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UNDERSTANDING *ACANTHASTER*

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Abstract. A fundamental understanding of the *Acanthaster* phenomenon - the outbreaks of the crown-of-thorns starfish - on the Great Barrier Reef has now emerged. This is a result of a concerted integrated research effort over the last decade, involving field, modelling and theoretical work. This new understanding requires that we reevaluate the nature of the outbreaks. It says that beneath the apparent complexity of waves of outbreaks travelling down the Reef lies the simplicity of a classic prey-predator stable limit cycle, which itself is clearly part of a family of dynamical behaviours for the phenomenon. It also says that the density of fish predators of juvenile starfish controls which of the family of behaviours is actually expressed. Finally, it suggests that the historic reduction of these fish populations by fishing, with the resulting series of waves of outbreaks, may now be causing irreversible degradation of the Great Barrier Reef.

Introduction

For many years, the *Acanthaster* story has been the best story in town for the world's coral reef scientists. It has all the elements of a ripping yarn: a sinister starfish, disastrous outbreaks destroying the very fabric of the coral reefs - the corals themselves, and endless controversy about the nature of the outbreaks. *What causes them? How much damage do they do? Can reefs recover from them? Should there be intervention to prevent outbreaks? What would constitute intervention, anyway?* Complexity and confusion abound. But often there comes a time in any story when the threads are pulled together - the denouement. This is when complexity gives way to simplicity, and confusion to understanding.

It is the central purpose of this essay to argue that this time has now come for *Acanthaster*. Now this is not to say that we now know all there is to know about this beast. Nor is it to say that we now know what to do. Rather it is to say that we now understand the broad shape of the phenomenon. Much work is needed to flesh out this understanding, but the direction in which progress is to be made is now clear, and we understand where we went wrong, as well as where we were right.

In building the argument that we now understand the animal *essentially*, I hope several things will emerge almost incidentally, but nevertheless importantly. In no particular order, they include what we now understand about coral reefs in general and, in particular, about the Great Barrier Reef (GBR); where we went wrong in the early days, and the lessons that has for ecologists; and what this new understanding tells us about what we may do about *Acanthaster*, and the lessons that has for reef managers.

The understanding that I discuss here is not revealed in any particular scientific paper, nor is it inside the skull of any particular scientist. It has been a work of many individuals, in a productive ferment of agreement and argument. Each paper, including this one, and each scientist, including this one, has a window on it. I cite the papers and acknowledge the scientists below.

But before the story, two caveats.

The first is that this is a story about the GBR, even though *Acanthaster* and its outbreaks are both widespread in the Indo-Pacific. My intention is to get the story right at its core, so to speak, where the starfish and its outbreaks have been most observed, even though I draw on lines of evidence from other regions, particularly from the Red Sea where there are intriguing similarities as well as differences (Moore 1990; Ormond et al., 1990).

Second, the story is concerned chiefly with circumstantial evidence. In this, it is distinguished from the sorts of scientific expositions which proceed in the traditional reductionist way through the marshalling of hardwon experimental data. But these approaches fall into the trap of *reasonableness* (Bradbury 1989), and they have, in large measure, failed to help us understand *Acanthaster*. So instead, I will follow Henry Thoreau's dictum 'Some circumstantial evidence is very strong, as when you find a trout in the milk' and present a case based so openly on circumstantial evidence that that rare creature, the reasonable reductionist, should find it convincing.

Thus this is not a review of what we know about *Acanthaster*. For that, see the admirable work of Moran (1986). Instead, it is a discourse about what we *understand* about the beast. Knowledge has to do with what is both true and believed to be true (Quine 1987), whereas understanding has a much more workaday guise. It has to do with seeing clearly the path by which we came to this present spot, and to where it seems to lead.

Acanthaster as a phenomenon

We pick up the story in the early 1980s and follow it through that decade. We went into the eighties with one sort of understanding of *Acanthaster* and emerged from it with a quite different one. In those years, two scientific discoveries were made in rapid succession. They mark the transition from the classical to the modern era in understanding *Acanthaster*. They are authentic scientific discoveries in three senses: they dramatically alter our understanding; they now, with hindsight, appear obvious, even trite, but yet they were not apprehended beforehand; and, lastly, they cannot now be *undiscovered*, so that all future understanding must take them into account.

I will describe these discoveries after I set the scene for the classical era from which they sprang. This period has been well reviewed by Moran (1986), a still significant work, indeed the highwater mark of the classical era. It was characterized by a steady increase in our knowledge of the biology of *Acanthaster*, of coral reef biology in general, and in, particular, of the recovery of coral communities after disturbance. Moran (1986) observed that the hypotheses concerning the origin of the outbreaks divided on the question of whether the outbreaks were natural or not, and to a lesser extent, on whether biological or physical events were the 'cause'. They united, however, in their emphasis of the singularity of that episode of outbreaks, a singularity expressed, for example, as the rare conjunction of favourable physical events or the novel effects of modern man on the pristine coral reef.

