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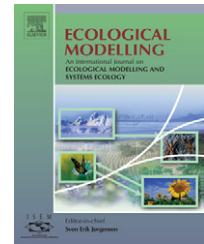
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Model of coral population response to accelerated bleaching and mass mortality in a changing climate

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ABSTRACT

We model coral community response to bleaching and mass mortality events which are predicted to increase in frequency with climate change. The model was parameterized for the Arabian/Persian Gulf, but is generally applicable. We assume three species groups (*Acropora*, faviids, and *Porites*) in two life-stages each where the juveniles are in competition but the adults can enter a size-refuge in which they cannot be competitively displaced. An aggressive group (*Acropora* species) dominates at equilibrium, which is not reached due to mass mortality events that primarily disadvantage this group (compensatory mortality, >90% versus 25% in faviids and *Porites*) roughly every 15 years. Population parameters (N individuals, carrying capacity) were calculated from satellite imagery and in situ transects, vital rates (fecundity, mortality, and survival) were derived from the model, field observations, and literature. It is shown that populations and unaltered community structure can persist despite repeated 90% mortality, given sufficiently high fecundity of the remaining population or import from connected populations. The frequency of disturbance determines the dominant group—in low frequency *Acropora*, in high frequency *Porites*. This is congruent with field observations. The model of an isolated population was more sensitive to parameter changes than that of connected populations. Highest sensitivity was to mortality rate and recruitment rate. Community composition was sensitive to spacing of disturbances and level of catastrophic mortality. Decreased mortality led to *Acropora* dominance, increased mortality led to *Acropora* extinction. In nature, closely spaced disturbances have severely disadvantaged *Acropora* populations over the last decade. Unless a longer (>10 years) disturbance-free interval can be maintained, a permanent shift away from *Acropora* dominance will be observed. A mortality rate of 99% in *Acropora*, as observed in 1996, is not sustainable if repetitive and neither is a disturbance frequency <15 years—each leading to population collapse. This shows that the severity and/or the spacing of the 1996–1998–2002 disturbances were unusual in frequency and duration.

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1. Introduction

That temperature anomalies cause coral bleaching and death has been demonstrated in countless studies, as has the fact that not all coral species are equally affected (Coles and

Brown, 2003). Among the corals, variable resistance to bleaching (Loya et al., 2001) may either be genetically determined at species-level or by distribution and environmental variability within any given reef (McClanahan et al., 2007). Among the more susceptible species, the genus *Acropora*, a dominant reef

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framework-builder in the Indo-Pacific and until fairly recently also in the Atlantic, is a conspicuous member.

A disadvantage or, worse, loss of *Acropora* as dominant species has important biological and geological implications stretching from changes in community structure to the near-cessation or switch-off of reefbuilding. It is unclear whether reef corals will be able to adapt to bleaching (Baker et al., 2004) or whether constantly upward-inching temperature excursions will cause extinction of species (Sheppard, 2003; McClanahan et al., 2007).

In the Arabian/Persian Gulf, *Acropora* is of overwhelming importance in the relatively species-poor assemblage that makes up the region's bioherms, biostromes and non-framebuilding communities. Up to six *Acropora* species occur, but species richness varies with recurring mortality events caused by strong cold- or hot-spells that primarily disadvantage *Acropora* species (Riegl, 1999, 2002, 2003; Purkis and Riegl, 2005). Since this genus is a dominant space-competitor, any mortality is truly compensatory (*sensu* Connell, 1978) with important implications for population and community dynamics (Connell, 1975). Riegl (1999, 2001) and Purkis and Riegl (2005) maintained that this repetitive mortality was necessary to explain assemblage structure and spatial patterns in nearshore biostromal and non-framebuilding communities. Little, however, is known about the vital rates (fecundity, mortality rates) and other population parameters that would make survival possible in such a dramatic disturbance regime.

With this background and scenarios of impending global warming (Sheppard, 2003), we were interested in modeling the dynamics of Arabian/Persian Gulf coral assemblages in a way that would allow us to better understand competition, population dynamics and how assemblage structure is maintained or altered. The same model would then allow us to forecast changes in various disturbance scenarios. But models of population dynamics and competition require estimates of population sizes, interaction parameters and fertilities for parameterization. Much of this information is not easy to come by, especially when working far from home base and in management environments that do not allow unhindered research. In our case, this led to a significant shortfall of baseline data, which we attempted to mitigate by using remote-sensing data, in particular the information on areas classified as corals (Purkis and Riegl, 2005), to upscale population size-estimates made in smaller areas.

Due to its extreme temperature environment, the Arabian/Persian Gulf has been presented as an ideal laboratory to evaluate coral reef persistence in global change conditions (Riegl, 2003). In the Arabian/Persian Gulf, reef corals already persist at temperatures forecast to affect many more temperate areas (Sheppard, 2003). Therefore, here developed model has relevance beyond the regional scope since the predicted rates and patterns of regeneration or collapse will be similar in other systems.

In this study we (1) build an ODE (ordinary differential equation)-based mathematical model of population and species-interactions to capture competitive dynamics, (2) use remote sensing to estimate some key population parameters of a model (N of corals at specific time-step, carrying capac-

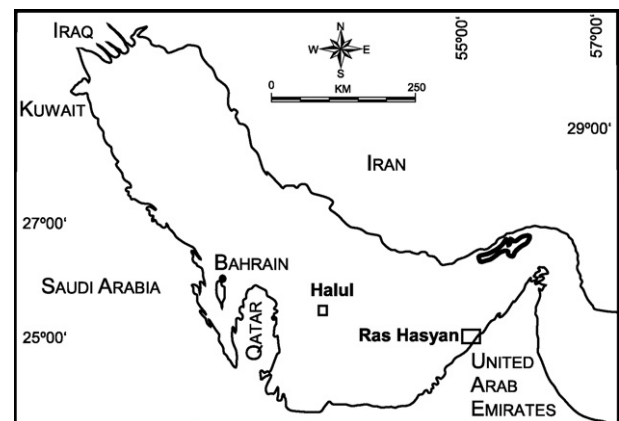


Fig. 1 – The Arabian/Persian Gulf and the two chosen study areas in U.A.E. (Ras Hasyan) and Qatar (Halul).

ity), (3) find the necessary vital rates using field observations, remote sensing and literature and examine their plausible ranges by sensitivity analysis, (4) verify whether such a community can theoretically persist in the postulated disturbance environment, (5) examine assemblage dynamics under different disturbance regimes and (6) forecast likely shifts or persistence of community patterns in a warming climate with increasingly frequent temperature-mediated bleaching events.

2. Study area

Our study area was defined by the gently sloping bathymetry of the Arabian homocline along the mainland coastline and highs produced primarily by salt diapirism that form banks and offshore islands (Purser and Seibold, 1973). With regards to the recent coral ecosystem, wind and waves are among the dominant determinants of temperature and turbidity. Land/sea breezes and the seasonal northerly Shamal winds influence local wave-induced currents and thus sediment transport, water clarity and habitat suitability for corals (Kirkham, 1998; Sheppard et al., 1992). The north-west trending coastline of the U.A.E. and the northern edges of the offshore islands are most strongly influenced by the Shamal due to absence of shelter by offshore barriers. Traditionally, these have been the areas with best coral framework development (Purser, 1973; Schlager, 2005).

Two systems were studied in greater detail (Fig. 1). Several square-kilometers between Jebel Ali and Ras Hasyan (United Arab Emirates) were investigated with 4-m resolution Ikonos satellite imagery and Halul Island (Qatar) was studied with 28-m resolution Landsat TM. Details of imagery and image processing are given in Purkis et al. (2005), Purkis (2005). The studied system near Ras Hasyan (U.A.E., Fig. 1) extended shore-parallel for ~7 km and ~1.5 km offshore, and attained a typical depth of 8 m. Previous studies (Riegl, 1999, 2002; Purkis and Riegl, 2005; Purkis et al., 2005) identified a complicated habitat mosaic of coral carpets (=biostromes), unconsolidated sand, macroalgae and seagrass, frequently underlain by hard-grounds (Shinn, 1969). Five coral assemblages of variable live cover occur:

- Large, well-spaced *Porites lutea* and other *Porites* mixed with other massive species; widely distributed on hardgrounds.
- Dense patches of tabular *Acropora clathrata* and *A. downingi* with 40–90% live substrate-cover within patches.
- Clusters of faviids (mostly *Platygyra daedalea*, *Cyphastrea serailia*, and *Favia* spp.) either widely spaced or densely packed.
- Widely spaced *Siderastrea savignyana* colonies on sandy hardground.
- Patches of densely packed (80% coral cover) columnar *Porites harrisoni* intermingled with faviids (*Favia* spp., and *Platygyra* spp.).

A comparable coral system exists around the offshore island Halul. The island is roughly circular with a discontinuous fringe of reefal coral associations (Purser, 1973; Schlager, 2005) and a relatively abruptly sloping shelf to about 20 m depth.

3. Materials and methods

3.1. Ecological background data

Baseline data regarding the biology of the system consist of series of 10 m and 50 m line transects as well as photo-transects taken between 1995 and 2007 between Jebel Ali and Ras Ghantoot, but also at Halul (2004, 2005, and 2006). Overall, 60 photo-transects, 155 line transects exist for the Jebel Ali/Ras Hasyan area, 10 photo- and 20 line transects for Halul and 2700 geo-referenced point observations for the Abu Dhabi and Qatar offshore islands. Some of these data and detailed methodologies are published elsewhere (Riegl, 1999, 2001, 2002; Purkis and Riegl, 2005; Purkis et al., 2005) and are used here as background information for the calibration of models.

Transects were geo-referenced at the beginning point and placement was originally stratified random in a geographical grid before detailed habitat maps were available (prior to 2002). Later, additional photo-transects were haphazardly placed within known sparse and dense coral areas for targeted sampling. Photo-transects consisted of overlapping photographs along a 10-m-long measuring tape. After merging images and digitizing coral outlines, images were re-gridded to unit pixel-size to allow area calculations. Point observations are short (10 s), geo-referenced video-clips that allow qualitative and some quantitative observations of coral populations.

