Interpreting the sign of coral bleaching as friend versus foe

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Abstract

Coral bleaching is a major concern to researchers, conservations and the general public worldwide. To date, much of the high profile attention for bleaching has coincided with major environmental impacts and for many the term coral bleaching is synonymously associated with coral mortality (so-called "lethal" bleaching episodes). Whilst this synonymous association has undoubtedly been key in raising public support, it carries unfair representation: non-lethal bleaching is, and always has been, a phenomenon that effectively occurs regularly in nature as corals acclimatize to regular periodic changes in growth environment (days, seasons etc). In addition, corals can exhibit sub-lethal bleaching during extreme environmental conditions whereby mortality does not occur and corals can potentially subsequently recover once ambient environmental conditions return. Perhaps not surprisingly it is the frequency and extent of these non- and sub-lethal processes that yield key evidence as to how coral species and reef systems will likely withstand environmental and thus climatic change. Observations of non- and sub-lethal bleaching (and subsequent recovery) are arguably not as readily reported as those of lethal bleaching since (1) the convenient tools used to quantify bleaching yield major ambiguity (and hence high potential for mis-identification) as to the severity of bleaching; and (2) lethal bleaching events inevitably receive higher profile (media) attention and so are more readily reported. Under-representation of non- and sub-lethal bleaching signs may over-classify the severity of bleaching, under-estimate the potential resilience of reefs against environmental change, and thus ultimately limit (if not depreciate) the validity and effectiveness of reef management policies and practices. Whilst bleaching induced coral mortality must remain our key concern it must be better

placed within the context of bleaching signs that do not result in a long-term loss of reef viability.

Introduction— Coral bleaching is a global phenomenon that continually draws widespread attention from both scientific and public arenas. Researchers strive to gain greater understanding of the fundamental mechanisms involved, variability that exists across species and geographical regions, and to refine models predicting likely impacts of future events towards reef susceptibility and resilience. Simultaneously, assessors, conservationists and managers have expanded our knowledge of both temporal and spatial variability in bleaching episodes and consequences for society. However, such widespread efforts have potentially come at a cost of how bleaching is uniformly perceived and thus the ultimate accuracy of conclusions returned of bleaching severity.

Anyone can in essence detect coral bleaching since the term simply refers to coral discolouration, specifically through loss of pigmentation (from corals' symbiotic microalgae, termed zooxanthellae, but also from the coral cnidarian host tissue) as well as loss of entire zooxanthellae cells from the cnidarian tissue (Brown 1997, Fitt et al. 2001, Smith et al. 2005). Importantly, "non-lethal" coral discoloration, and by inference coral bleaching, is and always has been a natural phenomenon that is driven by inherent system variability in environmental condition, such as temperature, light, sediment loading and salinity (Stimson 1997, Brown et al. 1999, Fagoonee et al. 1999, Fitt et al. 2000; also Lesser 2004, Baker et al. 2008; see Fig. 1) as well as biological interactions, including disease, and microbial and corallivore activity (Rosenberg et al. 2007, Rotjan & Lewis 2008). Bleaching is consequently a *sign* of numerous (not necessarily mutually exclusive) causative factors and in reality not straightforward to describe with a single underlying definition. For the purposes of this article we use the term bleaching to describe coral discolouration.

Given the link between coral colouration and variability of environmental condition, it was perhaps inevitable that reports of coral bleaching episodes have increased over recent decades as reef environments have simultaneously experienced an unprecedented rate of environmental change (e.g. Lesser 2004, 2007, Hoegh-Guldberg et al. 2007, Baker et al. 2008). Importantly, an increase in the amplitude and frequency of environmental variability beyond that of the *status quo*, i.e. beyond average cycles of days, seasons etc., exacerbates coral bleaching (Hoegh-Guldberg et al 1999, Lesser 2007, see also Baker et al. 2008). Here, corals may be driven towards "sub-lethal" stress (e.g. Fitt & Warner 1995, Fitt et al. 2001, Fig. 1) whereby bleaching does not result in coral mortality and is ultimately reversible should 'natural' scales of environmental variability return for sufficient time (Fig. 1). Sub-lethal bleaching thus in essence affords some capacity to ride out periods of 'stress' (*sensu* Obura 2009). However, under the most extreme or rapid environmental change, corals exhibit an irreversible "end point" of the bleaching process, that of coral mortality. Extreme loss of coral zooxanthellae cells and/or host tissue necrosis occurs to leave only the bare underlying $CaCO_3$ skeleton with no chance of recovery once favourable environmental conditions return. Such "lethal" bleaching induced coral mortality can result in negative cascade effects, via reductions to the net balance of reef accretion and the eventualchange in reef architecture that in turn impact reef form and function to the detriment of ecosystem diversity and service provision (e.g. Bellwood et al. 2006, Baker et al. 2008). Whilst these have direct consequences to the viability of populations directly dependent on reefs for subsistence, such cascades may further impact the aesthetic and diverse nature of reefs that ultimately

generates income. It is thus not surprising that both local and international emphasis has been increasingly placed on detecting bleaching events that lead to coral mortality.

