



## Demographic variation within spatially structured reef fish populations: when are larger-bodied subpopulations more important?

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### Abstract

Environmental heterogeneity frequently induces spatial variability in somatic growth, which can cause inter-population differences in reproductive output among organisms for which fecundity is dependent upon body size. Mean asymptotic body size,  $L_{\infty}$ , varies among populations of several reef fish species. Deterministic models suggest  $L_{\infty}$  has little effect on population growth, so subpopulations with larger  $L_{\infty}$  may not have disproportionate effects in sustaining an open system. We used a stochastic simulation model to examine the potential role of a larger  $L_{\infty}$  subpopulation in aspects of population dynamics beyond population growth under a range of assumptions about the prevailing recruitment relationships. We compared dynamics of a demographically homogeneous system with a system that included one subpopulation with 20% larger  $L_{\infty}$ . Despite the magnitude of the increase in  $L_{\infty}$ , mean population size and average time at large population sizes differed little between the homogenous system and that with the larger  $L_{\infty}$  subpopulation. However, including the larger  $L_{\infty}$  subpopulation did result in less time spent at very small population sizes, which could reduce extinction risks. Effects of the larger  $L_{\infty}$  subpopulation were most pronounced when a deterministic recruitment cycle was imposed in combination with high stochastic variability in recruitment. This was due to regular series of poor recruitment years shifting the population structure toward older cohorts where differences in body size (and reproductive output) between the larger  $L_{\infty}$  subpopulation and the other subpopulations were greatest. Differences were also greater when recruitment variability was regionally correlated. When recruitment variability was locally independent, the probability of system-wide declines was reduced because declines of individual populations at one time were replenished by unaffected neighbors in subsequent years. Our study suggests that variation in  $L_{\infty}$  within a network of

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interconnected subpopulations may not be an important determinant of population behavior under certain conditions, but might be important in coping with periods of persistent, system-wide recruitment failure.

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## 1. Introduction

Interactive effects of life history traits (i.e. fecundity, mortality, maturation, growth, reproduction) determine the dynamics of populations. Since Cole's (1954) seminal paper that developed theory for the population consequences of demographic processes operating at the level of individuals, there has been extensive incorporation of life history traits into population models, especially via matrix models. However, when spatially structured populations are considered, most models are constructed in terms of overall population growth without explicitly accounting for its constituent demographic rates. Yet, ecological conditions are rarely homogenous across a species' range, and this ecological variability can induce spatial variability in demography. When distinct populations of a given species interact through dispersal of some individuals as part of a metapopulation or other spatially structured population, demographic processes in one place can affect population dynamics on other habitat patches. Spatially structured models that account for particular life history traits provide the opportunity to examine the significance of spatial patterns in demography for population dynamics.

We focus our attention on tropical reef fishes, among which somatic growth is particularly responsive to local ecology (Jones, 1991). Fecundity among fishes and other taxa that produce large clutches (e.g. reptiles, marine invertebrates) is highly correlated with body size, so growth characteristics have consequences for reproductive output. Intraspecific spatial variation in growth rate and asymptotic body size,  $L_\infty$ , of reef fishes is commonly observed among populations (Choat and Axe, 1996; Hart and Russ, 1996; Newman et al., 1996; Meekan et al., 2001; Gust et al., 2002; Kritzer, 2002; Williams et al., 2003). Populations of reef-dwelling organisms are often segregated in space due to the patchy distribution of reef habitat, but habitat patches can be connected by dispersal of pelagic larvae. Consequently, coral reef sys-

tems are increasingly being modeled within the context of metapopulation theory and related concepts such as source–sink theory (Kritzer and Sale, 2004). Our question of interest concerns whether subpopulations with larger  $L_\infty$  within interconnected reef fish populations play a disproportionate role in sustaining the larger population.

The only previous study to examine the role of asymptotic size suggests that varying asymptotic size will not have substantial effects on marine population dynamics. Ebert (1985) performed sensitivity analysis of a matrix model of a sea urchin population with growth, maturity and longevity characteristics similar to many reef fishes. Ebert found that varying somatic growth rate had pronounced effects on population growth rate, but varying asymptotic body size had little effect. This suggests that while a subpopulation with higher growth rate will be more important, a subpopulation with larger  $L_\infty$  will have little additional effects on population dynamics of a larger open system relative to subpopulations with smaller bodied individuals. However, Ebert (1985) notes that his findings might be dependent upon the deterministic, equilibrium assumptions of his model, and DeAngelis (1988) argues that spatial and temporal heterogeneity can profoundly affect how we interpret demographic characteristics when using ecological models. Moreover, Ebert's study only addressed effects of asymptotic size on overall population growth rate. Gotelli (1991) notes that interesting and potentially important descriptors of population dynamics beyond population growth rate cannot be examined using matrix models and instead must be examined using numerical simulations.

We adopt a simulation modeling approach to examine whether a subpopulation with larger  $L_\infty$  within a spatially structured coral reef fish population may affect the long-term behavior of the population as a whole. Specifically, we evaluate the contribution of a subpopulation with larger  $L_\infty$  toward mitigating the adverse effects of variable and often low recruitment

relative to a system with homogeneous demographic traits among subpopulations in terms of three summary statistics. The summary statistics we use are the mean annual population size relative to a reference population size, and indices of *stability* and *vulnerability*. Stability is defined as the ability to maintain overall population size near the reference size. Vulnerability is defined as the propensity for overall population size to fall below an arbitrarily chosen lower threshold where it might be more prone to extinction. We explore the behavior of the simulated populations in response to different plausible ecological scenarios, including patterns of inter-subpopulation larval dispersal, deterministic cycles in recruitment, and different degrees of stochastic variability in recruitment that is either correlated among subpopulations or locally independent.

## 2. Methods

### 2.1. Background on model structure

The brief review of reef fish population ecology provided in this section is not intended to be comprehensive, but rather is intended to highlight empirical data that guided our model structure.

We simulate the dynamics of a system comprised of four subpopulations inhabiting distinct reefs (Fig. 1), one of which is given a larger  $L_\infty$  when spatial variability in demography is incorporated. We use four subpopulations in order to achieve a balance between minimizing model complexity while having the larger  $L_\infty$  subpopulation represent a minority of the overall system so as not to overstate its importance. Given the paucity of available information on larval dispersal (Kritzer and Sale, 2004), we consider a range of exchange rates among subpopulations. Post-settlement stage reef fishes are largely sedentary, so we assume there is no movement among reefs after the pelagic stage.

We address the alternative possibilities that variability in recruitment is regionally correlated (e.g. Myers et al., 1997) or independent among subpopulations (e.g. Doherty, 1987). The magnitude of temporal variability in replenishment of reef fish populations is high. Settlement can vary by up to an order of magnitude or more over even a few years (Doherty, 1991). Doherty and Fowler (1994) measured coefficients of variation

in annual settlement on seven reefs ranging from 0.6 to 1.7 over a 9-year-period. We also consider both random interannual variations in larval supply and random variation coupled with a deterministic cycle (see Fogarty et al., 1991). Several long-term recruitment time series exhibit cycles with an approximately 10-year-period (e.g. Johnson et al., 1986; Austin et al., 1996; Clark et al., 1999), so we adopt a 10-year-period when cyclical patterns are incorporated.

