazies. *Facies* 9, 173–284.
- Gili, E., 1993. Facies and geometry of Les Collades de Basturs carbonate platform, Upper Cretaceous, south-central Pyrenees. In: Simo, J.A.T., Scott, R.W., Masse, J.-P. (Eds.), *Cretaceous Carbonate Platforms*. Amer. Assoc. Petrol. Geol. Mem., vol. 56, pp. 343–352.
- Gili, E., Skelton, P.W., Vicens, E., Obrador, A., 1995. Corals to rudists—an environmentally induced assemblage succession. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 119, 127–136.
- Gill, G.A., Coates, A.G., 1977. Mobility, growth patterns and substrate in some fossil and recent corals. *Lethaia* 10, 119–134.
- Ginsburg, R.N., Schroeder, J.H., 1973. Growth and submarine fossilization of algal cup reefs, Bermuda. *Sedimentology* 20, 575–614.
- Glynn, P., 1976. Some physical and biological determinants of coral community structure in the eastern Pacific. *Ecol. Monogr.* 46, 431–456.
- Goldfuss, A., 1826–1833. *Petrefacta Germaniae*, 1, 1–252. Düsseldorf (Arnz).
- Gong, S.-Y., Wang, S.-W., Lee, T.-Y., 1998. Pleistocene coral reefs associated with claystones, Southwestern Taiwan. *Coral Reefs* 17, 215–222.
- Goreau, T.F., 1959. The ecology of Jamaican coral reefs. I. Species composition and zonation. *Ecology* 10, 67–90.
- Goreau, T.F., Wells, J.W., 1967. The shallow-water Scleractinia of Jamaica: revised list of species and their vertical distribution range. *Bull. mar. Sci.* 17, 442–453.
- Goreau, T.F., Yonge, C.M., 1968. Coral community on muddy sand. *Nature* 217, 421–423.
- Götz, S., 2003. Biotic interaction and synecology in a Late Cretaceous coral-rudist biostrome of southeastern Spain. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 187, 125–138.
- Graus, R.R., Macintyre, I.G., 1976. Light control of growth form in colonial reef corals: computer simulation. *Science* 193, 895–897.
- Grigg, R.W., Dollar, S.J., 1990. Natural and anthropogenic disturbance on coral reefs. In: Dubinsky, Z. (Ed.), *Ecosystems of the world, Coral reefs*, vol. 25. Elsevier, Amsterdam, pp. 439–452.
- Hallock, P., 1987. Fluctuations in the trophic resource continuum: a factor in global diversity cycles? *Paleoceanography* 2, 457–471.
- Hallock, P., 1988. The role of nutrient availability in bioerosion: consequences to carbonate buildups. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 63, 275–291.
- Hallock, P., Schlager, W., 1986. Nutrient excess and the demise of coral reef and carbonate platforms. *Palaios* 1, 389–398.
- Hayward, A.B., 1982. Coral reefs in a clastic sedimentary environment: fossil (Miocene, S.W. Turkey) and modern (Recent, Red Sea) analogues. *Coral Reefs* 1, 109–114.
- Hearn, C.J., Atkinson, M.J., Falter, J.L., 2001. A physical derivation of nutrient-uptake rates in coral reefs: effects of roughness and waves. *Coral Reefs* 20, 347–356.
- Helmuth, B., Sebens, K., 1993. The influence of colony morphology and orientation to flow on particle capture by the scleractinian coral *Agaricia agaricites* (Linnaeus). *J. Exp. Mar. Biol. Ecol.* 165, 251–278.
- Hillis, Z.M., Bythell, J.C., 1998. “Keep up or give up”: hurricanes promote coral survival by interrupting burial from sediment accumulation. *Coral Reefs* 17, 262.
- Hodgson, G., 1990. Tetracycline reduces sedimentation damage to corals. *Mar. Biol.* 104, 493–496.
- Höfling, R., 1989. Substrate-induced morphotypes and intraspecific variability in Upper Cretaceous scleractinians of the Eastern Alps (West Germany, Austria). *Mem. Assoc. Australas. Paleontols.* 8, 51–60.
- Höfling, R., 1997. Eine erweiterte Riff-Typologie und ihre Anwendung auf kretazische Biokonstruktionen. Bayer. Akad. Wiss., Mathematisch-Naturwiss. Kl., Abh., N.F. 169 (Bayer. Akad. d. Wiss., München, 127 pp).
- Hubbard, D.K., 1986. Sedimentation as a control of reef development: St. Croix, U.S.V.I. *Coral Reefs* 5, 117–125.
- Hubbard, D.K., 1997. Reefs as dynamic systems. In: Birkeland, C. (Ed.), *Life and death of coral reefs*. Chapman and Hall, New York, pp. 43–67.
