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Human-induced physical disturbances and their indicators on coral reef habitats: A multi-scale approach

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Abstract – This article aims to review 1) the major and most frequent human-induced physical disturbances and their consequences on coral reef habitats using a multi-scale approach, and 2) the scale-related indicators and conceptual aspects used to detect and measure the effects of these physical impacts. By physical disturbances, we mean direct perturbations that lead to the destruction/erosion of the carbonate framework. Human-induced direct physical disturbances are numerous from coastal development, tourism, harvesting, accidents and nuclear/weapon testing. Since methods for monitoring and measuring indicators are generally scale-implicit, coral reefs are first presented according to different ecological-spatial scales of organization, from colony to region (colony, reefscape, reef zone, whole reef, island and region). In this way, it is easier to link a couple {habitat, disturbance} to their potential indicators and to the descriptors they target. Three classes of descriptors, related to the response of the living component of coral reef ecosystem, are considered here: stony coral, reef fishes and the human uses. A synthesis of the different options for coral habitat assessments is proposed. We sort them according to their objectives (monitor, initial status or improvement of knowledge), their specificities (identification or not of a specific disturbances) and their scale of investigation (small, meso- or large scales). Usually, the majority of the indicators of human-induced disturbances are non-specific. They reveal that something is happening but not the actual causality and can only detect differences across time or space. A major weakness lies in the difficulty in deconvoluting the signals from a conjunction of stressors occurring at different scales. As such, a hierarchical concept of disturbances in coral reefs would be the next logical step to enhance our capabilities in monitoring and forecasting coral reefs status.

Key words: Coral reef / Physical disturbances / Habitat / Human-induced disturbances / Indicator

Résumé – Indicateurs des perturbations physiques et anthropiques de l'habitat corallien : une approche multi spatiale. Cet article a pour but d'examiner à travers une approche multi-spatiale 1) les principales et les plus fréquentes perturbations physiques sur l'habitat corallien et leurs conséquences, 2) les indicateurs de ces perturbations et les aspects conceptuels utilisés pour détecter et mesurer les effets de ces impacts. Seules, les dégradations physiques ayant un impact direct sur la destruction et l'érosion de la trame carbonatée du récif corallien sont considérées. Ce type d'impact, fréquent en milieu corallien, peut être généré par l'urbanisation du littoral, les activités touristiques (plongée sous-marine), la récolte d'organismes (piétinement, pêche à la dynamite), les essais nucléaires ou des accidents (échouage de navires). Les méthodes d'échantillonnage et les indicateurs utilisés pour le suivi des récifs étant reliés à l'échelle d'observation, les récifs coralliens sont abordés dans un premier temps en fonction de ces différentes échelles spatiales (colonie, paysage, partie du récif, récif en entier, île, région). De cette manière, il est plus facile de relier le tandem {habitat, perturbation} aux potentiels indicateurs et descripteurs ciblés. Trois classes de descripteurs reliées à la composante vivante de l'écosystème récifal sont considérées : les coraux constructeurs de récif, les poissons récifaux (Chaetodontidae) et l'homme à travers l'utilisation qu'il fait de l'écosystème. Une synthèse des différentes options pour évaluer l'état du récif corallien est proposée. Elles ont été sélectionnées en fonction des objectifs (suivi, état initial ou amélioration des connaissances), de leurs spécificités (identificateur ou non de la perturbation) et l'échelle d'investigation (petite, moyenne ou large). La majorité des indicateurs d'une perturbation anthropique n'est pas spécifique à un type de perturbation. Ils révèlent que quelque chose s'est passé, mais pas spécifiquement la cause actuelle de la perturbation ; ils ne peuvent donc que détecter des différences au cours du temps ou de l'espace. Un des obstacles pour détecter spécifiquement une perturbation réside dans la difficulté de dissocier les signaux d'un ensemble de stress qui se répercutent à différentes échelles spatiales. Ainsi, une approche conceptuelle hiérarchique de perturbations en milieu corallien serait la prochaine étape à franchir pour améliorer nos connaissances afin de mieux suivre l'état des récifs coralliens et anticiper leurs dégradations.

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1 Introduction

Coral reefs are characterized by their high species diversity and high gross productivity, among the highest of Earth's marine or terrestrial ecosystems (Connell 1978; Ray 1988). Coral reefs, frequently associated with seagrass beds and mangrove forests on tropical shorelines, supply vast numbers of people with goods and services such as seafood, recreational possibilities, and coastal protection providing significant aesthetic, cultural and economical benefits for many tropical countries (Done et al. 1996; Constanza et al. 1997; Berg et al. 1998).

Scleractinians (stony corals) are the main contributor of the reef framework since coral polyps secrete a carbonate skeleton at an average of 5 kg calcium carbonate per square meter (Kinsey 1985). The high calcification rates of these organisms are possible due to a symbiotic association with microscopic unicellular algae, the zooxanthellae that facilitate the growth and secretion of the calcium carbonate skeleton (Goreau 1959; Smith 1985; Gattuso et al. 1993, 1999). Crustose coralline algae, foraminifera and molluscs may also contribute significantly to the carbonate budget of a reef, which itself results from the accretion of the carbonate material at a geological scale. However, various agents balance continuously the calcification process through chemical, physical or biological erosion. As a result of a variety of environmental forcing and the duality between coral growth and carbonate dissolution/destruction, reefs provide a variety of three-dimensional complex habitats and niches for a variety of fish, molluscs, crustaceans and other reef-dwelling animals. The diversity of niches and habitats partially explain the diversity and structure of living community that exist on many coral reefs worldwide (Veron 1986; Done 1992).

Usually, ecologists consider as disturbances the factors that prevent calcification or enhance destruction/erosion of the carbonate framework. These disturbances play an important role in shaping continuously coral reef communities and their architecture (Connell 1978; Grigg 1983; Brown and Howard 1985; Hughes 1989; Grigg and Dollar 1990; Done 1992; Connell et al. 1997; Hughes and Connell 1999). Disturbances can be natural (e.g., ingestion by parrotfish of large amounts of coral rock, Bruggeman 1994; Peyrot-Claussade et al. 1995; sponges and echinoids grazing, Hutchings 1986) or induced by human activities.

