

## REVIEW

# Can Caribbean coral populations be modelled at metapopulation scales?

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**ABSTRACT:** Understanding and predicting the connectivity of coral reef organisms linked by larval dispersal is a key goal of tropical coastal ecosystem science and management. As oceanographers make advances modelling transport processes between reefs, ecologists should be prepared to embrace the population dynamics of organisms at larger metapopulation scales. A metapopulation is demographically closed but contains multiple open local populations. Metapopulation models of coral dynamics would aid the identification of larval source and sink areas and help identify the boundaries of demographically closed populations. Metapopulation models would also aid the understanding of species extinctions and help formulate transboundary management strategies to conserve ecosystem function. Existing metapopulation models are not spatially realistic or proven to represent physical and biological processes at appropriate spatial and temporal scales. Before more realistic alternatives can be established, further research is needed into (1) the larval transport between reefs (i.e. the coupling of reef-scale and oceanic models of water circulation, the pre-settlement mortality rates of larvae, and larval mobility in the water column), (2) the influence of larval supply on coral population dynamics at local (10s of kilometres) scales (i.e. processes of settlement behaviour, post-settlement mortality, and the pre-emption of space by algae), and (3) processes affecting the net fecundity of local populations (i.e. interactions of colony size, partial mortality rate, competition with algae, and the influence of habitat, physical disturbance, herbivore pressure, nitrification and sedimentation).

**KEY WORDS:** Coral · Metapopulation · Population dynamics · Model · Scale · Remote sensing · Connectivity

## INTRODUCTION

Empirical evidence and theoretical considerations show unequivocally that large-scale processes must be embraced if we are to understand the population dynamics of organisms which have a pelagic phase during their life history (Caselle & Warner 1996, Cornell & Karlson 1996, Hatcher 1997). At large scales, such organisms (e.g. sessile invertebrates, reef fish) form populations whose dynamics are open at the local scale (Warner & Hughes 1989, Gilpin & Hanski 1991, Gaines & Lafferty 1995, Alexander & Roughgarden 1996) but demographically closed at some larger

metapopulation scale beyond which the effective dispersal of larvae by oceanic and coastal currents ceases (Roughgarden & Iwasa 1986). In a coral reef context, the hydrological connectivity of local fish and invertebrate populations has important implications for the science underpinning coastal (Done et al. 1996) and fisheries management (Roberts 1997). For example, some coral reefs may be net sources of larvae to reefs downstream, whereas other reefs may be net larval sinks, reliant on sites upstream for their larval supply (Roberts 1997). Further, hydrological connectivity between ecosystems can lead to the transfer of pathogens, pollutants, nutrients and sediments, and therefore poor agricultural practices can affect coral reefs downstream (e.g. Nowlis et al. 1997) and possibly beyond international boundaries.

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In a paper on the transport envelopes of fish larvae between Caribbean reefs, Roberts (1997) identified groups of countries with interconnected coastal fish populations, suggesting that cooperative management was vital to sustain recruitment levels in the fishery. Whilst Roberts' (1997) assumption of passive larval dispersal by ocean currents has been criticised (Bellwood 1998, Sale & Cowen 1998), the need for models of larval transport between reefs is uncontested. Larval transport may be a highly localised phenomenon where marine larvae become entrained within coastal circulation (Olson 1985, Sammarco & Andrews 1988, Black et al. 1991, Black 1993) or where larvae are competent to settle soon after release (Carlson & Olson 1993). However, at the scale of inter-reef connectivity in the Caribbean, where entrained larvae may exist in the plankton for weeks to months (Roberts 1997), the destination of larvae is strongly influenced by meso-scale variability (e.g. Lee et al. 1994) at scales of several hundred kilometres and months to a year (Mooers & Maul 1998).

Reviewing oceanic circulation in the Intra-Americas Seas (IAS), Mooers & Maul (1998) concluded that the present understanding of mesoscale oceanic variability is confined to a few well-studied regions (e.g. Florida, the Gulf of Mexico) but by applying process-based theory of circulation from these areas to less studied areas of the IAS, and making field verifications, predictive simulation models of IAS circulation will be possible. It is conceivable, then, that ecologists may soon have better information on the transport envelopes between reefs which potentially provides new insight into the population dynamics of organisms which have a planktonic stage.

A number of attempts have been made to model the metapopulation dynamics of both sessile (Iwasa & Roughgarden 1986, Roughgarden & Iwasa 1986, Possingham & Roughgarden 1990, Preece & Johnson 1993, Stone et al. 1996) and mobile (Man et al. 1995) marine organisms, but, as I will show later, none are suitable for modelling fish or invertebrate metapopulations distributed across reefs of the Caribbean. Metapopulation models were originally conceived by Levins (1970) to describe a structureless network of conspecific populations whose dynamics were dominated by extinction and colonisation. This extreme view of metapopulations has been modified extensively in the last 30 yr (see Gilpin & Hanski 1991) with the emergence of spatially realistic models of real patch networks whose populations may be depressed rather than driven extinct (see Hanski & Simperloff 1997). A spatially realistic metapopulation model of scleractinian coral populations would be highly appropriate for investigating large-scale issues of reef sustainability such as the identification of larval source and sink areas (see

also Ogden 1997), investigating the vulnerability to and potential recoverability from major disturbances of local populations of sessile organisms, and identifying the boundaries of demographically closed populations (Grosberg & Levitan 1992). Realistic metapopulation models would also predict the effects of habitat loss on community structure and diversity (Stone 1995, Cornell & Karlson 1996), improve understanding of the competitive interactions between species or taxa with different dispersal abilities (Gaines & Lafferty 1995), and predict the long-term effects of massive bleaching events (Brown 1997) and disease outbreaks. Ultimately, the predictions of such models would improve the formulation of transboundary management strategies to conserve ecosystem function.