Increased bleaching monitoring efforts have importantly increased the scales of data available to assess coral bleaching patterns (Spalding 2009); however, it is important to realise that all reports of bleaching are dependent upon what we, as both non-specialist assessors and specialist researchers, perceive to be bleached coral, i.e. nature, extent and severity. Impact afforded by both public and academic media reports is inextricably linked to consequence, and so bleaching events that result in coral mortality will inevitably gain more attention than non-lethal bleaching events associated with 'natural' environmental fluctuations. Less than ca. 5% of all scientific publications consider natural variability of coral bleaching (as of 1st November 2009 *ISI Web Of Science, Thompson Scientific*); thus knowledge transfer of the patterns and processes of bleaching from the academic arena to non-specialists is arguably already weighted towards a synonymous association of bleached corals with (impending) mortality. Such potential unfair representation should raise serious concerned, in particular where non-specialists must be increasingly responsible for locally collating data sets of coral bleaching that drive the management or policy decisions.

It is undeniable that the common association between bleaching and mass coral mortality, in particular during recent thermal anomaly episodes, has been important for raising global support for reef research and conservation efforts. Following the 'precautionary principle' (see Raffensberger & Tickner 1999) to assume a worst case scenario following the appearance of signs of bleaching potentially supports initiation of at least some mitigation. However, understanding when bleaching is truly 'a problem'

and not part of the current *status quo* is a critical step if we are to generate the most informed and ultimately most effective management decisions. Bleaching induced mass mortality events undoubtedly have a resounding impact upon reef viability and economics; however, it is important that observations of bleaching not detrimental to coral viability, i.e. those indicative of a positive physiological response by corals to a change of their growth environment, are not misinterpreted as impending mortality and consequently that a reef is in a 'state of decline'.

The aim of this opinion article is thus to briefly highlight how signs of coral bleaching manifest in nature. In particular, how the capacity for positively responding (acclimatizing, *sensu* Gates & Edmunds 1999) to environmental change via physiology and behaviour carries a sign of bleaching that may (1) on occasion be misinterpreted as a stress response preceding mortality; and in fact (2) inform of species/systems that can best withstand stress conditions. For this, we consider how commonly used non-invasive tools, that have been increasingly contributing to global data bases quantifying coral bleaching, can yield signals that can be interpreted as both non-lethal and (sub)lethal responses. We further briefly discuss the implications of potentially misinterpreting non-lethal bleaching as impending mortality. Importantly, this is not a review of the coral bleaching phenomenon (but we refer the reader to comprehensive reviews by Glynn 1996, Brown 1997, Hoegh-Guldberg 1999, Fitt et al. 2001, Smith et al. 2005, Baker et al. 2008, Weiss 2008 and Baird et al. 2009; see also van Oppen & Lough 2009) but instead a call (1) for more accurate interpretation and communication of the sign (and hence severity) of bleaching; in doing so, (2) to re-focus effortstowards non- and sub-lethal bleaching (including subsequent recovery), i.e. those phenomena that receive less

attention and are perhaps less frequently reported, in understanding reef resilience under environmental change.

Observing bleaching as evidence of impending mortality— The term bleaching can be used to describe a continuum from non-lethal to lethal episodes; thus, it is no wonder that researchers are still yet to reach a consensus as to the primary mechanism by which corals most commonly bleach. Substantial research has been directed towards understanding sub(lethal) coral bleaching episodes so as to identify how environmental change will result in a loss of reef form and function. *In vivo* thermal stress studies have now documented a range of physiological mechanisms that act to reduce the net photosynthetic capacity of thermally sensitive genotypes of the corals' symbiotic zooxanthellae (Fitt et al. 2001, Smith et al. 2005, Baird et al. 2009, Takahashi et al. 2009). This loss of photosynthetic capacity appears to coincide with an increased net production of reactive oxygen species (ROS), which can damage a range of cellular components, such as lipids and proteins, to induce severe physiological malfunction (for work on zooxanthellae see Lesser 1996, 2006, Tchernov et al. 2004, Suggett et al. 2008). In all cases, zooxanthellae are lost from the corals' gastroderm tissue via expulsion or degradation (e.g. Gates et al. 1992, Dunn et al. 2002, Smith et al. 2005, Baird et al. 2009, Strychar & Sammarco 2009) presumably once physiological 'costs' effectively outweigh the advantages of maintaining the symbiosis. More recently, coral biologists have begun to acknowledge how the coral host itself can be negatively impacted by thermal stress, and thus its role in bleaching, via processes such as elevated ROS production by host tissues as well as loss of host tissue adhesion from the underling $CaCO_3$ skeleton (Downs

et al. 2002, Baird et al. 2009, Fitt et al. 2009, Vidal-Dupoil et al. 2009, but see also Gates et al. 1992).