Although the coral area at Ras Hasyan, monitored since 1995, was recently mostly destroyed by the development of artificial islands and causeways, community successional dynamics was still apparent, revisited and sampled and also described by Burt et al. (2008). Halul appears to be a key stepping-stone for the regeneration of SE Arabian/Persian Gulf coral populations, since it was one of the few sites with significant *Acropora* recovery. During extensive surveys between Qatar and Dubai, noteworthy *Acropora* populations were found in Qatar only at Umm al Arshan and Halul, in Abu Dhabi between Taweelah and Ras Ghanada and at Al Hila, in Dubai at Ras Ghantoot and some survivors near Ras Hasyan, and in Sharjah at Sir Abu Nuair. These sites are also home to

important communities of massive corals and connectivity can be assumed (own unpubl. data), which is important for the model.

3.2. The model

We base our assumptions of ecosystem functioning on dynamics observed prior to, during and in the aftermath of coral mass mortality caused by temperature anomalies in 1996, 1998 and 2002. In 1995, when some parts of the investigated system had presumably reached climax (Riegl, 1999), the following pattern was observed:

Well-defined patches of almost 100% and >100% (tables overtopping) of *Acropora* cover were observed. Underneath the tables was an understory of smaller massive colonies, a mixed assemblage of faviids, siderastreids and poritids. Sectioning massive corals and tagging of *Acropora* had yielded approximate growth rates of around 1–2 cm per year for massive corals and 5–10 cm per year for *Acropora*. Thus, the coral assemblage was partitioned into a dominant guild made up by tabular *Acropora* species (primarily *A. downingi* and *A. clathrata*) and a subordinate guild made up by the massive coral genera (primarily *Favia*, *Favites*, *Porites*, and *Pseudosiderastrea*). *Acropora* have more effective nematocysts than faviids and *Porites* allowing them to win in competitive interactions (Thomason and Brown, 1986; Baird and Hughes, 2000). Large massive colonies persisted despite being surrounded by a mostly closed canopy of *Acropora* if the massive colonies had grown to a size which made it impossible for the *Acropora* to overtop or kill them entirely when in physical contact. This usually meant a size of at least 30–50 cm diameter in hemispherical colonies. In the studied systems and in fact most Arabian/Persian Gulf coral assemblages, topography plays no role since virtually all colonies grow on the same substratum at the same height. This is due to the strong bioerosion that removes colonies after mass mortality events (for detailed discussion of this phenomenon see Riegl, 2001).

From these observations, the following dynamics was inferred.

- the assemblage can be divided into two major guilds: competitively dominant branching corals and competitively inferior massive corals, within which faviids aggressively dominate poritids.
- within the guilds, dynamics were assumed to be essentially neutral with no species capable of gaining a strong advantage over the others. Thus the dynamics of the entire community can be subsumed into few equations governing guild-behaviour.
- since large massive colonies persisted even in otherwise closed *Acropora* canopies, it was assumed that the competitively inferior massive colonies could grow into a size-refuge where displacement by others became impossible (Sebens, 1982). The mechanism of persistence would be taller size than neighboring *Acropora*, thus eluding being overtopped, and having enough tissue area that losses due to direct competition could not endanger the inferior competitor's survival.
- while *Acropora* were considered competitively always superior outside the size-refuge, they suffer repeated catas-

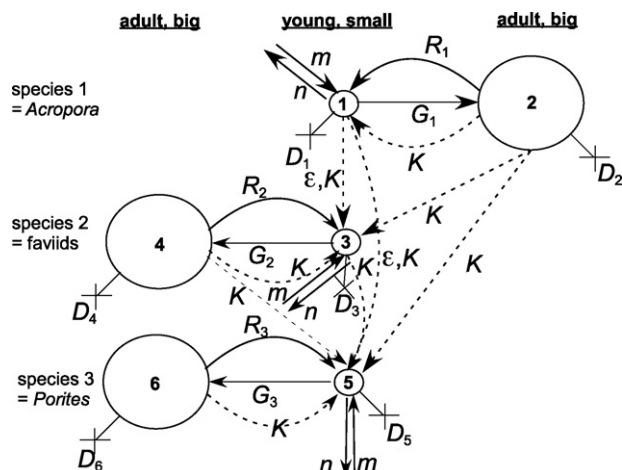


Fig. 2 – Structure of the model. m = migration term, D_i = mortality term, R_i = within-population recruitment term (ignoring immigration), G_i = growth term, ε = aggression term, which is $N_j(N_i R_i)/K$ if species j is aggressed upon by species i . K = carrying capacity term indicating that presence of stage i in species i has a negative influence on another stage/species at which the arrow is pointed. Arrows show the direction of an interaction. Solid arrows are growth-based interaction and point at the recipient of numerical increase, i.e., one stage grows or recruits into another. Dotted arrows are competitive interactions, the arrow points at the loser.

trophic mortality at roughly decadal scales (Riegl, 1999) as a true compensatory mortality (*sensu* Connell, 1978) that would only displace the dominant competitor, giving members of the inferior guild an opportunity to reach their size-refuge (Connell, 1975).

- all corals started as small, reproductively inactive colonies that grew, following a fixed ratio, into large colonies (Babcock, 1991; Hall and Hughes, 1996) (Figs. 2 and 3).

The above described mechanism is a case of Lotka-Volterra-type competition between the dominant and subordinate species. A similar system was developed by Sebens (1982) who modelled a competitively inferior species suffering mortality from a dominant species only at the smallest colony stage but that could also attain a size-refuge in which it was immune from competition. We extended this model to a three-species, two life-stages situation with more involved interactions. Only large specimens were considered fertile. Recruitment was allowed into any free cell, each cell could be settled only by one specimen, leading to a finite carrying capacity (K).

Small *Acropora* were modelled as follows:

$$\frac{dN_1}{dt} = \frac{R_1 N_2}{K} (K - N_1 - N_2 - N_4 - N_6) - N_1 (G_1 + D_1 + n) + m A \quad (1)$$

where dN_1/dt is the rate of change in abundance of the small stage of the dominant species as a function of fertility of the large specimens in the same species ($R_1 N_2$) with recruits only

allowed to settle into free space (thus subtraction of all large colony abundances from carrying capacity). Also, fragments of big *Acropora* can enter this group but fragment production rate is included in R_1 . Losses occur by growth into the large size-class (G_1) and mortality (D_1). Post-settlement mortality and death of early larval stages, which can be high (Mumby and Dytham, 2006), is included in R_1 . D_i ($i = 1, 3$, and 5) occurs in Eqs. (1), (3), and (5) and refers to diseases or predation on young colonies and can be ignored and included into G_i , in particular when the model focusses on big coral dynamics. We tested both approaches. An outside, connected, population (A) can add larvae to the focal population via a migration term m . Arabian/Persian Gulf *Acropora* are prone to local extinction during mass mortality, which requires another connected population for maintenance and regeneration of any local population. An emigration term (n) allows larvae to move from focal to connected population.

Acropora rapidly grow into big, aggressive colonies. Their rate of change dN_2/dt depends primarily on availability of small colonies and their success to reach the size-refuge ($G_1 N_1$), mortality rate (D_2), and the ability to out-compete other species, which is implicit in other species' carrying capacity being influenced by N_2 (see formulae (3) and (5)).

$$\frac{dN_2}{dt} = G_1 N_1 - D_2 N_2 \quad (2)$$

Faviids are massive corals with slower growth than *Acropora*, are competitively subordinate, but dominate *Porites*. Rate of change of small colonies depends on adult fertility ($R_2 N_4$), recruitment density is self-limited as well as by large colonies of the subordinate guild. Losses occur due to growth ($N_3 G_2$), other factors like diseases or predation (D_3) of direct competition (i.e., overgrowth in same cell) by *Acropora* recruits (Baird and Hughes, 2000). The likelihood follows Sebens (1982): space covered by any species is N_j , rate of contact per unit space with propagules of other species i is $N_j R_i N_i / K$ (i and j denoting different species); hence, if faviids are aggressed upon by *Acropora*, but not *Porites*, this is $N_3 R_1 N_2 / K$. Faviid recruits are also hindered by already settled *Acropora* of the small size-class (hence subtraction of N_1 from K). Again, immigration (m) and emigration (n) terms are added/subtracted.

$$\begin{aligned} \frac{dN_3}{dt} = & \frac{R_2 N_4}{K} (K - N_3 - N_1 - N_2 - N_4 - N_6) \\ & - N_3 (G_2 + D_3 + n + \frac{R_1 N_2}{K}) + m B \end{aligned} \quad (3)$$

Large faviid colonies have equivalent dynamics to large *Acropora*. They have reached a size-refuge and can no longer be killed by other species. They can lose tissue in competition, but would not die. Such tissue loss is shrinkage, but it is never sufficient to shrink back into N_3 and size-variability within the big size-class is ignored. Hence no term for subtraction is necessary. A mortality term (D_4) allows for inclusion of diseases and other non-catastrophic mortality.