In this paper I discuss the challenge of building population models suitable for predicting the metapopulation dynamics of scleractinian corals on Caribbean reefs. My intention is to highlight ecological questions for empiricists and modellers in order to take advantage of the metapopulation scales made possible by advances in oceanography. I begin by describing the design and objectives of metapopulation models and then review the problems and considerations which need to be embraced using interdisciplinary studies. I do not discuss in detail the difficulties of modelling IAS circulation since this has been reviewed elsewhere (e.g. Mooers & Maul 1998).

## DESIGN AND OBJECTIVES OF METAPOPOPULATION MODELS

The design of a metapopulation model will clearly depend on the question(s) being asked, and metapopulation models have biogeographic, genetic, evolutionary, and ecological interpretations (Hanski & Gilpin 1997, Hubbell 1997). Jackson et al. (1996) provide an evolutionary example for corals by describing how the turnover of Caribbean coral species during the early Pleistocene may have resulted from local extinction at latitudinal extremes after a rapid fall in sea level greatly reduced the number of available patches for cold-intolerant species. Jackson et al. (1996) referred to the metapopulation model of Nee & May (1992) which predicted that species of lower colonisation potential would go extinct first as available habitat decreases. The limited evidence supports this theory in that the life history strategy of acroporid corals, which replaced pocilloporids in terms of dominance, favours fast growth and the ability to track changes in sea level (Chappell & Polach 1991). Spatially realistic metapopulation models would also help clarify the roles of dispersal, disturbance frequency, and interspecific competition in explaining the apparently ubiquitous

distribution of coral species throughout the Caribbean on ecological and some geological time scales (Karlson & Cornell 1998).

I focus here, however, on ecological time scales of years to decades which are relevant to the population dynamics of many reef corals (Hughes 1996), although the longevity of some massive corals (e.g. *Montastraea annularis*) may exceed 200 yr (Hudson et al. 1994). Through their zooxanthellae symbionts, scleractinian corals fix carbon which is principally directed towards bioconstruction of the reef framework and trophic pathways throughout the ecosystem (for details see Dubinsky 1990, Johnson et al. 1995, Done et al. 1996, Opitz 1996, Hatcher 1997). Major reef-building corals, such as *Montastraea* spp., *Siderastrea siderea*, *Acropora* spp. and *Diploria* spp., generally attain large size and have a broadcasting life history strategy (Szmant 1986) which is relevant to metapopulation concepts of open or partially open local populations. The acroporids are probably an exception, however, due to their high rates of asexual reproduction by fragmentation (Highsmith et al. 1980, Neigel & Avise 1983), which for *A. palmata* can account for two-thirds of the colonies on a reef (Highsmith 1982). The aim here would be to

predict temporal changes in the abundance and size-frequency distribution of corals within local populations and their implications for reef function at local and metapopulation scales. I focus on this aspect of metapopulation modelling and discuss the definition of spatial scales for the model and some of the difficulties in modelling both the planktonic and benthic model components.

### DEFINING SPATIAL SCALES OF LOCAL AND METAPOPOPULATIONS OF CORALS

A metapopulation model requires at least 2 spatial scales: the local populations (Fig. 1) and the larger metapopulation.

Gaines & Lafferty (1995) defined open local populations as existing where 'Migration of individuals among local populations is common. In the case of marine species with long lived pelagic larvae, immigration is the only way that local populations increase in size. In such extreme open populations, local reproduction does not affect local population dynamics'. However, this definition is at odds with reef systems