It is perhaps difficult (but not impossible) to expect that one single mechanism will ever solely explain bleaching in nature since the variety and complexity of (stress-induced) bleaching mechanisms proposed to date come from a range of coral species and growth environments and inevitably reflect genotypic and phenotypic modifications of general patterns. One might expect that coral species under similar evolutionary constraints that govern fitness will exhibit similar bleaching mechanisms; specifically, exposure to environmental variability across the evolutionary age of any one species should be reflected in the ability to withstand subsequent environmental fluctuation. That said, the long-term advantages of tolerance, which likely carries significant energetic costs, must be weighted up against key life history traits such as the energy available for growth and fecundity. (e.g. Loya et al. 2001, West & Salm 2003, Yee et al. 2008). Similarly, expected traits will be further mediated by acclimatization or adaptation to local environmental pressures, including extreme environmental variability (e.g. Brown et al. 2002, Brown & Dunne 2008), and their association with zooxanthellae of alternative stress tolerances. General patterns of bleaching, as a precursor to impending mortality, amongst coral species (genera) are indeed observed in nature (eg. Hoegh-Guldberg & Salvat 1995, Loya et al. 2001, McClanahan et al. 2007); however, exceptions to such rules can convey key information and help elude to the full potential of reefs to withstand future environmental change.

Implicating the severity of coral bleaching is inherently dependent upon how accurate bleaching observations are as signs of (impending) mortality. Convenient (non-

invasive) assays have been developed to examine two common and inconspicuous associated bleaching traits: a loss of coral colour and/orphotosynthetic efficiency (e.g. Fitt et al. 2000, 2001, Smith et al. 2005). Technological advances combined with widespread availability of methods that quantify these traits have no doubt significantly contributed to the rise of bleaching reports in recent years (for more detail see Baker et al. 2008, Spalding 2009), in particular those of (impending) mortality; therefore, it is important to briefly consider these methods:

Assessment of changes to coral colour and intensity can in essence by made optically, i.e. by eye; however, a more robust semi-quantitative assessment can be made using a convenient reference colour chart. Each reference colour is graded to interpret the severity of bleaching and thus of coral (reef) viability (Siebeck et al. 2006). This method in particular is incredibly cheap to implement and can result in a wealth of data. More sophisticated but standardised (bio-optical sensor) techniques, such as spectroradiometry, which can be sensed both directly upon the coral surface (Rodriguez-Román et al. 2006) and remotely from the reef (Mumby et al. 2001, Manzello et al. 2009) can also be used to assay coral colour and hence be interpreted to represent bleaching, but are inevitably more expensive and thus relatively inaccessible to most non-specialists.

Despite the convenience of using coral colour, linking biomass with bleaching severity is fraught with difficulties for broad scale ecosystem assessments. Instead, approaches that examine physiological *performance* are more robust and can describe a response to environmental change at finer scales than through colour alone (e.g. Brown et al. 1999). For example, assessing photosynthetic viability can be made conveniently and rapidly but requires the use of a relatively expensive piece of hardware (an active

fluorometer). Even so active fluorometry has gained notable popularity amongst both the research and monitoring communities. In principle, this approach should be simple since it employs a 'point and shoot' procedure to obtain the parameter of interest, the photochemical efficiency, termed F_v/F_m (comprised of measurements of the minimum (F_o) and maximum (F_m) fluorescence yield, such that $F_v/F_m = [F_m - F_o]/F_m$, see Warner et al. in press). Numerous scientific publications have demonstrated that declines of F_v/F_m through changes of F_o and F_m, occur in response to heat stress for isolated zooxanthellae (e.g. Warner et al. 1999, Tchernov et al. 2004, Robison & Warner 2006, Suggett et al. 2008) but also intact corals (e.g. Warner et al. 1996, Hill & Ralph 2006, Warner et al. in press). As with coral colour, a scale of F_v/F_m is effectively used to provide a quantitative grade for coral (reef) viability.