$$\frac{dN_4}{dt} = G_2 N_3 - D_4 N_4 \quad (4)$$

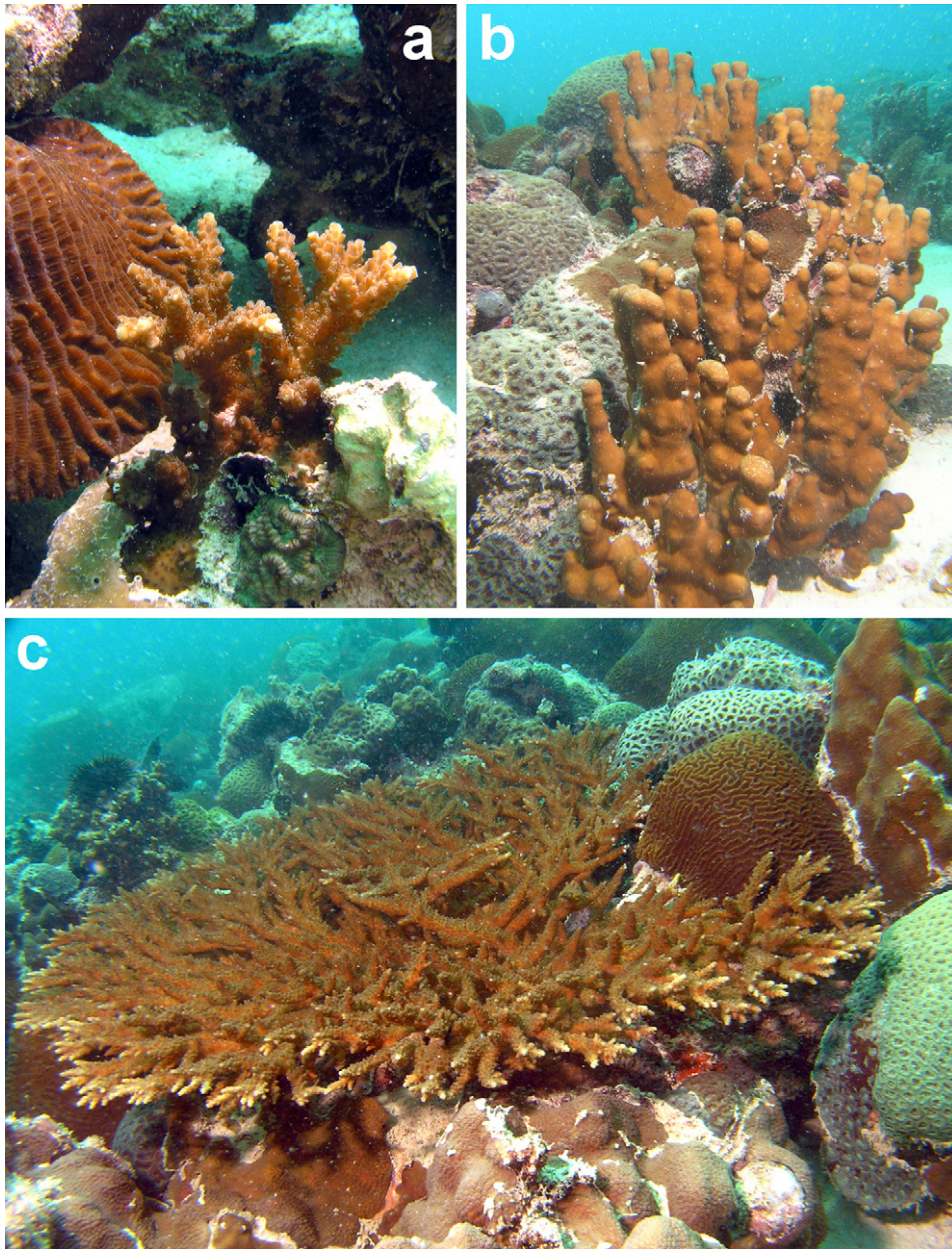


Fig. 3 – Dynamics as in Fig. 2 validated by photographs of actual interaction. (a) *Acropora downingi* and *Favia pallida* recruits settled on a *Porites lutea*; live *Porites* tissue is seen to the left of the *Acropora* recruit (b) large faviids competitively encroach on large *Porites harrisoni*, which is too big to be killed entirely (c) *Acropora downingi* overgrowing faviids, but most are too big to be killed (images by G. Foster).

Finally, small poritids are limited due to space pre-emption by all big and small colonies and loose in encounters with recruits of other species. A portion (N_5G_3) grows up into adults and reaches a size-refuge, in which neither *Acropora*, nor faviids can kill them. Some (m) immigrate from outside populations, some emigrate (n):

$$\frac{dN_5}{dt} = \frac{R_3N_6}{K} \left(K - \sum_{i=1}^6 N_i \right) - N_5 \left(G_3 + D_5 + n + \frac{R_1N_2}{K} \right) + mC \quad (5)$$

$$\frac{dN_6}{dt} = G_3N_5 - D_6N_6 \quad (6)$$

In these six equations, the constants R_i (intrinsic rate of increase), K_i (carrying capacity), D_i (death rate), G_i (growth rate into adults) and m, n (migration rates) are equivalent in meaning and subscripts denote unique treatment for each species.

Numerical approximations of the six ODEs were performed using the Matlab ODE solver implementing second-order Runge–Kutta methods (Gilat and Subramanian, 2008). Catas-

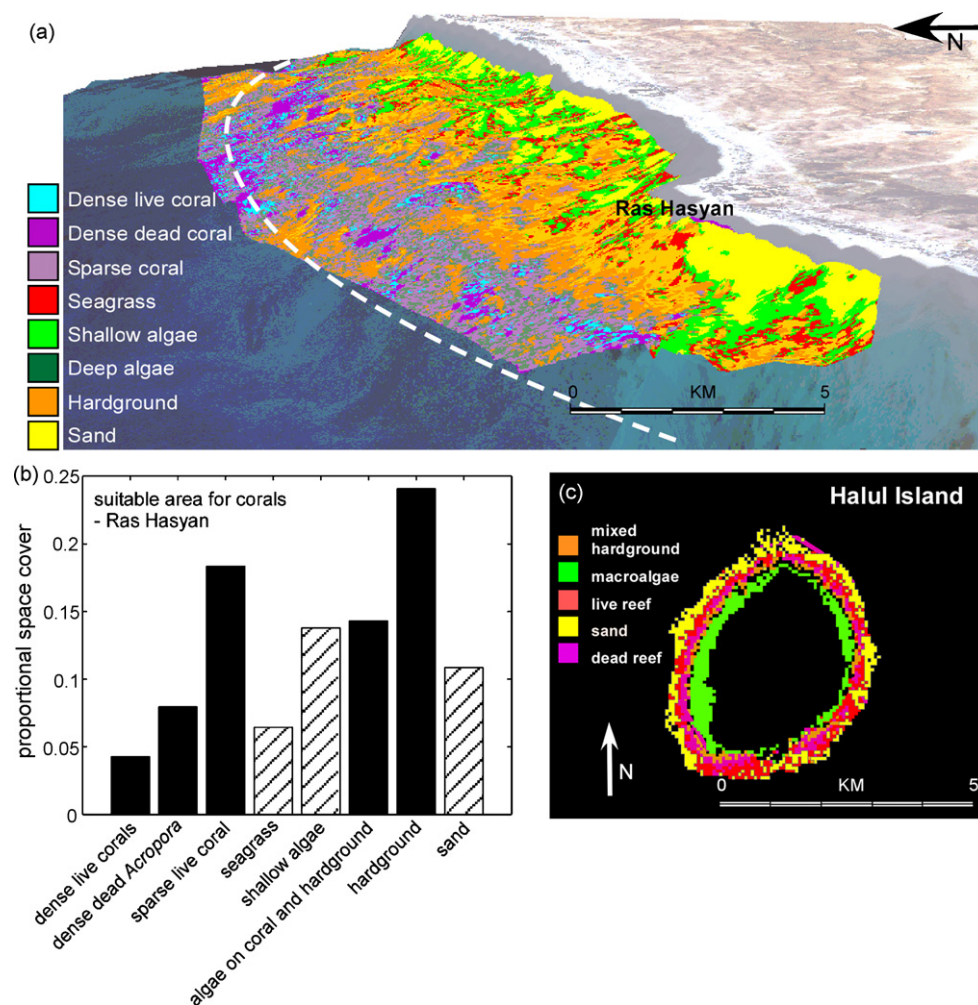


Fig. 4 – Space cover of environments in (a) Ras Hasyan area (c) and Halul using classification of satellite imagery. (b) Black bars show habitats used to estimate model parameters for Ras Hasyan. The equivalent was done in Halul (not shown). Striped bars are unsuitable for corals. Vertical exaggeration at Ras Hasyan in (a) 500-fold to show topography. The area has changed dramatically subsequent to this analysis due to major coastal construction (Burt et al., 2008).

trophic mortality was introduced as a multiplier of N_i after a certain number of solution steps.

3.3. Parameter estimation

To estimate population parameters, we combined remote sensing with in situ ground-truthing. From photo-transects we estimated how many corals occurred per unit area sparse or dense coral to calculate approximate numbers of corals per pixel. The dense coral area, dominated by *Acropora*, was delineated by GPS to allow differentiating *Acropora* pixels from those containing other genera. Ground-truthing consisted of differentially corrected GPS fixed localities of 5 m radius that were evaluated for type of bottom cover, percent cover of dominant bottom type, coral identity and cover (Purkis and Riegl, 2005; Purkis, 2005). Ceramic settlement tiles (five racks of 20 tiles each) were deployed during 2005/2006/2007 spawning seasons but low replication has not yet allowed useful estimates of recruitment. Thus, fertility parameters had to be estimated

from the model and from size/frequency distribution data obtained from photo-transects (see Section 3.3.2).

3.3.1. Population size

Population sizes were obtained by assigning coral density per unit area estimates obtained from digitized photo-transects and ground-control-points to color-coded habitat classes on classified satellite imagery (Fig. 4). This resulted in an estimated number of corals contained in pixels coded as dense and sparse coral. Carrying capacity of the system (K) was estimated as sum of all coral pixels plus all pixels including substratum onto which corals could recruit and form new coral patches (hardgrounds, dense dead coral, dead reef, etc.).

