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TRADITIONAL VS NEW APPROACHES FOR ASSESSING CORAL HEALTH: A GLOBAL OVERVIEW AND THE PARADIGM OF FRENCH POLYNESIA

Laetitia Hédouin
USR3278 EPHE CNRS CRIOBE, BP 1013, Moorea, French Polynesia. Laboratoire d'Excellence "CORAIL", BP 1013 Papetoai, Moorea, French Polynesia, Laetitia.hedouin@criobe.pf

Véronique Berteaux-Lecellier
USR3278 EPHE CNRS CRIOBE, BP 1013, Moorea, French Polynesia. Laboratoire d'Excellence "CORAIL", BP 1013 Papetoai, Moorea, French Polynesia

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TRADITIONAL VS NEW APPROACHES FOR ASSESSING CORAL HEALTH: A GLOBAL OVERVIEW AND THE PARADIGM OF FRENCH POLYNESIA

Laetitia Hédouin[1, 2] and Véronique Berteaux-Lecellier[1, 2]

Key words: coral heath, indicator, French Polynesia, stress.

ABSTRACT

Today, there is increasing concern regarding the capacity of Scleractinian corals to sustain the growing number of insults associated with global and local changes (*e.g.* global warming, ocean acidification, pollution). If corals are to exist, there is an urgent need to use indicators of coral health that provide insight into early sub lethal shifts in corals before the irreversible effects of exposure manifest at the population and community levels. This paper will provide an overview of the most relevant and appropriate indicators of coral health currently used in traditional monitoring programs (traditional approach) or those that could be used in a near future to improve assessment of coral health (new and proactive approach). In addition, by using French Polynesia coral reefs as a study case, this paper will present how coral health was assessed in the past and how it will be in a near future.

I. INTRODUCTION

Coral reefs are some of the most diverse, biologically complex and economically important marine ecosystems on earth. Scleractinian corals are the reef building species of these ecosystems. Unfortunately there is today a deep concern as to whether corals will survive shifts in the marine environment associated with global changes (global warming and ocean acidification; *e.g.* [12, 103] and local stressors (*e.g.* sedimentation, pollution, eutrophication; [31, 42, 46]. Changes in environmental conditions have serious implications for corals and some of the adverse effects are coral bleaching, decrease in growth, reduced reproductive outputs and in severe cases, coral death and loss of biodiversity, *e.g.* [22, 31, 60, 93]. At a local scale, corals of French Polynesia were affected by several bleaching events in the past (1983, 1987, 1991, 1994, 2002, 2003, 2007) [4, 6, 97], *Acanthaster planci* (crown-of-thorns starfish) outbreaks (1979-1986, 2006-2009) [56, 57], and cyclones (1983, 1991, 2010) [56, 97]. In addition to these disturbances, corals around the Society archipelago (the most populated and industrialized archipelago of French Polynesia) are also threatened by coastal development and changes in land use due to increasing anthropogenic pressures. Beside a scarcity of data on the degree of local stressors in French Polynesia, some coastal reef areas are subjected to severe sedimentation (up to 100 g m^2 d^{-1} [85]), inputs of nutrients [41], metal discharges (*e.g.* Cu levels up to 1140 mg kg^{-1}, Ni concentration up to 177 µg g^{-1} measured in reef sediments) [23, Hédouin, *personal data*] and pesticide pollution [80]. The health of corals in French Polynesia is or will be (in a near future) increasingly threatened by global stressors, local stressors, or by the combination of both. In this context, the question is how can we assess coral health within a manageable timeframe that allow implementing management actions in order to conserve coral biodiversity?

Health is defined as a relative occurring along "a continuum between two endpoints: absolute health (a state in which all functions are optimal) and death, which occurs when functions are so severely impaired that life is impossible. Between the two points there is a region of relative health that blends imperceptibly into a region that we can define as disease" [112]. The aim of this paper is to provide an overview of the most relevant and appropriate indicators of coral health currently used in traditional monitoring programs or those that could be used in a near future to improve assessment of coral health. Altogether such indicators will contribute to global projections and therefore to predictive models such as the recent work on determination of temporary refugia for coral reefs [99]. In addition, by using French Polynesia coral reefs as a study case, this paper will review how coral health was assessed in the past and how new indicators under development and innovative approach could improve the assessment of coral health in these islands.