The reappearance of outbreaks on the Great Barrier Reef in the early 1980s triggered the first discovery: that the outbreaks were a *phenomenon* not an *event*. We realised that the first outbreaks of the sixties and seventies has only been an *instance* of a something more general. This more general thing, this phenomenon, offered the hope of an understanding based not on more and more complete descriptions of the event - that is, natural history - but rather on a deeper and deeper embedding of the descriptions in a more general understanding - that is, science.

This discovery is not documented anywhere, because, whatever else it is (1), it is not the nature of the scientific literature to give a clear picture of how science is done. That is the task of the history of science, which is never easy, and of which this essay may be a part.

It is quite true that this discovery is trite and obvious (especially after the event), and so was probably unpublishable once it was made. Nonetheless, because of its effect on our subsequent understanding, it may turn out to be the most important thing ever discovered about *Acanthaster*. It can even be seen in the shadows of the next discovery which followed it more or less immediately: that the most likely area of scientific understanding in which to embed the phenomenon was ecology, in particular, population dynamics.

Thus two papers appearing independently and in quick succession (Antonelli and Kazarinoff 1984; Bradbury, Hammond, Moran and Reichelt 1985a) in the *Journal of Theoretical Biology* clearly mark the beginning of the modern era because they were both primarily concerned to embed the phenomenon firmly in the ecological theory of population dynamics. They both stressed the primacy of the interaction qua interaction as a driving force controlling outbreaks, and they both came to remarkably similar conclusions about the nature of that interaction: that it was some kind of limit cycle driven by the way in which starfish and coral, predator and prey, interacted.

Bradbury et al. (1985a, p. 69) declared 'The crown-of-thorns phenomenon... is, in essence, a prey-predator interaction. As such, the separate behaviour of prey and predator may appear confusing and unpredictable, while the dynamics of the pair object may be quite regular and predictable. The pair object is therefore the appropriate object of study'. This insight, while a commonplace now, was heretical to that group of scientists who had focussed primarily on the natural history of the starfish. Indeed, one eminent starfish biologist said to me at this time: 'What is this *interaction* you are talking about? Anyone can see that *Acanthaster* affects corals, but how can corals affect *Acanthaster?*'. This statement sadly highlights the limited penetration of modern evolutionary theory into wide areas of biology.

Per ardua...

These discoveries led to a resurgence and reorientation of *Acanthaster* research into three distinct lines - natural history, ecological theory and modelling experiments - each feeding on the others. The goal was to unlock the secrets of the population dynamics.

The broad outline of the natural history of *Acanthaster* on the GBR is now clear. It is the result of the systematic working through of the research program first described by Bradbury et al. (1985b). The distribution and abundance of the starafish and its impact on the coral populations is now known at the microscale [parts of reefs and times of *ca* 10^0 years] (Moran et al. 1985; 1988), the mesoscale [individual reefs and times of *ca* 10^0-10^1 years] (Moran et al. 1988), and the macroscale [the whole GBR and times of *ca* 10^1-10^2 years] (Moran et al. 1988; Johnson et al. 1989; Reichelt et al. 1990a). The pattern evident from these studies strongly suggests an underlying cyclicity of

1 Indeed, readers might be like to contemplate recent comments reported in The Economist of 16 February 1991. John Maddox, the editor of Nature, suggested that journals like his are mere archives for things everyone knows already, and Sydney Brenner of Cambridge University compared scientific publishing to 'incinerating the facts'.

outbreak and recovery at the mesoscale of individual reefs coupled with a larger wave-like process at the macroscale of the whole GBR.

This tantalising evidence of a well structured phenomenon where before there had only been a gallimaufry - a ragbag collection of (often conflicting) observations - spurred the theoreticians to seek the underlying controls of these dynamics. It seemed to them to be strong (circumstantial) evidence for a significant endogenous control of the phenomenon. Their work drew on our understanding of other outbreaking systems, thus anchoring the phenomenon firmly within the modern theory of population dynamics. Three groups (Antonelli et al. 1989; McCallum 1990; Parslow 1990), working at different levels of generalisation, physical scale and mathematical sophistication, quickly converged in their fundamental understanding of the theoretical aspects of the phenomenon: *Acanthaster* outbreaks on the GBR are instances of classic predator-prey dynamics. Their work concludes that stable limit cycles at the mesoscale of individual reefs and hydrodynamic connections between reefs for transport of starfish larvae are together sufficient to account qualitatively for the macroscale dynamics observed throughout the whole GBR (Antonelli et al. 1990).

