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DISENTANGLING TRAIT-BASED MORTALITY IN SPECIES WITH DECOUPLED SIZE AND AGE

- A manuscript for consideration as a Standard Paper in *The Journal of Animal Ecology* -

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Running title: Disentangling mortality for decoupled size and age
SUMMARY

1. Size and age are fundamental organismal traits and, typically, both are good predictors of mortality. For many species, however, size and age predict mortality in ontogenetically opposing directions. Specifically, mortality due to predation is often more intense on smaller individuals whereas mortality due to senescence impacts, by definition, on older individuals.

2. When size-based and age-based mortality are independent in this manner, modeling mortality in both traits is often necessary. Classical approaches, such as Leslie or Lefkovitch matrices, usually require the model to infer the state of one trait from the state of the other, for example by assuming that explicitly modelled age (or stage) class structure provides implicit information on underlying size class structure, as is the case in many species.

3. However, the assumption that one trait informs on the other is challenged when size and age are decoupled, as often occurs in invertebrates, fish, reptiles and plants. In these cases, age-structured models may perform poorly at capturing size-based mortality, and vice versa.

4. We offer a solution to this dilemma, relaxing the assumption that class structure in one trait is inferable from class structure in another trait. Using empirical data from a reef fish, Sparisoma viride (Scaridae), we demonstrate how an individual-based model (IBM) can be implemented to model mortality as explicit, independent and simultaneous functions of individual size and age – an approach that mimics the effects of mortality in many wild populations. By validating this ‘multi-trait IBM’ against three independent lines of empirical data, we determine that the approach produces more convincing predictions of size-class structure, longevity and post-settlement mortality for S. viride than do the trait-independent or single-trait mortality models tested.
Multi-trait IBMs also allow trait-based mortality to be modelled either additively or multiplicatively, and individual variability in growth rates can be accommodated. Consequently, we propose that the approach may be useful in fields that may benefit from disentangling, or investigating interactions among, size-based and age-based demographic processes, including comparative demography (e.g., life-history consequences of resource patchiness) and conservation biology (e.g., impacts of invasive predators on size structure but not lifespan of natives).

**Keywords:** Agent-based models (ABMs), coral reef fish, demography, individual-based models (IBMs), life histories, population dynamics, post-settlement mortality, predation, senescence, size escape.
INTRODUCTION

Size and age are two of the most fundamental traits in biology (DeAngelis and Huston 1987) and both traits may be reliable predictors of mortality (Hughes and Connell 1987). For example, individuals of many species experience elevated size-based mortality when they are small, often as a result of predation (e.g., Hixon and Carr 1997) but surviving individuals may later become increasingly vulnerable to age-based mortality, usually as a result of senescence (e.g., Caswell and Salguero-Gómez 2013). However, the fact that the traits tend to predict mortality in ontogenetically opposing directions is of concern when deciding whether to select a size-based or age-based population model. A classical solution to this dilemma is to explicitly model mortality as a function of one trait (the state variable) and then implicitly model mortality for the remaining trait within state variable classes (e.g., DeAngelis et al 1980). In study systems where the explicitly modelled trait (be that size, age or life stage) provides reliable information on the other trait, then the approach is valuable and matrix population models (Leslie 1945; Lefkovitch 1965) have rightfully become mainstays of ecology (Caswell 2001).

However, for organisms such as clonal invertebrates (Hughes 1984), marine fish (Choat et al. 2003), reptiles (Wikelski and Thom 2000) and perennial plants (Salguero-Gómez and Casper 2010), size and age are often poor proxies for one another. As a result, age-structured models logically may provide unreliable estimates of size-based mortality, and vice versa. We offer a solution to this problem using a complementary modelling approach that exploits the structural characteristics of individual-based models (IBMs). With ecological applications stretching back for many decades (Grimm et al. 2005), IBMs are computational models that consist of a virtual environment populated by modelled individuals (Grimm and Railsback 2004). Unlike most classical population models, which assume that individuals within a size/age class are identical
(Caswell 2001), IBMs can explicitly model individual variability in any characteristic of interest, such as vital rates, behaviour and/or phenotypic plasticity (Grimm et al. 2006; Dunlop et al. 2007). The fact that trait characteristics can be assigned at the level of individuals means that IBMs can be used to model complex problems with emergent properties, such as harvest-induced evolution of life-history traits in Atlantic cod (Dunlop et al. 2009) and costs associated with parental care in smallmouth bass (Dunlop et al. 2007). We highlight the fact that independent size and age variables may also be assigned to modelled individuals within IBMs, meaning that these models are not constrained to infer the state of one trait from the state of the other, as in the case of matrix models. As a result, size-based and age-based mortality processes may be allowed to afflict modelled individuals explicitly, simultaneously and independently, mimicking how mortality is likely to act on many organisms in the wild. We refer to this model structure as a ‘multi-trait IBM’.