Density-dependent regulation of reef fish populations is most commonly observed during early post-settlement life stages (reviewed by Doherty, 2002; Hixon and Webster, 2002). This density-dependent post-settlement mortality shows no evidence of over-compensation at high densities, so we assume an asymptotic relationship between larval supply to the reef and recruitment to the benthic population at maturity. The range of  $L_\infty$  variation among neighboring populations is approximately 5%–30% (Choat and Axe, 1996; Hart and Russ, 1996; Newman et al., 1996; Kritzer, 2002), so we incorporate an intermediate difference of 20% when spatial variation is introduced (Fig. 2). Parameter values are based upon the stripey bass *Lutjanus carponotatus* (Kritzer, 2002, 2004).

### 2.2. Model structure and parameter values

Length at age  $a$  on reef  $i$ ,  $L_{a,i}$ , was determined by a von Bertalanffy growth function specific to each reef:

$$L_{a,i} = L_{\infty,i} e^{-K_i a},$$

where  $K_i$  is a reef-specific growth coefficient that determines the curvature of the model. Base case systems were established with all reefs given the same  $L_\infty$  value of 250 mm. Simulation results for these base case systems were compared with results for systems with spatial variation in  $L_\infty$ , in which one reef was given a larger  $L_\infty$  value of 300 mm (Fig. 2). Values of  $K$  (0.8 year<sup>-1</sup> for  $L_\infty = 250$  mm and 0.65 year<sup>-1</sup> for  $L_\infty = 300$  mm) were chosen such that the somatic growth rate ( $\omega = KL_\infty$ ; Gallucci and Quinn, 1979) was comparable between subpopulations with differing values of  $L_\infty$  to avoid confounding effect of  $L_\infty$  with effects of somatic growth rate.

Weight at age  $a$  on reef  $i$ ,  $W_{a,i}$ , is determined from length by a cubic power function. Fifty percent of a cohort is mature at age 2 and 100% maturity is at age 3, with a maximum longevity of 20 years. The number

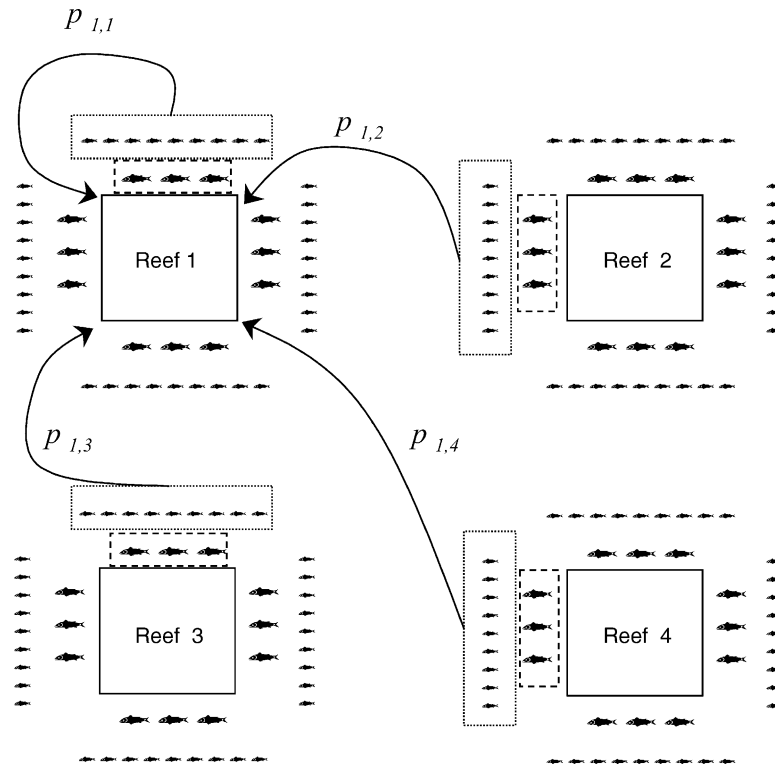


Fig. 1. Conceptual diagram of the hypothetical reef fish populations modeled in this study, illustrating the manner in which effective biomass for a given reef  $i$  (here reef 1) is calculated. The proportion of larvae (♠, larvae) dispersing to reef  $i$  from reef  $j$ ,  $p_{i,j}$ , determines the proportion of spawning biomass (♣, spawners) on reef  $j$  used to calculate the magnitude of larval supply to reef  $i$ . The spatial distribution of spawners and larvae around each reef is illustrative only.

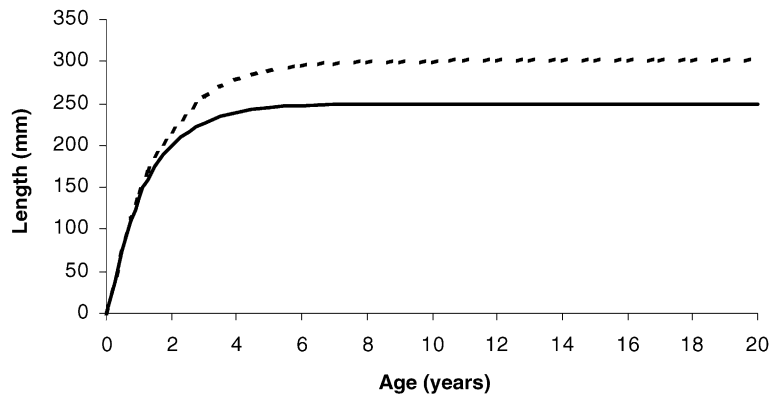


Fig. 2. Growth curve for all subpopulations in the base case system (solid line) and that for one subpopulation when spatial variation in asymptotic body size,  $L_{\infty}$ , is introduced (broken line). Early growth rates are similar, but diverge as different  $L_{\infty}$  of 250 and 300 mm are approached.

of fish of age  $a$  on reef  $i$  in year  $t$ ,  $N_{a,i,t}$ , is determined by survivorship from the previous year:

$$N_{a,i,t} = N_{a-1,i,t-1}e^{-M},$$

where  $M$  is the instantaneous natural mortality rate of fish aged 2 and older ( $0.21 \text{ year}^{-1}$ ). These demographic traits collectively determine the spawning biomass of subpopulation  $i$  in year  $t$ ,  $B_{i,t}$ :

$$B_{i,t} = \sum_{a=2}^{a_{\max}} W_{a,i} N_{a,i,t} m_a,$$

where  $m_a$  is the proportion of mature fish in age class  $a$ .

The model predicts recruitment to the spawning population at age 2 as a function of the ‘effective biomass’ of a given subpopulation. The effective biomass is the sum of a proportion of the biomass of all reefs in the system. The proportion of each reef’s biomass contributing to the effective biomass of a given reef is equivalent to the proportion of larvae that disperse to the reef of interest (Fig. 1). Specifically, the effective biomass of reef  $i$  in year  $t$  is:

$$EB_{i,t} = \sum_{j=1}^4 p_{i,j} B_{j,t},$$

where  $p_{i,j}$  is the proportion of larvae produced by reef  $j$  that disperse to reef  $i$ . Larval production is assumed to be a linear function of spawning biomass, so effective biomass is an index of larval supply. Inter-subpopulation dispersal probabilities varied among ecological scenarios modeled (see below).

An asymptotic density-dependent model of the Beverton–Holt form was used to determine recruitment of 2-year-olds to the spawning population of reef  $i$  in year  $t$ ,  $N_{2,i,t}$ , as a function of EB, 2 years earlier:

$$N_{2,i,t} = \frac{\alpha \cdot EB_{i,t-2}}{\beta + EB_{i,t-2}},$$

where  $\alpha$  is the juvenile carrying capacity of a cohort and  $\beta$  is the EB required to produce a recruitment of 2-year-olds equal to  $\alpha/2$ .