Of major concern is where measured changes in colour or photochemical efficiency are incorrectly interpreted as a sign of impending mortality but are in fact evidence of non-lethal bleaching, i.e. false positives are recorded. Identifying such false positives across species, environments and bioregions is in fact a crucial factor if we are to (1) better understand how systems tolerate or even positively respond via acclimatization/adaptation to disturbance events; and (2) accurately gauge the rate of system decline (and subsequent recovery). However, as is a common theme in modern sciences, relatively neutral findings such as non- and sub-lethal bleaching often do not reach the mainstream scientific literature or public media, especially when in competition with science thatreports mass mortality events.

When bleaching is 'beneficial' to corals: alternative perceptions— Non-lethal bleaching episodes carry fundamental information that demonstrates physiological flexibility to variable environmental conditions in space and time; such bleaching is of course beneficial to the persistence of corals across 'typical' scales of environmental variability (e.g. Falkowski & Dubinsky 1981; but see also Obura 2009). In particular, a "photo-acclimation model" can explain some instances of coral discoloration (and loss of photosynthetic efficiency) and hence the bleaching sign; this is particularly relevant in light of the non-invasive approaches that have contributed to the rapidly increasing global data sets of bleaching severity in recent years (above). Numerous publications from algal research demonstrate that a reduction in pigmentation per cell, in particular the major light harvesting pigment chlorophyll *a*, can occur as cells are solely exposed to elevated light intensity (e.g. MacIntyre et al. 2002, Hennige et al. 2009). Here, the discoloration that is observed is driven by an active safety mechanism designed to protect against over-excitation of the light harvesting apparatus, i.e. downregulation. Photoacclimation thus enables phototrophs to re-adjust their physiology to maintain optimal steady state growth as the (light) environment changes. Similar characteristics are observed for zooxanthellae within corals acclimating to a light gradient throughout the water column (Falkowski & Dubinsky 1981, Lesser & Gorbunov 2000) or experiencing seasonal increases of light exposure (Stimson 1997, Brown et al. 1999, Fagoonee et al. 1999, Fitt et al. 2000). Photoacclimation also exists in shallow waters where strong gradients of bleaching can exist across individual colonies in response to the predominant direction of light stress (see Brown & Dunne 2008, and references therein).

For many, photoacclimation typically refers to the response of the photosynthetic zooxanthellae within the coral host; however, the host has also been demonstrated to alter its pigmentation in response to light availability (Dove et al. 2006, D'Angelo et al. 2008). The reason for this is still not entirely clear but may act to support optimisation of the zooxanthellae' maximum photosynthetic efficiency via photoenhancement or photoprotection, depending on the light environment for growth. Similarly, polyp behaviour via tentacular contraction and expansion can modulate and hence optimise the light environment of the associated zooxanthellae (Levy et al. 2003), in particular during periods of environmental stress (e.g. Brown et al. 1994). In doing so, 'acclimatizaion' can alter pigmentation density and hence coral colour without any consequence to longer term coral viability; here, the use of coral colour alone to classify the severity of bleaching would likely result in an erroneous interpretation of bleaching as a negative rather than positive response to environmental change.

Photoacclimation not only potentially impacts the intensity of zooxanthellae and host coral colour but also the zooxanthellaes' photochemical activity. Photoprotection implicitly results in a greater proportion of the absorbed excitation (light) energy being dumped as heat to avoid excess activation of the photochemical reaction centres (for examples from corals and isolated zooxanthellae see Warner et al. in press). Consequently, the photochemical efficiency decreases under ever increasing light intensity. This phenomenon is easily observed from measurements of photochemical efficiency from active fluorometry, i.e. F_v/F_m, for strains of isolated zooxanthellae when grown under various light intensities (Robison & Warner 2006, Hennige et al. 2009) but also for corals across natural light gradients (Lesser & Gorbunov 2000, Iglesias-Prieto et

al. 2004, Winters et al. 2006, Hennige et al. 2008, Piniak & Brown 2009). Day-time

tentacularcontraction may also act to lower values of F_v/F_m (see Levy et al. 2003). Again,

under such conditions, active flourometry signals may also result in erroneous

interpretation of bleaching as a negative rather than positive response to environmental

change.

Fluorometry-based studies now highlight that acclimation in response to changes

in environment appear to be a major driver of variations of F_v/F_m in nature (Suggett et al.