Man-induced physical disturbances are numerous, including over-harvesting of reef organisms (Grigg 1984; Wells and Alcala 1987), coral mining (White 1987; Brown and Dunne 1988), destructive fishing methods (Carpenter and Alcala 1977; Alcala and Gomezn 1987; Gomez et al. 1987; McManus et al. 1997; Salvat et al. 2002; Erdmann 2000; Jackson et al. 2001; Fox et al. 2005) or uncontrolled land reclamation for tourism and coastal development (Tilmant 1987; Allison 1996; Hawkins and Roberts 1997; Guzman et al. 2003). The effects of these disturbances can be detected at different scales. These disturbances have direct consequences on stony corals ranging from colony to reef zone. With the expansion of human population on coastlines, and deforestation or intensive agriculture on the upstream watersheds, the increase in nutrient delivery (Marszaleck 1981a; Bell 1992; Naim et al. 2000), sediment and pollutant loads (Pastorok and Bilyard 1985) can have significant consequences at whole reef scale or even regional scale. Finally, activities occurring very far from the reefs may have consequences at a global scale. Indeed, greenhouse warming and global change are the usual suspects to explain more frequent occurrences of coral bleaching events, and may potentially increase hurricane frequencies and strengths (Knutson et al. 1998; Hoegh-Guldberg 1999; Kleypas et al. 2001). Human impacts and increased fragmentation of coral reef habitat have undermined reef resilience, making them much more susceptible to current and future climate change (Hughes et al. 2003). Being able to specifically identify the consequences of human actions on reef communities would be a valuable tool in terms of management. Unfortunately, it is not always easy to find the right key, or indicator, that will decode without ambiguity the signal of a human-induced stress on coral reefs.

This article aims to review:

- the major and most frequent human-induced physical disturbances and their consequences on coral reef habitats considering different levels of ecological organisation associated with various spatial scales (colony scale to region scale), and
- the scale-related indicators and conceptual aspects to detect and to measure the effects of these physical disturbances. By physical disturbances, we mean all events that lead to destruction/erosion of the carbonate framework of a colony, community or entire reef.

Within the limit of this article, we do not consider either man-induced non-physical disturbances such as chemical pollution, eutrophication, or thermal stress, nor non-human, natural, physical-perturbations, such as hurricanes, coral-bleaching events, or outbreaks of predators. Furthermore we will not address indirect perturbations such as global human induced greenhouse warming. Only direct perturbations will be specifically identified here.

2 Multi-scale habitat in coral reef environments

The habitat of an organism can be intuitively defined as the place where it lives, and which provides food, shelter and living space to the organism. More formally, a habitat can be defined as a spatially-bounded area, with a subset of physical and biotic conditions, within which the density of interacting individuals, and at least one of the parameters of population growth, is different than in adjacent subsets (Morris 2003). Then, habitat must be defined by the species and populations of interest, and in a manner that reflects underlying processes operating at appropriate spatial and temporal scales. Coral habitats can be classified according to an ecological function (e.g., nursery grounds) and/or according to a spatial or structural pattern (e.g., the distribution of living and non-living components). These approaches are not mutually exclusive, since function and structure are intimately linked at all levels of biological organization. A particular organism can occupy different habitats at different stages of its life and according to its activity (growth, foraging, sheltering and reproduction). This vision is compatible with a hierarchical, multi-scale presentation of reef habitats. For example, a colony is a habitat, but it is also submitted to a specific hydroclimate, which control a region. Since methods for monitoring and measuring indicators are generally scale-implicit, we propose a presentation by ecological-spatial scales (Fig. 1). This presentation makes easier to link directly a couple {habitat, disturbance} with its potential indicators (Sect. 4). Such a hierarchical decomposition is appropriate for complex systems (O'Neill et al. 1989; O'Neill 2001).

2.1 Level 1: Individual coral colony, community and reefscape

The level of habitat can be referred as a small-scale level: 1 to 10 m spatial unit. It corresponds to what most coral reef ecologists refer to when they use the concept of habitat. Individual coral colonies create a microcosm that offers shelter and food for various species. The success of coral recruitment depends upon a variety of environmental factors (temperature, light, sedimentation, salinity, nutrient regime, wave action and type of substrate). The spatial aggregation of coral colonies within a mono- or multi-specific community forms a "reefscape", which can be defined as an architectural unit. Within this unit of typically a width of a few tens of meters, habitats can be diverse, offering living space for various inhabitants (molluscs, crustaceans, fishes, algae, corals, etc.), which are involved in a complex web of ecological interactions.

2.2 Level 2: Reef zone, whole reef

We refer to this level of organization as the "meso-scale" level. Spatially, it typically ranges from few tens of meters to few kilometres. Depending on depth and hydrodynamic conditions, reefscape may change quickly or gradually within a reef zone and within the whole reef (Veron 1986). A complex reef may have several reef zones (fringing reef, barrier reef, reef flat, lagoon, patches, outer slope, channel, etc.), each of them potentially presenting several reefscapes. Conversely, a simple reef may have only a couple of reef zones and few reefscapes. Reef zones are large, yet, as a whole, they are under the influence of the same type of environmental or human forcing and will reflect the influence of perturbations in a relatively unimodal way. Thus reef zones are frequently considered as management units in integrated coastal management or monitoring programs.

2.3 Level 3: Island, region

We refer to this level of organization as the "large-scale" level. Spatially, it typically ranges from few hundreds of meters to hundred of kilometres. It embodies reef complexes, islands, archipelagos and groups of archipelagos belonging to the same unit in terms of biogeography or hydroclimate. Noteworthy at this scale is that interactions between the reef systems and other ecosystems (land, ocean) are implicit. A biogeography region can also be considered as one scale of habitat, since coral distribution and diversity depend on the environmental factors that trigger coral spawning, on the ocean-circulation patterns that physically control the dispersal of passive larvae and, ultimately, evolutionary processes (Veron 2000; Achituv and Dubinsky 1990). This scale is relevant here because it is often considered for management purposes. For instance, network of protected areas or conservation actions are defined within an island, a reef tract, or an archipelago under the same jurisdiction.

3 Human disturbance categories and their effects on coral habitats

The major anthropogenic disturbances affect the physical structure of coral habitats at each organisational level (Table 1). Here, a disturbance is an event that alters the physical environment and/or limits the availability of essential resources (e.g., available substrate) (Pickett and White 1985). This inventory may not be completely exhaustive, but it highlights the major perturbations that have been documented in coral reefs. Furthermore, it is not straightforward to discriminate the relative contributions of natural or man-induced perturbations to the resulting community structure (Grigg and Dollar 1990; Hatcher et al. 1989) since cascading or convoluted effects are common at various time-scales (Quinn and Dunham 1983; Karlson and Hurd 1993; Adjeroud 1997). This convolution of processes explains why management decisions and actions are not a simple endeavor (Fig. 2).