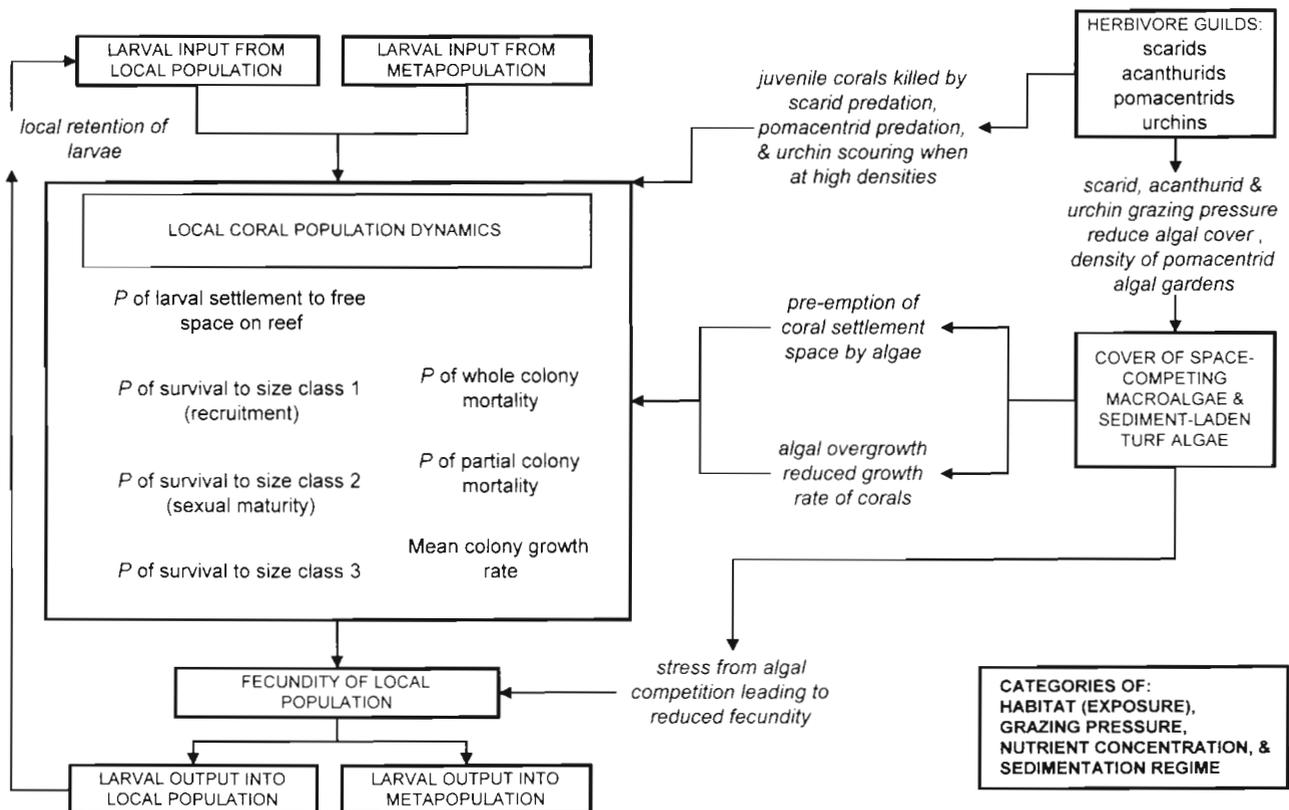


Fig. 1. Representation of processes affecting local coral population dynamics showing larval exchange with the metapopulation. The model should be parameterised for varying categories of habitat (exposure), grazing pressure, nutrient concentration and sediment regime which are putatively the major external controls affecting the coral population dynamics. *P*: probability

with high local retention of larvae (i.e. where local reproduction may affect local population dynamics) and a more appropriate definition can be extracted from Hanski & Simperloff (1997), who state that 'individuals practically share a common environment', which might refer to local levels of the most important processes controlling coral population dynamics at a practicable scale for modelling (Fig. 1). These processes are described in detail later but may include herbivory (fishing intensity and *Diadema antillarum* densities), suspended sediment regime, nutrient concentration, physical wave exposure and potential larval supply (proximity to nearest source of larvae).

Choosing an appropriate spatial scale to represent local populations is difficult because of (1) the paucity of geographic data on local processes (e.g. herbivory) and reef attributes such as size, and (2) the computer tractability of simulations (i.e. the maximum number of local populations that can be simulated, depending on the complexity of the model). Oceanic models can predict circulation (and therefore estimate larval supply) on a grid representing 20 km by 20 km cells (Gao & Mooers 1996, cited in Mooers & Maul 1998), and the World Conservation Monitoring Centre (WCMC) has estimated coral reef area at a resolution of 1 km<sup>2</sup> (Spalding & Grenfell 1997). However, there is little consistency in definition of 'coral reef' in the WCMC coverage and future coral reef mapping initiatives at local and regional scales should adopt a standardised classification scheme or protocol (Mumby & Harborne 1999). Where water conditions permit (ca horizontal Secchi distance > 15 m and depth < 20 m), estimates of coral reef area and distribution can be improved using satellite remote sensing. Mumby et al. (1997) demonstrated that the satellite-borne sensor Landsat Thematic Mapper provides the most cost-effective means of making detailed (<30 m pixel size) maps of coral reef distribution over hundreds of kilometres. Each image covers approximately 185 km × 185 km and the creation of an accurate (thematic accuracy ca 70%), region-wide coverage is feasible. Satellite images of coral reefs also provide a semi-quantitative distribution of suspended sediment concentration in surface waters (Clark 1993) which may help make a crude categorisation of sedimentation at the scale of local coral populations. Similarly, coarse levels of eutrophication may be inferred from a time series of chlorophyll concentrations within coastal areas, which can now be obtained synoptically throughout the IAS using data from the satellite-borne sensor SeaWiFS (Sea-viewing Wide Field-of-view Sensor; for overview, see Acker 1997).

In short, further remote sensing is required to develop a grid-based model of coral reef distribution, coral reef area, and physical environmental conditions (e.g. water quality). This will need to be augmented by

additional field data on ecological processes (e.g. herbivore biomass) and reef status (e.g. size-frequency distribution of corals) and might be partly achieved (1) by review of the descriptive literature on coral reef communities (particularly the Atoll Research Bulletin), (2) by interaction with REEFBASE, the global database on coral reef status (McManus & Ablan 1997), (3) through regional networks of coastal ecosystem monitoring such as CARICOMP (Caribbean Coastal Marine Productivity; Ogden et al. 1997, Woodley et al. 1997), and (4) using the results of rapid reef assessment surveys focused on coral mortality, herbivore guilds and algal functional groups (e.g. the Atlantic & Gulf Reef Assessment exercise, R. N. Ginsburg pers. comm.). On a cautionary note, however, the predictions of models can only be as good as the data they are based on and therefore sensitivity analyses should be carried out to examine the influence of say the standard error of local coral cover estimates on the predictions of the model.

Given the uncertainty in defining the extent of local populations, it may prove more realistic to derive probabilistic boundaries to metapopulation size rather than attempt to describe the absolute extent of any metapopulation. For example, transport envelopes could be estimated representing the probability that reefs receive 10, 30, 50, and 100% of propagules from within the envelope.