The modelling studies parallel the field studies in terms of scale: for example, Hogeweg and Hesper (1990) and Reichelt et al. (1990b) at the microscale; Green (1990) at the mesoscale; Bradbury, Van der Laan and Macdonald (1990) and Van der Laan and Bradbury (1990) at the macroscale. Simple empirical discrete event models like these explore the shape of the envelope of possible *Acanthaster* dynamics. They show that the observed dynamics, especially at the larger scales, are part and parcel of a wider array of behaviours, only some of which have been observed in the field. The cyclically outbreaking populations observed on individual reefs are phenomenologically continuous with historically 'stable' low density nonoutbreaking populations, and with metastable, chronic, medium density 'outbreaks' (Bradbury et al. 1985a; Moore, 1990), and even chaotic populations (Bradbury et al. 1985c). Similarly, the wave-like propagation of outbreaks observed throughout the GBR is phenomenologically continuous with synchronised global outbreak pulses, with system-wide chaos, and with widespread, but nonpropagating, outbreaks. It is important to note that *phenomenologically continuous* does not mean that the epiphenomena of the population dynamics are continuous, indeed they may be highly discontinuous (Bradbury and Antonelli, 1990).

These three strands themselves interact. The natural history derives its sense of direction from (and is prevented from falling into stamp-collecting by) the imperatives of the other two, both voracious consumers of field data. The theoretical work and the field work help define the envelope of possible worlds that the modelling work can explore. The modelling and the field work in their own distinct ways provide rich grounds in which to test the theoretical work.

Together these strands open up the possibility of attacking *cause*. Together they say that *Acanthaster* dynamics are explicable in terms of the modern theory of population dynamics, that the observed dynamics are the result of strong feedbacks within the interaction, and that the observed dynamics are themselves embedded in a wider universe of possibilities (2). Thus *cause* can be understood to be that set of controls which result in the observed dynamics and not in other possible dynamics (Bradbury and Antonelli 1990).

... ad astra

This new picture of the *shape* of the phenomenon is quite clear, but very different from the prevailing views at the beginning of the eighties. That earlier view was characterised by strong polarisation (Moran and Bradbury 1989). On the one hand, there was a view that the outbreaks were, if not isolated and singular events, then at least unusual but natural, and one from which reefs recovered fully. Outbreaks were, it was thought, the result of a conjunction of unusual (usually) physical circumstances, such as particularly favourable settlement for starfish larvae. This view took no account of the interactive nature of the process. Nor could it, because that would admit to its potential for recurrence.

The other view was that the outbreaks were singular events driven by singular changes in the reef itself. Thus an otherwise rare species, the starfish, became uncharacteristically abundant, and the outbreak itself, as well as causing damage, became the harbinger of a deeper disturbance in the system.

The new view is not an amalgam of the earlier views, nor has it been achieved by all workers, but by sufficient of those actively working on the process for it to be considered a new paradigm.

It says that *Acanthaster* outbreaks are neither particularly novel nor particularly natural (indeed these appellations do not help our understanding much at all). Rather they are instances of a more general phenomenon - the interaction between a predator and its prey. The particular manifestation of the phenomenon, which we observe as an outbreak, is *caused* by the working through of the set of controls on the interaction.

This *cause* I have deliberately italicised to emphasise its triviality. It is essentially free of the understanding

2 They also say, almost incidentally, that the idea of external physical (noninteracting) processes controlling the dynamics is implausible.

we seek. But it should not be dismissed because it bears the same relation to something more fundamental, which is understanding, that the outbreaks themselves do to the phenomenon. Since the cause tells us *how* the outbreaks occur, we can now make progress on *why* they occur. We can now begin to understand.

To touch cause

Cause can be seen as the particular instances of the controls of the population dynamics, just as the outbreaks themselves are particular instances of the more general phenomenon. Thus cause tells us how the particular instance, the outbreak occurs, while an understanding of the controls tells us why one particular instance of the phenomenon and not another should occur.

Three studies examine the nature of the controls on the phenomenon, building on the works just discussed which reveal the dynamics.