The basis of all optical classifications and maps were satellite images (IKONOS and Landsat ETM7 11-bit multispectral satellite image, 4 m and 28 m pixel-size, respectively). Details about image processing, ground-truthing and the approach taken to obtain maps are given in Purkis (2005) and Purkis

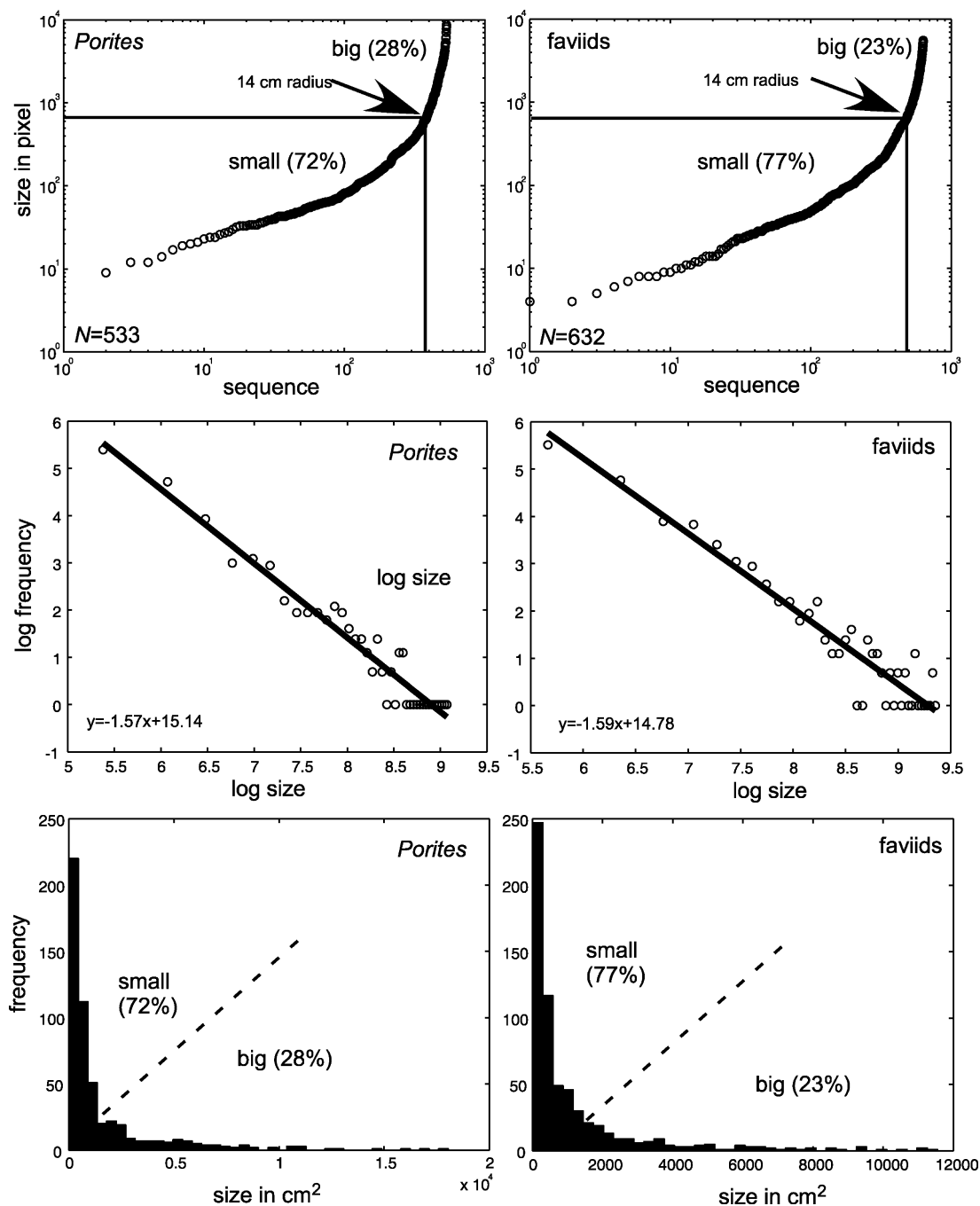


Fig. 5 – Sizes of coral colonies as determined from photo-transects. One square meter is covered by 4800 pixels (1 pixel = 2.08 cm²). Faviids and *Porites* showed similar distributions. Regressions (solid lines, middle panel) are highly significant ($p < 0.01$).

et al. (2005). Bathymetry for depth correction of spectral reflectance values was obtained from acoustic surveys and tidally corrected against data from in situ loggers. Image classification was conducted by unsupervised k-means clustering and a multivariate normal probability driven classifier (Purkis and Pasterkamp, 2004) after masking of pixels outside the depth-resolution of the images and without coral. Imagery was classified into pixels containing: corals (either dense or sparse as determined by ground-truthing), dead corals (mostly dead and overgrown *Acropora* killed in 1996) mixed

hardground (bare, sparsely coral-, and sparsely algal-covered hardgrounds). Other categories, even if present, (Fig. 4) were not used for the model. Classification accuracy was validated by extensive ground-truthing (Ikonos map overall accuracy 81%, Landsat map 72%). Accuracy differences were largely due to different spatial resolution (pixel size) and the size of the studied areas (Purkis et al., 2005; Purkis and Riegl, 2005). Confusion existed primarily between algae and seagrass, bare versus sparsely covered hardgrounds and between coral and algae since dead coral (killed in 1996/1998; Riegl, 1999, 2002; Purkis

and Riegl, 2005) had dense algal overgrowth. These inaccuracies had little influence on coral population estimations.

At Ras Hasyan, *Acropora* colonies prior to mass mortality had mean sizes between 0.5 m and 0.8 m radius, which allows 2 large colonies to occupy a single 4 m × 4 m Ikonos pixel. A total of 293,316 pixels were classified as dense dead coral suggesting a total population of big *Acropora* tables of 586,632 prior to mass mortality. Among dense *Acropora*, few other corals were found and no massives were assigned to these pixels. The 157,567 pixels assigned to dense live coral consisted primarily of large massive corals, with attending small colonies and recruits. Average colonies covered 0.02–0.03 m² (see Section 3.3.2) and we assigned 10 massive colonies to each pixel, which was plausible in comparison with photo-transects. Another 677,763 pixels were assigned as sparse corals and we assigned 5 corals per pixel. This suggested a total population of 4,964,485 massive corals. We partitioned this number between faviids and *Porites* according to the distribution observed in photo-transects (54% *Porites* and 46% faviids) and within each group, partitioned between “small” and “big” according to Fig. 5. For *Acropora* we assigned 52/48% small/big (see Section 3.3.2). The total theoretical carrying capacity was considered to consist of all suitable substratum for coral growth in the entire area—a sum of dense dead, dense live and sparse coral covered areas plus the area of bare hardground, which summed to 888,056 pixels. Thus the entire area available for coral growth was 2,016,703 pixels. If we assume that these pixels will be mostly covered by the most aggressive corals (*Acropora*) in the climax community, but that under each *Acropora* table at least one subordinate coral will persist, then we obtain a carrying capacity of 1 coral m⁻² or a total of 8,066,812 colonies, given the 4-m pixel-size of the image.

At Halul, 350 Landsat pixels were classified as “live reef”, 275 as “dead reef”, and 139 as “mixed hardground” (Fig. 4). Of the entire area classified as “live reef”, *Acropora* was only encountered in the SE-quadrant, about 12.5% of the area, or 39,375 m². *Acropora* colonies occurred on average with 5 m spacing or clumps of up to 4 colonies with inter-cluster distance of 20 m. Thus we estimated one *Acropora* colony every fifth meter square (i.e., 1 per 25 m²) leading to a total population estimate of 1575 colonies. The remaining 87.5% of the classified “live reef” area were covered by massive corals at higher density with smaller colonies than *Acropora*. We assumed one colony per square-meter, leading to an estimated population size of 275,625 massive colonies, partitioned into 54% *Porites* (107,163 small and 41,674 big) and 46% faviids (97,625 small and 29,161 big) using the approximation obtained at Ras Hasyan. Total carrying capacity was calculated as the area classified as “live reef” presently bearing live coral, plus the area classified as “dead reef”, which had been bearing live coral until only a few years ago, plus the area classified as “mixed hardground”, because it could have been bearing corals before, certainly was suitable habitat for corals, and could conceivably be colonized. Therefore, total carrying capacity assuming a limit of 1 coral per square meter was 687,600 corals. During the surveys, no *Acropora* was found that exceeded one square meter in size. If they obtained larger sizes, they would overtop other corals and by this mechanism the density of 1 coral per square meter would be maintained, supporting above simplified density assumption.

3.3.2. Coral demographic parameters

Little information is available about the vital rates (fecundity, settlement of spat, survivability, and general mortality) that are needed to evaluate our hypothesis of repetitive mortality or to parameterize a model. We were therefore forced to estimate the relevant parameters from the data and literature available. We used photo-transects to determine the size-frequency distribution of corals. Photo-transects were digitized into color-coded bitmaps and the areas of all corals in the chosen species groups (faviidae: *Favia* spp, *Platygyra daedalea*, *Cyphastrea* spp., *Pseudosiderastrea tayamai*; *Porites*: *Porites lutea*, *P. solida*, *P. harrisoni*) were evaluated for size. A total of 1165 colonies were counted. In a log-log plot of size versus frequency (Fig. 5), both faviids and *Porites* showed an inflection point at 160 pixels (333 cm²), which equates to radii of about 14 cm, at which sizes increased more rapidly. This change was more pronounced in *Porites* than in faviids and was considered the cut-off point between the functional groups “small” and “big” due to the apparent change in dynamics. In faviids/*Porites*, 77/72% of the population were small, 23/28% were big. This size-distribution compares to Bak and Meesters (1999) and Meesters et al. (2001) for several Caribbean species of massive coral. Average faviid size was 272 cm² (~9 cm radius), average *Porites* size was 372 cm², (~11 cm radius). In *Acropora*, it was more difficult to estimate the frequency of big versus small colonies. In the regenerating phase after mortality events, we observed only recruits, and in the dominating phase in between disturbances, the large adult colonies frequently precluded settlement within the dense coral areas. We therefore assumed that 48% of all colonies were big, 52% small, which corresponded to values obtained from random photo-transects and is a useful mean in comparison with other studies (Smith et al., 2005). However, this analysis is less precise than that for *Porites* and faviids.

For the estimation of graduation rates into the next size-class, we used the approach of Fong and Glynn (1998) and divided growth rate by the width (i.e., colony diameter) of the size-class. *Acropora* linear extension rates are around 5–10 cm per year (Coles and Fadlallah, 1991), versus 1 cm per year for poritids and 1.5 cm for faviids (own unpublished data based on growth-band measurements). We considered *Acropora* to enter the “big” size-class at 20 cm radius ($G_1 = 0.25$) with a conservative growth assumption of 5 cm per year, faviids ($G_2 = 0.11$) and *Porites* at 14 cm radius ($G_3 = 0.07$). Immigration and emigration rates were varied between uniform and random, depending on model run. If random, n and m were assigned random numbers from a Gaussian distribution with mean 0 and variance 1.