#### THE PLANKTONIC COMPONENT OF THE METAPOPOPULATION MODEL

Several marine metapopulation models have no spatial structure and make the simplifying, but clearly inappropriate, assumption of complete mixing of larvae and that patches have equal access to the larval pool (e.g. Iwasa & Roughgarden 1986, Roughgarden & Iwasa 1986, Man et al. 1995, Stone et al. 1996). An appropriate model of larval dispersal needs 2 principal components: (1) the geographic transport of larvae between reefs, which depends on the velocity and vertical stratification of oceanic and coastal currents, and the motility of larvae, and (2) the survivorship of larvae over time.

#### Geographic transport of larvae in coastal and oceanic currents

The swimming speeds of coral planulae are orders of magnitude less than those of oceanic currents (Hodgson 1985, Carlon & Olson 1993) so assumptions of passive dispersal by oceanic currents may be valid in general (Harrison & Wallace 1990). However, variations in

wind velocity will greatly affect dispersal (Willis & Oliver 1988) and the buoyancy of larvae tends to decrease with time (Babcock & Mundy 1996), meaning that vertical mixing in the water column should be taken into account. Existing oceanic circulation models incorporate vertical structure in the water column by using multiple depth strata (ca 25), principally focused at the ocean surface and near the benthos (C. N. K. Mooers pers. comm.).

While existing oceanic models of IAS mesoscale circulation have good vertical resolution, one of the main problems in predicting the supply of larvae to a reef (and indeed larval output from a reef) is the reconciliation of horizontal scales between these oceanic models, which have a minimum grid size of ca 20 km (Mooers & Maul 1998), and the vertically integrated fluid dynamic models used to predict circulation around coral reefs, which typically have grid sizes of hundreds of metres (e.g. Black 1993, Kraines et al. 1998). Preece & Johnson (1993) created a cellular automaton model of coral populations of the central Great Barrier Reef (see also Johnson & Preece 1993) and used larval retention coefficients, predicted by vertically integrated fluid dynamic models (Black et al. 1990), to simulate connectivity. Although the model was not spatially realistic (e.g. it did not include realistic reef shapes, sizes, or hydrological conditions), this method may be appropriate for bridging the scales of oceanic and reef circulation models but further modelling activities are required to characterise larval retention regimes for generic reef shapes, areas, depths, weather conditions and circulation parameters (*sensu* Black 1993). Further, the disparity in spatial scales between oceanic and reef circulation models may be reduced in the foreseeable future by nesting high resolution grids within oceanic models, possibly attaining resolutions of 1 to 5 km (C. N. K. Mooers pers. comm.).

#### Survivorship of larvae in the plankton

Broadcast planulae develop for a minimum of 4 to 6 d prior to becoming competent to settle and metamorphose (see review by Harrison & Wallace 1990) and settlement must take place within 3 to 4 wk or else planulae will have insufficient energy reserves to metamorphose (Richmond 1988). However, virtually nothing is known about larval mortality rates other than mortality may increase whilst in the vicinity of reefs, mainly due to planktivorous reef fish (Hamner et al. 1988, Westneat & Resing 1988) and that the larvae of brooding Caribbean corals (e.g. *Agaricia agaricites*, *Porites astreoides*, and *Siderastrea radians*) are highly palatable to damselfish and wrasse (Lindquist & Hay 1996). Recent developments in larval genetics, permit-

ting molecular tagging (see comments by Ogden 1997), may, in future, provide insights into larval behaviour. Experiments may be designed where tagged larvae are released into natural systems whose flow regimes are well studied and periodic plankton sampling should aim to differentiate larval mortality rates from losses of plankton due to diffusional and advective transport processes.

#### THE LOCAL POPULATION COMPONENT OF THE METAPOPOPULATION MODEL

The following section reviews current understanding of coral population dynamics and the scales of causative processes. From a metapopulation modelling perspective, it is critical to understand the processes governing the recruitment of corals to a population (i.e. relationship between larval supply and recruitment), and the net fecundity (larval output) of the population (Fig. 1).

#### Larval settlement

Models of barnacle metapopulation dynamics along the coast of California (Possingham & Roughgarden 1990, Alexander & Roughgarden 1996) use diffusive and advective models of larval transport and estimates of larval mortality rate to predict the supply of larvae to suitable habitat. Larval settlement is then manipulated using a coefficient. Unfortunately, there are no benchmark estimates of larval settlement rate available to reef ecologists since the processes affecting coral recruitment, namely, larval supply, settlement behaviour, the availability of free space, and post-settlement mortality, are poorly understood (Babcock & Mundy 1996).

The settlement behaviour of planulae has been studied intensively but many observational studies are inconclusive because of the difficulties in inferring active substratum selection when stochastic larval supply and patchy post-settlement mortality are not recorded. In general, however, larvae appear to prefer rough surfaces (Lewis 1974, Carleton & Sammarco 1987, Smith 1997) which may enhance attachment (see review in Harrison & Wallace 1990). Chemical cues are known to induce larvae of some genera (e.g. *Agaricia*) to settle on encrusting red algae (Morse et al. 1988); other species (e.g. *Favia fragum*) prefer to settle near conspecifics (Lewis 1974); whilst others are inhibited by secondary metabolites from other taxa such as soft corals (Maida et al. 1995). Settlement characteristics may be highly species-specific (Morse et al. 1988, Carlon & Olson 1993).

In a unique experimental study, Babcock & Mundy (1996) investigated the survivorship and settlement behaviour of larvae from the broadcast spawning corals *Platygyra* and *Oxypora*, whose adult populations are stratified by depth. Adult patterns of distribution were not attributable to depth-related mortality rates of settled larvae, suggesting that either the supply of larvae differs with depth for the 2 species or the mortality rates of larger corals are depth-dependent and species-specific. Another important result of the study was that no microhabitat had persistent advantages in terms of recruit survivorship. For the first 4 mo after larval attachment, survivorship was highest for recruits attached to under surfaces where sediment accumulation was reduced. However, this pattern was reversed after 4 mo because the higher growth rate of corals attached to vertical and upper surfaces provided an escape from mortality due to larger size (sensu Hughes & Jackson 1985). Thus, Babcock & Mundy (1996) concluded that there may be no single optimum settlement orientation for larvae as survivorship varies with habitat, sediment regime, and coral size.