- Hubbard, J.A.E.B., Pocock, Y.P., 1972. Sediment rejection by recent scleractinian corals: a key to the palaeo-environmental reconstruction. *Geol. Rundsch.* 61, 598–626.
- Hubbard, D.K., Miller, A.I., Scaturro, D., 1990. Production and cycling of calcium carbonate in a shelf-edge reef system (St. Croix, U.S. Virgin Islands): applications to the nature of reef systems in the fossil record. *J. Sediment. Pet.* 60, 335–360.
- Hughes, T.P., 1994. Catastrophes, phase shifts and large-scale degradation of a Caribbean coral reef. *Science* 265, 1547–1551.
- Hughes, T.P., Jackson, J.B.C., 1985. Population dynamics and life histories of foliaceous corals. *Ecol. Monogr.* 55, 141–166.
- Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B.C., Kleypas, J., Lough, J.M., Marshall, P., Nyström, M., Palumbi, S.R., Pandolfi, J.M., Rosen, B., Roughgarden, J., 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* 301, 929–933.

- Hunte, W., Wittenberg, M., 1992. Effects of eutrophication and sedimentation on juvenile corals. II. Settlement. *Mar. Biol.* 114, 625–631.
- Huston, M.A., 1985. Patterns of species diversity on coral reefs. *Ann. Rev. Ecol. Systemat.* 16, 149–177.
- Insalaco, E., 1996. Upper Jurassic microsolenid biostromes of northern and central Europe: facies and depositional environment. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 121, 169–194.
- James, N.P., Ginsburg, R.N., 1979. The seaward margin of Belize barrier and atoll reefs. Morphology, Sedimentology, Organism Distribution and Late Quaternary History. *Int. Assoc. Sediment. Spec. Publ.*, vol. 3. Blackwell, Oxford (191 pp).
- James, N.P., Macintyre, I.G., 1985. Carbonate depositional environments, modern and ancient. Part I: Reefs. Zonation, depositional facies, and diagenesis. In: Warme, J.E., Shanley, K.W. (Eds.), Carbonate depositional environments, modern and ancient, Colorado School of Mines Quart., vol. 80. Colorado School of Mines Press, Golden, Colorado, p. 3 (70 pp).
- Johannes, R.E., 1980. The ecological significance of the submarine discharge of groundwater. *Mar. Ecol. Progr. Ser.* 3, 365–373.
- Johnson, D.P., Risk, M.J., 1987. Fringing reef growth on a terrigenous mud foundation, Fantome Island, central Great Barrier Reef, Australia. *Sedimentology* 34, 275–287.
- Johnson, C.C., Sanders, D., Kauffman, E.G., Hay, W.W., 2002. Upper Cretaceous reefal patterns and processes affecting their development and demise. In: Kiessling, W., Flügel, E., Golonka, J. (Eds.), Phanerozoic Reef Patterns. *Soc. Econ. Pal. Min. Spec. Publ.*, vol. 72, pp. 549–585.
- Jokiel, P.L., 1978. Effects of water motion on reef corals. *J. Exp. Mar. Biol. Ecol.* 35, 87–97.
- Kiessling, W., 2002. Secular variations in the Phanerozoic reef ecosystem. In: Kiessling, W., Flügel, E., Golonka, J. (Eds.), Phanerozoic Reef Patterns. *Soc. Econ. Pal. Min. Spec. Publ.*, vol. 72, pp. 625–690.
- Kiessling, W., Flügel, E., Golonka, J., 1999. Paleoreef Maps: evaluation of a comprehensive database on Phanerozoic reefs. *Am. Assoc. Petrol. Bull.* 83, 1552–1587.
- Kiessling, W., Flügel, E., 2002. PaleoReefs—a database on Phanerozoic reefs. In: Kiessling, W., Flügel, E., Golonka, J. (Eds.), Phanerozoic reef patterns. *Soc. Econ. Pal. Min. Spec. Publ.*, vol. 72, pp. 77–92.
- Kinsey, D., Davies, P., 1979. Effects of elevated nitrogen and phosphorus levels on coral reef growth. *Limnol. Oceanogr.* 24, 935–940.
- Kleypas, J.A., 1996. Coral reef development under naturally turbid conditions: fringing reefs near Broad Sound, Australia. *Coral Reefs* 15, 153–167.
- Koop, K., Booth, D., Broadbent, A., Brodie, J., Bucher, D., Capone, D., Coll, J., Dennison, W., Erdmann, M., Harrison, P., Hoegh-Guldberg, O., Hutchings, P., Jones, G.B., Larkum, A.W.D., O'Neill, J., Steven, A., Tentori, E., Ward, S., Williamson, J., Yellowlees, D., 2001. ENCORE: the effect of nutrient enrichment on coral reefs. Synthesis of results and conclusions. *Mar. Poll. Bull.* 42, 91–120.