Coastal development, tourist activities, harvesting pressure, accidents and nuclear/weapon testing are the main stressors (Table 1). The increase of human populations on coastal areas promotes constructions and land reclamation for airports, roads, ports, marinas, houses and hotels. This does not only sacrifice reef zones (meso-scale disturbance), but often requires the extraction of coral boulders (small-scale disturbance) in areas that lack alternative building material (e.g., Brown and Howard 1985; Salvat 1987; White 1987). Land reclamation is not limited to modern or developing space-limited countries. Traditional way of life of the Kuna Yala Indians in San Blas archipelago (Panama), and limited space on inhabited islands also result in extensive coral mining and "reef flat filling" (Guzman et al. 2003). At small-scale (colony), tourists eager to enjoy coral reefs can have significant effects by trampling, anchoring, snorkelling, diving or boat groundings (Tilmant 1987; Hawkins and Roberts 1992; Clarke et al. 1993; Allison 1996; Jameson et al. 1999; Tratalos and Austin 2001; Zakai and Chadwick-Furman 2002). At small-scale (colony or community), harvesting using destructive fishing methods, such as dynamite or cyanide fishing, "muro-ami" (driving of fish into large nets attached to the reef) and traps, have a high negative impact (Alcala and Gomez 1987; Eldredge 1987; Gomez and Alcala 1987; Munro et al. 1987; Randall 1987; Johannes and Riepen 1995). Such practices are prohibited in some countries (e.g., Philippines) but laws are not always enforced (Alcala and Gomez 1987). Bombing for military training had a great impact on the reef framework, for instance in Los Vieques Islands (offshore Puerto-Rico). Accidents, which include ship grounding, had a harmful effect on coral reef habitat from colony scale to reef zone (Dollar and Grigg 1981; Hatcher 1984; Hudson and Goodwin 2001). Finally, nuclear testing performed on South Pacific atolls (e.g. Mururoa, Bikini) had significant impacts at meso-scale level

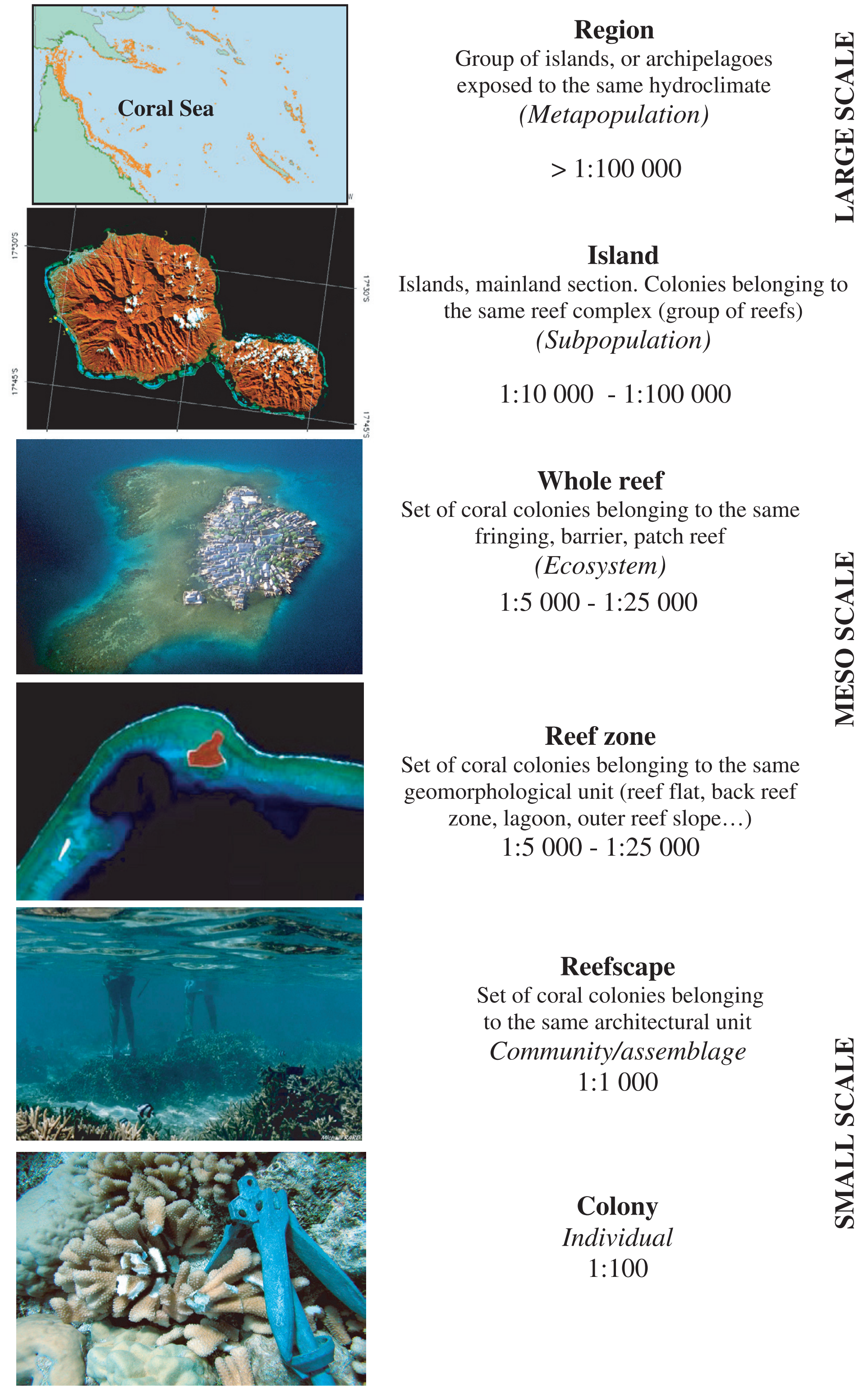

Fig. 1. Multi-scale presentation of coral reef habitats. For each spatial scale (on the right), the spatial pattern (in bold), the ecological function (in italic) and the representative scale are mentioned. Pictures illustrating the small and meso-scales present some related human-induced physical disturbances. Namely, coral colony debris due to anchoring, fishermen walking on a branching coral dominated lagoon reefscape in La Reunion Island, crater generated by atmospheric nuclear blast on the inner slope of the rim of Bikini atoll (Marshall Islands) and land filling of a patch reef flat using coral colonies from the forereef of the same reef in San Blas island (Panama). Island-scale is illustrated by Tahiti island where coastal barrier reefs and fringing reefs are dominant. Region scale is illustrated by the Coral Sea basin which is rimed by the major reef systems of the western Pacific (in orange, incl. New Caledonia, Vanuatu, Salomon Islands, Papua New Guinea and the Great Barrier Reef of Australia. Map source: Reefbase).

Table 1. Characteristics of the major anthropogenic perturbations that affect the physical structure of the habitat by mechanical destruction of stony corals. See Figure 1 for explanation of the spatial scales. Rs: reversible in the short term (years), Rl: reversible in the long term (decades), I: irreversible. 1: punctual, 2: punctual to chronic, 3: chronic. *: speculative factor, as no case-study was reported.