Paper submitted 08/31/11; revised 07/03/13; accepted 08/13/13. Author for correspondence: Laetitia Hédouin (e-mail: Laetitia.hedouin@criobe.pf).
[1] USR3278 EPHE CNRS CRIOBE, BP 1013, Moorea, French Polynesia.
[2] Laboratoire d'Excellence "CORAIL", BP 1013 Papetoai, Moorea, French Polynesia.

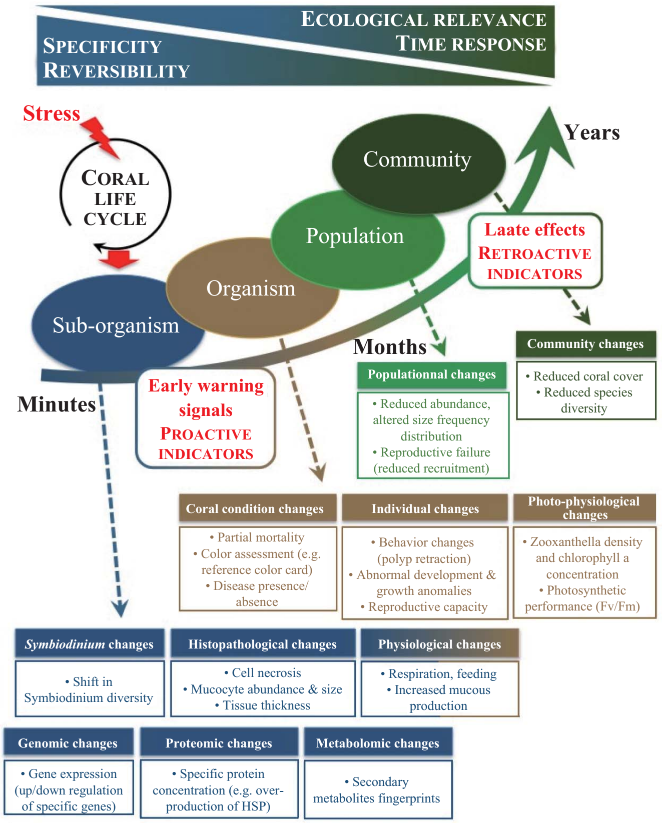

Fig. 1. Coral responses to stress at different levels of biological organization: from early warning signals to late effects.

II. OVERVIEW OF INDICATORS AVAILABLE TO ASSESS CORAL HEALTH

When exposed to environmental stressors, all animals initially manifest the exposure as shifts in gene expression. If the stressor persists, these changes at the molecular level are reflected at ever increasing levels of biological organization, first in cells, tissues and organ (sub-organismal changes, See Fig. 1), then in organisms (by *e.g.* behavior changes), leading eventually as reduced growth and reproductive failure; and finally to death as the coping mechanisms are overwhelmed (Fig. 1). Thus, signs of stress are visible at different biological organization scales (from early sublethal changes in the gene expression to much later manifestations of exposures like coral mortality and changes in community structure) and across a range of timeframes (from minutes to years) (Fig. 1).

1. Indicators at the Community and Population Levels

Traditional monitoring approaches focus on the latter end of this timescale and commonly evaluate the response of corals to stress at population and community levels. Visual transect surveys allow assessing rapidly and easily the coral abundance, coral cover, and genera composition in a given station. These indicators are currently used in several monitoring programs locally (*e.g.* CRAMP in the state of Hawaii [48], Polynesia Mana Network in French Polynesia, Australian Institute of Marine Science Long-Term Monitoring Program in Australia [22, 68]), and worldwide (*e.g.* ReefCheck). These monitoring networks provide valuable and detailed descriptions of coral health status over long-term changes, from months (*e.g.* recent mortality) to years (*e.g.* changes in composition, coral cover). Effects of stress on coral health are thus easily estimated with the decrease of coral cover (*e.g.* a major decline of coral cover on the Great Barrier Reef from 28 to 13.8% over the period of 1985-2012 [22]) or with the reduction in coral diversity over time (species richness decreases by 61% after the 1998 bleaching event at Sesoko Island [60]; species richness decreases up to 60% in reefs subjected to land-based pollution, [29]). Such coral health indicators are very successful at documenting degradation of coral health *a posteriori* (*e.g.* death of corals, loss of species) and are qualified as "retroactive" indicators. Despite the high ecological relevance of this traditional approach to assess coral health, these changes at the population and community levels unfortunately tend to be less sensitive and less specific than changes occurring at the subcellular or individual levels (Fig. 1). Indeed, since they are generally detectable when irreversible environmental damages have already occurred, they do not provide information on coral health status that is temporally relevant to proactively managing the resources.