3.3.3. Vital rates

3.3.3.1. Model formulation describing recruitment rate. Field observations support our model assumption of continued recruitment immediately after disturbance events. In 1999, 58 *Acropora* recruits of 7.6 ± 3.5 cm diameter (suggesting that they were at least 1-year old and had settled in 1997 or 1998) and some bigger (of several years age, i.e., >10 cm diameter) colonies were found in a small area that would not have held more than 5800 adult colonies. From this a 1% survivorship assumption can be derived for the 1996 event. Also Fadlallah (1996) showed that *Acropora*, even if stressed, have at least a limited ability to finish the gametogenic cycle and produce

propagules. *Acropora* usually spawn in early summer, thus both heat- and cold-anomalies occur after spawning which potentially allows some spat to survive (Loya et al., 2001). For the model, we assume that recruit settlement was equally spread over dense and sparse coral areas as well as hard-ground. This coincides with observations of recruitment onto all available suitable substrata (unpublished own data; Purkis and Riegl, 2005).

However, reproductive rates for all coral groups in the Arabian/Persian Gulf were unknown. Since we knew N_i for all species and K from the satellite images (see Section 3.3.1) and G_i (see Section 3.3.2), we were in a position to explicitly solve for D_i in Eqs. (2), (4), and (6), provided D_i in Eqs. (1), (3), and (5) (juvenile mortality) were set to zero. Once D_i values were obtained ($D_2=0.27$, $D_4=0.37$, and $D_6=0.18$), we could then calculate R_i values ($R_1=0.4$, $R_2=1$, and $R_3=1.1$). For the calculations we considered migration (both in- and out-) zero, since we were interested in the stability of the local population.

Such a model implicitly expects constant environment and constant variables and we were primarily interested in exploring whether the corals could also survive under different disturbance scenarios. Therefore, we considered these values primarily as guide for the range within which to search for variables that would allow the population to persist in the disturbed environment.

We evaluated our model under assumptions of constant fertility and settlement (=constant R) as well as under assumptions of stochastically varying R . To achieve the latter, R was assigned a random number value from a Gaussian distribution with mean zero and variance 1. This adds realism, since recruitment processes have been observed to be variable in time (Fong and Glynn, 1998; Smith et al., 2005).

3.4. Sensitivity analysis

To assess which parameters most strongly affected model behavior, and to evaluate the realism of the estimation of values where little empirical basis existed, we varied those parameters obtained by explicit solution. Analyses are based on the effect of a change in one parameter with all others kept the same, i.e., local sensitivity. Equations were plotted with variable parameters and inspected to ensure that resultant curves did not deviate significantly. Two indices examined effects of parameter changes: (1) total values index (TVI): mean of ratios of all population sizes at end of numerical experiment over sizes at beginning (N_{1-6}). Index shows whether overall coral cover at end is reconciled with expectation of reaching levels comparable to beginning, (2) *Acropora* index (AI): sum of all small plus big populations other than *Acropora* over sum of small plus big *Acropora* populations. It indicates community structure, i.e., abundance ratio at end of numerical experiment compared to beginning; default value ~ 4 (see Tables 2 and 3) allowed to vary from 8.06 to 2.01 (i.e., halved *Acropora* abundance to doubled *Acropora* abundance).

3.5. Isolated versus connected population

Our model aims at evaluating effects of mass mortality. Based on observations in the field, between 90% and 99% of all *Acro-*

pora can succumb to such events. But our observations also suggest that the severity of mortality may be strongly influenced by local variables and may not be uniform over the entire region. After the 1996 mass mortality, which killed about 99% of corals in the Ras Hasyan area, some surviving populations that had suffered less mortality were found at nearby Ras Ghantoot and Deira. It is conceivable that such populations can act as a larval reservoir for resettlement of the denuded areas since wind and tide-driven long-shore currents frequently reverse and connect these sites that are only separated by few dozen km. We thus considered our population model in two distinct settings:

- an isolated population with no external larval input at all.
- two openly connected populations that can exchange propagules freely during every recruitment event either at fixed or random rates.

In the latter case, we simultaneously solved 12 ODEs, 6 for each population (a focal population and a connected population) consisting of the 2 guilds: dominant (*Acropora*), and dominated (faviids, and *Porites*). The focal and the connected population could have the same vital rate, or R_i was varied as a Gaussian random number, giving each (sub)population a unique dynamics. Connectivity via m and n was either held constant (at arbitrary values 0.1 or 0.01) or was also assigned a random number from a Gaussian distribution with mean zero, variance and standard deviation unity. We used Gaussian random numbers centered on zero because they favor low recruitment rates over occasional high rates. This is reminiscent of the situation in coral reefs where high-recruitment events are rarer than low-recruitment events (Mumby and Dytham, 2006). A , B , and C of formulae (1), (3), and (5) then became the appropriate N_i of the connected population.

3.6. Disturbance dynamics

Coral assemblages in the SE Arabian/Persian Gulf have been identified to be strongly influenced by temperature-related mortality events (Sheppard et al., 1992; George and John, 1999, 2000; Riegl, 1999, 2001, 2002; Purkis and Riegl, 2005). Disturbances are repetitive and most likely cyclic in nature. Bleaching events with region-wide coral mortality were observed in 1996, 1998 and 2002 (George and John, 1999, 2000; Riegl, 1999, 2003; Sheppard and Loughland, 2002; Purkis and Riegl, 2005; Burt et al., 2008). A previous mortality event in Dubai in the early 1980s is recorded by Holt Titgen (1982) and Shinn (1976) describes a large-scale *Acropora* kill on the Qatar east coast in 1964. We used the HadISST dataset (Reynolds and Smith, 1994) to identify peaks in temperature excursion in order to verify the known mortalities and learn about others. During these anomalies, preferentially *Acropora* are killed (Shinn, 1976; Riegl, 1999; Purkis and Riegl, 2005). In areas where *Acropora* was killed, massive corals (mainly faviidae and *Porites*) persisted and increased in size (Riegl, 2003).

The HadISST temperature data set suggested that the mass mortality events, which could be clearly pinpointed from literature records and own observation, likely had strong local drivers. In the 1×1 geographic degrees and monthly averaged dataset, the temperature spikes were generally not very

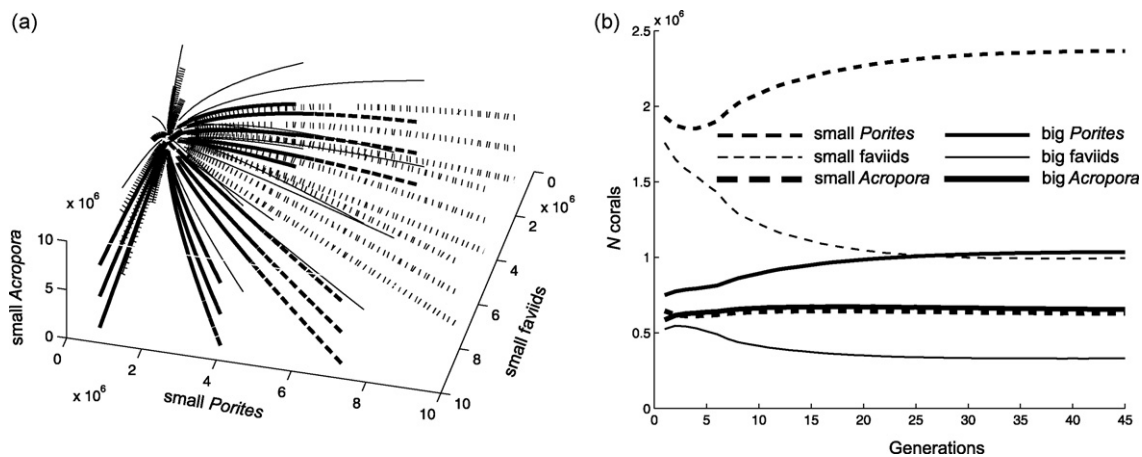


Fig. 6 – Intrinsic properties of the model: (a) 3d phase-plane solution of trajectories of competitive interaction between the small stages of all species. All converge towards a narrow region of *Acropora* dominance and (b) the species groups in Eqs. (1)–(6) parameterized from satellite imagery and photo-transects (Table 1) reach carrying capacity and then remain stable. *Porites* should be most frequent, then *Acropora*, then faviids.

obvious, with the exception of 1998, which clearly was an unusually hot year. The 1964 mass mortality in Qatar recorded by Shinn (1976) fell into a warmer-than-usual period, with 1964 being clearly a hot summer with a preceeding warm and a following cold winter. Ruiz-Sebastian et al. (personal comment and in preparation) suggest that the combination of cold winter/hot summer predisposes corals to bleaching. Therefore, there is a possibility that both a hot summer and then an unusual, but brief, cold-spell in winter could have damaged the corals. A mass mortality near Jebel Ali around 1980 (Holt Titgen, 1982) coincided with the highest positive seasonally adjusted summer temperature anomaly (1980) between 1969 and 1987 followed by a cold winter and an even hotter summer. 1987/1988 had hot summers and warm winters without mortality. Mass mortality occurred in 1996 during a hot summer and in 1998 during the hottest summer on record. In summer 2002 corals bleached severely but mortality was low (Riegl, 2003; Purkis and Riegl, 2005). In the summers of 2006–2008, mild bleaching with hardly any mortality occurred. Although too short to allow generalizations, the sequence of major coral mortality events 1964–1981–1996, coupled with characteristics of the areas coral build-ups (or, rather, lack thereof), suggests that a roughly 15–17-year cycle of recurring mass mortality, predominantly in the genus *Acropora* exists (Riegl, 1999).