Ormond et al. (1990) use field and modelling results to argue that a lethrinid-like fish predator of juvenile starfish is a critical control. This paper extends the understanding of the dynamics gained in the theoretical work of Antonelli et al. (1989) and McCallum (1990) and the empirical work of Moore (1990). Bradbury et al. (1990), in the second study, using a simple, empirically based cellular automata model, confirm that predator control, of exactly the type postulated by Ormond et al. (1990), is a plausible process. Moreover this model gives biological meaning to some parameters controlling the dynamics in the Antonelli et al. (1989) model. The third study, Bradbury and Antonelli (1990), is a theoretical analysis of the nature of the phenomenon's controls. It too confirms the significance of predation on the starfish as a major control, while arguing that other controls, grouped as *weather* and *place to live,* also have important roles to play.

Taken together, these papers suggest the following. The interaction between *Acanthaster* and coral on the Great Barrier Reef is manifested across a range of (sometimes discontinuous) dynamics, the most obvious of which we call an outbreak. That instance of the phenomenon is the result of the particular instances of the controls affecting the interaction. Change in any one control is itself insufficient to 'cause' an outbreak, since there are at least several interacting controls for the phenomenon. However, one control, the suite of lethrinid-like fish predators of the starfish, dominates the most dramatic shifts in the dynamics - from stable low density starfish populations to starfish outbreaks.

The new lessons - change on the GBR

It should now be clear why I asserted that the outbreaks are neither particularly novel nor particularly natural. The dynamics that give rise to the outbreaks are perfectly natural in the sense that they are embedded in the life histories of the starfish and coral, and so beyond human intervention. Yet (some of) the controls may themselves have their intensities altered by human intervention, so that some instances of the phenomenon may be novel. Because of this, it now becomes possible to talk sensibly about the nature and role of human intervention in the phenomenon (3).

The simplest things that may be said, as a result of this new understanding, may have enormous consequences. But they follow logically and inexorably from that understanding.

The first of these is that the GBR is changing. Its changes under evolutionary and ecological pressures are now compounded by changes due to man. Thus to say that the Reef is pristine is a nonsense. It has not been so since man, including aboriginal man, began exploiting it. It has more of the attributes of a heavily exploited system than anything else, and has had for many years. This should come as no surprise to anyone familiar with Saville-Kent, whose subtitle to his 1890 book was... Nor should it come as a surprise that the suite of lethrinid-like fish predators discussed above have had their density reduced on the GBR by commercial fishing over the last twenty years or so (Steven, *pers. comm*). In this sense, reductionists may say with perfect internal consistency, even if befuddled externally, that human intervention has caused the outbreaks.

Indeed, the system may have already changed as a result of the two earlier outbreak episodes. A model by Done et al. (1989) suggests that the long lived and slow growing massive corals may not recover their earlier abundances in the relatively short intervals between outbreak episodes, thus leading to change in the community structure of the system. Field evidence of Endean et al. (1989) supports this. More recently, Robert Seymour and I have completed a new model of the phenomenon which shows that the historical outbreak data fit a damped series of global pulses ending with the whole system in a degraded state. Perhaps we are witnessing an historic shift from the travelling outbreak wave to the global pulse (predicted in earlier models) with the shift brought about by the repeated passes of the wave itself.

Importantly, these changes are systemic. They show that the GBR behaves as a system, and the change at one scale or level of organisation propagate to and are manifested at other scales and levels (Bradbury and Mundy 1989). They also show that the changes are not necessarily cyclic, that the system may not return to any earlier state.

The second point is that managing the system must be viewed in the light of system change. That is, it has

3 That is intervention in the phenomenon beyond observing it, as a good Heisenbergian might say.

less to do with returning the system to some putative pristine state than with channelling the change in some broad direction.

Specifically, control of outbreaks may be possible, but not in the ways that have been discussedd hitherto (Zann and Weaver 1989). Since the outbreaks are an emergent property of the present state of the GBR, removal of adult starfish on a few individual reefs will have little or no effect on the process as Yamaguchi (1986) noted in Japan. Such efforts only toy with the epiphenomena. Control, to be effective, needs to focus on changing the values of the system's control variables, which are things like predators, a place to live and weather, and not on changing the values of the state variables, such as the corals and the starfish. Moreover, the control variables need to be changed globally, over the whole (or large parts of the) GBR, and not locally on individual reefs.

Given that the only control that we are likely to be able to influence is the predators, and that we are witnessing the effects, as repeated waves of outbreaks, of an historical global reduction in this control, we are forced to conclude that the only reasonable possibility for control lies in a global increase in predators. Since the predators are part of a commercial fishery, we arrive at the interesting notion that, globally, the GBR may not be a multiple use resource.

Lastly we note that a management ethos underpinned by the assumptions that the GBR is mostly pristine, with only local degradation, largely stable, and capable of multiple use in different localities does not sit well with the evidence that the GBR is largely exploited, with system wide degradation, rapidly changing, and incapable of multiple use.

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