We applied a multi-trait IBM to investigate the relative influences of size-based and age-based mortality on the Caribbean stoplight parrotfish *Sparisoma viride* (Bonnaterre 1788, Plate 1). We used the species’ well-studied life history and ecology to hypothesize that size-based and age-based mortality act in ontogenetically opposing directions. This hypothesis is based on two lines of reasoning. Firstly, size-based mortality impacts strongly on fish through predation, which disproportionately targets small individuals (Sparre and Venema 1998; Almany and Webster 2006). Empirical data for *Sparisoma spp.* (including *S. viride*) indicate that mortality rates may be as high as 0.97 within the first three months after larvae settle to the reef from the plankton (Vallès et al. 2008). However, the probability of mortality declines as individuals grow to approach a predation-escape size (Mumby et al. 2006). Consequently, size is likely to be a good predictor of mortality in small *S. viride* but its utility should diminish as an individual grows.
Secondly, aging can also influence mortality in fish through a variety of mechanisms (Comfort 1963; Reznick et al. 2002). In parrotfishes such as *S. viride*, changes in behaviour and commensurate energy investment can occur with changes in sex and/or social status. Acquiring a territory, in particular, demands increased time investment in patrolling, chasing conspecific males and mating (Robertson and Warner, 1978; vanRooij et al. 1996b), all of which reduce time available for feeding and thus energy available for somatic repair. In *S. viride*, territoriality necessarily occurs later in life because individuals are obliged to first change sex and then enter a non-territorial ‘bachelor’ phase until the opportunity to acquire a territory arises (vanRooij et al. 1996b). Logically, the longer that a male spends guarding a territory, the greater the magnitude of accumulated degeneration, and using age as a predictor of mortality may thus improve model performance.

*Sparisoma viride* may even experience negative effects of aging without changing sex or status, owing to the species’ considerable investment in reproduction. Life history theory holds that organisms differentially allocate limited resources between processes such as growth, repair and reproduction to maximise fitness (Beverton and Holt 1959; Charnov and Berrigan 1991). Investment in reproduction, in particular, may require costly trade offs in survival, and in model organisms such as *Drosophila* spp. (Sgrò and Partridge 1999) and *Caenorhabditis elegans* (Gems and Riddle 1996), elevated rates of mating cause commensurate increases in senescence. The existence of senescence-induced mortality is thus a plausible hypothesis in a reef fish such as *S. viride*, which often mates every day, all year round (vanRooij et al. 1996a). Classical theories of senescence even suggest that elevated predation (extrinsic mortality) could hasten the onset of senescence (intrinsic mortality) but evidence for this has been elusive in fish populations (Reznick et al. 2004).
As a result of the characteristics of *S. viride* highlighted above, we expected that a multi-trait IBM that decomposed mortality into ontogenetically opposing size-based and age-based components may outperform single-trait or trait-independent mortality models at reproducing the complex demographic patterns observed in *S. viride* field data. We tested our hypothesis by conducting simulations that incorporated mortality functions of increasing complexity, ranging from a trait-independent null model, to an age-based model, followed by a size-based model, and finally a multi-trait model. We validated each model against three independent sources of empirical demographic data for *S. viride*, comprising: (1) size-class structure; (2) maximum lifespan; and (3) juvenile mortality rates, and found that the multi-trait model provided the best predictions of all three.