The mortality during these events was known from previous transect studies and was <25% for massive corals but at least 90% for *Acropora* (Riegl, 1999, 2003). Therefore, we evaluated the model with mortality settings 25% for massive corals and 90% or 99% for *Acropora*. While transect studies suggested that *Acropora* mortality was near-total, no regeneration could have been observed in 1999 if nothing at all had survived, yet recruits and some larger colonies were encountered. Thus we assumed a 1–10% survival of large and small *Acropora*. Catastrophic mortality was modeled by reducing input N_i by 99%, 90% (in *Acropora*) or 25% (in faviids and *Porites*) at defined time-steps. This mortality was thus extraneous to regular population dynamics and not included as a factor in formulae (1)–(6).

4. Results

4.1. Assumption of constant rates—model runs for Ras Hasyan

In the first instance, we wanted to know whether the envisaged dynamics, as defined by the six ODEs, had at all the capability of reproducing community dynamics as observed in the field. Parameters were needed to fulfil the hypothesis that these coral assemblages had indeed been subjected to repetitive mass mortality but yet had persisted. We examined whether on a set disturbance frequency with a set mortality rate, a perpetually regenerating population was indeed possible. We assumed the population levels of 1995 as the baseline since at this time, the abundance of corals had been estimated and we could tune the model towards reaching comparable levels ($TVI \sim 1.7$, $AI \sim 4$). Sensitivity analysis used TVI to evaluate effects of parameter variation on overall coral populations, AI to evaluate deviations in community composition.

In the field, we had observed disturbances twice with 15-year, and once with 17-year recurrence. As a first step, we assumed a constant 15-year disturbance cycle recurring 100 times. Under assumption of constant reproductive rate R_i , the parameters derived by explicit solution allowed a regularly recurring disturbance of 90% mortality in small and big *Acropora*, 25% in small and big faviids and *Porites* every 15 years for 1500 years (a time-period of relative environmental constancy in the region) with recovery to pre-disturbance levels (set at 1995 values). Longer runs (>1500 years) did not change the outcome. However, in the isolated population with no larval import ($m=0$), we had to adjust the R_1 (*Acropora* rate of increase) from 0.4 to 0.88, to avoid its extinction. Without this increase ($R_1=0.4$), larval import had to support regeneration of the decimated *Acropora* population. Suitable values were a stable outside population of N_2 (the start and 1995 values) with $m=0.12$. None of the other parameters required adjustment.

To evaluate stability we calculated the system's Jacobian and its eigenvalues. We arrived at a dominant, negative, real eigenvalue (-0.95) and two small, complex eigenvalues. This suggested stability, i.e., the system would converge towards a stable region if allowed to reach climax. In a 3d phase-plane solved for the small stages (big stages show little competitive interaction) trajectories converge towards, but do not meet in, a single point (Fig. 6a). The complex eigenvalues suggested some oscillation (Edelstein-Keshet, 2005). The properties of the three differential equations contain the possibility that the assemblage could converge to a region where the dominant *Acropora* eventually out-competes the other species (Fig. 6a). Since the vital rates were calculated from values in a community where they coexisted, the model in the present parameterization (Table 1) allows coexistence (Fig. 6b).

Sensitivity analysis examined possible ranges of parameter variability without changing outcomes (Table 2). The connected model allowed wider variability of parameters than the isolated population model, and both were most sensitive to variations in R_i and D_i . Variability of catastrophic mortality (Table 3), an extraneous factor to the population model, primarily affected species composition (*Acropora* outcompeting other species at lowered mortality = declining AI) but did not strongly affect TVI. The model was very sensitive to spacing of mass mortality events (Table 3). Shorter intervals led to marked decreases, longer intervals to marked increases in *Acropora* dominance. Mortality spacing could vary between 10 and 20 years to maintain a community roughly comparable to that used as baseline.

The model also allowed different ways of treating small colony mortality. It could be included in G_i , since higher small coral mortality would result in a lower transfer rate into the bigger size-class. More independent small colony dynamics can be modeled with a separate mortality term (D_1 , D_3 , and D_5). In this case, however, explicit solution for D_i and R_i values is not possible and we also lacked field-derived, realistic values. After explicit solution for D_2 , D_4 , and D_6 (with D_1 , D_3 , and $D_5 = 0$) we found by iteration that mortality could be partitioned ~10/90% between small/large colonies while still obtaining a comparable outcome (unpartitioned mortality: TVI = 1.06, AI = 2.07; partitioned mortality: TVI = 0.89, AI = 4.79). Again, wider variability of D_i was possible in the connected, rather than the isolated, model (Table 2).

Next, we tested these assumptions in a more realistic disturbance scenario (Fig. 7). We assumed for want of better data that the same number of corals as in 1995 had existed in 1949 at the start of model runs. Thermal anomalies were detected in 1949, 1964, 1981, 1996, 1998 and 2002. The severities of mortality were kept constant: small and large *Acropora* were reduced by 90%, while small and large faviids were reduced by 25% (Fig. 7a). In order to maintain the *Acropora* population, its R value had to be raised from 0.4 to 0.87. When this was done, *Acropora* populations were found to strongly rebound without outside larval input, as did faviids and *Porites*, until the closely spaced 1996–2008–2002 disturbance tripelet did not allow sufficient time for population recovery, pushing all populations to very low levels, and *Acropora* to extinction. Faviids and *Porites* showed strong signs of recovery from 2002 to 2008 and had almost attained full population level (Fig. 7a). In the connected model ($R_1 = 0.4$, $m = 0.12$, and $A = \text{const}$, Table 1), *Acropora* was

Table 1 – Population parameters used to model coral assemblages. Values are based on measurements from monitoring (mortality at disturbance), from satellite imagery (N_i), calculation based on photo-transects (growth rates), explicit solution from the equations (fertility, big and small colony mortality), and iteratively determined settings (migration rate).

	<i>Acropora</i>	Faviids	<i>Porites</i>	Carrying capacity	Disturbance sequence
Fertility per colony					
N_{small} Ras Hasyan	Basic: 0.4; disturbed: 0.88 or random	1 or random	1.1 or random	Ras	100*15 yr, or
N_{big} Ras Hasyan	645,295	1,758,421	1,930,192	Hasyan: 8066812;	15–17–15–2–4–6
N_{small} Halul	586,632	525,242	750,630	Halul: 687600	
N_{big} Halul	1706	97,625	107,163		
Small colony mortality	1575	29,161	41,674		
Big colony mortality	0 or 0.3	0 or 0.4	0 or 0.02		
Growth to bigger size	0.27 or 0.24	0.37 or 0.33	0.18 or 0.16		
Neighboring population size Ras Hasyan	0.25	0.11	0.07		
Neighboring population size Halul	0 or 586,632 (constant) or random	0 or 1,758,421 (constant) or random	0 or 1,930,192 (constant) or random		
Migration rate	0 or 1575 (constant)	0 or 29,161 (constant)	0 or 41,674 (constant)		
Mortality at disturbance	0, 0.12, 0.01 or random	0, 0.12, 0.01 or random	0, 0.12, 0.01, or random		
	90% or 99%	25%	25%		

Table 2 – Local sensitivity of the model to single parameter variation (column 1) with the others held constant. Sensitivity is evaluated with respect to total values index (TVI) and *Acropora* index (AI) both in the isolated case (column 3) and allowing immigration from an outside population of fixed value (column 5).

Local sensitivity (model time 1500 years, disturbances every 15 years)				
Varied factor	Value in unconnected model (1 population)	Allowed variability, multiplication factor	Value in connected model (2 populations, $m = 0.12$)	Allowed variability, multiplication factor
R_i	0.88, 1, 1.1	0.98–1	0.4, 1, 1.1	0.5–1
R_1 only	0.88	0.98–1	0.4	0.1–1
G_i	0.25, 0.11, 0.07	0.9–1.1	0.25, 0.11, 0.07	1–5
D_i	0, 0.27, 0, 0.37, 0, 0.18	1–1.05	0, 0.27, 0, 0.37, 0, 0.18	1–2
D_i	0.03, 0.24, 0.4, 0.33, 0.02, 0.16	0.95–1.01	0.03, 0.24, 0.4, 0.33, 0.02, 0.16	0.1–2
K	8,066,812	0.1–5	8,066,812	1–3
m	0	n.a.	0.12	0.3–1.5
A	0	n.a.	586,632	0.3–1.5
B	0	n.a.	0	n.a.
C	0	n.a.	0	n.a.
Disturbance interval				

Note: $i = 1, \dots, 6$; allowed variability range set by AI span 8.06–2.01.

able to recover after the 1996/1998/2002 events due to constant larval subsidy from outside (Fig. 7b).

Following model runs addressed the question whether the *Acropora* population, with unaltered recruitment or mortality rates, could sustain itself if 99% mortalities, as observed in 1996, were the recurrent norm. We used the same realistic disturbance frequency (15–17–15–2–4–6 years) as above. While faviids and *Porites* persisted through the disturbances with 25% mortality, and showed strong recovery after the three short-interval disturbances (2–4–6 years), *Acropora* was only capable to persist in the system with larval import from a constant-size, large ($A = 586,632$) outside population, it went extinct without larval subsidy. This suggested that the 1996 mortality was unusual in its severity and would cause significantly altered community structure if such disturbances became the norm. However, both in the field and the connected model *Acropora* persisted through the disturbances and had staged a moderate come-back by 2008 (see also Burt et al., 2008). This suggested that outside populations had replenished the locally depleted populations. We are aware of areas having escaped both the 1996 and 1998 mortalities that could have served as larval sources for the investigated populations (Riegl, 1999, 2002). Larval sources likely will not remain constant as assumed above, but will fluctuate. Next, we considered two fully connected populations and allowed continuous larval import/export, assuming that the focal and connected populations had the same vital rates and population parameters. This is likely a conservative underestimation of the realistically available pool of corals, however, it allows for expansion/depression of the available larval pool as all populations fluctuate. We forced both populations to fluctuate synchronously (i.e., region-wide, uniform impact of mortality event), but one population to subsidy the other with more larvae than it received itself ($m = 0.12$, $n = 0.01$ in the receiving population; $m = 0.01$, $n = 0.12$ in the donor population), simulating an upstream/downstream effect. *Acropora* went extinct after two (donor population) or three (receiving population) disturbances, while faviids and *Porites* expanded. Persistence of the connected population was only possible with another sizeable and stable donor population (Fig. 7b), simultaneous depression of focal and connected population severely disadvantaged *Acropora* to the point of virtual extinction ($N_i \text{ Acropora} < 10$ at the end of model runs, Fig. 7c). Larval retention increased populations, larval export reduced populations but more than one connected population would have been necessary to maintain a big enough larval pool to compensate for the heavy mortality with $R_1 = 0.4$. With $R_1 = 0.88$, *Acropora* populations persisted until the 1996/1998 combined events. We deduce that populations as observed prior to the 1996 event could only have existed if recurrent mass mortality did not exceed or reach 90% on a regular basis and a sufficiently large larval pool for local recovery subsidy was available, confirming the 1996 mortality and the close spacing of the 1996/1998/2002 events as unusually severe.