2009); thus, solely relying on changes of F_v/F_m to inform of stress-inducing bleaching

may in many instances prove misleading. That is not to say fluorometry is an obsolete

tool for monitoring coral viability; however, in order to determine whether variations of

F_v/F_m are in fact the result of photoinhibition (and thermal stress) rather than from

photoacclimation requires a much more sophisticated examination of the underlying

nature by which F_v/F_m varies, i.e. F_o and F_m (as described by Gorbunov et al. 2001,

Rodriguez et al. 2008, also Warner et al. in press). Here, a simple set of 'rules' can be

employed to essentially deconvolute changes of F_o and F_m into signatures of stress

(photodamage and photoinhibition) versus acclimation. Importantly, such analyses will

inevitably require a more detailed treatment of the fluorescence data. Also, the 'rules'

required to deconvolute changes of F_o and F_m into stress versus acclimation will be very

different according to the protocols and instrumentation used to generate the fluorescence

yields (see Suggett et al. 2003, Warner et al. in press). Given these additional constraints,

fluorometry may prove less desirable to non-specialists as a convenient point and shoot

"coral health meter", at least initially.

In addition to photoacclimation, changes to the (photosynthetic) community composition can also result in major variations of F_v/F_m and pigment concentration and hence colour (Suggett et al. 2009). For any population within the community the relative abundance of genotypes will be the direct result by which the environment at any one time favours some and discriminates others. The zooxanthellae community within the coral holobiont is no exception and the relative abundance of zooxanthellae genotypes of different stress tolerance is well known to alter temporally and spatially with environment (e.g. Iglesias-Prieto et al. 2004, Thornhill et al. 2006); in fact, such alterations may actually be a pre-requisite for the long term viability of the coral-zooxanthellae symbiosis with environmental change (Buddemeier & Fautin 1993, Baker et al. 2004, see also Baker et al. 2008). The zooxanthellaecommunity can be altered by 'shuffling' (*sensu* Baker 2003, Berkelmans & van Oppen 2006) between existing or acquiring (switching to) new zooxanthellae genotypes. Shuffling amongst the existing zooxanthellae community is analogous to up and down regulation of the existing gene pool and thus be considered acclimation by the holobiont. In contrast, conferral of this new genetic signature to the next holobiont generation or indeed zooxanthellae switching at any time is an adaptive response. Regardless of the process, a change in the zooxanthellae community will have a significant impact upon the zooxnathellaes' photochemical efficiency (F_v/F_m) and amount of pigmentation per cell, and ultimately coral colour (Hennige et al. 2009), i.e. again confound the measurements gained from 'convenient' and readily available assays used to grade (sub)lethal bleaching:

Laboratory investigations of zooxanthellae of a range of tolerances to light and heat stress demonstrate that under the same growth conditions more tolerant strains

generally have higher values of F_v/F_m and pigmentation per cell (Robison & Warner 2006, Hennige et al. 2009); as such, replacement of sensitive with tolerant zooxanthellae under stress will likely yield increases of F_v/F_m and zooxanthellaes' (and hence coral) colour. Whilst these increases would not be interpreted as a stress response *per se*, they might be erroneously interpreted to be photosynthetic recovery by the original (pre-stress) community. By the same reasoning, should corals switch or shuffle in favour of more stress sensitive zooxanthellae genotypes over time (for this to happen it would be assumed that returning the community back to dominance by stress sensitive genotypes provides some benefit to the growth and viability of the host under optimum environmental conditions), decreases of F_v/F_m and pigmentation per cell would be induced that may be interpreted as a sub(lethal) bleaching response. Either way, altering the symbiont community structure is a compounding factor that will influence how the dynamics associated with bleaching rate and recovery are interpreted and subsequently documented.

Interpreting the severity of bleaching through patterns of bleaching— In turning to *how* (photo)acclimation, acclimatization and adaptation can provide a plausible alternative (non-lethal) sign of bleaching, it is important to consider *when* such bleaching might be mis-interpreted as (sub)lethal bleaching episodes. Seasonal increases in light intensity and availability are most often accompanied by increases in seawater temperature. As such, corals will be left susceptible to the proximal increase in light availability unless they can tolerate the increases in temperature. Researchers attempting to identify the primary environmental factor inducing mortality have repeatedly shown that whilst