Beverton–Holt curves of different shapes were initially compared to assess the influence of the parameters  $\alpha$  and  $\beta$ , for which plausible values are unknown. The maximum recruitment level,  $\alpha$ , was arbitrarily set at 10,000 fish, which essentially scales

population size. Stock-recruitment curves of differing steepness were then generated by using  $\beta$  values ranging from 15% to 50% of the biomass of a base case subpopulation if  $\alpha$  were maintained indefinitely,  $B_{\max} = \sum_{a=2}^{a_{\max}} \alpha e^{-M(a-2)} m_a W_a$ , which was approximately 12,000 metric tons. Note that  $B_{\max}$  is distinct from the virgin biomass,  $B_0$ , which is a product of the recruitment function, and therefore, cannot be used to set its parameters. Preliminary simulations revealed that systems with  $\beta$  values less than 20%  $B_{\max}$  were so productive that they remained at large sizes in all ecological scenarios. In contrast, systems with  $\beta$  values greater than 40%  $B_{\max}$  were so unproductive that they crashed in a large number of simulations regardless of the values of other parameters. Therefore, a  $\beta$  value of 30%  $B_{\max}$ , or 3600 tons, was used as an intermediate value between excessive and insufficient reproductive potential.

When cycles in recruitment were modeled, recruitment was determined using the baseline  $\alpha$  for the first 5 years and then a value 20% of the baseline  $\alpha$  for the next 5 years. Stochastic interannual variation was added to the model by multiplying EB, and therefore, larval supply, by a random variate before it was used to predict recruitment to the adult population by either the constant or cyclical function. Random variates were drawn from log-normal distributions with a mean of 1 and coefficients of variation,  $CV_L$  (standard deviation when mean is 1), that ranged from 0.5 to 2.0 in different scenarios. We address the alternative possibilities of regionally correlated variability and variability that is independent among subpopulations by multiplying EB of all subpopulations by the same random variate in some scenarios and by using unique random variates for each subpopulation in other scenarios. We ran preliminary simulations of base case systems using values for proportional larval retention by each subpopulation,  $p_{i,i}$ , ranging from 0.1 to 1.0 to select values for subsequent simulations comparing base case with spatial variation case systems. Larvae in excess of the proportion retained by a subpopulation were distributed equally among the remaining reefs, so  $p_{i,j} = (1 - p_{i,i})/3$  for all  $j \neq i$ .

### 2.3. Modeling approach and summary statistics

Monte Carlo simulations were performed for base case and spatial variation case systems using scenarios

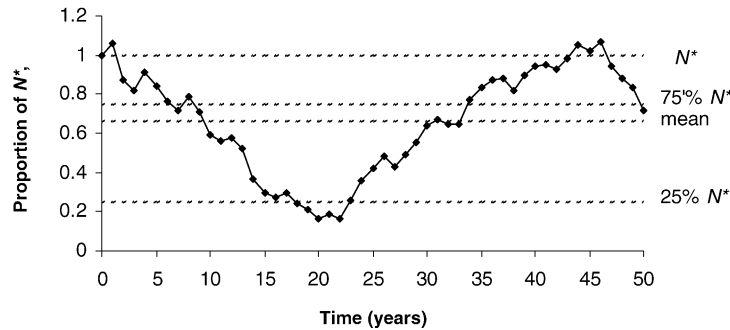


Fig. 3. A 50-year-trajectory within a hypothetical 500-year time series of total population size for a simulated system of interconnected reef fish subpopulations illustrating the manner in which summary statistics were calculated. Mean population size was measured as a percentage of a reference population size ( $N^*$ ) calculated from a deterministic simulation. The index of stability,  $I_S$ , is the percentage of years the overall population size is greater than 75%  $N^*$ . The index of vulnerability,  $I_V$ , is the percentage of years the overall population size is less than 25%  $N^*$ . Here, these summary statistics would be 66%, 48%, and 10%, respectively.

defined by a dispersal pattern, degree of  $CV_L$ , spatial correlation of variability in larval supply (i.e. regional or independent among reefs) and temporal constancy of the underlying recruitment function (i.e. constant or cyclical). Prior to introducing stochastic variability in larval supply a 200-year deterministic run of the model was performed for a given combination of parameters. This was done to eliminate effects due to starting conditions by establishing a constant overall population size in the case of a constant recruitment function or a repeated cycle of population sizes in the case of a cyclical recruitment function. A 200-year run was more than sufficient to stabilize the behavior of the deterministic model. A reference population size,  $N^*$ , was then calculated as the average population size over the final 10 years of the deterministic run to serve as a basis for assessing the performance of the system when environmental stochasticity was added. The value of  $N^*$  is the equilibrium population size when the recruitment function is constant, as opposed to the average over a full cycle when the recruitment function is cyclical.

Having established  $N^*$  for a given system (base case or spatial variation) under a given recruitment function and dispersal regime, 100 individual time series of 500 years each were then simulated for each level of  $CV_L$  and each spatial scale of stochastic variability in larval supply. Each time series commenced with the population size and structure at the end of the deterministic run. From each time series, three summary statistics were calculated. Firstly, we calculated the

mean proportion of the reference population size over the 500-year time series (Fig. 3). Secondly, we calculated the proportion of years the overall population size remained above 75%  $N^*$  as an index of stability,  $I_S$  (Fig. 3), which Holling (1973) defined as the capacity for a population to maintain its size near an equilibrium value. A third summary statistic was the proportion of years the overall population size fell below a lower threshold of 25%  $N^*$  as an index of vulnerability to drop to population sizes that may be more prone to extinction due to catastrophic events,  $I_V$  (Fig. 3). The effects of introducing a subpopulation with a larger  $L_\infty$  were then assessed by comparing the mean values of these indices over all time series for a given scenario between the base case system and that with spatial variation in  $L_\infty$ .

### 3. Results

We first summarize initial deterministic simulation results that established the reference population sizes. Next, we summarize preliminary stochastic simulations that determined the influence of dispersal patterns under different assumptions about the constancy of the recruitment function and the spatial scale at which recruitment variability is correlated. We then describe the patterns in the three summary statistics when recruitment variability is independent among local subpopulations, followed by results when recruitment variability was regionally correlated.



### 3.1. Deterministic simulations: reference population sizes

Base case systems operating under a common recruitment function (i.e. constant or cyclical) had the same  $N^*$  regardless of the dispersal scenario used because demographic traits were homogenous ( $N^* = 177,039$  for constant recruitment function;  $N^* = 86,610$  for cyclical recruitment function). In contrast,  $N^*$  differed slightly among dispersal scenarios for spatial variation case systems due to differential distribution of the marginally greater reproductive output from the higher  $L_\infty$  subpopulation. The  $N^*$  values differed among dispersal scenarios by <1% for the constant recruitment function (all  $N^*$  approximately 182,000) and by <2% for the cyclical recruitment function (all  $N^*$  approximately 92,000). Furthermore, although  $N^*$  values were always greater for spatial variation case systems relative to base case systems with a common recruitment function, the differences were small for either recruitment function (<3% of the base case  $N^*$  for the constant recruitment function; <7% of the base case  $N^*$  for the cyclical recruitment function). By assessing population behavior relative to different reference values, we ran a risk of understating the effects of the subpopulation with larger  $L_\infty$  by holding those systems to a higher standard. However, the similarity among  $N^*$  values for systems with a common dispersal and recruitment regime suggests that population behavior was assessed relative to comparable benchmarks, while underscoring the limited effects of  $L_\infty$  on system performance under equilibrium conditions (Ebert, 1985).