Type of perturbation	Spatial scale	Duration	Resilience	Creation of a new habitat	References
- Discharge of solid wastes	Colony to Reefscape	2	Rs	Possible	Laist (1987)
- Collecting				No	Grigg (1984), Wells and Alcala (1987)
- Dredging/coral mining - Coastal reclamation	Colony to reef zone	3	I to Rl	Possible	Bak (1978), Salvat et al. (1979), Wolanski et al. (1984), Marszaleck (1981b), Salvat (1987), White (1987), Brown and Dunne (1988), Shepherd et al. (1992), Clarke et al. (1993), Hawkins and Roberts (1994), White et al. (1997)
- Beach construction operation			I	No	Mergner (1981), White (1987)
- Outfall installation - Coastal defence installation			I	Possible	Mergner (1981), White (1987)
- Terrigenous inputs		2	Rs	No	Loya (1976), Mergner (1981)
- Offshore drilling			Rl	Possible	Hudson et al. (1982), White (1987)
- Displacement of coral boulders			Rs	Possible	Porcher (1993)
- Destructive fishing practices			I	Possible	Carpenter and Alcala (1977), Alcala and Gomez (1987), Polunin et al. (1983), Eldredge (1987), Gomez et al. (1987), Munro et al. (1987), Randall (1987), Galvez and Sadorra (1988), MacAllister (1988), Rubec (1988), Saila et al. (1993), Pauly et al. (1989), McManus et al. (1997), Riegl and Luke (1998), Erdmann (2000), Jackson et al. (2001), Fox et al. (2005)
- Trampling			Rs	Possible	Woodland and Hooper (1977), Liddle and Kay (1987), Kay and Liddle (1989), Hawkins and Roberts (1992)
- Boating/mooring - Snorkelling/diving			Rs	Possible	Davis (1977), Dollar and Grigg (1981), Tilmant (1987), Neil (1990), Hawkins and Roberts (1992, 1993), Clarke et al. (1993), Rinkevitch (1995), Allison (1996), Jameson et al. (1999), Tratalos and Austin (2001)
- Ship grounding		1	Rl	Possible	Hatcher (1984), Bablet and Perrault (1987), Littler and Littler (1999), Bruckner and Bruckner (2001), Hudson and Goodwin (2001)
- Nuclear blasts testing	Colony to whole reef	2	I	Possible	Lewis (1971)
- Oil spill	Colony to region	2	Rs	No	Johannes et al. (1972), Reimer (1975), Loya (1976), Loya and Rinkevich (1980), Knap et al. (1983), Dodge et al. (1984), Fucik et al. (1984), Bak (1987), Loya and Rinkevich (1987), Burns and Knap (1989), Jackson et al. (1989), Guzman et al. (1991), Guzman and Jimenez (1992), Burns et al. (1993), Guzman and Holst (1993), Epstein et al. (2000), Stejskal (2000)
- Introduction of alien coral species*		1	I	Possible	Eldredge (1987)

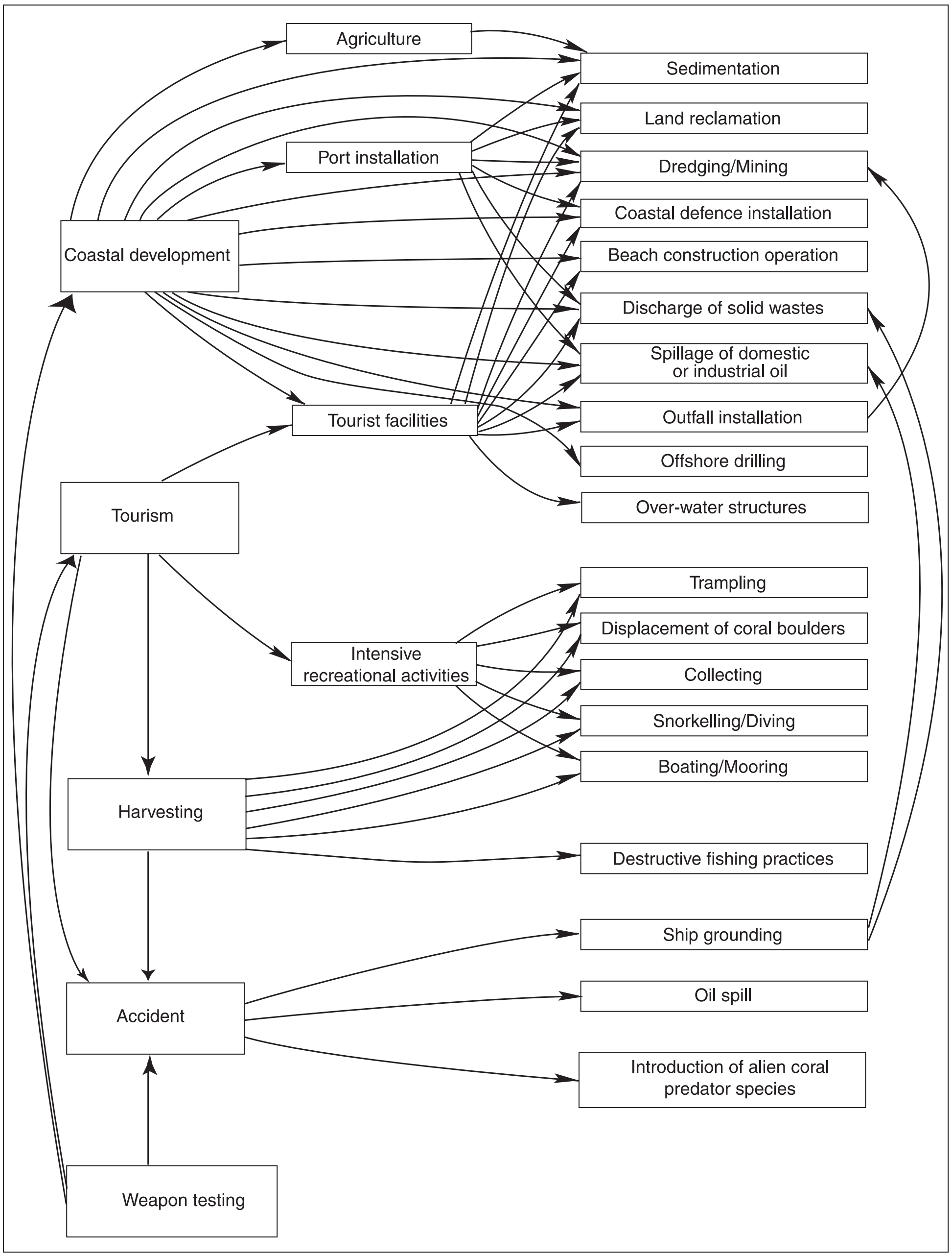

Fig. 2. Cascading causes of coral reef physical degradation. As an example of this "domino effect", nuclear weapons tests done 40 years ago have themselves directly damage the physical foundation of pinnacles or atoll rims, but they are also the initial factor that makes now possible the lucrative wreck-diving activities in "nuclear lagoons" such as Bikini, which itself promote fishing for feeding local and tourist populations and tourist facilities development, which itself enhance the risks of accidents.

on the structure of several sections of the rims and large pinnacles. In Mururoa atoll (French Polynesia), cracks appeared in lagoon bommies and the southern rim collapsed due to the explosion shock wave (Bouchez and Lecomte 1995). In Bikini atoll (Marshall Islands), the first aerial explosions created huge craters along the atoll's rim (Fig. 1).