- Kühn, O., 1925. Variationsuntersuchungen an rezenten Korallen und ihre Anwendung auf die Fossilien. *Verh. Zool. Bot. Ges. Wien* 1925, 129–134.
- Larcombe, P., Costen, A., Woolfe, K.J., 2001. The hydrodynamic and sedimentary setting of nearshore coral reefs, central Great Barrier Reef shelf, Australia: Paluma shoals, a case study. *Sedimentology* 48, 811–835.
- Larcombe, P., Carter, R.M., 2004. Cyclone pumping, sediment partitioning and the development of the Great Barrier Reef shelf system: a review. *Quaternary Sci. Rev.* 23, 107–135.
- Lasker, H.R., 1980. Sediment rejection by reef corals: the roles of behavior and morphology in *Montastrea cavernosa* (Linnaeus). *J. Exp. mar. Biol. Ecol.* 47, 77–87.
- Leinfelder, R.R., 1994. Karbonatplattformen und Korallenriffe innerhalb siliziklastischer Sedimentationsbereiche (Oberjura, Lusitanisches Becken, Portugal). *Profil* 6, 1–207.
- Leinfelder, R.R., Krautter, M., Latenser, R., Nose, M., Schmid, D.U., Schweigert, G., Keupp, H., Brugger, H., Herrmann, R., Rehfeld-Kiefer, U., Schroeder, J.H., Reinhold, C., Koch, R., Zeiss, A., Schweizer, V., Christmann, H., Menges, G., Luterbacher, H., 1994. The origin of Jurassic reefs: current research developments and results. *Facies* 31, 1–56.
- Leinfelder, R.R., Schmid, D.U., Nose, M., Werner, W., 2002. Jurassic reef patterns—the expression of a changing globe. In: Kiessling, W., Flügel, E., Golonka, J. (Eds.), Phanerozoic Reef Patterns. *Soc. Econ. Pal. Min. Spec. Publ.*, vol. 72, pp. 465–520.
- Lewis, J.B., 1976. Experimental tests of suspension feeding in Atlantic reef corals. *Mar. Biol.* 36, 147–150.
- Lewis, J.B., 1987. Measurement of groundwater seepage flux onto a coral reef: spatial and temporal variations. *Limnol. Oceanogr.* 32, 1165–1169.
- Lewis, J.B., Price, W.S., 1975. Feeding mechanisms and feeding strategies of Atlantic reef corals. *J. Zool. London* 176, 527–544.
- Logan, A., 1988. Sediment-shifting capability in the recent solitary coral *Scolymnia cubensis* (Milne-Edwards and Haime) from Bermuda. *Bull. Mar. Sci.* 43, 241–248.
- Loya, Y., 1976. Effects of water turbidity and sedimentation on the community structure of Puerto Rico corals. *Bull. mar. Sci.* 26, 450–466.
- MacDonald, I.A., Perry, C.T., 2003. Biological degradation of coral framework in a turbid lagoon environment, Discovery Bay, north Jamaica. *Coral Reefs* 22, 523–535.
- Macintyre, I.G., 1988. Modern coral reefs of western atlantic: new geological perspective. *Amer. Assoc. Petrol. Geol. Bull.* 72, 1360–1369.
- Maniwavie, T., Rewald, J., Aitsi, J., Wagner, T.P., Munday, P.L., 2001. Recovery of corals after volcanic eruptions in Papua New Guinea. *Coral Reefs* 20, 24.
- Marshall, S.M., Orr, A.P., 1931. Sedimentation on Low Isles reef and its relation to coral growth. *Scientific reports of the Great Barrier Reef Expedition* 1/5, 93–132.
- Martin, R.E., 1996. Secular increase in nutrient levels through the Phanerozoic: implications for productivity, biomass, and diversity of the marine biosphere. *Palaios* 11, 209–219.
- Martin, J.M., Braga, J.C., Rivas, P., 1989. Coral successions in Upper Tortonian reefs in SE Spain. *Lethaia* 22, 271–286.
- Masse, J.-P., Philip, J., 1981. Cretaceous coral-rudist buildups of France. In: Toomey, D.F. (Ed.), European Fossil Reef Models. *Soc. Econ. Pal. Min. Spec. Publ.*, vol. 30, pp. 399–426.

- Mayer, A.G., 1918. Ecology of the Murray Island coral reef. Carnegie Inst. Washington publ. 213, 9, 3–48.