### 3.2. Preliminary stochastic simulations

Before conducting the comparison of the base case and spatial variation case systems, we ran a series of simulations of base case systems with the highest degree of variability in larval supply ( $CV_L = 2.0$ ) to select dispersal scenarios for the comparative modeling. These simulations revealed that values of all three summary statistics were similar across larval retention values when variability in larval supply was correlated among subpopulations (Fig. 4). Values of  $I_S$  were also similar among larval retention values when variability in larval supply was independent among subpopulations (Fig. 4B). Conversely, when subpopulations experienced independent fluctuations in larval

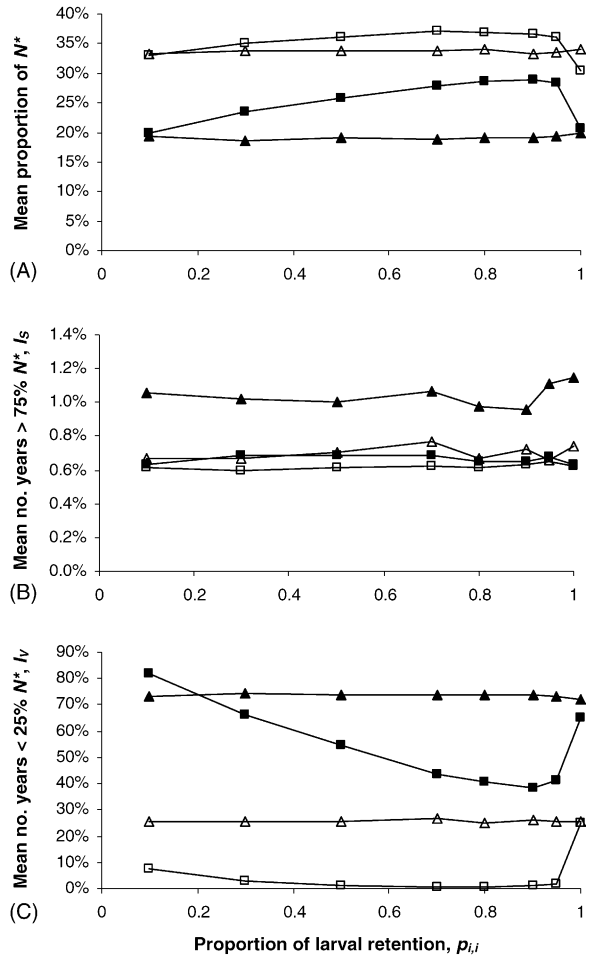


Fig. 4. Effects of proportion of larval retention by each subpopulation,  $p_{i,i}$ , on the value of three summary statistics: mean annual proportion of  $N^*$  (A); index of stability,  $I_S$  (B); and index of vulnerability,  $I_V$  (C). Scenarios included either a constant (open symbols) or cyclical (filled symbols) recruitment function, and stochastic variability in larval supply that was either correlated among reefs (triangles) or locally independent (squares). All simulations modeled a base case system with a coefficient of variation in larval supply,  $CV_L$ , of 2.0.

supply, values improved for the mean annual population size (i.e. increased) and  $I_V$  (i.e. decreased) up to larval retention values of approximately 0.9 (Fig. 4A and C). Thereafter, values of these summary statistics quickly became much poorer as proportional retention approached 1.0 (Fig. 4A and C). Consequently, comparisons between base case and spatial variation case systems were made using a single intermediate larval retention value (0.5) when variability in larval supply

was correlated among subpopulations and a range of larval retention values (0.1, 0.3, 0.7, 0.9) when variability was independent among subpopulations.

The comparisons of summary statistics across retention values also illustrate two patterns that are generally maintained throughout the simulations. Firstly, values of summary statistics were generally poorer when recruitment went through a deterministic cycle in addition to stochastic variability (Figs. 4–6). This is due to the regular and predictable series of poor recruitment years experienced when the recruitment function cycles. Secondly, values of the summary statistics were nearly always poorer when variability in larval supply was correlated among subpopulations as opposed to being independent among reefs (Figs. 4–6). This is due to an averaging effect when variability is locally independent, whereby exceptionally poor recruitment events do not affect the overall system and individual subpopulations diminished by poor recruitment can quickly recover through replenishment from unaffected neighbors. The only exception to these trends were for  $I_S$  at the highest level of stochastic variability ( $CV_L = 2.0$ ), where values were highest when recruitment was cyclical and regionally correlated (Fig. 4B). However, all values of  $I_S$  were small at this highest level of stochastic variability, as was the magnitude of the differences among the recruitment scenarios.

### 3.3. Locally independent variability in larval supply

There was a consistent pattern of decline in all three summary statistics (i.e., decrease in the mean annual population size and  $I_S$ , and increase in  $I_V$ ) with increasing variability in larval supply (Fig. 5). At low and intermediate values of  $CV_L$  (0.5–1.5), the decline in mean annual population size (Fig. 5A) is due to a general lowering of the upper bounds of population fluctuations (decreases in  $I_S$ ; Fig. 5B) without reduction of the lower bounds below 25%  $N^*$  ( $I_V$  values  $\approx 0$ ; Fig. 5C). However, at the highest value of  $CV_L$  considered, the continued reduction of mean annual population size corresponds with lower population sizes that often fall below the 25%  $N^*$  threshold (Fig. 5C).

There were small but consistent differences in mean annual population size between the base case and spatial variation case systems across all levels of  $CV_L$  (Fig. 5A). In contrast, differences in  $I_S$  values between

the two systems varied among  $CV_L$  values.  $I_S$  values were similar at  $CV_L = 0.5$ , with population size above 75%  $N^*$  in more than 80% of the years on average in each time series when the recruitment function was cyclical and above 75%  $N^*$  100% of the time when the recruitment function was constant (Fig. 5B). Similarly, both the base case and spatial variation case systems were almost never above 75%  $N^*$  with  $CV_L$  values of 1.5 and 2.0 for both recruitment functions (Fig. 5B). However, at  $CV_L = 1.0$ , differences in  $I_S$  between the base case and spatial variation case systems were apparent. The values of  $I_S$  decreased slightly with increasing larval retention probabilities, but the magnitude of differences between base case and spatial variation case systems was generally consistent (Fig. 5B). Also, the relative decrease in  $I_S$  from  $CV_L = 0.5$  to 1.0 for both systems was much more pronounced with the cyclical recruitment function than with the constant function (Fig. 5B).

Periodic declines in overall population size below 25%  $N^*$  did not occur for either base case or spatial variation systems under either recruitment or any dispersal regimes when  $CV_L = 0.5$  or 1.0 and only very rarely when  $CV_L = 1.5$  (Fig. 5C). This pattern was generally the same under the constant recruitment function when  $CV_L$  reached 2.0, but  $I_V$  values ranged between 30% and 82% at  $CV_L = 2.0$  when the recruitment function was cyclical (Fig. 5C). In the scenarios where variability in larval supply was independent among reefs, the largest differences among dispersal patterns and the largest effects of a larger  $L_\infty$  subpopulation were evident at  $CV_L$  of 2.0 in combination with a deterministic cycle in recruitment. Declines in overall population size below 25%  $N^*$  were progressively less common as proportional larval retention increased from 0.1 to 0.9, with  $I_V$  at  $p_{i,i} = 0.9$  less than half that at  $p_{i,i} = 0.1$  (Fig. 5C). Concomitant with these changes, the absolute differences in  $I_V$  between the base case and spatial variation case systems decreased from 12% to 8% as  $p_{i,i}$  increased from 0.1 to 0.9, but the relative differences increased from 15% to 23% the  $I_V$  value of the base case system (Fig. 5C).