The human disturbances listed above have various effects that differ in their mode of action, their spatial scale, their intensity and their duration. The same exact disturbance may have a different effect (or perturbation) depending on the moment it strikes the reef and where. For example, dredging and terrigenous inputs, which have important impacts on fringing reef communities of high islands, have generally a negligible impact on the outer slope of high islands and atolls (Salvat et al. 1979; Augustin et al. 1997; Adjeroud et al. 2002; Fabricius 2005). In contrast, diving, ship grounding and nuclear blast testing may affect lagoonal as well as outer reef slope coral communities. Despite their negative effects, some modes of perturbation may effectively create a new coral habitat. This aspect is particularly important for the management and rehabilitation of disturbed areas (Salvat et al. 2002). In general, the effects of disturbances depend on the temporal and spatial reference scales under consideration, their frequency, the ecological history of the site (e.g., chronology of the previous perturbations), the structure (growth forms, etc.) of the impacted communities, the geomorphology and depth of the reef zone, the confounding influence of any other physical or biotic stresses (Connell 1978; Hughes 1989; Grigg and Dollar 1990; Karlson and Hurd 1993; Meesters and Bak 1993; Hughes 1994; Bak and Nieuland 1995; Connell et al. 1997).

These perturbations may have short-term or immediate direct consequences, as well as long-term and indirect effects mostly at small and meso-scales. Most of the perturbations, compiled in Table 1, affect coral habitats at these two scales. We have not identified a direct human-induced physical perturbation that is specific to the large-scale level. It is only through repetition or generalisation of small-scale disturbances, throughout a region or an island, that human induced physical perturbations become large-scale level disturbance. Otherwise, there are several examples of meso-scale level disturbances that have second-order large-scale influences. For instance, the dredging of a pass in an atoll is a reef-zone physical disturbance, but the resulting modification of the water exchanges between lagoon and ocean may have significant consequences on the equilibrium of the whole island. Several anthropogenic disturbances may look relatively minor compared to natural disturbances, such as cyclones or submarine earthquakes (Hatcher et al. 1989). However, human impacts, when combined with natural disturbances, may significantly affect the recovery process of a reef, particularly since they are often chronic rather than infrequent (Connell et al. 1997).

Some of the disturbances are well documented (e.g., destructive fishing practices), whereas other were rarely studied (e.g., bombing or nuclear blasts testing) (Table 1). In general, physical disturbances result in a reduction in the three dimensional structural complexity of the reefs, reducing the availability of shelters for associated organisms (Aroson and Swanson 1997). Physical destruction may not necessarily kill coral colonies entirely. However, even partial mortality and weakening may favour pathogens infestation and reduce the reproductive potential of individuals (Hunte and Wittenberg 1992; Ward and Harrison 2000; Hall 2001; Nugues and Roberts 2003). Even if coral colonies are not directly damaged, the sediment and rubbles produced by human activities may cover and bury the coral community in place ("smothering" effect). Discharge of solid wastes and oil spill may also cover, totally or partially, the coral colonies in place. There is no real evidence that oil floating above the corals causes noticeable damage, but one may assume that corals living near the surface can be coated by oil and consequently impacted in their physical structure. For further explanations on the perturbations and their effects, we have listed the most relevant literature.

It is often difficult to estimate the duration of the effects associated to a particular perturbation. In fact, several perturbations, such as trampling, collecting, destructive fishing practices or bombing have effects that may be infrequent or chronic. However, other perturbations, such as dredging and beach construction operation, are often chronic, whereas ship grounding can be considered as infrequent perturbations. The impacted coral communities may be irreversibly damaged, or may recover partially or totally. The resilience (i.e., capacity to recover) of the coral community depends on the characteristics (intensity and duration) of the perturbation and on the initial community or colony structure (Connell et al. 1997). It depends also on functional processes (such as herbivory), and the functional overlap (or redundancy) of multiple species in an ecosystem (Nyström et al. 2000; Nyström and Folke 2001; Belwood et al. 2004), on the availability and abundance of local larvae, and on the connectivity with other reef habitats and larval supply (Obura 2005). The concept of "spatial resilience" is differentiated from that of ecological resilience by recent authors (Nyström and Folke 2001; Bengtsson et al. 2003), most important in terms of the spatial scale over which it is applied. Ecological resilience generally applies to properties within the spatial boundaries of an ecosystem. In coral reef studies, this is generally considered to extend up to tens and sometimes hundred kilometres (Obura 2005). Spatial resilience extends beyond this to include large scale functions and processes beyond boundaries of an ecosystem unit. For a coral reef, this would include the processes of connectivity to other reefs by currents and larval dispersal, large-scale oceanographic phenomena such as upwelling in adjacent system and other features that may occur over hundreds to thousands of kilometres (Obura 2005). Furthermore, chronic and low level perturbations may cause more damage to the reefs in the long term than discrete and highly destructive events, because the former do not allow sufficient time for recovery (Davis 1977; Dustan and Halas 1987; Tilmant 1987). Nevertheless, dredging, coastal reclamation, beach construction operation, and coastal installations generally imply that impacted communities have few chances to return to their initial state (i.e. irreversible impacts) (Table 1). For other discrete and weak perturbations, such as collecting, mooring and boating, or snorkelling and diving, impacted communities may return rapidly (years) to their initial structure. For larger scars, due to large ship grounding for instance, recovery time may be higher (decades). In some case, the extent of the disturbances may not prevent communities to return to their initial structure. For destructive fishing practices, small-scale impacts (e.g., individual blasts) do not alter significantly the community structure, whereas generalisation of these impacts at larger scale (e.g., several densely spaced blasts over large portions of a reef) may eventually alter the community structure and the environment, and thereby greatly reduce the potential and rate of recovery (McManus et al. 1997; Riegl and Luke 1998).

Some perturbations may create a new coral habitat (Table 1). For example, dredging, coastal reclamation, sewage discharge and coastal defence installations, or offshore drilling may create a new substrate that can be colonized by corals, thus forming a habitat for other reef species. Trampling, displacement of coral boulders, boating/mooring, snorkelling/diving, ship grounding, destructive fishing practices, discharge of solid wastes, and nuclear blasts testing may form accumulation of dead and live coral rubbles, which may provide habitat for certain fish species (Riegl and Luke 1998). In contrast, beach construction operations, terrigenous inputs, collecting, and oil spill have never been associated with the creation of new habitats. Historical trajectories of reef degradation extending back thousands of years, provide a powerful tool to explain global patterns and causes of ecosystem collapse, as well to predict future ecosystem states, through an understanding of the sequence of species and habitat loss (Pandofi et al. 2003).