- McCall, J., Rosen, B., Darrell, J., 1994. Carbonate deposition in accretionary prism settings: early Miocene coral limestones and corals of the Makran mountain range in southern Iran. *Facies* 31, 141–178.
- McClanahan, T.R., Obura, D., 1997. Sedimentation effects on shallow coral communities in Kenya. *J. Exp. Mar. Biol. Ecol.* 209, 103–122.
- McConnaughey, T.A., Whelan, J.F., 1997. Calcification generates protons for nutrient and bicarbonate uptake. *Earth-Sci. Rev.* 42, 95–177.
- McCook, L.J., 1999. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18, 357–367.
- McCook, L.J., Jompa, J., Diaz-Pulido, G., 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19, 400–417.
- McCoy, E.D., Heck, K.L., 1976. Biogeography of corals, seagrasses, and mangroves: an alternative to the center of origin concept. *Syst. Zool.* 25, 201–210.
- McCulloch, M., Fallon, S., Wyndham, T., Hendy, E., Lough, J., Barnes, D., 2003. Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. *Nature* 421, 727–730.
- Miller, R.L., Cruise, J.F., 1995. Effects of suspended sediments on coral growth: evidence from remote sensing and hydrologic modeling. *Remote Sens. Environ.* 53, 177–187.
- Mitchell, S.F., 2002. Palaeoecology of corals and rudists in mixed volcanoclastic-carbonate small-scale rhythms (Upper Cretaceous, Jamaica). *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 186, 237–259.
- Muscatine, L., 1973. Nutrition of corals. In: Jones, O.A., Endean, R. (Eds.), *The geology and biology of coral reefs*, vol. 2. Academic Press, London, pp. 77–115.
- Muscatine, L., 1990. The role of symbiotic algae in carbon and energy flux in reef corals. In: Dubinsky, Z. (Ed.), *Ecosystems of the World, Coral Reefs*, vol. 25. Elsevier, Amsterdam, pp. 75–87.
- Muscatine, L., Porter, J.W., Kaplan, I.R., 1989. Resource partitioning by reef corals as determined from stable isotope composition. I. $\delta^{13}\text{C}$ of zooxanthellae and animal tissue vs. depth. *Mar. Biol.* 100, 185–193.
- Naim, O., 1993. Seasonal responses of a fringing reef community to eutrophication (Réunion Island, Western Indian Ocean). *Mar. Ecol. Progr. Series* 99, 291–320.
- Nose, M., 1995. Vergleichende Faziesanalyse und Palökologie korallenreicher Verflachungsabfolgen des iberischen Oberjura. *Profil* 8, 1–237.
- Nugues, M.M., Roberts, C.M., 2003. Partial mortality in massive reef corals as an indicator of sediment stress on coral reefs. *Mar. Poll. Bull.* 46, 314–323.
- Olivier, N., Carpentier, C., Martin-Garin, B., Lathuilière, B., Gaillard, C., Ferry, S., Hantzpergue, P., Geister, J., 2004. Coral-microbialite reefs in pure carbonate versus mixed carbonate-siliciclastic depositional environments: the example of the Pagny-sur-Meuse section (Upper Jurassic; northeastern France). *Facies* 50, 229–255.
- Oppenheim, P., 1930. Die Anthozoen der Gosauschichten in den Ostalpen. Oppenheim, Berlin-Lichterfelde (publ. on own expense, 604 pp).
- Pandolfi, J.M., 2002. Coral community dynamics at multiple scales. *Coral Reefs* 22, 12–21.
- Pandolfi, J.M., Bradbury, R.H., Sala, E., Hughes, T.P., Bjorndal, K.A., Cooke, R.G., McArdle, D., McClenachan, L., Newman, M.J.H., Paredes, G., Warner, R.R., Jackson, J.B.C., 2003. Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301, 955–958.
- Pastorak, R.A., Bilyard, G.R., 1985. Effects of sewage pollution on coral-reef communities. *Mar. Ecol. Progr. Series* 21, 175–189.
- Perrin, C., 2002. Tertiary: the emergence of modern reef ecosystems. In: Kiessling, W., Flügel, E., Golonka, J. (Eds.), *Phanerozoic Reef Patterns*. Soc. Econ. Pal. Min. Spec. Publ., vol. 72, pp. 587–621.
- Perry, C.T., 1996. Distribution and abundance of macroborers in an upper Miocene reef system, Mallorca, Spain: implications for reef development and framework destruction. *Palaios* 11, 40–56.
- Perry, C.T., 1998. Macroborers within coral framework at Discovery Bay, north Jamaica: species distribution and abundance, and effects on coral preservation. *Coral Reefs* 17, 277–287.