temperature induces photosystem de-activation, the rate at which this occurs will be dependent upon light availability (e.g. Lesser 1996, Robison & Warner 2006). An inherent positive association between light availability and seawater temperature would suggest that the ultimate capacity for acclimatizaton/adaptation (within the genetic constraintsof different coral species or indeed genera), i.e. non-lethal bleaching capacity, needs to be considered a key property determining the ultimate resistance to sub(lethal) bleaching. It is plausible to expect that strong patterns of acclimation to seasonal changes of light and temperature are evidence of physiological flexibility to environmental change. Similarly, that species found across extremes of light environment will also likely exhibit the greatest tolerance to variable environmental growth conditions and thus transient periods of stress (e.g. Yee et al. 2008). What is important to consider is that species observed to be paler, and thus bleached, when light and temperature are highest (and potentially most variable) may inevitably be misinterpreted as susceptible to (sub)lethal bleaching when in fact they may prove to be most tolerant. Indeed, seasonal co-variability between incident light intensity and seawater temperature may even imply that reef assessors would be more aware of the probability (perhaps even more actively looking for incidences) of (sub)lethal bleaching during periods when corals are most actively acclimatizing to high light. Such potentially fundamental concepts cannot be addressed at present but clearly warrant further attention, not only from the point of view of the underlying mechanisms that afford physiological flexibility but also how such observations are ultimately reported and applied.

Inevitably more elaborate analyses of bleached corals for characteristics such as tissue quality (e.g. Rodrigues & Grottoli 2007) may help to confirm the true nature of the

observed bleaching sign as non-lethal or (sub)lethal; however, these additional analyses not only require more sophisticated techniques that are rarely available but also undermine the advantages afforded by primary (non-invasive) assessment tools, i.e. their rapid *in situ* application with high spatial and temporal coverage by non-specialists. Therefore, it will be critical to set additional criteria if reef assessors are to continue to rely on measures of coral colour and/or F_v/F_m and simultaneously minimise incidents of false positives. In all cases, these criteria must consider localised changes of both biotic and abiotic (physic-chemical) variables, a statement that may seem obvious but still seems to elude many small scale assessments. Such criteria have been documented elsewhere but we briefly synthesise as follows:

Firstly, quantifying the cycle with which corals respond to regular, environmental change (Stimson 1997, Brown et al. 1999, Fagoonee et al. 1999, Fitt et al 2000, Downs et al. 2002) will enable assessors to place the incidents of bleaching within the context of a 'business as usual' scenario (Winters et al. 2006, Weeks et al. 2008, Piniak & Brown 2009). In particular, such continuous observations will identify (i) the species that discolour seasonally; (ii) the nature (pattern) and extent to which these species discolour, and thus whether some species are genetically more prone to always being lighter in colour than many other species on the same reef, such as *Astreopora gracilis*. Here, understanding species-specific trends of tissue retraction in response to smaller scale variability (e.g. daily, tidal) will also be important; and (iii) quantify these various changes relative to the extent of environmental change. Variability of the extent of bleaching within species, systems should ultimately provide an index phenotypic (and genotypic) tolerance to environmental change. Of course such observations require some

level of interpretation relative to any potential shifting baseline between geographic location (Manzello et al. 2007) and as longer-term environmental (climatic) change progresses (e.g. Berkelmans 2008, Weeks et al. 2008). For example, these observations may need to further account for any potential localised adaptation that may occur. Without this detailed understanding of the system in question it is clear that opportunistic and/or sporadic assessments of bleaching at reef sites may result in a higher frequency of false positives and consequently a greater likelihood that a bleaching episode will be incorrectly declared and that stress tolerantcorals are labelled as stress sensitive.

Secondly, it is important that we differentiate bleaching responses (non-lethal and (sub)lethal)) amongst the key reef architect species to understand potential consequences to the ecology of reef systems, require more detailed physiological understanding of the major reef formers. Studies generally acknowledge that species of Acroporidae and Pocilloporidae are often more susceptible than species of Poritidae and Favidae, to lethal bleaching (e.g. Hoegh-Guldberg & Salvat 1995, Loya et al. 2001, Obura 2001, McClanahan et al. 2007) under relatively low levels of residual environmental variability. Such differential susceptibility appears to correspond with alternative bleaching processes inherent to fast growing opportunistic ("type-1", Obura 2001) versus slow growing persistent ("type-2") coral species (e.g. Buddemeier & Fautin 1993, Fig. 1). Typically, type-2 species exhibit sub-lethal bleaching unless exposed to sudden and extreme (high residual) levels of environmental change (Fitt & Warner 1995, Fig. 1). Many instances of thermal induced (e.g. El Niño) mass coral bleaching events appear to induce a rapid loss of coral tissue to reveal the skeletons across large areas dominated by opportunistic (branching) species, i.e. a type-1 thermal stress. However, more localised

stress events, in particular when stressors act in concert, may impact many more persistent species within the coral community. Understanding such species-specific differential characteristics of bleaching in response to stress thus has major consequences for reef structure and analysis of the community structure of the system in interest may subsequently provide a baseline for interpreting how productivity and biodiversity will likely be impacted by future thermal anomalies.