Sedimentation appears to be particularly important in determining early mortality at both microhabitat scales (Maida et al. 1994, Gleason 1996) and reef scales (Hunte & Wittenberg 1992). Sediments can affect larval settlement directly by preventing secure attachment and indirectly by altering larval settlement behaviour. Increased water turbidity could make more cryptic habitats too dark, either increasing mortality rates in these refugia (due to decreased coral growth rate) or forcing larvae to settle on more exposed upper surfaces where sediment levels or grazing intensity may be higher, possibly increasing juvenile mortality rates (Maida et al. 1994).

The effects of nutrification (increased ambient nutrient concentrations) on coral settlement are only beginning to emerge. Ward & Harrison (1997) manipulated nitrogen and phosphorus concentrations on adults and larvae of *Acropora longicyathus* and found that increases in both nutrients reduced the settlement of spat and that their effects were synergistic. The mechanisms by which elevated nutrients prevent settlement are not understood but may involve blooms of cyanobacteria which release toxins to prevent larval attachment. Conversely, Ward & Harrison (1997) found that larvae released from adults which had been incubated in a nitrogen-rich environment showed high levels of settlement when released in ambient seawater. Corals are nitrogen-limited so the settlement success of larvae developing in nitrogen-rich conditions might be attributable to a release from this limitation enabling greater amino acid production which confers greater protection from ultraviolet radiation. Larvae

released from eutrophic reefs may therefore have greater survivorship than those from oligotrophic reefs whereas larval settlement on eutrophic reefs may be severely reduced. Whether these patterns hold for other species remains to be seen.

### Post-settlement mortality and recruitment

Empirical data on coral recruitment in the Western Atlantic are unequivocal in the numerical dominance of recruits from brooding species and paucity of recruits from species which broadcast their gametes (Bak & Engel 1979, Rogers et al. 1984, Hughes 1985, Smith 1992, 1997). More experimental work is needed to explain the low levels of recruitment observed for the latter group (i.e. to assess the relative importance of larval supply, settlement behaviour, and post-settlement mortality).

In general, recruitment of corals has been shown to be space-limited (i.e. positively correlated to free space available) in Jamaica (Hughes 1985) and the Great Barrier Reef (Connell et al. 1997), but recruitment also shows great temporal variation (Gleason 1996, Connell et al. 1997) and spatial variability on a wide range of scales including continental shelves (Sammarco 1991), between reefs (Fisk & Harriott 1990), and within sites (Babcock 1989, Smith 1992, Baird & Hughes 1997). Available empirical evidence suggests that post-settlement mortality in corals is high (Smith 1997), but the density dependence (or otherwise) and scale dependence of such processes are poorly understood and difficult to infer from observational studies (Caley et al. 1996). This difficulty arises throughout benthic ecology because observations of persistent and variable age-class strength in a population, which are usually inferred to indicate density-independent mortality (e.g. Victor 1986), may occur in the presence of density-dependent mortality (Holm 1990). Further, variable post-recruitment mortality may obscure the relationship between recruitment and year-class strength even in the absence of density-dependent mortality (Warner & Hughes 1989). Caley et al. (1996) point out that experiments should manipulate entire cohorts over a number of years in order to examine the effects of recruitment on age distributions and overall population size.

The feeding activities of herbivores can have positive and/or negative effects on coral recruitment (Fig. 1). Dense aggregations of *Diadema* (Sammarco 1980, Rylaarsdam 1983) and intense fish grazing (Bak & Engel 1979, Sammarco 1991, but see Birkeland 1977) may overgraze the substratum preventing successful coral recruitment. Conversely, Birkeland (1977) found that intermediate grazing pressure on Caribbean reefs

promoted coral settlement by removing fouling turf and macroalgal canopies, and Morse et al. (1988) suggested that grazers may facilitate establishment of specific (though unidentified) red coralline algae, which in turn promotes settlement of *Agaricia humilis* through chemical cues. The adaptive significance of settlement cues from coralline algae and direct grazing effects on recruit survival have not been fully explored. Studies of feeding selectivity by the parrotfish *Sparisoma viride*, which is capable of killing coral recruits, revealed an active avoidance of coralline algae (Bruggeman et al. 1994) but, again, the coralline species concerned were not identified. If the same coralline species were avoided by parrotfish and induced settlement of invertebrate larvae, one might investigate the importance of parrotfish grazing as a selective agent favouring the (co)evolution of larval settlement cues from coralline algae.