- Perry, C.T., 1999. Reef framework preservation in four contrasting modern reef environments, Discovery Bay, Jamaica. *Jour. Coastal Res.* 15, 796–812.
- Perry, C.T., 2003. Coral reefs in a high-latitude, siliciclastic barrier island setting: reef framework and sediment production at Inhaca Island, southern Mozambique. *Coral Reefs* 22, 485–497.
- Perry, C.T., Bertling, M., 2000. Spatial and temporal patterns of macroboring within Mesozoic and Cenozoic coral reef systems. In: Insalaco, E., Skelton, P.W., Palmer, T.J. (Eds.), *Carbonate platform systems: components and interactions*. Geol. Soc. London, Spec. Publ., vol. 178, pp. 33–50.
- Perry, C.T., Macdonald, I.A., 2002. Impacts of light penetration on the bathymetry of reef microboring communities: implications for the development of microendolithic trace assemblages. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 186, 101–113.
- Perry, C.T., Lacombe, P., 2003. Introduction: marginal and non-reef building coral environments. *Coral Reefs* 22, 427–432.
- Pfister, T., 1977. Das Problem der Variationsbreite von Korallen am Beispiel der oligozänen *Antiguastrea lucasiana* (DEFRANCE). *Eclogae geol. Helv.* 70, 825–843.
- Pfister, T., 1985. Coral fauna and facies of the Oligocene fringing reef near Cairo Montenotte (Liguria, northern Italy). *Facies* 13, 175–226.
- Philipp, E., Fabricius, K., 2003. Photophysiological stress in scleractinian corals in response to short-term sedimentation. *J. Exp. Mar. Biol. Ecol.* 287, 57–78.
- Polsak, A., 1981. Upper Cretaceous biolithitic complexes in a subduction zone: examples from the Inner Dinarides, Yugoslavia. In: Toomey, D.F. (Ed.), *European Fossil Reef Models*. Soc. Econ. Pal. Min. Spec. Publ., vol. 30, pp. 447–472.
- Pomar, L., 1991. Reef geometries, erosion surfaces and high-frequency sea-level changes, upper Miocene Reef Complex, Mallorca, Spain. *Sedimentology* 38, 243–269.

- Porter, J.W., 1976. Autotrophy, heterotrophy, and resource partitioning in Caribbean reef-building corals. *Amer. Natur.* 110, 731–742.
- Potts, D.C., 1983. Evolutionary disequilibrium among Indo-Pacific corals. *Bull. Mar. Sci.* 33, 619–632.
- Potts, D.C., 1984. Generation times and the Quaternary evolution of reef-building corals. *Paleobiology* 10, 48–58.
- Potts, D.C., Done, T.J., Isdale, P.J., Fisk, D.A., 1985. Dominance of a coral community by the genus *Porites* (Scleractinia). *Mar. Ecol. Progr. Ser.* 23, 79–84.
- Rawlins, B.G., Ferguson, A.J., Chilton, P.J., Arthurton, R.S., Rees, J.G., Baldock, J.W., 1998. Review of agricultural pollution in the Caribbean with particular emphasis on small island developing states. *Mar. Poll. Bull.* 36, 658–668.
- Rehfeld, U., Ernst, G., 1998. Hydrozoan build-ups of *Millepora irregularis* sp. nov. and fungiid coral meadows of *Cunulites Alloitau* (Anthozoa)—palaeoecological and palaeoceanographical implications for the Upper Cretaceous of north Cantabria (northern Spain). *Facies* 39, 125–138.
- Reitner, J., 1986. A comparative study of the diagenesis in diapir-influenced reef atolls and fault block reef platform in the Late Albian of the Vasco-Cantabrian basin (Northern Spain). In: Schröder, J.H., Purser, B.H. (Eds.), *Reef Diagenesis*. Springer, Berlin, pp. 186–209.
- Renema, W., Troelstra, S.R., 2001. Larger foraminifera distribution on a mesotrophic carbonate shelf in SW Sulawesi (Indonesia). *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 175, 125–146.
- Riding, R., 2002. Structure and composition of organic reefs and carbonate mud mounds: concepts and categories. *Earth-Sci. Rev.* 58, 163–231.
- Riegl, B., 1995. Effects of sand deposition on scleractinian and alcyonacean corals. *Mar. Biol.* 121, 517–526.
- Riegl, B., 2001. Inhibition of reef framework by frequent disturbance: examples from the Arabian Gulf, South Africa, and the Cayman Islands. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 175, 79–101.
- Riegl, B., Branch, G.M., 1995. Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonaceans (Lamouroux 1816) corals. *J. Exp. Mar. Biol. Ecol.* 186, 259–275.