Thirdly, and following the above considerations for different bleaching responses, observing the bleaching pattern at the coral colony level yields key clues as to the nature of bleaching and thus interpretation of its severity towards overall reef health, for example, corallivore grazer (Rotjan & Lewis 2008) or microbial (Rosenberg et al. 2007) activity. Both processes can severely impact upon coral viability and ultimately kill the entire colony in extreme cases.

Towards a 'fairer' picture of coral bleaching— Increased awareness of bleaching and the common association with environmental (thermal) stress will no doubt lead to some misreporting of reefs as being under threat or in decline, in particular if the precautionary principle is in effect. Any efforts to improve bleaching predictions (Van Hooidonk & Huber 2009) are inherently dependent upon the accuracy of data available to truth current algorithms. A key objective is of course to minimise false positive reports of (sub)lethal bleaching; however, a more pressing need is to maximise reporting of non- and sub-lethal bleaching along with other key information of environment and species so that we can more confidently identify positive as well as negative outcomes of bleaching episodes. This is perhaps most relevant to local economies dependent on the presence of 'healthy

reefs' that literally cannot afford for incidents of bleaching to be misinterpreted and consequently misreported. In particular, spot-checks on rarely visited areas may increase the likelihood of yielding false positives and thus misclassify how sensitive these areas are to thermal stress; such false positives also increase the likelihood that a system or species is identified as being able to recover (the rate and extent) post stress. Either way, misidentifying a bleaching event as lethal has immediate consequences to larger scale data sets that collate global information for improving environmental (e.g. Lesser 2007, McClanahan et al. 2007) or systematic (e.g. Riegl & Purkis 2009) models for bleaching predictions. Erroneous data will ultimately limit, perhaps even misinform, the predictive power of forecasting models (see Van hooidonk & Huber 2009) and so constrain the accuracy of information required to target management of larger scale reef systems.

At local to regional scales, false positive reports of lethal bleaching (orconversely non-reports of non- and sub-lethal bleaching) have clear implications for identifying which areas of reef, and ultimately species, require preferential and targeted management. Informing how best to currently conserve species from direct anthropogenic pressures, such as coral harvesting (mining), fishing and tourism, requires fundamental knowledge of the bleaching susceptibility of the key species for the system in question. Indeed, sensitivity and susceptibility scoring of different species is an important tool for conservationists (West & Salm 2003, McClanahan et al. 2007), in particular when sensitivity scoring can be placed within the context of the general ecology of a species that accounts for differences in key life history traits. Arguably, only through such an ecophysiological approach is it possible to understand the relevant conservation priority for a species and its overall vulnerability to anthropogenic impacts (including thermally

induced bleaching) (Loya et al. 2001, Yee et al. 2008); for example, highly sensitive type-1 opportunistic species often exist on reefs in high abundance when environmental conditions are optimal. Such high abundance, which is supported by high growth rates and fecundity, could thus be considered a survival strategy, in particular since the probability of colonising into refuges from environmental stress is increased (West & Salm 2003); high abundance of a species is not generally associated with vulnerability, but could thus be considered an index of high conservation priority. An alternative argument (although not necessarily mutually exclusive), is that most effort should be placed on conserving less susceptible persistent (type-2) species since these will likely be the key reef architects under future climate scenarios; that is of course unless species that are typically type-1 are able to adapt (see Baker et al. 2008, Berkelmans 2008, Jones 2008).

Generating the most accurate picture of bleaching susceptibility of key reef forming species and hence reef systems will therefore be critical for communities to ultimately implement any effective adaptive capacity for sustainability and income (see McClanahan et al 2008). Identifying reefs that are highly susceptible to, or indeed are already experiencing, (sub)lethal bleaching may indirectly win public and economic support in the short term. Indeed, one empirical study has suggested that bleaching will unlikely deter tourists from visiting (Andersson 2007); however, it is hard to imagine that impacted reefs will be as desirable as unimpacted reefs longer-term. Such concerns are certainly paramount for small island states, whose economy is ultimately dependent upon their environments being 'desirable'. Unfortunately, through this reasoning comes a potential warning that reef managers and policy makers may not perceive it economically

viable to declare true incidents of bleaching (i.e. ignoring the precautionary principle), at least in the short term. In particular, where new advice conflicts with already instigated adaptive practices that may have been established based on limited data. Of course this would have severe implications.