### 3.4. Regionally correlated variability in larval supply

Like the results for locally independent variability in larval supply, values of all summary statistics wors-



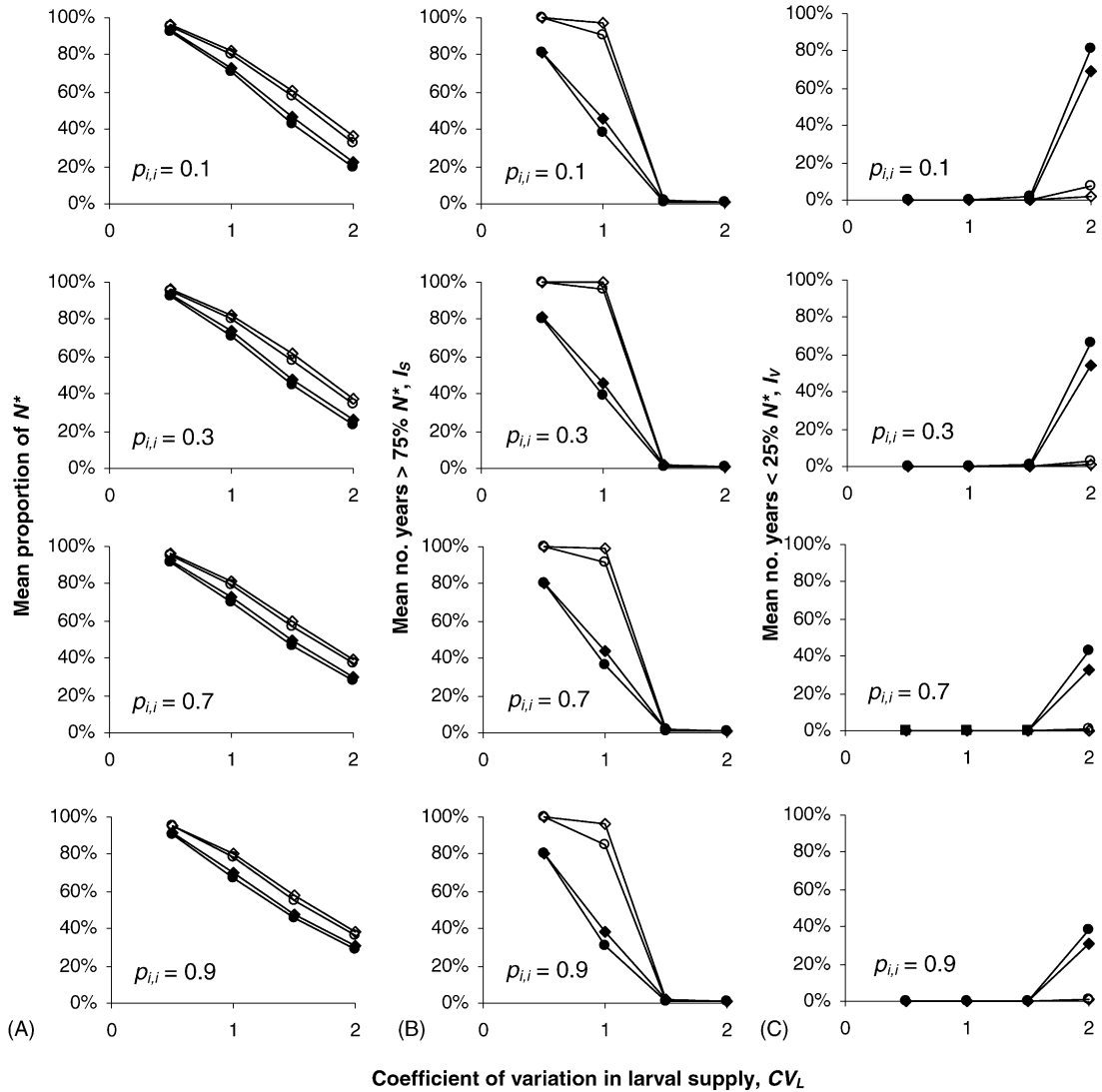


Fig. 5. Mean annual proportion of  $N^*$  (A); index of stability,  $I_S$  (B); and index of vulnerability,  $I_V$  (C), at different levels of variability in larval supply,  $CV_L$ , for base case (circles) and spatial variation case (diamonds) systems modeled with a constant (open symbols) or cyclical (filled symbols) recruitment function. Proportional larval retention by each subpopulation,  $p_{i,i}$ , varied among scenarios and is indicated on each plot. Stochastic variability in larval supply was independent among subpopulations.

ened as the degree of variability increased (Fig. 6). Furthermore, changes in summary statistics across values of  $CV_L$  followed the same general patterns as those when variability was regionally correlated. Values of the mean annual population size and  $I_S$  were most similar between the scenarios with locally (Fig. 5A and B) and regionally correlated variability in recruitment (Fig. 6A and B). In contrast, differences between the

results for locally independent and regionally correlated variability in larval supply were greatest for the values of  $I_V$ . Firstly, when the recruitment function was cyclical, declines in overall population size below 25%  $N^*$  were much more common at  $CV_L = 1.5$  when variability in larval supply was regionally correlated (Figs. 5C and 6C). Furthermore, there was a clear difference between the two systems with the spatial variation case

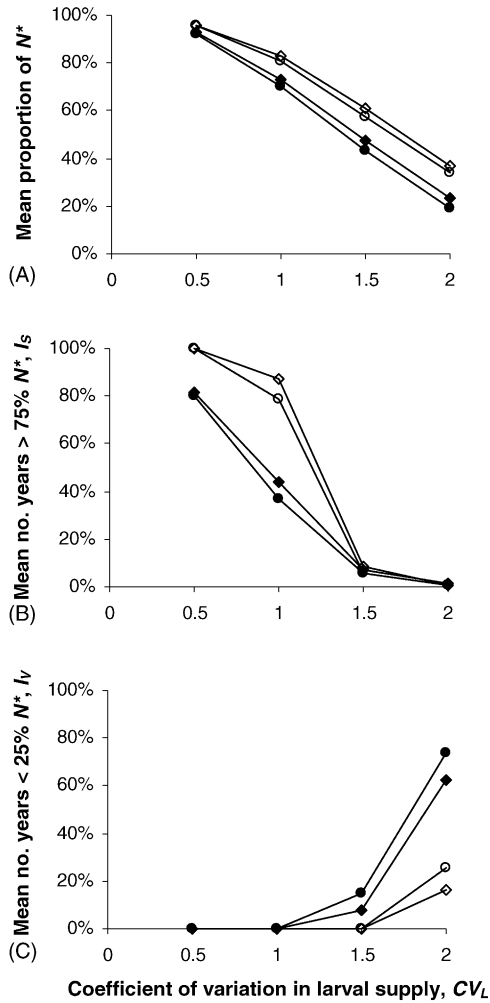


Fig. 6. Mean annual proportion of  $N^*$  (A); index of stability,  $I_S$  (B); and index of vulnerability,  $I_V$  (C), at different levels of variability in larval supply,  $CV_L$ , for base case (circles) and spatial variation case (diamonds) systems modeled with a constant (open symbols) or cyclical (filled symbols) recruitment function. Proportional larval retention by each subpopulation was 0.5. Stochastic variability in larval supply was correlated among subpopulations.

system falling to very low population sizes about half as frequently as the base case system (Fig. 6C).