For this reason, there is an urgent need to shift from observation of coral decline to proactive assessment of coral health [27] in order to obtain relevant information on a shorter timeframe. Such proactive approach for assessing coral health provides the capacity to implement management strategies aiming at reducing environmental stressors before the exposures kill corals. A large number of works has emerged this last decade on the response of corals to different global (*e.g.* temperature, acidification) and local stressors (*e.g.* pollution, salinity, sedimentation) at lower levels of biological organization, from molecules to individual changes. These studies highlighted a multitude of proactive indicators of coral health, each of them characterized by advantages and disadvantages. This paper, as a non-exhaustive review, will only discuss changes in coral biology that are, to our personal point of view, the most promising and relevant indicators of coral health.

2. Indicators at the Sub-Organism Level

1) Genomic Changes

Environmental stressors will affect the normal biological function of the corals and the most immediate effects, after activation of latent anti-stress cellular pathways, will be changes in gene expression initiated to offset the impacts and return the biology to the homeostatic condition. The discovery of new gene-based biomarkers relies on the availability of genome information. However, genomic approaches were limited during years by the paucity of genetic information. Recently due to the development and optimization of sequencing technologies [61, 81] and their growing affordability, this gap is now disappearing and the new area of next-generation sequencing is delivering more and more information for a number of representative corals. Two whole genome sequencing projects of the coral genus *Acropora* [87] (www.coralbase.org) and several coral transcriptomes (*e.g. Porites, Acropora* and *Pocillopora*; http://www.bio.utexas.edu/research/matz_lab/matzlab/Data.html, http://cnidarians.bu.edu/PocilloporaBase/cgi-bin/index.cgi, [98]) have recently been made available to the scientific community.

Several approaches may be used today to identify key genes of interest as potential biomarkers of corals exposed to environmental disturbances, such as cDNA microarray (*e.g.* [14, 39, 86], 454 or illumina RNAseq processes (*e.g.* [65, 107]) but also Suppression Subtractive Hybridization technique (SSH) [105, 106]. The growing interest for the development of gene-based stress markers for corals using such genomic techniques lies in the timeframe of coral response (few minutes to hours), compared to physiological or tissular changes (from hours to weeks). As an example, while a down regulation of two genes (Pdcyst-rich and PdC-Lectin, by 10-fold and 101 fold decrease, respectively) was observed for the coral *Pocillopora damicornis* exposed to temperature increase [105], these changes in gene expression patterns occur before any visible signs of symbiosis breakdown appeared. This clearly reveals the high interest of gene-based stress markers to detect the effect of stress before the breakdown of the symbiosis, and therefore their proactive usefulness to assess coral health.

While promising for proactive management (precise, fast response, small coral sampling <1 cm^2), these methods are still expensive, difficult, and could be logistically difficult in some isolated areas. In addition, recent studies revealed that certain genes may be differentially expressed across a colony (*e.g.* between the tip and base of coral branches [13]), but also the existence of a high natural gene expression variation across several colonies [39]. These works highlight the need for deeper understanding of the intra and inter-variation of coral transcriptomic before further uses of these changes as indicators.

2) Proteomic Changes

Likewise genomic biomarkers, proteomic biomarkers have received an increasing concern these last years, and stress-overproduced proteins in widely diverse taxa were identified in response to stress [96]. These include proteins involved in metabolic condition, oxidative stress and xenobiotic response (*e.g.* ferrochelatase, chloroplast, Heat Shock Protein – Hsp-70 and 60, ubiquitin, Mn and Cu superoxide dismutase –SOD-, glutathione, cytochrome P450 [25, 26, 82]; temperature [26, 32]; heat [26]). A molecular biomarker system (MBS) was developed for *Montastraea faveolata* to gain deeper understMERCCing of proteomic changes and to test their usefulness as proactive tools to assess coral health [26]. They showed significant changes in coral characterized by *e.g.* production increase of LPO and ubiquitin in heat-stressed corals in the light in comparison to those exposed to heat-stressed in the dark. In addition, since the induction of several Hsps of 70 kDa, 60 kDa and 35 kDa in the coral *Acropora grandis* was observed after a 5 h treatment at 35°C [32], this highlights that changes in corals are detectable with a very short timeframe (few hours). More recently proteomic changes were also revealed in coral endosymbionts in response to stress (*e.g.* caffeine [77]; temperature [111]). In the latter work, a viral replication protein was overexpressed (114-fold increase) in the endosymbiont-enriched fraction of the coral *Stylophora pistillata* in response to thermal stress, which could lead to increasing viral load and susceptibility to coral disease.