Modelling and empirical studies are needed to assess the effects of major space occupiers on coral recruitment. It is clear from the discussion above that larval settlement is inhibited by macroalgae and sediment-laden turf algae (Fig. 1), yet very little is known of the spatio-temporal dynamics of these space competitors and their effects on the survivorship of corals. Several issues need to be resolved for a clearer understanding. First, what effect does algal overgrowth exert on the survivorship of coral recruits, and how does survivorship vary with (1) the species and biomass of alga, (2) the duration of overgrowth, and (3) the size of coral recruit? Second, what are the spatial dynamics of algal cover in relation to its effect on the survivorship of recruits? In terms of recruitment dynamics and the role of available space, the 2 questions are intimately linked. For example, imagine that a 6 mo old recruit could withstand macroalgal overgrowth for 2 mo without a significant decline in survivorship, and that the coral must grow for 2 yr to become large enough to escape algal-induced mortality. Then the appropriate question for studies (and models) of recruitment dynamics would be: what is the total percent cover of substratum experiencing macroalgal overgrowth for periods less than 2 mo during a 2 yr period? Thus, the role of algal cover in preventing recruitment may be underestimated by studies estimating average algal cover at reef or site scales because, while average cover may appear to be stable at this scale, the total area covered by algae for 2 mo periods may differ markedly. De Ruyter van Stevenick & Breeman (1987) studied the cover of *Lobophora variegata* at a depth of 25 m in Curaçao and found no significant changes in cover at the reef scale but cover in individual quadrats, measuring 11 by 16 cm, varied from 10 to 90% during the same period (1 yr). Clearly, spatio-temporal scales of algal patch

dynamics must be studied in greater detail, and in relation to the principal structuring processes of different herbivore guilds (Hay & Taylor 1985, Carpenter 1986, Foster 1987, Steneck 1989), potential productivity and regrowth capability (Steneck & Dethier 1994), and detachment by physical disturbance (Carpenter 1986).

Ultimately, empirical and modelling methods might try to identify the 'recruitment potential' of reefs with various structural complexity (see Steneck 1993), algal cover, grazing regime, wave exposure, and sediment regimes. I define the recruitment potential of a reef as the probability that a competent larva reaching a reef will settle and reach recruit size (ca 1 cm), but more appropriate definitions may be prompted by further studies. Models should be spatially explicit in order to incorporate the complex spatial interactions of the aforementioned processes, but emphasis must be placed on modelling the simplest set of parameters capable of affecting recruitment dynamics. Model predictions should aim to describe a probability distribution of recruitment levels for reefs experiencing different intensities of biological and physical processes. For example, the recruitment potential of an exposed fore-reef with many large herbivorous parrotfish, few *Diadema*, and low sedimentation rate may be 0.02 (SE 0.1) but only 0.001 (SE 0.04) where herbivory is reduced. Burrows & Hawkins (1998) describe a cellular automaton approach to modelling algal patch dynamics on temperate rocky shores and this principle might be adapted by reef ecologists (see also Caswell & Etter 1993).

### Coral growth and mortality

The growth rates of most major reef-building corals (e.g. *Montastraea annularis*) decrease with depth (Highsmith et al. 1983, Huston 1985) although Bosscher & Meesters (1993) found growth to be light-saturated to a depth of 15 m and then sharply light-limited to 30 m. Juvenile growth rates are high (van Moorsel 1988) and, although growth can be indeterminate (Sebens 1987), relative growth rate decreases with increasing coral size and age partly due to increased rates of partial colony mortality and possibly by greater energetic investment in sexual reproduction (Hughes & Connell 1987). Bleaching events can cease coral growth even in large corals such as *Montastraea* spp. (Goreau & Macfarlane 1990) but the anticipated deleterious effects of nutrification and sedimentation on growth rate are less clear.

Tomascik & Sander (1985) found that eutrophication generally decreased the growth rate of *Montastraea annularis* in Barbados but that suspended particulate matter (SPM) could have variable effects on growth

depending on concentration. At intermediate SPM concentrations, corals may derive nutrients from particulate matter, whereas high SPM concentrations may be deleterious by smothering polyps and reducing light availability to zooxanthellae. Increased nutrient concentrations can have indirect effects on coral growth rate (1) by promoting the cover of space competitors including macroalgae (Littler et al. 1993) and sponges (Wilkinson 1987, Aerts & van Soest 1997) which potentially increases the incidence of competitive interactions and reduces growth rate (Tanner 1995), and (2) by promoting phytoplankton blooms which reduce the transmission of light to the benthos, thus reducing rates of photosynthesis (D'Elia & Wiebe 1990). Direct effects of nutrients on coral growth rates are difficult to summarise because of the variation in nutrient concentration, application frequency, and duration of manipulative experiments. It would appear, however, that increased nitrogen can decrease the translocation of photosynthates from zooxanthellae to host thus reducing calcification rates (McGuire & Szmant 1997, Steven & Broadbent 1997) and that phosphorus may interfere with calcification by acting as a crystal poison (Hoegh-Guldberg et al. 1997).

Many metapopulation models (e.g. Caswell & Cohen 1993, Tilman et al. 1994, Man et al. 1995, Stone et al. 1996) assume that disturbance leads to complete extinction of species on a patch but, during ecological time scales, such severe effects of disturbance are not appropriate for open populations of marine organisms which may show greater resistance to extinction (Caley et al. 1996, Connell et al. 1997). A more suitable model would allow local populations to be depressed but rarely driven to extinction. Mortality rates of adult corals are principally size-dependent (Hughes & Jackson 1980, 1985, Hughes & Connell 1987, Meesters et al. 1997), and to some extent age-dependent (Hughes 1984, Bak & Meesters 1998). Whole colony mortality is greatest for small corals whereas the incidence of partial colony mortality from various biological (e.g. parrotfish grazing, disease) and physical (e.g. abrasion) sources increases with colony size (Hughes & Jackson 1985, Bak & Meesters 1998). Bak & Meesters (1998) studied the partial mortality of massive corals in Curaçao at shallow sites of 6 to 10 m depth. They concluded that the modal size frequency class (on logarithmic axes) of each species might constitute a critical colony size where the relative importances of whole and partial colony mortality are reversed. Whether this result is site-specific is uncertain, but, if true, may help parameterise models of coral population dynamics by distinguishing the incidence of whole colony and partial colony mortalities (Fig. 1).