- Risk, M.J., Sammarco, P.W., Edinger, E.N., 1995. Bioerosion in *Acropora* across the continental shelf of the Great Barrier Reef. *Coral Reefs* 14, 79–86.
- River, G.F., Edmunds, P.J., 2001. Mechanisms of interaction between macroalgae and scleractinians on a coral reef in Jamaica. *J. Exp. Mar. Biol. Ecol.* 261, 159–172.
- Roberts, H.H., 1987. Modern carbonate-siliciclastic transitions: humid and arid tropical examples. *Sediment. Geol.* 50, 25–65.
- Roberts, L.G., Harriott, V.J., 2003. Can environmental records be extracted from coral skeletons from Moreton Bay, Australia, a subtropical, turbid environment? *Coral Reefs* 22, 517–522.
- Roberts, H.H., Wilson, P.A., Lugo-Fernandez, A., 1992. Biologic and geologic responses to physical processes: examples from modern reef systems of the Caribbean-Atlantic region. *Cont. Shelf Res.* 12, 809–834.
- Rogers, C.S., 1983. Sublethal and lethal effects of sediments applied to common Caribbean reef corals in the field. *Mar. Poll. Bull.* 14, 378–382.
- Rogers, C.S., 1990. Responses of coral reef and reef organisms to sedimentation. *Mar. Ecol. Progr. Series* 62, 185–202.
- Rose, C.S., Risk, M.J., 1985. Increase in *Clino delithrix* infestation of *Montastrea cavernosa* heads on an organically polluted portion of the Grand Cayman fringing reef. *Mar. Ecol.* 6, 345–363.
- Rosen, B.R., 1982. Darwin, coral reefs, and global geology. *BioScience* 32, 519–525.
- Rosen, B.R., 1984. Reef coral biogeography and climate through the Late Cretaceous. In: Brenchley, P. (Ed.), *Fossils and climate*. John Wiley, Chichester, pp. 201–262.
- Rougerie, F., Fagerstrom, J.A., 1994. Cretaceous history of Pacific Basin guyot reefs: a reappraisal based on geothermal endo-upwelling. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 112, 239–260.
- Roy, K.J., Smith, S.V., 1971. Sedimentation and coral reef development in turbid water: Fanning Lagoon. *Pac. Sci.* 25, 234–248.
- Sadler, P.M., 1981. Sediment accumulation rates and the completeness of stratigraphic sections. *J. Geol.* 89, 569–584.
- Sammarco, P.W., 1996. Comments on coral reef regeneration, bioerosion, biogeography, and chemical ecology: future directions. *J. Exp. Mar. Biol. Ecol.* 200, 135–168.
- Sammarco, P.W., Risk, M.J., 1990. Large-scale patterns in internal bioerosion of *Porites*: cross continental shelf trends on the Great Barrier Reef. *Mar. Ecol. Progr. Ser.* 59, 145–156.
- Sanders, D., 1998. Tectonically controlled Late Cretaceous terrestrial to neritic deposition, Gosau Group, Northern Calcareous Alps (Tyrol, Austria). *Facies* 39, 139–178.
- Sanders, D., 2003. Syndepositional dissolution of calcium carbonate in neritic carbonate environments: geological recognition, processes, potential significance. *J. African Earth Sci.* 36, 99–134.
- Sanders, D., Baron-Szabo, R., 1997. Coral-rudist bioconstructions in the Upper Cretaceous Haidach section (Northern Calcareous Alps, Austria). *Facies* 36, 69–90.
- Sanders, D., Baron-Szabo, R.-C., in press. Cretaceous bioconstructions and coral-dominated assemblages in relation to depositional environment, Eastern Alps. In: Hubmann, B., Piller, W. (Eds.), *Fossil Reefs of Austria*. Österr. Akad. Wiss., Erdwiss. Komm., Vienna.
- Sanders, D., Höfling, R., 2000. Carbonate deposition in mixed siliciclastic-carbonate environments on top of an orogenic wedge (Late Cretaceous, Northern Calcareous Alps, Austria). *Sediment. Geol.* 137, 127–146.
- Sanders, D., Pons, J.M., 1999. Rudist formations in mixed siliciclastic-carbonate depositional environments, Upper Cretaceous, Austria: stratigraphy, sedimentology, and models of development. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 148, 249–284.
- Sanders, D., Pons, J.M., 2001. Stratigraphic architecture of a Santonian mixed siliciclastic-carbonate succession (Catalonian Pyrenees, Spain). *Facies* 44, 105–136.

- Sanders, D., Kollmann, H., Wagreich, M., 1997. Sequence development and biotic assemblages on an active continental margin: the Turonian–Campanian of the Northern Calcareous Alps. *Bull. Soc. géol. France* 168, 351–372.