Secondly, at  $CV_L = 2.0$ , the values of  $I_V$  with the cyclical recruitment function were higher when variability in larval supply was regionally correlated than when larval supply was locally independent, except when the local retention probability was 0.1 (Figs. 5C and 6C). Moreover, the  $I_V$  values for both

systems at  $CV_L = 2.0$  with the constant recruitment function were much greater when variability in larval supply was regionally correlated than when it was locally independent (Figs. 5C and 6C). Like the results for locally independent variability in larval supply, there was an effect of including the larger  $L_\infty$  subpopulation, as  $I_V$  values for the spatial variation case were lower than the base case by 9% and 11% with the constant and cyclical recruitment functions, respectively (Fig. 6C). These differences represent relative changes from the base case of 36% and 15%.

## 4. Discussion

### 4.1. The significance of spatial variation in $L_\infty$

We examined population behavior in terms of mean population size over a time series, as well as frequency of population sizes at both the upper and lower bounds of the range of fluctuations, under a variety of ecological scenarios. The general results of our simulations are summarized in Table 1. The results are most striking for the lack of large differences, despite the magnitude of the demographic variation introduced. Spatial differences in  $L_\infty$  of 20%, or even less, in field studies result in strong statistical significance (Hart and Russ, 1996; Newman et al., 1996). Yet, there were generally very small differences in all summary statistics under most scenarios modeled. This is despite the fact that the power relationship between length and weight means a 20% difference in  $L_\infty$  results in an approximately 75% difference in asymptotic weight, and weight is the determinant of reproductive output. However, effects of the larger  $L_\infty$  subpopulation were evident when recruitment was cyclical, temporal variability in recruitment was high, and especially when variability in recruitment was regionally correlated. This illustrates that the ecological significance of biological patterns is highly dependent upon context, even when statistical significance is strong (also see Weinberg et al., 1986).

The inclusion of a larger  $L_\infty$  subpopulation had the greatest effect in reducing time spent at small population sizes, and this may be important for the persistence of subpopulations. It is well-known that populations are more susceptible to additional impacts such as invasive species introductions (e.g. Smith, 1968) or habitat degradation (e.g. Nickelson and Lawson, 1998)

Table 1  
Qualitative summary of simulations comparing dynamics of hypothetical spatially structured coral reef fish populations<sup>a</sup>

| DFDF                                | Mean relative $N$ | Stability  | Vulnerability  |
|-------------------------------------|-------------------|--|--|
| Local variability in recruitment    |                   |  |  |
| Constant recruitment function       | BC $\approx$ SV   | BC $\approx$ SV at $CV_L = 0.5, 1.5, 2.0$<br>BC < SV at $CV_L = 1.0$ | BC $\approx$ SV  |
| Cyclical recruitment function       | BC $\approx$ SV   | BC $\approx$ SV at $CV_L = 0.5, 1.5, 2.0$<br>BC < SV at $CV_L = 1.0$ | BC $\approx$ SV at $CV_L < 2.0$<br>BC $\gg$ SV at $CV_L = 2.0$ ;<br>values decrease as proportional larval retention increases |
| Regional variability in recruitment |                   |  |  |
| Constant recruitment function       | BC $\approx$ SV   | BC $\approx$ SV at $CV_L = 0.5, 1.5, 2.0$<br>BC < SV at $CV_L = 1.0$ | BC $\approx$ SV at $CV_L < 2.0$<br>BC $\gg$ SV at $CV_L = 2.0$   |
| Cyclical recruitment function       | BC $\approx$ SV   | BC $\approx$ SV at $CV_L = 0.5, 1.5, 2.0$<br>BC < SV at $CV_L = 1.0$ | BC $\approx$ SV at $CV_L < 1.5$<br>BC $\gg$ SV at $CV_L \geq 1.5$  |

<sup>a</sup> Results indicate differences between base case systems (BC) within which demography is homogeneous across subpopulations and spatial variation case systems (SV) within which one out of four subpopulations has a larger asymptotic body size,  $L_\infty$  (quantitative results presented in Figs. 5 and 6). Population dynamics were assessed by three summary statistics: the mean annual population size relative to a reference size ( $N^*$ ), the mean number of years spent above 75%  $N^*$  (stability), and the mean number of years spent below 25%  $N^*$  (vulnerability) (see text and Fig. 3 for further details).

when at small sizes, which results in higher extinction risk. Even if extinction is not a likely threat, the recovery time needed to re-build to large size is much longer from small population sizes (Hutchings, 2001). Our model did not include Allee effects or other negative changes in demographic rates at small population sizes. Allee effects would further affect both extinction risk and recovery time (Dennis, 2002). If we had included such effects, the larger  $L_\infty$  subpopulation might have periodically become a true source for its neighbors either by re-establishing populations after local extinction or through supplemental replenishment that avoided local extinction in the first place (i.e. rescue effects).

The most pronounced effects of the larger  $L_\infty$  subpopulation were evident when recruitment was cyclical and stochastic variability was high. A deterministic recruitment cycle ensures that poor recruitment years are not episodic events to be immediately followed by strong offsetting pulses, but rather that low recruitment events will occur in consecutive series and systematically diminish overall population size. Stochasticity exacerbates this problem by driving average population size below that achieved under deterministic conditions (Dennis, 2002). Somatic growth differences in our model resulted in increasing differences in body size with increasing age (Fig. 2). In the absence of a cycle in recruitment, young age classes comprise the

majority of the population. Therefore, Ebert's (1985) finding that somatic growth rate has greater effects on population growth rate than does  $L_\infty$  reflects the influence of the former on body size in the more abundant young age classes, while the latter has more influence on body size in the less abundant older age classes. In our model, differences in body size between the two somatic growth functions are least at young age classes (Fig. 2), so the larger  $L_\infty$  subpopulation provides relatively little additional reproductive output under conditions of average (but variable) recruitment. However, when a series of poor recruitment years results in small cohorts at young age classes, older age classes represent a larger proportion of the population. This shift in age and size structure results in greater relative differences in overall replenishment potential between a base case subpopulation and the subpopulation with larger  $L_\infty$ .

Cole's (1954) classic paper on the links between life history traits and population dynamics revealed a paradox in that a semelparous reproductive strategy generally results in a higher population growth rate relative to iteroparity, yet iteroparity is much more common in nature. Subsequent work by Murphy (1968) and Schaeffer (1974) illustrated that this conclusion quickly changes when the natural world is viewed as dynamic rather than static. Warner and Chesson (1985) also adopted a more dynamic view of the world and addressed not

simply random variability in reproductive success but rather persistent recruitment failure interspersed by occasional successes. They formalized the concept of the storage effect, which attributes greater importance to longevity in enabling persistence through poor years. The storage effect is a useful concept for interpreting our results, because the effects of the larger  $L_{\infty}$  subpopulation were contingent upon exactly the sort of shift in population structure toward older age classes that the storage effect implies. Our study shows how the storage effect in combination with spatial variation in growth can increase the resilience of spatially structured populations. Habitat patches that allow resident animals to attain larger body sizes can result in storage of greater reproductive potential among older age classes. The higher fecundity produced on those patches can then be spread throughout an open system, resulting in faster system-wide recovery from population declines.