4.2. Using the model from Ras Hasyan to forecast dynamics at Halul

The coral community around Halul was also severely impacted in 1998. Its corals could, via other islands or directly,

Table 3 – Effect of variability in catastrophic mortality and event-spacing on model outcomes; (a) column one are the factors by which N_i will be multiplied (values sequential for $i = 1 \dots 6$) after each 15 years of model run over 1500 years (connected *Acropora* populations $R_1 = 0.4$, $m = 0.12$, $A = 586,632$, $B = 0$, $C = 0$; $D_{1.5} = 0$). Decreasing values of AI show increased competitive dominance of *Acropora* in lower disturbance scenarios. Higher values in N_i multiplication factor correspond to higher survival. (b) Spacing of events and their influence.

(a) Mortality multiplication factor for N_1 through N_6	<i>Acropora</i> index (AI)	Total value index (TVI)
0.05, 0.05, 0.7, 0.7, 0.7, 0.7	4.54	1.88
0.1, 0.1, 0.75, 0.75, 0.75, 0.75	4.23	1.73
0.2, 0.2, 0.80, 0.80, 0.80, 0.80	3.60	1.56
0.3, 0.3, 0.85, 0.85, 0.85, 0.85	3.05	1.41
0.4, 0.4, 0.90, 0.90, 0.90, 0.90	2.57	1.29
0.5, 0.5, 0.95, 0.95, 0.95, 0.95	2.17	1.18
(b) Spacing of mass mortality events		
5 year	12.55	1.45
10 year	6.72	1.70
15 year	4.23	1.73
20 year	2.99	1.70
25 year	2.29	1.66

be connected to the Ras Hasyan populations and support them with larvae. Halul is upstream of Ras Hasyan with regards to wind-driven surface circulation as measure by holey sock drogues (D. Olson and J. Hoolihan, pers. comm.). We used vital rates obtained from Ras Hasyan (better and more data than at Halul, but presumed equivalent population dynamics) and population parameters obtained from the Halul Landsat TM scene to examine trajectories. Disturbances were identical to those assumed for Ras Hasyan (15–17–15–2–4–6). Coral populations persisted through six disturbance cycles with a 1949 starting population at 2005-level (earliest available field population estimates). Regeneration and die-back patterns led to the same observed community shift away from *Acropora* towards *Porites* dominance. The smaller habitat at Halul saturated faster than at Ras Hasyan, if given a large connected population for larval import ($m = 0.12$, and $A = 586,632$), and the population moved further towards the internal equilibrium (*Acropora* dominating even the smaller sizes of the other groups) after 47 years. With larval import from only a small population ($m = 0.12$, and $A = 1575$), the *Acropora* population stayed small and went extinct after the 1996/1998 disturbances.

4.3. Assumption of stochastic rates

While we were able to recreate stable dynamics under assumptions of constant recruitment and larval import, we nonetheless have to acknowledge that the world is not constant. Thus, the model would be even more plausible if a comparable outcome was achieved with stochastic rates. We assigned Gaussian random numbers to R_i , m and n and we used the realistic disturbance scenario (15–17–15–2–4–6) and simultaneously solved for 12 connected populations (2 for each size-class). Model sensitivity to R_i was confirmed by *Acropora* and faviid decline with random R_i and the system moving towards *Porites* dominance. Random larval import/export (m , n random, R_i fixes as in Table 1) did not change patterns but led to faster decline and extinction than with constant rates (pattern comparable to Fig. 7b). Also in stochastic simulations, *Acropora* did not withstand the high-disturbance frequency from 1996 to 2002.

We next investigated whether populations could be maintained over a 1500-year period with random disturbances, but fixed R_i (0.4, 1, 1.1). Single-run simulations (15-year 90% *Acropora*, 25% faviid and *Porites* mortality cycle) showed violent swings within and among populations. Averaged over 500 trials, *Acropora* could not persist. In agreement with the already established sensitivity to spacing of mass mortality, random assignment of event-spacing sooner or later brought several closely spaced events and caused *Acropora* extinction. This suggests that if our model really adequately models natural dynamics, thermal anomalies indeed must follow cycles of between 10 and 20 years in nature.

5. Discussion

Our model supports the notion that coral communities can indeed persist under a repetitive disturbance regime with approximately 15-year cycles as suggested by us in earlier papers (Riegl, 1999, 2002; Purkis and Riegl, 2005) and is also supported by recent reports from the field (Burt et al., 2008). However, dependent on the parameterization of the model, in particular dependent on assumptions of fertility and connectivity, the overall dynamics and ecological implications vary.

The model clearly shows that the 99% mortality suffered by *Acropora* along the U.A.E. coast in 1996 must have been unusual, since we could not find any realistic parameters (i.e., falling within constraints in Tables 2 and 3) that would allow survival under repeated such mortalities. The greatest mortality rate an *Acropora* population could endure repetitively was 90%. Apparently, repetitive 25% population reductions are no problem for faviid and *Porites* populations. Not only was 1996 an unusually severe disturbance, the close spacing of the 1996, 1998 and 2002 crises had a significant effect by causing a shift in the populations towards functional (very low abundance), or complete *Acropora* extinction. Thus, even if Arabian/Persian Gulf coral assemblages are apparently adapted to disturbances (Riegl, 1999; Burt et al., 2008), increased severity and frequency thereof, as predicted by global-change scenarios (Sheppard, 2003) would lead to shifts in community structure. *Acropora* would be lost, either completely or at least as dominant

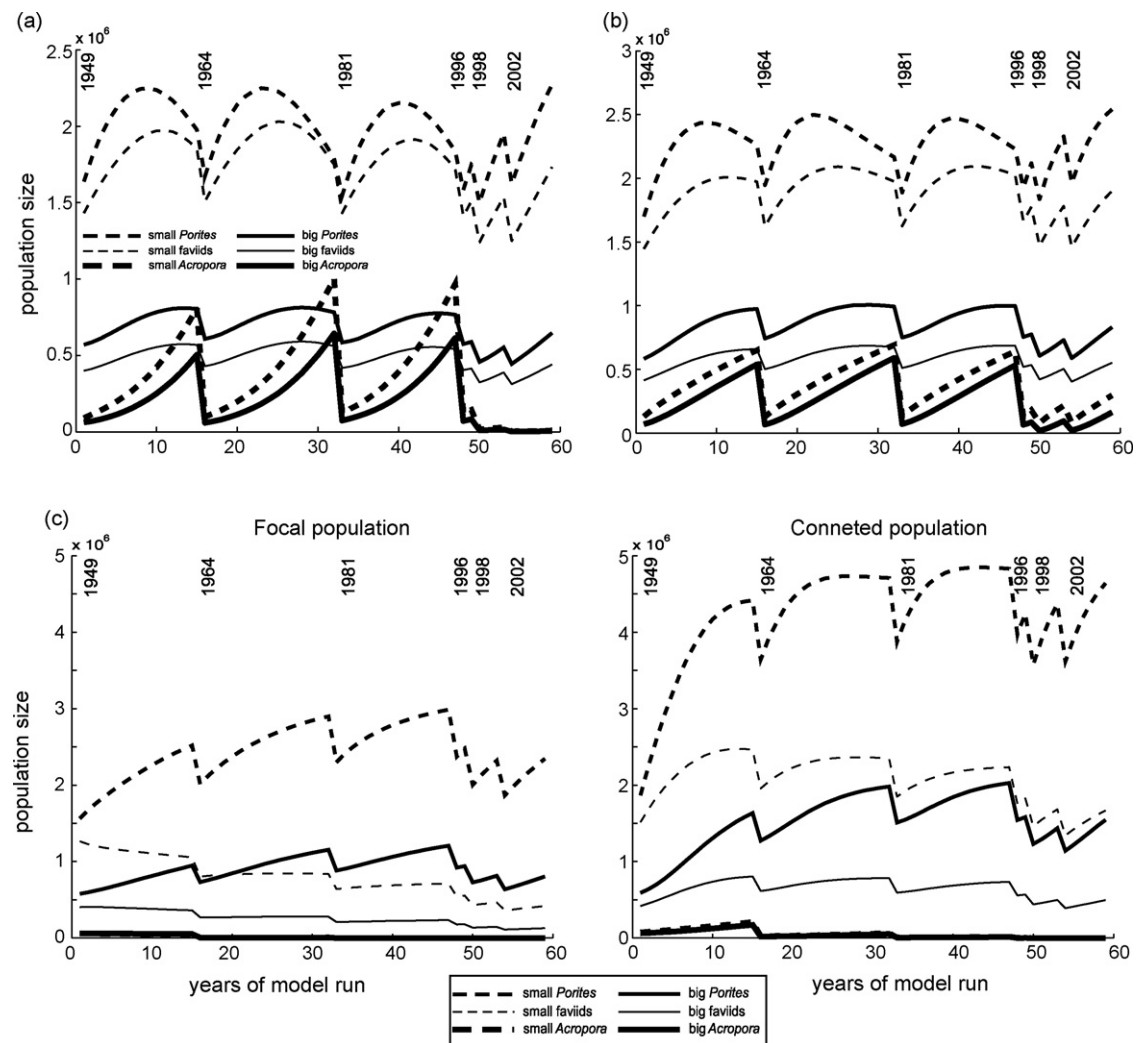


Fig. 7 – Model of six disturbance cycles (shown by year in which disturbance occurred) that suggests persistence of the coral assemblage in the postulated disturbance regime. (a) Isolated populations at Ras Hasyan ($m=0$, $R_1=0.87$, 90% mortality in *Acropora*, 25% in *faviids* and *Porites* at each disturbance; D_1 , D_3 , and $D_5=0$). (b) Connected populations at Ras Hasyan ($m=0.12$, $A=586,632$, $R_1=0.4$, 90% mortality in *Acropora*, 25% in *faviids* and *Porites* at each disturbance; D_1 , D_3 , and D_5 included as in Table 1). (c) Ras Hasyan, dynamically connected populations ($m=0.12$, $n=0.01$ in receiving population, $n=0.12$, $m=0.01$ in donor population; $R_1=0.4$, 90% mortality in *Acropora*, 25% in *faviids* and *Porites* at each disturbance; D_1 , D_3 , and D_5 included as in Table 1). The far lower *Acropora* values than in (a) and (b) are due to simultaneous depression in population levels in focal and connected population.

species. Extrapolating to all reef areas of the world, one could surmise that more rapidly repeated and severe bleaching events will leave a depauperate community of only few but very robust species.