Proteomic approach represents a powerful tool for assessing changes in coral biology and identifying set of biomarkers. However, a lack of field validation exists similarly to gene-based biomarkers and serious efforts have to be deployed to fill this gap in order to develop and efficiently implement such indicators in the near future. The storage of coral samples for proteomic at -80°C or in liquid nitrogen remains a strong limitation for expanding these tools on a broader scale.

3) Metabolomic Changes

The metabolomic approach is now widely used to study the interactions of living organisms with their environment [38]. This quantitative and qualitative approach of secondary metabolites present in cells is complementary to gene expression and fleshes out the activities of biosynthetic routes set up in response to environmental variations. Thus, to obtain a more comprehensive view of the response of organisms facing external stresses, such an approach performed in parallel to the genetic, transcriptomic and cytologic approaches, is of upmost interest [16]. The demonstration of a correlation between the presence of certain metabolites (*e.g.*: zooxanthellatoxin) and a specific stress will be, where appropriate, used as a biomarker [95]. While zooxanthella metabolites and their role in symbiosis have already been studied [38, 113], data on secondary metabolites in corals are very scarce. Nevertheless, the metabolomic analysis performed on the soft coral *Nephthea spp*., disclosing a relationship between water quality and terpenoids (antipredators) amount notably (Januar *et al*. [47] and the results obtained by Boroujerdi *et al*. [16] on the coral pathogen *Vibrio coralliilyticus* in response to extreme conditions, support the richness of a such approach to provide an integrated view of the functional state of an organisms in response to stress. Metabolomic approach is a new and developing tool that could play a central role in the biomarker field for a proactive assessment of coral health in the next future.

4) Cellular and Tissular Changes

Changes at the tissular level are also potential proactive indicators of coral health. A recent study of Ainsworth *et al.* [9] indicated that thermal stress responses occur in the host tissues of the coral *Acropora aspera* in the days before the onset of coral bleaching, by observing reductions in thickness of coral tissue layers and apoptosis of the cells prior to reduction in symbiont density. Moreover, when exposed to mild to moderate sedimentation, the coral *Montastrea cavernosa* showed clear evidences of histopathological changes after a week, characterized by changes in size and appearance of mucocytes and tissue swelling (*e.g.* [100, 101]. Even though few studies have considered using histopathological changes in corals as proactive indicators of coral health, results from available literature indicated that they constitute a new insight for coral health diagnosis with a timescale of days to week(s) (*e.g.* [9, 29, 44, 73]. The histopathological condition of corals is scored based on a semi-quantitative scale (expressed as presence/absence of various changes in cells and tissues [100] or quantitative scale for some specific changes (*e.g.* nematocyst density, [17]). Despite on broader scale for monitoring coral health, the sampling and fixation of corals for histological studies is easy and fast (48 h in formalin solution, then transfer to EtOH) and could be perform by trained persons, the preparation of histological slides require a well-equipped laboratory and the assessment of histopathological changes may suffer from bias linked to the degree of expertise of the slide reader.

5) Symbiodinium Clade Changes

Scleractinian corals rely on the mutualistic symbiosis between the coral and zooxanthellae belonging to the genus *Symbiodinium*. When corals are exposed to environmental stressor, the symbiotic relationship between coral and zooxanthellae may break down and bleaching occurs. Bleaching is characterized by a loss of color corresponding to zooxanthella loss and/or algal pigment loss [34]. The genus *Symbiodinium* is genetically diverse with nine divergent lineages (clades A to I, [11, 75]) that exhibit a diverse range of functional and physiological properties. For example, corals harboring clade D *Symbiodinium* are more thermo-tolerant (*e.g.* [15, 37, 59]), but the coral fitness may suffer from the energetic cost of clades D (*e.g.* reduction in growth and reproduction [50, 51]). Clade A is less beneficial to corals (lower rate of carbon fixation) and the symbiosis is closer to parasitism than mutualism [92]. A single colony of coral may harbor multiple clades (*e.g.* [33, 89]. When corals are exposed to stress, corals may acclimatize to the changes in environmental condition by symbiont 'switching' (acquisition of new symbionts from the surrounding environment) or symbiont 'shuffling' (changes in the relative abundances of each symbiont clade) [90]. For example, Jones *et al*. [49] showed that after the 2006 bleaching event at Keppel Islands (Great Barrier Reef), the coral *Acropora millepora* initially harboring predominantly the *Symbiodinium* type C2 switched to D or C1 predominance (for corals that survived to bleaching).