**METHODS**

**SPECIES, STUDY SITE AND FIELD DATA**

The stoplight parrotfish, *Sparisoma viride* (Scaridae), is a protogynous hermaphrodite whose grazing of benthic algae is critical for the maintenance of ecological functions in Caribbean coral reefs (Mumby *et al.* 2004). Following a planktonic larval phase, individuals of this species settle to the reef at a size of ~10 mm (vanRooij *et al.* 1996a) after which they may transition through four life phases (life cycle stages, Plate 1), namely (1) juvenile, (2) mature female, (3) bachelor male and (4) territorial male. The phases are sequential but not obligate and transitions are mediated by social factors (vanRooij *et al.* 1996b). Post-settlement juveniles reach sexual maturity at ~150 mm, after which individuals may remain female or change sex (vanRooij *et al.* 1996b). Mature females either join harems guarded by territorial males in the deeper reef front area, or they join the roving groups in the shallower areas (vanRooij *et al.* 1996b). Multiple females from both deep and shallow groups spawn daily with each territorial male (vanRooij *et
In addition to the non-haremic females, the shallow groups also contain post-transition males that have not yet acquired a territory. These ‘bachelor’ males do not spawn, but instead invest in rapid growth, which may maximise their ability to take over a territory, should the incumbent male die. Territorial males guard harems of females in the forereef areas, and spawn daily (vanRooij et al. 1995). Although the ecology of the species is unusual, it is by no means unique for a reef fish (Warner 1984).

In order to construct and validate our *S. viride* IBM, we collated empirical data for somatic growth rates, population size structure, maximum lifespan and juvenile mortality, which are the best demographic data available for this species. We gathered data for growth rates and size classes (Fig. 1) at the fringing reef at Karpata in Bonaire, Netherlands Antilles, between August 1988 and January 1992. This region is a marine reserve where spear fishing has been banned since 1971 and the *S. viride* population was unexploited (vanRooij et al. 1996a). The population was at stationary equilibrium during the data-gathering period, with no significant variation in adult density or spatial distribution of fish between reef zones (vanRooij et al. 1996b). We obtained lifespan values from Choat et al. (2003), who conducted the most comprehensive study of *S. viride* age-based demographics by sampling 417 individuals across the length of the western Atlantic, quantifying otolith (ear stone) annual rings to age individuals. The maximum observed lifespan was nine years, which is here assumed as the maximum lifespan of the species. We used juvenile mortality rates from Vallès et al. (2008) who quantified the fate of a cohort of settling *Sparisoma* spp., including *S. viride*, in Barbados, West Indies, finding that 0.97 of settlers died within three months of arriving at the reef from the plankton.
Our IBM simulated population dynamics through an iterative process. At each monthly time step, the model added individuals to the population, which grew according to empirical rates from Bonaire (Table 1) and died according to the mortality function (below) being assessed in that particular simulation. The model was implemented in Matlab (ver. R2010a). We describe the model structure in terms of its main vital rates: recruitment, growth and mortality.

**MODEL STRUCTURE - RECRUITMENT**

Individuals joined the simulated population at a size of 10 mm and an age of one month, which are the empirical size and age values associated with the arrival of *S. viride* settlers from the plankton (vanRooij *et al.* 1996a). We modelled settlement size as a constant because an empirical size distribution is not available at such a small scale. We did not model per capita rates of reproduction because post-settlement processes decouple numerical relationships between adults and recruits in reef fish (Hixon and Carr 1997). Instead, we assumed that recruitment was sufficient to offset mortality in the Bonaire population, which remained at stable equilibrium during the sampling period (vanRooij *et al.* 1996b). Consequently, the models were allowed to draw in the number of recruits they required to maintain population densities near the empirical mean of 441 individuals ha⁻¹.

**MODEL STRUCTURE - GROWTH**

We modelled somatic growth quasi-continuously (mm scale at monthly time steps) using the von Bertalanffy growth function (*VBGF*; von Bertalanffy 1934), a widely used equation for fish growth (Sparre and Venema 1998):

\[
L(t) = L_\infty (1 - e^{-K(t-t_0)})
\]  