At larger spatial scales, storm and hurricane damage is highly patchy (Woodley et al. 1981, Edmunds & Wit-

man 1991, Witman 1992, Bythell et al. 1993a,b, Rogers 1993). For example, the effects of Cyclone Ivor on the Great Barrier Reef were patchy at scales of tens to hundreds of metres within 50 km of the 'eye' of the storm (Done 1992). With the exception of shallow water acroporids, large reef-building massive corals tend to be more resistant to storm damage than smaller encrusting species (Jackson & Hughes 1985) although the strength of coral attachment to the substratum is predicted to be the main factor determining dislodgement rates (Massel & Done 1993). Models of the effects of storms on reefs (e.g. Hughes 1984, Andres & Rodenhouse 1993) and empirical studies (e.g. Hughes 1989, Done 1992, Witman 1992, Connell et al. 1997, Lirman & Fong 1997, Rogers et al. 1997) are unequivocal in pointing out the importance of considering the historical regime of disturbances when attempting to predict or interpret the effect of any individual disturbance (Hughes 1989). For example, the negative effect of Hurricane Hugo in 1989 on coral cover in St. John (U.S. Virgin Islands) was so severe that more recent hurricanes (Luis and Marilyn) in 1995 did not, on average, depress coral cover further (Rogers et al. 1997).

It may be impossible to simulate hurricane-induced mortality events at reef scales because of the stochastic spatio-temporal patchiness in severity and frequency of disturbance (Done 1992). However, small-scale (10s of kilometres) stochastic modelling with depressed (damaged) coral populations simulated at scales of hundreds of metres (see above) may predict the probability distribution of various small-scale outcomes over a given time interval (e.g. net change of coral size-frequency distribution at kilometre scales). Probabilistic outputs would then be inserted into larger-scale models (i.e. the representation of local populations within the metapopulation) in an attempt to bridge the gap in scale between models. Conceptually, the metapopulation model may then simulate the recovery of coral populations from hurricanes where the effects of each hurricane are chosen pseudo-randomly from the probability of small-scale outcomes. The problem of simulating major disturbances may be reduced at evolutionary and geological temporal scales. Treml et al. (1997) reconstructed the paths of hurricanes in the Lesser Antilles over the past 500 yr and found that the spatial distribution of hurricane paths was not random at century scales but the incidence of individual storms is unpredictable.

#### Intra- and intertaxon competitive interactions

Since the die-off of *Diadema antillarum* in 1983–94 (Lessios et al. 1984) some Caribbean coral reefs may have undergone a phase change in community struc-

ture toward greater macroalgal biomass and often to the detriment of coral populations (De Ruytner van Stevenick & Bak 1986, De Ruytner van Stevenick & Breeman 1987, Hughes et al. 1987, Lessios 1988, Levitan 1988, Carpenter 1990, Hughes 1994, Bak & Nieuwland 1995). At a regional scale, the importance of bottom-up (nitrification; Lapointe 1997) versus top-down (reduced herbivory; Hughes 1994, 1996) explanations for phase changes remains contentious, although the large spatial scale, sequence, and nature of changes would tend to support the latter hypothesis (with local exacerbation by nitrification and historical hurricane disturbances). In practice, these changes in reef community structure probably mean that macroalgae and turf algae are the dominant space competitors with coral colonies rather than other corals (Fig. 1; Rogers 1993). In Curaçao, De Ruytner van Stevenick et al. (1988) found that growth rates of the brown macroalga *Lobophora variegata* were reduced by 35% when in contact with small corals but that algal-coral overgrowth continued. In Australia, Tanner (1995) found that macroalgal competition reduced growth rates of (semi-)encrusting acroporid corals but not bushy (erect) pocilloporids. Further research is needed into the consequences of algal-coral competition, particularly when viewed at large spatial scales (10s of kilometres). For example, how is 'algal-coral overgrowth' mediated by the size, morphology, and species of coral, wave exposure, light intensity (depth), and nutrient concentration? Although interspecific competition between corals is typified by competitive networks (Buss & Jackson 1979, Chornesky 1989, Lang & Chornesky 1990) which have been modelled (Karlson & Jackson 1981, Karlson & Buss 1984), algal-coral competition may be more predictable, lending itself to the simpler approach of modelling competitive hierarchies (see metapopulation models by Caswell & Cohen 1993, Stone et al. 1996).

### Coral fecundity

The puberty size of corals is size-dependent (Soong 1993) and usually larger in species which broadcast rather than brood their larvae (Harrison & Wallace 1990). Puberty sizes and fecundities in Caribbean corals are well known though varied even within species (Szmant 1991, Soong & Lang 1992, Soong 1993). Population models need to investigate the interactions of puberty size, partial colony mortality, and stress on the overall fecundity of the local population of corals. Models will have to take account of the age of corals because matrices of size-frequency distribution cannot simply be multiplied by the appropriate size matrix for fecundity. A reproductively mature colony that is

reduced below puberty size by partial colony mortality may still reproduce (depending on whether central reproductive areas of the colony remain intact), albeit with reduced fecundity (Hughes 1984, Szmant-Froelich 1985).

More research is needed into the effects of stress on the proportion of gravid polyps per colony, their gonad density, and gamete production. Effects of nitrification and sedimentation on coral fecundity have not been extensively studied although both appear to suppress fertility (Kojis & Quinn 1984, Tomascik & Sander 1987). Competitive interactions also affect fecundity (Fig. 1). Tanner (1995) found that the fecundity of *Acropora palifera* on the Great Barrier Reef was halved when in contact with macroalgae. Szmant (1991), working on *Montastraea annularis*, found that zones of polyps (a few centimetres wide) were infertile if in contact with other macro-organisms due to the high defence and growth demands of these polyps. These are small-scale observations and their effects at larger scales are unknown, largely because of the ethical considerations in removing tissue from many colonies (A. M. Szmant pers. comm.) and the time required for histological analysis. Extensive observations during spawning events may be the only feasible means of seeking further insight into large-scale effects on fecundity.