As such, genotypic shifts in symbiont communities are observed in response to changes in environmental conditions. Monitoring shift of *Symbiodinium* diversity in corals and more specifically shift towards clade D *Symbiodinium* [91] appear as an interesting proxy of coral health. Long-term *in situ* monitoring of *Symbiodinium* composition in corals is still scarce (*e.g.* [59]), but needs to be performed to provide a baseline of temporal changes of *Symbiodinium* community in corals. Molecular techniques necessitate a small portion of corals, but there is still a scarcity of information on changes in *Symbiodinium* community across a whole colony (*e.g.* difference between top and bottom exists; [84]) and how to sample corals in order to efficiently use *Symbiodinium* community as a good proxy of coral health. In contrary to coral proteomic, storage of corals tissues is easy (most commonly in EtOH > 70%, salt-saturated DMSO buffers, Gaither *et al*. 2011, or in guanidine lysis buffer and conservation at 4°C until analyses [74]).

3. Indicators at the Organism Level

1) Photo-Physiological Changes

The degree of bleaching can be characterized by measuring the zooxanthella density and chlorophyll a and c2 concentrations present in coral tissues, providing thus an overview of the photo-physiological performance of a coral. Such changes in coral biology are interesting indicators of health due to their rapid responses (> hrs) to environmental stressors (*e.g.* pollution, temperature; [52]), but they required coral sampling (> 2-3 cm^2, destructive technique) and laboratory processing which increase the cost and time of analyses, and reduce the spatial scale for coral health assessment.

It is also now possible to assess the *in hospite* photosynthetic efficiency of the *Symbiodinium* inside coral tissues using a Diving-PAM (based on the Pulsed Amplitude Modulated fluorometry). This non-destructive technique allows investigators to take rapid and non-invasive measurements of coral photo-physiology. This technique has been successfully used to assess the photo-physiological status of corals exposed to various stressors, such as heat (*e.g.* [54]), sedimentation (*e.g.* [72]) and pollution (*e.g.* cyanide, [53]). Even though the use of Diving-PAM for assessing the photosynthetic efficiency of *Symbiodinium* is promising as proactive indicator, most of the works has been until now investigated through laboratory experiments (in controlled stress conditions) and short-term *in situ* experiment. The lack of long-term *in situ* validation combined with the expensive cost of the Diving-PAM may explain the delay in this technique on broader scales to assess coral health.

2) Biological Condition Changes

Biological condition of coral colonies may be characterized *in situ* by assessing *e.g.* coral bleaching degree, partial mortality, or percent live tissue. Indeed, depending on the intensity and duration of stress, various degree of bleaching could be observed *in situ* in corals, from pale to completely bleach. While visual assessment of coral bleaching is very common, it is highly dependent of each observer. To counterpart this, a Coral Color Reference Card (CCC) has been developed to improve the objectiveness during assessment of coral bleaching [88]. The main advantage of the CCC is that it allows a fast, cheap, easy, and non-destructive assessment of coral health on broader spatial scale (*e.g.* [64]). However this method remains more qualitative than quantitative. Assessing the degree of coral bleaching *in situ* provides useful information on the health status of coral (from normal to highly stressed) before the coral dye, on a timescale from days to weeks. Unfortunately, when bleaching is visually observed *in situ*, the breakdown of the symbiosis already occurred and fast (*e.g.* hours to few days) management actions (*e.g.* shading, reducing local stressors) have to be deployed to improve coral survival.

Corals are modular colonial organisms and they are able to survive with some death of parts of their living tissue. This particular aspect of corals has been explored and the frequency of partial mortality (i.e. proportion of live coral colonies that were partially dead [24]) as well as the percentage of partial mortality on a colony (i.e. the amount of dead tissue per colony [67]) are other indicators of coral health derived from coral mortality. One of the main advantages of using coral partial mortality as indicators of coral health is that signs of partial mortality can be observed before the whole colony died. Therefore, such changes could be use as a proxy of the negative effects on the whole coral colony fitness (*e.g.* reduction of coral energy reserves, growth, reproduction, and size), but more importantly they provide evidence of changes in coral health occurring before irreversible changes (death of the whole colony if stressors persist). Quantifying changes in partial mortality is cheap, fast and simple.

Moreover since partial mortality or coral bleaching degree is simple and measured by a visual assessment, local communities could be trained and thus participated in the assessment of coral health of their own reefs. Such collaboration between scientists and local communities allows therefore assessing coral health on larger spatial scales, an example of such program is currently developed in Hawaii, with the "Eyes of the Reef" network (http://reefcheckhawaii.org/eyesofthereef.htm), where local communities monitor and report coral bleaching and diseases.