(1)
where \( L(t) \) is the individual’s length (mm) at time \( t \) (months), \( L_{\infty} \) is the individual’s asymptotic length, \( K \) is the rate at which the curve approaches \( L_{\infty} \), and \( t_0 \) is the value when the function intercepts the horizontal (time) axis. Somatic growth rates vary by life phase in the Bonaire \( S. \ viride \) population (vanRooij et al. 1995) and we structured the IBM to capture this variability by creating Gaussian distributions of \( L_{\infty} \) for each life phase (Table 1) from the size ranges of asymptotic individuals in mark-recapture data from Bonaire (vanRooij et al. 1995). The model assigned a value of \( L_{\infty} \) to each newly generated individual by randomly sampling from the distribution for juveniles (\( \mu = 305 \text{ mm} \pm 16 \text{ mm S.D.} \)). Because \( L_{\infty} \) and \( K \) are negatively correlated (Pilling et al. 2002), a corresponding value for \( K \) was assigned to that individual using the coefficients of linear regressions of \( K \) on \( L_{\infty} \) for \( S. \ viride \) otolith data (Bozec et al. 2014):

\[
\ln(K) = 10.87 - 1.92 \ln(L_{\infty})
\]

MODEL STRUCTURE – LIFE PHASE TRANSITIONS

Although somatic growth was quasi-continuous in the IBM, life phase (or stage) transitions were implemented probabilistically as individuals grew past size-class thresholds. To do so, we first calculated the empirical mean proportions observed for each life phase within 50 mm length classes in the field data (Fig. 1 and Table 2). We then used these proportions to calculate the probability of transitioning from phase \( i \) to \( j \) as each individual grows past the threshold between successive length classes \( L \) and \( L_j \) using the equation:

\[
Pt_{ij} = \left( \frac{L_{ij} - L_{ij(\text{non})}}{L_i} \right)
\]
where \( L_{ij} \) is the total proportion of phase \( j \) in class \( L_i \), \( L_{ij(non)} \) is the non-transitioning proportion of phase \( j \) in class \( L_i \) (i.e., individuals that have already transitioned phase prior to growing into \( L_i \)), and \( L_i \) is the proportion of phase \( i \) in class \( L \). Substituting the observed life phase proportions (Table 2) into equation 3 yields the following transition probabilities:

\[
Pt_{ij} = \begin{cases} 
(Ju \rightarrow Fe) & 1.00, \text{ if } L = 150; \\
(Fe \rightarrow Ba) & 0.04, \text{ if } L = 200; \\
(Fe \rightarrow Ba) & 0.13, \text{ if } L = 250; \\
(Fe \rightarrow Ba) & 0.24, \text{ if } L = 300; \\
(Ba \rightarrow Te) & 0.38, \text{ if } L = 300; \\
(Ba \rightarrow Te) & 0.51, \text{ if } L = 350;
\end{cases}
\]

where \( Ju \) is juvenile phase, \( Fe \) is adult female phase, \( Ba \) is bachelor male phase, \( Te \) is territorial male phase, and \( L \) is individual body length (mm). Note that: 1) the life phase of all fish smaller than 150 mm was juvenile (vanRooij and Videler 1997); 2) the life phase change from juvenile to adult female at 150 mm was obligatory (vanRooij and Videler 1997); 3) it was not possible to transition from adult female to territorial male without first transitioning to bachelor male (vanRooij and Videler 1997); and 4) life phase transitions are irreversible in \( Sparisoma viride \) (Robertson and Warner 1978).

After a transition had occurred, the IBM ensured that the growth of each individual retained trajectory memory so that a fast-growing juvenile became a correspondingly fast-growing mature female and so on (Kirkpatrick and Lofsvold 1992). To do so, each time an individual transitioned to a new phase, the IBM used a \textit{trajectory index}, \( t \), to assign a value of \( L_{\infty} \) from the new growth distribution that corresponded to the location of its initial value of \( L_{\infty} \) within the juvenile distribution:
For example, the mean and standard deviation of the juvenile $L_\infty$ distribution are 305 mm ± 16 mm (Table 1). If the IBM created an individual that was randomly assigned an $L_\infty$ value of 297 mm as a juvenile, that value would be 8 mm smaller than the mean, which equals -0.5 standard deviations from the mean, so $t=-0.5$. Each time that individual subsequently transitioned phase, it would be re-assigned a value of $L_\infty$ that was -0.5 standard deviations from the mean of the new $L_\infty$ distribution, ensuring that the individual’s position within each $L_\infty$ distribution remained consistent as the individual grew. The new value of $K$ would then be assigned as above, using equation 2.

\[
t = \frac{L_{\infty initial} - L_{\infty juvs}}{\sigma_{juvs}}
\]