### TESTING PREDICTIONS FROM METAPOPOPULATION MODELS

A great limitation of modelling at large scales is the difficulty in testing predictions of the model, particularly since most empirical studies are conducted at relatively small scales (Gaines & Lafferty 1995, Caley et al. 1996). One method of testing metapopulation-scale predictions is the reconstruction of well-documented large-scale phenomena such as the phase changes on reefs during last 2 decades (Hughes 1994). In future, long-term geographic trends in the dynamics of coral populations from regional monitoring programmes (e.g. CARICOMP; Ogden et al. 1997) may provide partial support for metapopulation model predictions. However, for reasons outlined earlier, it is inadvisable to infer specific demographic processes from data on adult population dynamics unless entire cohorts (including recruits) are monitored. There is still a paucity of data on recruitment levels on Caribbean reefs and future monitoring efforts might consider including such data.

Investigations of gene flow may shed light on estimates of population connectivity (Palumbi 1994, Shulman & Bermingham 1995, Ayre et al. 1997). Although low levels of gene flow may indicate infrequent larval exchange, high levels of gene flow among sites do not

necessarily imply high levels of larval exchange during *ecological* time frames because even low levels of larval exchange may maintain gene flow (Sammarco & Andrews 1988). Generally, reef-dwelling invertebrates with limited pelagic dispersal have been found to have restricted gene flow (e.g. Ayre & Dufty 1994, Burnett et al. 1995) whereas species with broadcast-spawning or long-lived brooded larvae have higher gene flow due to greater inter-reef connectivity (e.g. Burnett et al. 1994, Ayre et al. 1997). However, evidence is also emerging that gene flow may be restricted even in areas which are anticipated to have strong larval connectivity. Working on *Acropora palifera* and *Pocillopora damicornis* at One Tree Island, Australia, Benzie et al. (1995) found a 10-fold drop in gene flow between reef crest populations and those inhabiting lagoon and microatoll areas. Such genetic isolation is difficult to reconcile given the expected exchange of larvae across the reef crest during periods of inundation, which may suggest that (currently unknown) local selective forces may be responsible. A more extreme deviation of expected gene flow was recently reported for the Pacific giant clam *Tridacna maxima* where gene flow ran perpendicular to present-day ocean currents (Benzie & Williams 1997). In some areas and for some taxa, dispersal events may be episodic so that measured gene flow may still reflect oceanic circulation patterns when sea levels were different to those today. A spatially hierarchical examination of genotypic variation in Caribbean corals is long overdue but, given the arguments made above, any interpretation of gene flow must have both ecological and geological perspectives.

## CONCLUSIONS

The title of this paper asks whether Caribbean coral populations can be modelled at metapopulation scales. The answer is almost certainly 'Not yet'. Whilst some simple patch-extinction models (Nee & May 1992, Tilman et al. 1994) may predict loss of species if their habitat is reduced, these methods best lend themselves to evolutionary studies involving loss of genera during geological time scales (e.g. Jackson et al. 1996, but see Stone et al. 1996). Despite attempts to represent coral reef connectivity on cellular automata (Preece & Johnson 1993), no coral reef metapopulation model is spatially realistic or proven to represent physical and biological processes at appropriate spatial and temporal scales.

Understanding the role of spatio-temporal heterogeneity in physical and biological processes on population dynamics is a central goal of ecology (Levin 1992, Aronson & Precht 1997). Patchy processes on

coral reefs can lead to large-scale heterogeneity in ecosystem structure. For example, Edmunds & Bruno (1996) found large variations in benthic community structure at kilometre scales around Jamaica, and Aronson & Murdoch (1997), surveying coral community structure of forereefs throughout the Florida Keys, found greater variation at among-reef scales (10 km) than at sub-reef (1 km) and regional (100 km) scales. Throughout this paper, I have echoed the words of others and called for further empirical research into the spatial dependency of processes, most of which have been studied at small spatial and temporal scales. Spatial modelling will be instrumental in improving our understanding of the interactions of complex processes. Model simulations may, for example, seek to predict the recruitment potential of reefs with different physical and biological characteristics. While simulation modelling will fail to provide simple biological rules governing community structure (*sensu* Judson 1994), its strength may be an ability to predict the relative probabilities of particular ecological outcomes (e.g. success of recruitment) for inclusion in larger-scale metapopulation models. Simplification of real ecosystems will have to be attempted where possible. Here, I propose a focus on major reef-building corals (except acroporids) which probably have more open population dynamics than smaller species which brood their offspring. Although this abstraction ignores a significant component of many coral assemblages, it may simplify the model because massive reef builders tend to be long-lived and have moderately stable population dynamics (Hughes & Jackson 1985, Bythell et al. 1993a).

Conceptually, local populations of corals would be represented in various 'phases' of community structure (Knowlton 1992), depending on local conditions of say grazing pressure and eutrophication, and the history of disturbance and recruitment. Further modelling and empirical studies are needed to understand the causative processes and stability of phase changes in community structure, with particular focus on the importance of larval supply, settlement and post-settlement processes. Only then will metapopulation scales of larval connectivity be interpreted and modelled meaningfully. However, even simple metapopulation models can exhibit complex behaviour (Gaines & Lafferty 1995) so testing the internal workings and predictions of a more complex metapopulation model may constitute the greatest challenge of all.

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