3) Reproductive Changes

Coral parents which experienced high levels of environmental stressors may reduce the amount of resources allocated toward reproduction and consequently it may result in reduction of reproductive success and output (*e.g.* [79]). Therefore, assessing sublethal effects on the reproductive biology of corals can provide a useful index of reproductive effort (*e.g.* fecundity index defined as the number of egg/planula per polyp [58, 94, 109]; size of eggs, volumes of testes materials [10, 35]). Based on available literature, assessing changes in coral reproductive effort represent a promising indicator of coral health for corals exposed to local and global stressors. For example, when exposed to elevated nitrogen, the coral *Acropora longicyathus* produced significantly fewer and smaller eggs and contained less testes material than controls [109]. Changes in coral fecundity is also noticeable after bleaching event: bleached coral colonies at Heron Island Reef displayed smaller eggs and fewer polyps containing eggs than unbleached colonies [108]. In addition, the impacts of bleaching on gametogenic cycle remains noticeable nine months after the event, indicating that even though visually (after ecological surveys) corals look to have recovered from bleaching (regained their colour), internal damages persist with time after the bleaching (reduction in reproduction success). This clearly emphasizes the need to combine changes at population and community levels to individual changes in corals in order to better assess the health of corals. However, assessing coral fecundity requires a good understanding of coral gametogenesis cycle in order to sample corals at specific stages of the cycle. Moreover, coral reproductive effort can only be used for one to three months before coral spawning for broadcasting corals, which inhibits the use of this indicator on a regular basis (*e.g.* every two months). As for histopathological changes, assessing coral fecundity require the use of histological techniques and their inconvenience (time-consuming, need of well equipped laboratory for histological processing). Nevertheless, compare to histopathological changes, assessing coral fecundity presents the advantages of being quantitative (*e.g.* size and number of eggs).

4. Changes in Early Life Stages as Indicators of Coral Health?

Coral health is mainly assessed by looking at biological changes of adult corals, however the renewal and persistence of coral population are definitely linked to the survival of early life stages of corals. The main indicator of coral health used until now on offspring is the recruitment of corals: the transition between the pelagic and benthic phase. A large number of surveys were performed worldwide on coral recruitment and provide useful data on the recruitment at specific location, time, and depth (*e.g.* [1, 3]). The recruitment is a traditional indicator that provides information on larval supply at one site. For broadcast corals (that release gametes in the water column), decrease in recruitment rates could be due to a decrease of larval supply (as for brooder corals), but also of a reduction of gamete fertilization success or abnormal embryonic/larval development due to environmental stressors present in the marine environment (*e.g.* [42, 46]). There is still a crucial lack of information between the first hours of coral life (just after coral spawning and their recruitment).

While theoretically, most of the changes in coral biology (*e.g.* molecular, histo-pathological, physiological changes) used to assess health of adult corals could be transferred to early life stages (*e.g.* transcriptomic techniques are currently used on larvae of corals [40, 63], the scarcity of releases of early life stages of corals during spawning events (*e.g.* few nights per year for *Montipora*, *Porites*, *Acropora* sp.) make such indicators of coral health inappropriate to proactively preserve the early life stages of corals. Effects of stress on early life stages for most coral species cannot be assessed on a monthly or bi-annually timescale as for adult corals. Therefore, proactive health indicators of early life stages of corals cannot be developed easily. In that context, proactive measures need to be developed to protect and enhance their survival during the pelagic phase. This could be realized by assessing their sensitivity to various stressors (*e.g.* temperature, sedimentation, pollution, or combination of stress) in order to determine the adequate quality environment for survival. These criteria on marine water quality could be useful to anticipate the negative effects of environmental stressors on the survival of early life stages and provide managers and politics guidelines to, for example, reduce pollutant loads or sediment discharges. Such changes in water quality through proactive actions at a local scale will help enhancing coral renewal and persistence before irreversible effect occurs. For example, toxicological studies on copper (Cu) observed that 50% of fertilization success of *Acropora surculosa* was inhibited by copper concentration of 45.2 μg l^{-1} [104]. Since Cu concentration up to 30 μg l^{-1} is encountered in polluted tropical marine area [62] by improving water quality guidelines (i.e. decreasing Cu levels in tropical seawater), fertilization success of coral gametes could be enhance. As such, each step of life cycle of coral early stages will be enhanced, and finally a higher number of recruits will be able to settle. Enhancing water quality guidelines is of high concern today, especially when local stressors could decrease the resistance of corals to global stressors. A recent study of Negri and Hoogenboom [66] indicated that halving copper concentration in seawater improves the tolerance of *Acropora* sp. coral larvae to thermal stress. Since the combination of local and global stressor is a developing scenario, assessing the sensitivity of early life stages of corals is the first glance to proactively improve their survival and appears as a promising approach for the future.