4 The measure of physical disturbances on coral reef habitats

4.1 Scale-dependent indicators of disturbance effects on coral reef habitat structure

The most usual indicators are related to habitat and/or to physical disturbance of habitat (Table 2). Indicator variables are listed according to the spatial scale of the descriptor they are expected to capture. We focus on the three most common categories of descriptors:

- *the stony coral* itself;
- *reef fishes* represented by Chaetodontidae among which many species are coral feeders and dependent of the coral reef habitat, and
- *the human uses* which could have an impact on coral reef habitats. Various variables are proposed as indicators to evaluate the impact of disturbance on these descriptors. We also indicate the methods generally used to obtain data on these variables (see English et al. 1994 for details on the classical methods used to monitor coral reefs), and the sampling unit of the method.

At colony scale (*stony corals* descriptors), the reproductive output (number of planulae per tissue volume) could decrease after repeated breakage (Rinkevich and Loya 1989; Van Veghel and Bak 1994; Rinkevich 1995). This decrease of spawning rate could be followed by a decrease in recruitment rate (number of new corals settling per substratum unit) (Richmond 1997; Zakaï et al. 2000). Recruitment intensity itself may be a useful measure to check if physically damaged reefs are in a way of recovery or not (Kojis and Quinn 2001). To date, the possibility of using other aspects of coral biology as indicators of environmental stress has seldom been explored. Noteworthy are measurements of coral tissue abrasion (damaged tissue that exposed the underlying intact coral skeleton, according to Riegl and Velmirov 1991; Hawkins et al. 1999; Zakai and Chadwick-Furman 2002) or partial mortality in massive corals (percentage of dead surface area per colony according to Brown and Howard 1985; Nugues and Roberts 2003). Nugues and Roberts (2003) proposed the 50%-threshold in dead coral tissue per colony as a simple stress indicator. Such variables may provide a rapid and effective means of detecting sediment stress on coral reefs, for example after dredging operations.

At reefscape or reef zone scale (corresponding to community/assemblage at ecological level), live coral cover and colony number are widely used in coral reef monitoring programs to assess coral reef health (e.g., Global Coral Reef Monitoring Program, Reef Check). The ratio of standing dead coral cover to total cover of both live and dead corals (Gomez et al. 1994) or linear quotes of live coral cover (>75%: excellent, 50–75%: good, 25–50%: fair, <25%: poor) (Gomez and Yap 1988) are also used. Their use as indicators of reef condition in "snapshot" survey is based on the assumption that "healthy" reefs should have high coral cover and coral density (Gomez and Yap 1988; Aronson et al. 1994). However, this assumption could be erroneous in some cases (Thomason and Roberts 1992). Moreover, sites with very high percentage of live coral cover are frequently composed of large monospecific stands of corals, with low coral diversity and spatial complexity (Roberts and Ormond 1987). Nevertheless, in some cases, the percentage of live branching corals or branching associated to live tabular corals has been used to characterise habitat complexity (Chabanet et al. 1997; Lewis 1998). Percentage of live coral cover could be used with other indices such as conservation classes that more accurately predict habitat complexity (Edinger and Risk 2000). Conservation value are estimated using r-K-S (ruderal/competitor/stress-tolerators) ternary diagrams based upon the relative abundance of standardized coral morphology categories: *Acropora* corals as disturbance-adapted ruderals (r), branching non-*Acropora* corals and foliose corals as competition-adapted (K) and massive and submassive corals as stress-tolerators (S). Then, reefs are classified from class 1 ($S > 60\%$) to class 4 ($\%\ r, K, S$ approximately equal). Other authors also estimated habitat complexity from coral morphological diversity (Roberts and Ormond 1987). Indexes of structural complexity or rugosity (ratio contour tape lengtht on stretched tape lengtht) have been also suggested (Risk 1972; Luckhurst and Luckhurst 1978; Dahl 1988). Williams and Polunin (2000) estimated the structural complexity of the substratum on a 6 point-scale (0: no vertical relief to 5: exceptionally complex with high coral cover and numerous caves and over-hangs). Related also to colony scale, "breakage variables" could be used as an indicator of diving pressure in the form of broken coral rubble (Hawkins and Roberts 1994, 1997) or loose fragments adjacent to branching colonies (Zakai and Chadwick-Furman 2002).

At whole reef scale (corresponding to ecosystem at ecological level), clear-cut zonation patterns in a form of serial change in community structure with an increase of water depth are long-established features of shallow water communities. Undisturbed situations provide clear sequences of community changes along transects, while the sequences appear disrupted after dredging operations (Clarke et al. 1993). Following this example, Clarke et al. (1993) proposed an index (Index of Multivariate Seriation) that measures the degree to which a coral community compares relative to a linear sequence. Furthermore, attributes such as "Reef Quality Index" (quality not acceptable if hard coral cover $< 30\%$, recently broken coral >5%, recently dead coral $> 3\%$ and coral rubble cover $> 5\%$ according to Jameson 1998) or "Coral Damage Index" (quality not acceptable if broken coral colonies $\geq 4\%$, coral rubble cover $\geq 3\%$ according to Jameson et al. 1999, 2001) could be used globally to gauge the severity and extent of physical damages, and focus managers on areas that need dive site management programs (e.g. mooring buoys).

Using *fish communities* descriptors, Chaetodontidae (butterflyfish) have been proposed as indicator of coral reef "vitality" (e.g. Reese 1981; Sano et al. 1984; Öhman et al. 1998). The underlying simple hypothesis is that since some feed on corals, if corals decline, then populations of corallivorous butterflyfish should also decline or change their feeding

Table 2. Descriptors (stony corals, butterflyfish and human uses), indicators of the impact of physical disturbances related to spatial scale (and ecological function in italic). The major references, the sampling size and the protocols usually used to obtain data of the descriptor attribute are also mentioned. LIT: Line Intercept Transect, PIT: Point Intercept Transect, RST*: Remote Sensus Techniques in development. Ref: same ref. than for abundance except the ones in italic.