Shifts in population structure driven by a deterministic recruitment cycle will occur regardless of the scale at which stochastic variability in recruitment is correlated. Therefore, the results of the model were qualitatively similar when variability in larval supply was independent among reefs and when it was correlated among reefs. However, the results differed quantitatively, with poorer values of the summary statistics and greater differences between the base case and spatial variation case systems when recruitment was correlated among reefs. This is consistent with a common feature of metapopulation theory, which is that synchrony in population fluctuations tends to destabilize populations and raise extinction risks (Hanski, 1999). In real populations of reef fishes, it is likely that fluctuations in settlement of post-larval juveniles will entail both region-wide and reef-specific components. Large-scale oceanographic and meteorological conditions can affect survivorship or growth of larvae, which would induce recruitment fluctuations that are similar among locations. On smaller spatial scales, slight temporal deviations in current speed and direction can determine the success of larval delivery to specific reefs, which will result in independent fluctuations among reefs.

#### 4.2. Model results and empirical data

Available recruitment time series data for coral reef fishes are too short to determine whether the long-

term cycles that made a subpopulation with larger  $L_{\infty}$  more important are evident in nature. However, age frequency data for *L. carponotatus*, the species used to parameterize the model in this study, suggest that such cycles might exist in nature at some times and/or places but not others. The age structure of *L. carponotatus* populations at the Palm Island group on the central Great Barrier Reef shows a regular exponential decline in frequency with increasing age (Fig. 7C) that matches the stable age distribution resulting when recruitment is temporally constant in the model (Fig. 7A). In contrast, the age structure at the Lizard Island group on the northern Great Barrier Reef shows a series of strong cohorts at older age classes and consequent shift in the age structure away from dominance by the youngest age classes (Fig. 7D). This pattern approximates the simulated age structure when the recruitment function is cyclical in the model (Fig. 7B). If these patterns persist beyond the nearly two decades spanned by these age frequency data, then there is greater potential for subpopulations with larger  $L_{\infty}$  in the Lizard Island group region to play a disproportionate role in sustaining the regional open population than comparable subpopulations in the Palm Island group region where a shift in age structure is not evident.

Doherty (2002) reviewed recruitment data for coral reef fishes and found that recruitment rates were generally low with occasional strong pulses. Furthermore, this general pattern was stronger at isolated oceanic islands or at the periphery of species' ranges. For example, Caley (1995) compared recruitment patterns of a wide variety of species between Lizard Island, located within the main tract of the GBR, and One Tree Island, located at the southern extent of the GBR within the Capricorn–Bunker group of reefs. He found that recruitment rates were much lower and more variable at One Tree Island than at Lizard Island. Therefore, subpopulations with larger  $L_{\infty}$  may be more likely to have greater importance in sustaining larger interconnected populations at range limits and isolated sites given the greater potential for shifts in population structure toward older age classes caused by low recruitment events. Isolated oceanic islands might seem to have less potential for demographic structuring within the system because of their more limited spatial extent. However, pronounced demographic variation can be seen on relatively small spatial scales in site-attached reef fishes. For example,

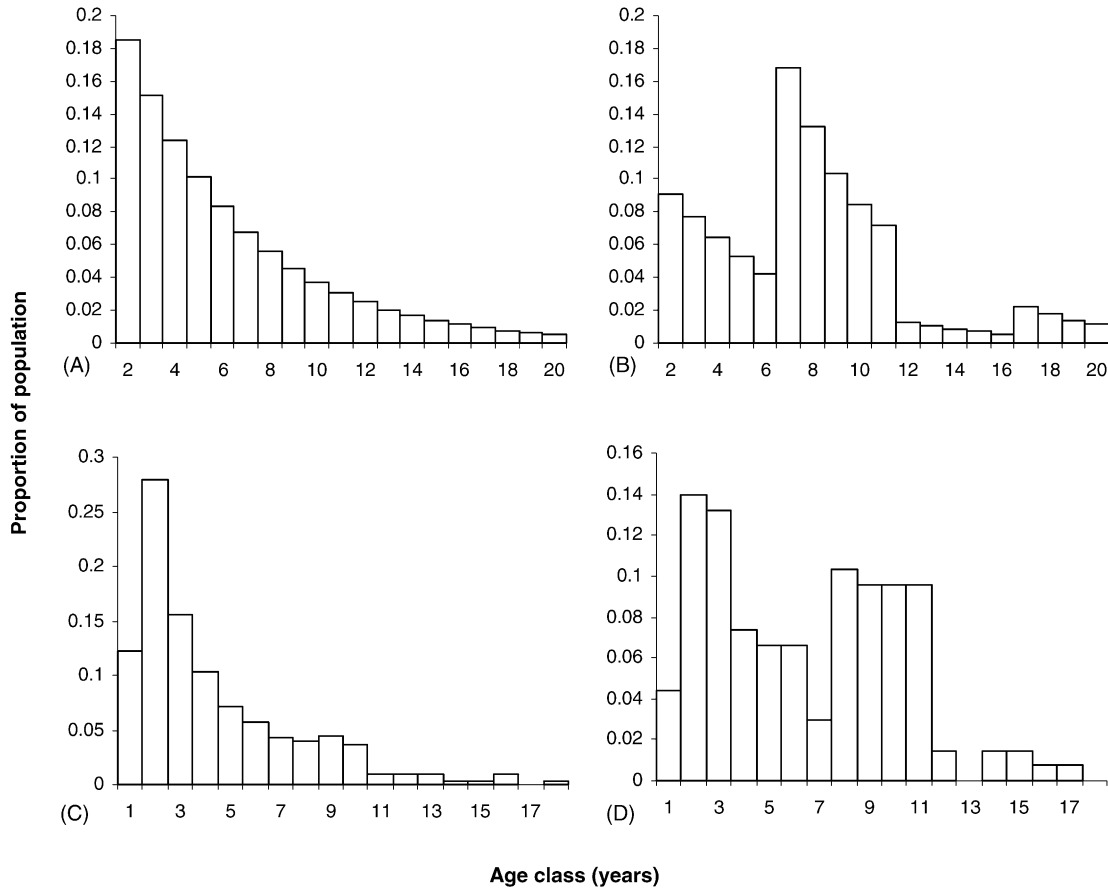


Fig. 7. Age frequency distributions generated by deterministic simulations that assume a temporally constant recruitment function (A) and a cyclical change in the recruitment function every 5 years (B), and empirical age frequency data for the Palm (C) and Lizard (D) Island groups, Great Barrier Reef. Simulated age frequency distributions begin at age 2 because the model only tracks population dynamics from maturity onward. The empirical data suggest that either recruitment scenario can be experienced in nature. Data are from Kritzer (2002).

Aldenhoven (1986) reports 10-fold differences in mortality of a small butterflyfish among different reef zones within a single contiguous reef system at Lizard Island.