MODEL STRUCTURE - COMPLEXITY

Optimal complexity, that is the number of parameters at which model ‘payoff’ is maximised, is not achieved in the same way in bottom-up, process-based models such as IBMs as in most classical models (Grimm and Railsback 2004). In the latter, there is a negatively linear relationship between model payoff and the number of parameters, meaning that more complex models must be penalised to account for the fact that fit systematically improves as parameters are added (Akaike 1974). In bottom-up models, on the other hand, the trade-off curve of complexity versus payoff is humped, such that model payoff initially increases as parameters are added, before subsequently declining as the model becomes saturated (Grimm et al. 2005). Payoff is thus maximised at an intermediate level of complexity, dubbed the Medawar Zone (Loehle 1990), and in the application of IBMs to ecology, optimal model complexity may best be determined by comparing the patterns that emerge from the model against patterns observed in the study system (Grimm and Railsback 2004).
Keeping the other components of the models unchanged, we examined four IBMs that employed mortality functions of varying complexity to calculate the probability of mortality for each individual at each time step. The mortality functions implemented in the four IBMs were as follows:

1. **Null model: Coefficient of natural mortality (CNM)**

   The simplest IBM we tested treated mortality as a constant decay in the density of year classes, governed by the parameter $M$, which is the exponent of the rate of decay. This function is known as the *coefficient of natural mortality (CNM)*, and it is commonly used to infer fish mortality rates (Gislason *et al.* 2010), including *S. viride* (Paddack *et al.* 2009). The CNM implicitly assumes that all individuals have a constant probability of mortality, regardless of size or age. For the purposes of comparing mortality functions where age and/or size are important predictors, here we considered the CNM our null model. In the CNM function, the individual’s probability of mortality at each monthly time step was given by:

   \[
   P_m = 1 - e^{M/12}
   \]

   where more negative values of $M$ increase the decay rate of the function.

2. **Age-based model**

   The second IBM included a function where only the individual’s age was a predictor of its mortality. We used the Gompertz function (Gompertz 1825), which is a special case of the generalized logistic function originally developed to model mortality in humans and has since found widespread application in demography (Olshansky and Carnes 1997) and gerontology.
(Jucett and Rosenberg 1993). In the age-based model, the probability of mortality was given by:

\[ P_m = 1 - e^{b \cdot e^{c \cdot t}} \]  

where \( t \) is the individual’s age (months), and \( b \) and \( c \) are parameters of the Gompertz function.

More negative values of \( b \) displace the mortality curve to the left, hastening the onset of senescence, and more negative values of \( c \) increase the growth rate of the function.

3. **Size-based model**

In the third IBM, we implemented mortality as a sole function of individual body size. We used the quadratic mortality model of Kirkpatrick (1984), which is a widely used, flexible equation that allows mortality to be modelled as a range of u-shaped or monotonic functions of body size.

In our size-based model, the probability of mortality was given by:

\[ P_m = m_1(L^* - L)^2 + m_2; \quad m_1, m_2 > 0 \]  

where \( m_1 \) controls the vertical intercept, \( L^* \) is the x-axis value (body size) at which the probability of mortality is minimised and \( m_2 \) defines the lower vertical boundary of the function.

4. **Multi-trait model**

Our final model predicted the probability of mortality for each individual as an additive but opposing function of both its size and age, whereby the probability of mortality was negatively influenced by increasing body size (Fig. 2A) whilst simultaneously being positively influenced by increasing age (Fig. 2B). The multi-trait IBM modelled the size-based component of mortality as an exponentially diminishing function of body size, representing elevated mortality in early stages that decreases as a predation escape size is approached. The multi-trait IBM then
modified this probability, such that an individual that survives size-based mortality became increasingly likely to succumb to age-based mortality as the individual gets older:

\[ P_m = (1 - aL^f) + (aL^f)(1 - e^{rt}/e^d) \]  

(8)

where \(a\) and \(f\) define an exponential mortality function that diminishes with the individual’s length (\(L\), mm). Respectively, \(r\) and \(d\) control the rate of change and the horizontal displacement of the exponential mortality function of age (\(t\)).