Our variable interpretation of the nature of the coral bleaching sign no doubt relates to the ambiguity with which the term 'bleaching' has been used in both the scientific and public arenas in recent years. However, it is now critical that we as reef researchers, assessors and managers correctly identify whether episodes are indeed (sub)lethal, and potentially detrimental to long term reef form and function, or non-lethal and part of the natural process of reef environmental and biological variability. Furthermore we should make the most of the considerable effort that is currently invested in reef monitoring by ensuring that episodes of short term bleaching (non-l and sub-lethal, followed by recovery) is given merit and heightened importance so that we gain a greater understanding of true system and species variability, variability in this sense potentially being a sign of partial resilience. For this, it is a priority that we evaluate key questions: Whether or not (1) the frequency of environmental induced (sub)lethal bleaching events has indeed increased to the extent stated (or can some be explained as non-lethal events)? (2) Variability of bleaching extent inherent to any given species or system can be considered a key parameter reflecting flexibility and hence long-term viability (rather than an artefact that simply clouds current attempts to correlate bleaching extent with broad scale changes of environment)? (3) Increased awareness has simultaneously led to increased sampling effort (with the probability for a greater return

of false positives)? and (4)The frequency of reporting is a function of the willingness to report incidents (the precautionary principle)?

It is most likely that the increased frequency in reports ultimately carries all four factors, the relative importance of each being dependant on site, time of year that sampling occurs and the degree of experience and expertise of the reef assessors. Of key priority is the interpretation of the generic bleaching sign solely as (impending) coral mortality. Instead it is imperative that researchers focus on the nature and extent of the *variability* of bleaching (within and between species, systems etc.) to more accurately gauge the capacity for potential resilience based on current physiological and genetic plasticity. Ultimately, convenient techniques for grading bleaching, which are perhaps our only means to generate the quantitative data needed to improve the temporal and spatial resolution of bleaching observations worldwide, can do this if data is better considered within their limitations (as briefly outlined here).

Importantly, in minimising false-positive reports of (sub)lethal bleaching also comes the need to improve how well we communicate the nature of bleaching, in particular through the mainstream media and to the general public. Importantly, it is all of our responsibility to alter the public perception that 'bleaching is always bad'. Unfortunately, mass mortality caused by bleaching, and the potential for impending mass mortality events, will likely always result in higher media coverage when compared to research that points to natural (non-lethal) variability of coral colour. To this end a greater degree of knowledge exchange is needed between coral researchers and assessors and the outcomes of such research and collaboration need to be fed back to managers and policy makers. It is ultimately up to the research community to ensure that such issues are

resolved so the limited resources and efforts available to monitor/quantify bleaching can be used most effectively and appropriately.

What is clear is that we must move beyond the most common perception that discoloured corals are always less 'healthy'. In particular , non-lethal (and arguably sub-lethal) bleaching events are part of a natural rhythm that enables corals to successfully respond to environmental variability or indeed, in the case of corallivore and microbial activity, contributes to sustaining trophic interactions and hence reef biodiversity. For this, it is imperative that the coral reef management *community* play a greater role: we need to understand the mechanisms of environmental resilience of key architect species, appreciate the variability between the different mechanisms, understand the important of refuge environments thereby incorporating such environments into management plans, and make the most (practically and theoretically) out of the high effort already invested in coral monitoring programmes. As such, the different 'types' of bleaching are accurately identified and reported, not only in the scientific literature, but in a format accessible and therefore suitable to wider society and to policy makers in particular.

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Figure 1. Schematic representation of bleaching (extent of discolouration) in response to environmental perturbation, as expressed by the residual (to the variance 'typically' expected for any given time point) of one or more factors regulating coral growth and physiology, e.g. light, temperature. Note that we use the term residual here to reflect change across the long term running average and thus is different to NOAA's coral bleaching anomaly products. Both changes to the amplitude (broken black line) and wavelength (solid black line) of the residual variance determines extent of bleaching attained, in particular via a relatively short duration of extreme environmental change or a longer duration of lower level but cumulative environmental change. Non-lethal bleaching occurs when the residuals = zero (equivalent to "business as usual" variability over any given time period, days, months etc.) and results in acclimatization. In contrast, introduction of a low level of residual variability induces enhanced discolouration. Corals that remain viable through a period of residualvariability exhibit sub-lethal bleaching and can undergo one of two subsequent fates: (A) recovery should 'typical' levels of environmental variability return, i.e. zero residuals; or (B) cumulative move towards lethal-bleaching (mortality) should subsequent environmental perturbations occur before recovery. Note the gradient (rate) of bleaching will be set according to the physiological tolerance (range and thresholds) to environmental variability: most 'sensitive' corals require relatively little residual variance to induce lethal bleaching (often expressed as type-1 corals); in contrast, most 'tolerant' corals express sub-lethal (type-2) bleaching unless a single environmental perturbation has high enough residual variance to immediately induce mortality (C) (e.g. Fitt & Warner 1995).