- Santisteban, C., Taberner, C., 1988. Sedimentary models of siliciclastic deposits and coral reefs interrelation. In: Doyle, L.J., Roberts, H.H. (Eds.), *Carbonate-clastic transitions, Developments in Sedimentology*, vol. 42. Elsevier, Amsterdam, pp. 35–76.
- Schlager, W., 1981. The paradox of drowned reefs and carbonate platforms. *Geol. Soc. Amer. Bull.* 92, 197–211.
- Schlichter, D., Brendelberger, H., 1998. Plasticity of the scleractinian body plan: functional morphology and trophic specialization of *Mycedium elephantotus* (Pallas, 1766). *Facies* 39, 227–242.
- Scoffin, T.P., 1992. Taphonomy of coral reefs: a review. *Coral Reefs* 11, 57–77.
- Scoffin, T.P., Brown, B.E., Dunne, R.P., Le Tissier, M.D.A., 1997. The controls on growth form of intertidal massive corals, Phuket, South Thailand. *Palaios* 12, 237–248.
- Senowbari-Daryan, B., Zühlke, R., Bechstäd, T., Flügel, E., 1993. Anisian (Middle Triassic) buildups of the northern Dolomites (Italy): the recovery of reef communities after the Permian/Triassic crisis. *Facies* 28, 181–256.
- Simo, A., 1993. Cretaceous carbonate platforms and stratigraphic sequences, south-central Pyrenees, Spain. In: Simo, J.A.T., Scott, R.W., Masse, J.-P. (Eds.), *Cretaceous carbonate platforms*, Amer. Assoc. Petrol. Geol. Mem., vol. 56, pp. 325–342.
- Smith, S.V., Buddemeier, R.W., 1992. Global change and coral reef ecosystems. *Ann. Rev. Syst.* 23, 89–118.
- Smithers, S., Lacombe, P., 2003. Late Holocene initiation and growth of a nearshore turbid-zone coral reef: Paluma Shoals, central Great Barrier Reef, Australia. *Coral Reefs* 22, 499–505.
- Sorokin, Y.I., 1990. Plankton in the reef ecosystem. In: Dubinsky, Z. (Ed.), *Ecosystems of the World, Coral Reefs*, vol. 25. Elsevier, Amsterdam, pp. 291–327.
- Souter, D.W., Lindén, O., 2000. The health and future of coral reef ecosystems. *Ocean and Coastal Management* 43, 657–688.
- Sprachta, S., Camoin, G., Golubic, S., Le Campion, Th., 2001. Microbialites in a modern lagoonal environment: nature and distribution, Tikehau atoll (French Polynesia). *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 175, 103–124.
- Stafford-Smith, M.G., 1993. Sediment-rejection efficiency of 22 species of Australian scleractinian corals. *Mar. Biol.* 115, 229–243.
- Stanley Jr., G.D., 1981. Early history of scleractinian corals and its geological consequences. *Geology* 9, 507–511.
- Stanley Jr., G.D., 2003. The evolution of modern corals and their early history. *Earth-Sci. Rev.* 60, 195–225.
- Stanley Jr., G.D., Swart, P.K., 1995. Evolution of the coral-zooxanthellae symbiosis during the Triassic. *Paleobiology* 21, 179–199.
- Stanton Jr., R.J., Flügel, E., 1987. Paleocology of Upper Triassic reefs in the Northern Calcareous Alps: reef communities. *Facies* 16, 157–186.
- Stehli, F.G., Wells, J.W., 1971. Diversity and age patterns in hermatypic corals. *Syst. Zool.* 20, 115–126.
- Stössel, I., 1999. Rudists and carbonate platform evolution: the Late Cretaceous Maiella carbonate platform margin, Abruzzi, Italy. *Mem. Sci. Geol.* 51, 333–413.
- Taberner, C., Bosenice, D.W.J., 1985. Ecological succession from corals to coralline algae in Eocene patch reefs, Northern Spain. In: Toomey, D.F., Nitecki, M.H. (Eds.), *Paleoalgology*. Springer, Berlin, pp. 225–235.
- Tanner, J.E., 1995. Competition between scleractinian corals and macroalgae: an experimental investigation of coral growth, survival and reproduction. *J. Exp. Mar. Biol. Ecol.* 190, 151–168.
- Tanner, J.E., 1997. Interspecific competition reduces fitness in scleractinian corals. *J. Exp. Mar. Biol. Ecol.* 214, 19–34.
- Tanner, J.E., Hughes, T.P., Connell, J.H., 1994. Species coexistence, keystone species and succession in coral assemblages: a sensitivity analysis. *Ecology* 75, 2204–2219.