#### 4.3. Comparison with other modelling studies

Mathematical models of coral reef fish systems can be grouped into several broad categories. The earliest reef fish models focused on the most complex levels of ecological organization and addressed community dynamics and species coexistence (Chesson and Warner, 1981; Sale, 1982; Warner and Chesson, 1985), while later work has examined trophodynamics (Grigg et al., 1984; McClanahan, 1995; Arias-

Gonzalez, 1998). However, the majority of mathematical modelling work applied to reef fish systems has examined single-species ecology. Single-species models fall into two main categories: those focused on pelagic larval dispersal and recruitment (e.g. Danilowicz and Sale, 1998; Cowen et al., 2000; Armsworth et al., 2001) and those that address post-settlement population dynamics, often including dispersal and recruitment processes as well. Our study falls into this latter category.

Models of post-settlement reef fish populations have increased considerably in detail. Warner and Hughes (1988) examined the roles of recruitment (from indeterminate sources) and mortality in determining the size of a local population. Demartini (1993) built a more complex model to assess the efficacy of marine pro-

tected areas for management of reef fishes. His model included spatial structure and more detailed life history traits, but also lacked any relationship between larval production and recruitment. Man et al. (1995) used a spatially structured patch-occupancy model to also examine management using protected areas. This model did include a larval production–recruitment relationship in that colonization of empty patches was dependent upon dispersal from occupied patches. However, the presence–absence resolution of the model meant that demographic detail was excluded. Crowder et al. (2000) added local demography to a spatially structured model, again in the context of marine protected areas, although this was limited to overall population growth and not individual life history traits. Punt et al. (2001) and Mapstone et al. (2004) developed a series of spatially structured simulation models to design a large-scale adaptive management experiment, analyze its results, and evaluate alternative management strategies, including the use of marine protected areas. Versions of their models included individual variation in somatic growth rate, regional variation in density, and local and regional correlations in recruitment. Armsworth (2002) also included individual demographic traits in a spatially structured reef fish population model. His model included more complex inter-reef connectivity scenarios than those that we considered, but did not consider spatial heterogeneity in demography. An important question for future work will be the relative roles of demographic variability (as we address herein) and position within the connectivity matrix (as addressed by Armsworth, 2002) in determining both the importance of individual local populations and overall system persistence.

At the time of Warner and Hughes' (1988) reef fish population model, DeAngelis (1988) anticipated that models of aquatic systems in general would need to increase in complexity. He argued that demographic structure and spatial heterogeneity would need to be included because seemingly small details, which are often excluded to achieve broader generality and analytical tractability, can be key features driving population dynamics. Ecological modelling efforts have since reinforced his argument. For example, Lirman (2003) used a stage-based model of tropical coral population dynamics to illustrate the effects of storm frequency on demographic structure. Interestingly, his results show that while large, established colonies provide the most

reliable source of reproductive output, high storm frequency shifts the importance toward small coral fragments which sustain the population through stressful periods when large colonies are destroyed and new recruits are rare. This result is analogous to our finding that prolonged periods of poor recruitment place greater weight on older and normally less abundant age classes (although we show a shift in importance toward older age classes while Lirman shows a shift toward younger age classes). This theme is not unique to marine systems. Lattera and Solbrig (2001) used a simulation model to demonstrate that the importance of different seed dispersal strategies is dependent upon the frequency of fires. Their model also showed effects of the degree of spatial synchrony in fires in determining the more effective dispersal strategy, which parallels our finding that spatial synchrony in recruitment failure makes a larger-bodied subpopulation more important. Similarly, Mooij et al. (2002) stress the importance of spatial synchrony in droughts in determining population dynamics of Florida snail kites. Therefore, our study continues a trend toward greater detail and complexity in population models generally, and of reef fishes in particular, which allows greater insights into the importance of unique system-specific features (e.g. fires and droughts on land, or oceanographic events in the sea).

#### 4.4. Extensions of the model

We assumed that there were no correlations among demographic traits. We made this assumption to avoid confounding effects of variation in  $L_{\infty}$  with effects of associated variation in correlated traits. However, higher growth rate and/or  $L_{\infty}$  can result in higher survivorship if susceptibility to predation decreases with increasing body size, as well as lower survivorship if there is a physiological trade-off between growth and mortality (e.g. Mulligan and Leaman, 1992). The former situation would increase the effects of spatial variation in  $L_{\infty}$ , while the latter situation would reduce those effects.

In addition to correlations between growth and mortality, other life history relationships we did not consider could likewise alter our results. We assumed that fecundity is a linear function of body weight, which means that only overall biomass and not population size structure determines reproductive output. This as-



sumption can be invalid for some species in at least two ways. Firstly, egg production can be a non-linear function of body size. Sadovy (1996) notes that relative fecundity is a constant proportion of body size when the exponent of the length–fecundity relationship is around 3, but this exponent can be as high as 5 for some fish species. Therefore, an equivalent mass of fish at two different spawning sites can produce very different numbers of eggs depending upon the sizes of individuals that comprise each local biomass. However, even if instantaneous fecundity is linear across fish weights, Sadovy (1996) also notes that larger fish might spawn over more protracted periods than do smaller fish. There is some evidence that this occurs in *L. carponotatus* (Kritzer, 2004). Longer spawning seasons among larger fish would result in greater cumulative fecundity over the breeding season. Non-linear size-specific fecundity or longer spawning seasons among larger fish would increase the effects of a larger  $L_\infty$  subpopulation.

The effects of a larger  $L_\infty$  subpopulation would be reduced if  $L_\infty$  were a function of population density. Density-dependent effects on somatic growth rate have been demonstrated among reef fishes (reviewed by Jones, 1991). In contrast, effects of density on  $L_\infty$  have not been thoroughly examined, but  $L_\infty$  does not correlate with density among neighboring populations of *L. carponotatus* on the central Great Barrier Reef (Kritzer, 2002). If density-dependent effects do operate and larger  $L_\infty$  only occurs when density is low, then reproductive output would be reduced by the presence of fewer individuals in large  $L_\infty$  subpopulations despite the larger body sizes and higher fecundity of those individuals.

Our results underscore the role of temporal change in the effects of particular demographic traits, and therefore, particular subpopulations. The effects of spatial variation in  $L_\infty$  in our model were time-dependent and contingent upon prevailing environmental conditions causing sequences of poor recruitment. Thomas and Kunin (1999) make a strong case for the transitory nature of population characteristics and argue that subpopulations are unlikely to fall neatly into categories such as ‘source’ or ‘sink’. Instead, they argue that the relative reproductive potential of any individual population, and therefore, its importance to a larger system, will change through time in response to changes in local and regional conditions. We con-

sidered only temporal changes in reproductive success through deterministic recruitment cycles and stochastic variability. Local demography was constant. However, demographic traits can vary through time as well as space, and temporal variation can also affect the relative contribution of a local population. For example, larger  $L_\infty$  among some subpopulations of the surgeonfish *Acanthurus nigrofuscus* reported by Hart and Russ (1996) was attributed to increased availability of algal food sources following reduction in coral cover due to crown-of-thorns starfish outbreaks. Recovery of impacted reefs could reduce  $L_\infty$  of resident surgeonfish populations, while outbreaks on previously unaffected reefs could raise local  $L_\infty$ . Virgl and Messier (2000) studied a spatially structured muskrat population and document the type of temporal shifts in spatial characteristics that might become evident among reef fish populations through longer term studies. Extensions of the simulation framework that we have used here would be a productive means of exploring a range of hypotheses regarding the importance of spatio-temporal dynamics of different population parameters in spatially structured populations. The outcomes of such simulation studies would provide a sound basis for the design of focused field programs to provide empirical tests on a range of taxa under different environmental conditions.

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