	Spatial scales	Indicators	References	Sampling size	Protocols
STONY CORALS	**Colony** *(inidvidual)*	*Reproduction* Reproductive output, settlement rate	Van Veghel and Bak (1994), Richmond (1997), Zakai et al. (2000), Fox (2004)	100–200 cm^2	Microscopic examination, settlement plates (tiles) collected *in situ*
		Damage Tissue abrasion	Brown and Howard (1985), Hawkins and Roberts (1997), Hawkins et al. (1999), Zakai and Chadwick-Furman (2002)	10 m	Transects (LIT), photographs, RST* (reflectance)
		Partial mortality in massive corals	Ginsburg et al. (1996), Nugues and Roberts (2003)	1–40 m^2	Belt transects, quadrats, photographs
	Reefscape / Reef zone *(Community/ assemblage)*	*«Reef vitality»* % hard coral cover	De Vantier (1986), Gomez and Yap (1988), Grigg and Dollar (1990), Naim (1993), Aroson et al. (1994), English et al. (1994), Chabanet et al. (1997), Lewis (1997, 1998), Mumby et al. (2001)	20 m 1–300 m^2 ± 100 km^2	Transects (LIT, PIT) Quadrats, belt transect, video mapping Manta tow, Hyperspectral airbone survey*
		Coral vitality index	Dustan (1994), Gomez et al. (1994)		
		Morphology % lifeform % tabular and/or branching coral	Edinger and Risk (2000) Chabanet et al. (1997), Lewis (1998), Joyce and Phinn (2002)	20–50 m 100–300 m^2	Transects (LIT), Video mapping, Bidirectional reflectance of corals*
		Architecture Structural complexity, rugosity	Risk (1972), Luckhurst and Luckhurst (1978), Williams and Polunin (2000), Brock et al. (2004)	25 m 1 m^2	Transects (LIT) Lidar airbone survey*
		«Breakage» *% broken corals (BC)* *% BC adjacent to branching corals*	Rogers et al. (1983), Hawkins and Roberts (1994, 1997) Zakai and Chadwick-Furman (2002)	20 m 1–10 000 m^2	Transects (LIT, PIT) Belt transect, quadrats (± photographs)
	Whole reef *(Ecosystem)*	*«Zonation pattern»* Index of Multivariate Seriation	Clarke et al. (1993)	10 m	Transects (LIT)
		Aesthetic Reef Quality Index (RQI) Coral Damage Index (CDI)	Jameson (1998) Jameson et al. (1999, 2001)	10–20 m ± 100 km^2	Transect (LIT) Daily observations (boats, divers, snorkelers…)
FISHES	**Reefscape / Reef zone** *(Community/ assemblage)*	Abundance	*Reese (1981)*, Sano et al. (1984), Williams (1986), Roberts and Ormond (1987), Hourrigan et al. (1988), Bouchon-Navaro and Bouchon (1989), *Fowler (1990), Cox (1994)*, Öhman et al. (1998), Cadoret et al. (1999)	20–50 m 40–200 m^2	Transects (LIT, PIT) Belt transect, point counts, video
		Species richness	Ref, Bell and Galzin (1984), Findley and Findley (1985)		
		Territory size, monogamous pairs occurrence	Reese (1981), Hourrigan et al. (1988), Crosby and Reese (1996)		
USES	**Whole reef**	Diver carrying capacity	Dixon et al. (1993), Chadwick-Furman (1996), Hawkins and Roberts (1997), Zakaï and Chadwick-Furman (2002)	± 100 km^2	Census from plane or boat Questionnaires, survey of dive centres
	Island	Diver preference	Andersson (1998), Williams and Polunin (2000)	± 100 km^2	Questionnaires, underwater survey (fish and habitat)

behaviour. However, in some cases, the actual correlation was low (Roberts and Ormond 1987; Fowler 1990). Nevertheless, species richness and abundance of chaetodontids have often been included into monitoring programs since volunteers without specific experience can easily conduct surveys on these easy-to-identify populations (Hodgson 1999; Conand et al. 2000; Crosby and Reese 1996).

The human uses of coral reef ecosystems is represented here by recreational scuba diving activities which is an important and growing component of the tourism market (Moberg and Folke 1999). The diver preferences for certain reef attributes were classified by Williams and Polunin (2000). These authors rank 14 attributes (e.g. "reef structure", "big fish", "variety of fishes", "variety of corals", "coral cover", "unusual fish", "sponges", etc.) on a scale from 0 (not at all important) to 5 (most preferred). Furthermore, some authors used the concept of "diver carrying capacity" which is the number of dives per site and per year that a reef can tolerate without becoming significantly degraded (Dixon et al. 1993; Chadwick-Furman 1996; Hawkins and Roberts 1997). Hawkins and Roberts (1997) suggests that reefs in the Red Sea and Caribbean can sustainably support around 5000−6000 dives per site per year, but that greater levels of use cause a rapid rise in diver damages.

Most of the variables measure disturbance effects on scale ranging from individual to community (Table 2). There is a paucity of indicator variables measuring habitat attributes at large spatial scale. These variables are less common because of the cost linked with this kind of studies and the difficulties to carry them out. Using remote sensing techniques, environmental impacts could be easier to measure at larger scales. For instance, remote sensing observations provide unambiguous measurement of changes in shorelines and alteration of reef zones due to land reclamation, dredging or waste disposal (e.g. the so-called "trash island" in Male atoll, Maldives). Several of these techniques are still largely exploratory and have not been validated on a sufficient number of case studies. Nevertheless, we mention key reports that clearly offer interesting perspectives in measuring synoptically coral mortality, using airborne hyperspectral data (Mumby et al. 2001), reef rugosity using LIDAR, i.e. airborne laser (Brock et al. 2004), habitat diversity and patchiness using high resolution satellite imagery (Andréfouët et al. 2003), and changes in habitat structure using time-series of images (Palandro et al. 2003). In addition, at colony-scale, *in situ* optical techniques now investigate the possibility to diagnose early a perturbation using changes in the reflectance or fluorescence of the colonies. Changes in optical measurement reveal changes in pigmentation potentially linked to a stress (Yamano et al. 2003). Finally, current research also assesses the variability of colony-scale reflectance according to their morphology (Joyce and Phinn 2002).

4.2 Strategy and criteria for assessing and monitoring coral reef habitat

Managers have to consider various options when conceiving an assessment of a coral habitat. Our goal is not to propose an exhaustive guideline on indicator selection, but to provide references and underline key concepts as sequentially presented (Fig. 3).

It is common sense to state that selection of the most appropriate bioindicators for a particular assessment or monitoring program depends on the objectives of that program (Dale and Beyeler 2001). We identified three broad categories of objectives (Fig. 3):

- To monitor trends in habitat conditions across time, in order to measure whether specific management actions improved habitats conditions, or whether the habitat has reached a level of disturbance for which some type of actions are required (*Objective O1*). The monitoring can be specifically designed to address one pre-identified disturbance, or can target a wide spectrum of disturbances.
- To make a single assessment of the initial status of the environment (*Objective O2*). This status describes habitat conditions after a perturbation has been identified (e.g. ship grounding), or draws an initial picture of habitat conditions before some type of planed disturbances occur (e.g. dredging). This objective can be a prelude to objective O1 (monitoring).
- To improve knowledge and use of existing indicators or test new indicators *(Objective O3*).
  This methodological objective is generally designed to improve the cost-effectiveness of currently applied methods. It aims to test experimentally some hypothesis or it tries to identify hypotheses that will be tested afterwards.

In addition, a management plan can be designed specifically to address one type of disturbance (*Hypothesis H1*), but some organisations have launched general monitoring plan at large scale for an entire region without a specific disturbance in mind (*Hypothesis H2*). The objectives will have to be carefully considered within these broad limits.