Our model contributes to a better understanding of the vital rates necessary to survive the predicted disturbance regime, and an estimation of maximum severity of repetitive disturbances. Due to their aggressive superiority, the analytic solution required *Acropora* to have a fertility of 0.4 surviving recruits per adult colony, the lowest of the modelled species. Sensitivity analysis showed that R_1 could vary between 0.2 and 0.4 in the connected case (Table 2) which put it very close to values in the literature. While this is higher than the fertilities of 0.1 assumed by Lirman (2003) for Caribbean *A. palmata*, our model did not separate asexual from sexual recruitment. Since

the latter is included in our R_1 values, and Arabian/Persian Gulf *Acropora* are as capable of asexual reproduction as those in the Caribbean (pers. observation), our estimated fertility rates do not deviate much. However, in the disturbed case (repetitive 90% mortality) in an isolated population with fixed vital rates, we had to adjust the *Acropora* fecundity to 0.88 in order to avoid extinction. A constant fertility of 0.2–0.4 was only possible with continuous and assured import of larvae.

The required fertility for *faviids* are higher than, those of *Porites* comparable to estimates in the literature (Babcock, 1991; Schloeder and Guzman, 2008). We believe our rates to be realistic based on calculations of plausible numbers of polyps and published per-polyp fecundity rates (Table 4).

Even if herein established fecundity differs from other reef areas, strong local variability cannot be discounted. Fecundity

Table 4 – Approximation of fertility to verify the fertility assumptions required for our model to allow a sustainable coral population despite recurring mass mortality. Values for gonads and eggs taken from Mumby and Dytham (2006).

	<i>Acropora</i>	Faviids	<i>Porites</i>
Average colony size in cm ²	3848	272	372
Number of polyps per cm ²	2	1	18
Number of gonads per polyp	6	6	6
Number of eggs per gonad	2	2	2
Number of gametes per average colony	92,363	3264	80,352
Gamete survival required for model fecundity	0.000004–0.000008	0.0003	0.00001

could be higher in Gulf coral communities because larvae settle into a strongly unsaturated environment with much freely available space. High urchin abundances ($\sim 5\text{ m}^{-2}$, unpubl. data) efficiently control macroalgae populations (Carpenter, 1986) and create abundant competition-free space for larvae to settle when coral populations are low. This is in contrast to the Caribbean, where an absence of urchins has repeatedly been blamed for strong presence of macroalgae with concomitant reduction of settlement space and survival of coral larvae (Hughes, 1994; Mumby et al., 2006, 2007).

One weakness of our model is that it ignores all other trophic compartments, such as herbivores (fishes or sea-urchins) that have a demonstrated effect on the survival and recruitment of corals (Mumby et al., 2006). However, while the Arabian/Persian Gulf moves towards a generally over-fished state, like all other oceans of the world (Bellwood et al., 2004), fish density in the study area did not decline until very recently (Riegl, 2002; own unpubl. data) and high urchin abundance suggests efficient, un-impacted herbivory. Therefore, our model presents an admittedly coral-centric view of dynamics in an otherwise little modified ecosystem.

Our model suggests that isolated populations require far more stability in parameters than connected populations, and are therefore less buffered against environmental perturbations. In the case of an isolated population, it was not possible to vary parameters as widely as in the connected case and still obtain consistent results (Table 2). Connectivity therefore is essential for population survival (Cowen et al., 2007). We consider our model parameters and outcomes most realistic in the case of connected populations. Our model also underlines the importance of the size of a connected population. *Acropora* survival was only possible with a stable, sizeable population as larval donor. Once the connected population fluctuated at the same intensity as the focal population, *Acropora* went extinct (Fig. 7c). This mechanism underlines the importance of refuges that maintain large populations and can act as “reseeded batteries”.

It is likely that mortality levels per disturbance indeed vary strongly and are not constant as assumed in our model. Any downward adjustment in mortality level would allow lower recruitment rates, but the relatively low sensitivity of the model to variability in catastrophic mortality suggests that internal factors, such as recruitment, are more important. Coral survival (as measured by TVI) in the harsh environment simulated by the model is founded in fecundity rather than resistance and lowered mortality in response to stressors. However, community structure was strongly influenced by mortality events, because compensatory mortality (Connell, 1978) was observed at several levels. Firstly, if *Acro-*

pora were not severely disadvantaged by the mortalities, they out-competed the other species until these only maintained large colonies within their size-refuge (Sebens, 1982). We saw this in the field (Purkis and Riegl, 2005; Burt et al., 2008) as well as in the simulations. A preferential mortality of *Acropora* always leads to an increase in the other species.

Demographic and environmental stochasticity compromised populations, leading to loss of *Acropora* and dominance by *Porites*. In many areas of the Arabian/Persian Gulf, *Porites* is dominant and *Acropora* rare, even though suitable habitat is available. This is the case in regions with a harsher environment (Gulf of Salwah, Yasat Islands, Khor Odaid area; Sheppard and Loughland, 2002) where temperature excursions are higher and less predictable. This community pattern may be a result of long-term *Acropora* decline, caused by reduced or variable fertility and disturbances at more rapid and irregular recurrence. With disturbances potentially becoming more severe, more frequent and less predictable (Sheppard, 2003), the entire Gulf may be moving towards this trajectory, putting the future of *Acropora* as a dominant species into doubt.

If we accept as premise that either unusual cold (Coles and Fadlallah, 1991) or hot events (George and John, 1999; Riegl, 1999; Purkis and Riegl, 2005) cause mass mortality, then no direction for evolutionary change towards either hot- or cold-adaptation should be expected. Any alleles that impart a generally wide temperature tolerance should be selected for. If the herein described population oscillations were purely caused by unidirectional stresses (i.e., only heat or only cold), the population genetic outcome should be easily predictable: rapidly the allele with the tolerance for the highest (or lowest) temperature should dominate, since the high mortality (90% or >90%) certainly would depress the evolutionary fitness of the worse-adapted allele. In the present case, the alleles of the zooxanthellae are of importance, since coral death is mostly due to high- or low-temperature-induced bleaching. However, while our direct observations can only confirm hot-kills, the literature (Shinn, 1976; Coles and Fadlallah, 1991) clearly implicates cold-kills as well, which would negate directional evolution towards either hot- or cold-adaptation. Lack of information regarding the proportion of hot- to cold-kills made us refrain from quantitative analysis. The closely spaced hot-kills of the late-1990s and early 2000s may have led to a phenotypic shift towards more hot-adapted corals, in particular *Acropora*. Riegl (2003) illustrates bleached faviids and unbleached *Acropora* in 2002—a clear reversal of the situation in 1996, where the mortality pattern was exactly the opposite. During the hot summers of 2007 and 2008, only mild bleaching without mortality was observed. Indeed our model supports

data in Baker et al. (2004), who found most Arabian/Persian Gulf *Acropora* to contain the temperature-tolerant zooxanthellae clade D.

Confusion of adaptive trajectories may be introduced by connectivity between populations. Our model shows the importance of large connected populations for larval import (Caley et al., 1996). The severity and cause of mass mortality may vary among localities due to the shallow, enclosed and high-latitude position of the Gulf. Thus, different phenotypic shifts might be observed among populations if some had experienced cold-kills while others experienced hot-kills. In this case, connectivity within an open population has important implications. Different mortality may lead to different population sizes, which is important for population persistence. If populations were simultaneously and uniformly depressed in our model, not enough propagules were available and extinction ensued. But if a large population was available for larval import, focal and/or connected populations (*Acropora*, faviids, *Porites*) persisted. Depending on the regional cause for mortality, different parts of the same open population or metapopulation (*sensu* Hanski, 1994) could follow independent population trajectories. As long as any one part of the (meta)population might survive and be available for re-seeding the denuded area, little evolutionary pressure would be exerted onto any genotype. By finding refuge within any given sub-population and acting as a weed (i.e., rapidly occupying and giving-up free space—as evidenced by the absence of reefal frameworks. If corals persisted, frameworks would form; Riegl, 2001), even genotypes apparently badly adapted to the presently observed environmental stress could prevail. Thus, cold-adapted as well as hot-adapted alleles might persist in the population.

It appears, however, that hot-kills will likely become the norm (Sheppard and Loughland, 2002; Sheppard, 2003; Nasrallah et al., 2004) and that mortality will be uniform and synchronized across the region. This makes major and permanent shifts in community structure (i.e., loss of *Acropora*) a likely scenario. However, zooxanthellae in the Gulf are mostly of the hot-adapted D-clade (Baker 2004). This, combined with the theoretical and empirically proven capability of Arabian/Persian Gulf corals to persist in a high-disturbance environment may give these corals an edge in their struggle for survival in an anthropogenically altered climate, provided disturbances do not become more frequent.

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