- Tanner, J.E., Hughes, T.P., Connell, J.H., 1996. The role of history in community analysis: a modelling approach. *Ecology* 77, 108–117.
- Thacker, R.W., Ginsburg, D.W., Paul, V.J., 2001. Effects of herbivore exclusion and nutrient enrichment on coral reefs macroalgae and cyanobacteria. *Coral Reefs* 19, 318–329.
- Titlyanov, E.A., Titlyanova, T.V., Leletkin, V.A., Tsukahara, R., van Woessik, R., Yamazato, K., 1996. Degradation and regulation of zooxanthellae density in hermatypic corals. *Mar. Ecol. Progr. Series* 139, 167–178.
- Tomascik, T., Sander, F., 1985. Effect of eutrophication on reef-building corals. I. Growth rate of the reef-building coral *Montastrea annularis*. *Mar. Biol.* 87, 143–155.
- Tomascik, T., Sander, F., 1987a. Effect of eutrophication on reef-building corals. II. Structure of scleractinian coral communities on fringing reefs, Barbados, West Indies. *Mar. Biol.* 94, 53–75.
- Tomascik, T., Sander, F., 1987b. Effect of eutrophication on reef-building corals. III. Reproduction of the reef-building coral *Porites porites*. *Mar. Biol.* 94, 77–94.
- Tudhope, A.W., Scoffin, T.P., 1994. Growth and structure of fringing reefs in a muddy environment, South Thailand. *J. Sediment. Res. A* 64, 752–764.
- Turnsek, D., 1997. Mesozoic corals of Slovenia. *Znanstvenoraziskovalni center SAZU, Založba ZRC, Ljubljana* (512 pp).
- Weber, J.N., 1974. Basis for skeletal plasticity among reef-building corals. *Geology* 2, 153–154.
- Wesseling, I., Uychiaoco, A.J., Alino, P., Aurin, T., Vermaat, J.E., 1999. Damage and recovery of four Philippine corals from short-term sediment burial. *Mar. Ecol. Progr. Ser.* 176, 11–15.
- Wilson, M.E.J., 2002. Cenozoic carbonates in Southeast Asia: implications for equatorial carbonate development. *Sediment. Geol.* 147, 295–428.
- Wilson, M.E.J., Rosen, B.R., 1998. Implications of paucity of corals in the Paleogene of SE Asia: plate tectonics or centre of origin? In: Hall, R., Holloway, J.D. (Eds.), *Biogeography and geological evolution of SE Asia*. Backhuys Publishers, Leiden, pp. 165–195.
- Wilson, M.E.J., Lokier, S.W., 2002. Siliciclastic and volcanoclastic influences on equatorial carbonates: insights from the Neogene of Indonesia. *Sedimentology* 49, 583–601.

- Wittenberg, M., Hunte, W., 1992. Effects of eutrophication and sedimentation on juvenile corals. I. Abundance, mortality and community structure. *Mar. Biol.* 112, 131–138.
- Wood, R., 1993. Nutrients, predation and the history of reef building. *Palaios* 8, 526–543.
- Wood, R., 1995. The changing biology of reef building. *Palaios* 10, 517–529.
- Woodley, J.D., 1992. The incidence of hurricanes on the north coast of Jamaica since 1870: are the classic reef descriptions atypical? *Hydrobiologia* 247, 133–138.
- Woolfe, K.J., Larcombe, P., 1998. Terrigenous sediment accumulation as a regional control on the distribution of reef carbonates. In: Camoin, G.F., Davies, P.J. (Eds.), *Reefs and carbonate platforms in the Pacific and Indian Oceans*. Spec. Publ. Int. Assoc. Sediment, vol. 25, pp. 295–310.
- Woolfe, K.J., Larcombe, P., 1999. Terrigenous sedimentation and coral reef growth: a conceptual framework. *Mar. Geol.* 155, 331–345.
- Yamashiro, H., Nishihira, M., 1998. Experimental study of growth and asexual reproduction in *Diastrea distorta* (Michelin, 1843), a free-living fungiid coral. *J. Exp. Mar. Biol. Ecol.* 225, 253–267.
- Yentsch, C.S., Yentsch, C.M., Cullen, J.J., Lapointe, B., Phinney, D.A., Yentsch, S.W., 2002. Sunlight and water transparency: cornerstones in coral research. *J. Exp. Mar. Biol. Ecol.* 268, 171–183.
- Yonge, C.M., 1930. *A year on the Great Barrier Reef*. Putnam, London (246 pp).
- Zankl, H., Schroeder, J.H., 1972. Interaction of genetic processes in Holocene reefs off North Eleuthera Island, Bahamas. *Geol. Rundsch.* 61, 520–541.