A variety of indicators with different generic properties need to be considered (Jope 2001). *Stressor indicators* measure the stressor itself (e.g., sediments in the water column after a dredging operation). The drawback is that there is no indication of consequences on the habitat themselves. *Exposure indicators* measure the amount of stressor to which the habitat is exposed (e.g., number of reef-walkers in a tourist area). These could be used as a diagnostic indicator as they are specific to the stressor. *Response indicators* measure changes occurring on the habitats (e.g., coral cover); however they do not necessarily identify the cause of the changes. The specificity of a response indicator is a key criterion. Response indicators can be specific and have a threshold or gradual response to a specific type of disturbance. Non-specific indicators will reveal that something is happening but not the causality. However, a range of non-specific indicators may be better than one specific indicator to draw the status of habitats at different scales. Most of the variables or attributes are *response indicators* (Table 2) as they measure changes occurring in the system (Jope 2001). They provide a better indication of ecological attribute conditions (habitat component), than ecological effects due to a specific disturbance. For example, by the time census methods have detected broken corals, these corals have already suffered damage and further efforts must focus on preventing more damage and death. Conversely, "diver carrying capacity" may be considered as *exposure indicator* as it measures

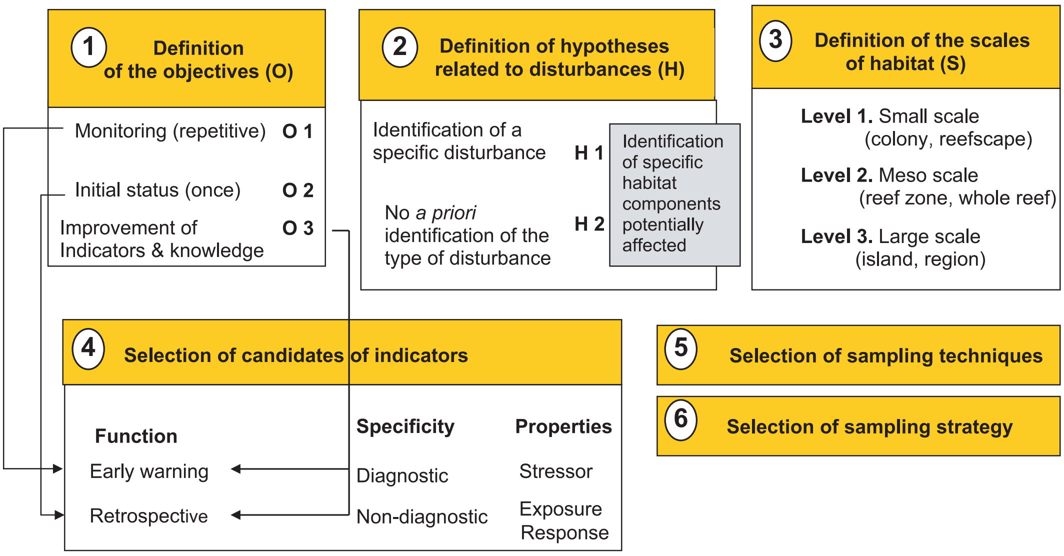

Fig. 3. Framework of sampling design for assessing indicators (e.g. coral reef habitat).

the amount of stressor to which the system is exposed. If specific to the stressor, this indicator may be considered as a diagnostic indicator. Non-diagnostic indicators may reflect changes (Rapport et al. 1985; Jope 2001), but not specifically to one of the disturbances (Table 1).

To complete this general classification of indicators, other properties such as sensitivity (the capacity to reveal gradations in response to stress) are of interest (Jameson 1998). This anticipatory quality specifies whether the indicator can provide *early-warning* signal (useful in case of monitoring trends in environmental conditions over the time), or is *retrospective*, providing evidence of ecosystem change after the change has occurred (Rapport et al. 1985).

The scale of work is one of the main considerations. Scale in this context depends directly on the objectives and the hypotheses which depend on the considered specific disturbance. Willingness to draw a general picture of coral habitats (Objective O2) without specific disturbances in mind (Hypothesis H2) will imply that a wide range of scale needs to be addressed. For instance, reefscape (or community) to regions can be studied by multiplying the numbers of regional sites where community measurements will be performed. Unfortunately, no single indicator is applicable directly across all spatial scales of concern (Dale and Beyeler 2001). Therefore, combining indicators at different levels of the biological organisation represents an optimal strategy, because these measures serve different purposes, from individual to communities (Hallock et al. 2004). Measures on colony potentially provide the earliest warning of possible deterioration while measures on community give a better indication of the ecological importance and magnitude of the disturbances and their consequences on communities including humans (Rapport et al. 1985; Underwood and Peterson 1988). Indicator selection depends on several additional criteria: the intrinsic quality of the measure itself (depending of the sampling techniques and of the choice of the variable) and the "effectiveness" that gather sampling strategy and the statistical analysis.

4.3 A hierarchical concept of disturbance in coral reefs in perspectives

Using a multi-scale approach allows to present the various indicators of (physical) disturbances in a logical suite. However, there is still a lack of explicit relationship between the observed physical impacts on reefs and what these impacts means in terms of alteration of the biological processes occurring on the reef. Another framework focussing on ecosystem functions and integrating the notions of disturbance, levels of organisation, scale, and indicators of perturbations could be a next logical step. Pickett et al. (1989) have proposed such a conceptual framework. By organising each ecological question within a so-called hierarchical model, they distinguish among entities (the object of interest, susceptible of being disturbed), function (set of interactions among entities), and structure (resulting complex of interacting entities). Though conceptually interesting and theoretically better suited to analyse multi-stressor effects throughout different ranges of scales and functions, the design and selection of indicators remain quite problematic. It is definitely recommended that scientists try to visualize the integration of methods within such conceptual frameworks (Hallock et al. 2004). However, the amount of indicators practical for managers remains limited, but new developments still occur. For instance, recent advances in molecular biology should aid in the accurate diagnostic of coral condition by "visualizing" coral stress using Molecular Biomarker System (MBS) or gene expression. For the first step, MBS was use to assess the physiological status of coral challenged under heat stress, using specific cellular and molecular parameters (Downs et al. 2000). However, transplantation experiments must be conducted to examine how stressors in natural populations induce gene expression and to determine whether these potential diagnostic indicators are effective and specific.

5 Conclusion

Indicators are essential tools for monitoring the state of the coastal environment. They can inform managers and policy makers of the effectiveness of strategies in achieving sustainability and need to be based on rigorous scientific, social and economic research. However, the suite of options for managers is limited. This review shows that the majority of the indicators of human-induced physical disturbances are non-specific. They can be categorized in few categories based on their properties, but they can't solve all problems. We followed a multi-scale discussion which eventually shows the difficulties for the managers and scientists to have a continuum of answers and indicators across space and time. Tools are needed to identify and rank coral responses to multiple stressors and to determinate which stressors having the greatest effects. Theoretically, a hierarchical scheme could be a logical new integrating scheme since they target functions across scales, but similar models are still in their infancy in the case of coral reef ecosystems. On a practical standpoint, managers and policymakers still need to understand the effects of man-induced disturbances, be able to properly assess these damages, and develop subsequent restoration and conservation efforts on reefs under their stewardship.

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