III. HOW WAS AND WILL BE CORAL HEALTH ASSESSED IN FRENCH POLYNESIA?

Most of the research carried out on corals until now in French Polynesia (Fig. 2) was mainly focused on ecological observations and used mainly "traditional indicators" to assess coral health on adult stages (*e.g.* [2, 5, 7, 55, 56]). A recent compilation of the researches performed at Tiahura and/or Vaipahu on the North coast of Moorea revealed a strong shift in coral composition, with coral assemblages being dominated by *Acropora* species in 1979 to a dominance in *Pocillopora* and *Porites* species in 2009 [97]. These works provided useful information on the dynamics of coral population and communities in Moorea exposed to anthropogenic and natural disturbances and served as identifying the dominant threats for coral reefs of French Polynesia, such as the 2006-2009 outbreak of *Acanthaster planci*, which led to a gradually decrease of coral cover from 40% in 2005 to less than 5% in 2010 [57]. The occurrence of several bleaching events in the past in French Polynesia also provided an opportunity to assess *in situ* the population and community level response of corals to rising seawater temperature [69, 70, 71]. Such works were relevant for our understanding on how corals resist and recover *in situ* to rising seawater temperature and emphasized notably the differential bleaching intensity (*e.g.* 37% of colonies showing signs of bleaching in 2007 vs 55% in 2002 [71]), but also the differential susceptibility among coral genera. For example, during the 2002 Moorea bleaching event, corals with massive or plating morphologie (*e.g. Porites* sp.) were less susceptible than their branching counterparts, (*e.g. Acropora*) [70].

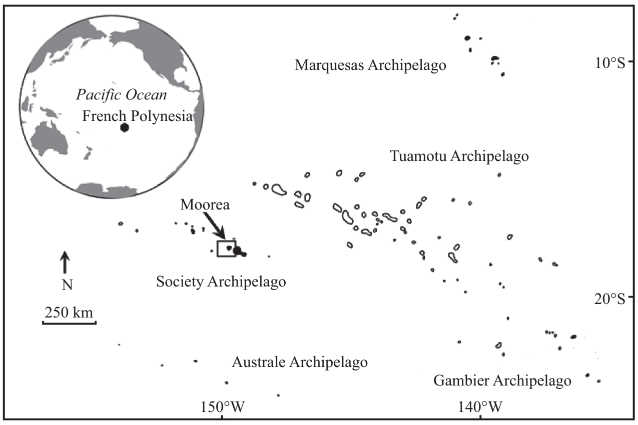

Fig. 2. Map of French Polynesia.

While a large number of studies were localized in Moorea, since 1993 coral health assessment in French Polynesia has been extended to a broader scale through the "*Polynesia mana*" network that allows using photoquadrats to assess changes at the population and community levels (*e.g.* changes in coral cover, species diversity) in seventeen stations located on the outer-reef of ten islands of French Polynesia from four archipelagoes (Society, Tuamotu, Marquesas, and Austral, see Fig. 2) biennially (www.criobe.pf/observatoire/). Since 2008, this broad monitoring program has been extended to other islands of the South Pacific (*e.g.* Cook Islands, Kiribati, Tonga, Wallis & Futuna). This network developed in French Polynesia documents the current state of corals facing global and local changes at the population and community levels and also the changes over time. For example, data from this monitoring revealed that the bleaching events of 1998 and 2002 decreased coral cover up to 35% in several islands [102]. Such information is particularly relevant for politics and managers to improve the adaptive management actions of coral reefs at a local scale, which has the potential to reinforce the resistance and resilience of coral reef ecosystems to face global stressors (rising seawater temperature and ocean acidification).

While the monitoring of coral health at the population and community levels is well established in French Polynesia (*e.g. Polynesia Mana* network, Moorea Coral Reef Long-Term Ecological Research, http://mcr.lternet.edu), increasing efforts need to be approached to understand the mechanisms for how organisms interpret and respond to their environment at lower level of biological organization. In this context, recent works performed in French Polynesia in controlled conditions provide the first glimpse on how corals will be able to face two major threats in the future, ocean acidification [19, 20, 21] and rising seawater temperature [110]. The latter work is currently exploring the response of the coral *P. damicornis* notably to temperature using an integrated approach of novel "omics" technologies, genomic and metabolomics, to improve our understanding of physiological processes. This approach will be particularly useful to get more insights into the cascade of cellular events occurring in coral biology under stress, starting from differential gene expression patterns, which may result in changes in the production of secondary metabolites, and thus into the identification of new proactive coral health indicators targeting the response of coral host, algal symbiont or both.

Algal symbiont is assumed to play a key role in coral resistance and resilience to stress. Nevertheless, despite there has been important progress in our understanding of the success of coral-*Symbiodinium* symbiosis under stress these last 20 years, it is only recently that *Symbiodinium* community changes have received increasing attention in French Polynesia. The study of Putnam *et al*. [78] shed new lights on *Symbiodinium* assemblages in various coral species in Moorea reefs, revealing the high flexibility of the *generalist* corals *Acropora* and *Pocillopora vs* the low flexibility of *specifist* corals such as massive *Porites*. Further works are also beginning to elucidate the temporal and spatial changes in symbiont diversity in corals (*P. damicornis*, *Acropora cytherea* and *Porites rus)* inhabiting various fringing reefs of Moorea in order to assess whether shift in symbiont community can be an efficient *in situ* proxy of coral health, especially in areas subjected to various local environmental changes [83].

Coral research developed in French Polynesia did not only focus on adult corals, and early life stages have been considered especially through monitoring of recruitment patterns since 2000 around Moorea Island. This monitoring of coral recruits indicates that the number of recruits is low (average 40 recruits m^{-2} $year^{-1}$ [3]) compared to other tropical areas (Great Barrier Reef, up to 4590 recruits m^{-2} $year^{-1}$ [45]). However since recruitment patterns were only studied in Moorea (*e.g.* [8, 30]), before using recruitment patterns as coral health indicators, there is a critical need to investigate coral recruitment on broader geographical scales in order to determine baseline levels of recruitments for pristine areas of French Polynesia (such as islands of Tuamotu archipelago). Nonetheless, most of the information on the early life stages is focused on coral recruits, the pelagic life stages of corals (gametes and larvae) remaining largely unknown in French Polynesia. The only available published work that we are aware of aimed at studying coral sexual reproduction in Moorea is a study by Carroll *et al*. [18], which reported spawning events of *Acropora* sp. in Moorea in October and November. The paucity of information on pelagic life stages in French Polynesia represents significant hurdles to understanding how stressors alter the early life stages of corals. In this context, a major effort is currently centralized on coral sexual reproduction of other coral genera in French Polynesia to identify spawning periods [43]. Such information will ultimately enable us to answer important questions on the sensibility of early life stages of corals in response to various stress, taking into consideration the species and stage of corals, and to identify potential management actions at a local scale allowing mitigating the deleterious effects of stress on these key life stages for the renewal and persistence of coral populations.

IV. CONCLUSION

Based on the review on worldwide ongoing research, it is critical to continue improving the assessment of coral health (*e.g.* through *in situ* validation of various biomarkers) in order to develop capacity allowing to proactively assessing coral health. We believe the emergence of interdisciplinary studies combining the field of genomic, proteomic, metabolomics is a promising one, which will provide a fuller picture of the response of coral holobiont to stress, and will generate a substantial body of evidence for the identification of new proactive coral health indicator(s).

For years, monitoring of coral health in French Polynesia was mainly performed using traditional indicators (reflecting changes over months to years) on adult and recruit stages, but it is today obvious that new approach for coral assessment is required, if corals are to persist through better management. Exploring the response of corals in a changing environment at various degree of biological organization (from subcellular to individual changes) will allow to identify changes in coral biology that could be detected before irreversible changes occur (at population and community levels). The ultimate goal being to implement new proactive indicators of coral health into the current traditional monitoring programs is present in French Polynesia. Indeed, a combination of traditional and proactive indicators of coral health in French Polynesia will provide greater insight into the biological effects of global and/or local stressor on coral health and provide a much more powerful approach to diagnose the state of health of organisms exposed to stress. An integrated approach of traditional (long-term responses) and new indicators (short-term responses) seems today the best solution to efficiently assess coral health and provide information on a timeline that allows the implementation of efficient management strategies for the protection and conservation of the world's resource of coral reef ecosystem. The development of such coral health assessment will address an important component of the science necessary to proactively manage and conserve the biodiversity of these important ecosystems.

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