**MODEL VALIDATION**

Although the length data simulated by the IBM were quasi-continuous (mm scale at one month increments), the data were subsequently classified into 50 mm bins to match the format of the original field data (Fig. 1). We then used the field data to validate the four IBMs for the goodness of their predictions of: (1) the population size structure observed in Bonaire (Fig. 1; vanRooij et al. 1996a); (2) the maximum observed lifespan (i.e., nine years; Choat et al. 2003) and (3) empirical estimates of juvenile mortality (i.e., 0.97 after 3 months; Vallès et al. 2008). We used grid-search optimization to minimize the value of a weighted objective function (\(\delta\)), which was the absolute difference between each simulated size class frequency and the corresponding observed size class frequency, expressed as a proportion of the observed class frequency, and these differences were then summed for the eight classes, such that:

\[ \delta = \sum_{i=1}^{8} \left| \frac{\overline{F}_i - \overline{X}_i}{\overline{X}_i} \right| \]  

(9)

where \(i\) represented the size classes, \(\overline{F}\) was the mean simulated class frequency, and \(\overline{X}\) was the mean observed class frequency. The goodness-of-fit of the four models was assessed using two-sample Pearson’s chi-square tests to compare the mean size-class densities of the model outputs.
against those of the Bonaire field data, with the null hypothesis being that both sets of values were drawn from the same distribution.

Regardless of the model under consideration, all of the simulated populations stabilised before 200 time steps (Figs 4A, D, G & J), which translates to ~17 years. To eliminate transient dynamics, these pre-equilibrium outputs were discarded and models were resampled from the subsequent 100 time steps.

In order to assess the robustness of the best fitting model to the aforementioned assumptions (variable recruitment, nonlinear mortality functions), a sensitivity analysis was conducted. We increased the fitted parameters by 10% one at a time and calculated the effect on $\delta$ (equation 9).

The sensitivity of $\delta$ to model parameters was quantified as the divergence from the value of $\delta$ that had been obtained when all of the optimal parameter values were used together in the model.

This means that the model is most sensitive to the parameter(s) that caused the greatest divergence of $\delta$.

RESULTS

We describe the results of the four models in turn, analysing the performance of each model in replicating empirical values for: 1) size class structure, 2) maximum lifespan, and 3) juvenile mortality.

1. **Null model: Coefficient of natural mortality (CNM)**

**Fitted parameters:** The optimised model with constant mortality (Fig. 3, top row) predicted the coefficient of natural mortality at -0.26, which is the exponent of the population decay rate, and a settlement flux of 6 individuals $\text{ha}^{-1} \text{mo}^{-1}$. The predicted mean population density was considerably below the empirically observed value of 441 individuals $\text{ha}^{-1}$ (dashed line in Fig.)
Model validation: (1) Size class structure: the model successfully predicted six out of the eight size classes to within the 95% confidence intervals of the field data (Fig. 3C). However, the two smallest classes (0-50 mm and 51-100 mm individuals) were underestimated. A two-sample chi-square test suggested that the class densities produced by the CNM model fail to fit the field data population distribution ($\chi^2_7 = 73.65; P < 0.001$).

(2) Maximum lifespan: The model predicted a maximum lifespan of 16 years (Fig. 3B), which is 1.78 times the observed maximum lifespan of nine years (Choat et al. 2003).

(3) Juvenile mortality: the CNM null model predicted juvenile mortality at 0.06 after three months, whereas empirical mortality rate at Barbados was found to be 0.97 (Vallès et al. 2008).

2. Age-based mortality

Fitted parameters: Our second IBM modelled as a function of age (Fig. 3, second row) using the Gompertz equation, for which the best fitting values were $b = -5.45$ (horizontal displacement of the function that predicts the onset of senescence) and $c = -0.005$ (growth rate of the function).

The model predicted a settlement flux of 4 individuals ha$^{-1}$ mo$^{-1}$. The simulated population density stabilised below the empirical density (dashed line, Fig. 3D).

Model validation: (1) Size class structure: For six out of the eight size classes again, as in the CNM, the age-based model replicated empirical densities to within the 95% confidence intervals of the field data but, also as with the CNM model, it failed to predict the two smallest classes (Fig. 3F). The class densities produced are unlikely to be from the same distribution as the field data ($\chi^2_7 = 83.07; P < 0.001$).

(2) Maximum lifespan: The age-based model overestimated lifespan, predicting a maximum of 12 years, or 1.33 times the observed lifespan (Fig. 3E).

(3) Juvenile mortality: the age-based model predicted that 0.02 of settlers would have died by the third month, compared to the empirical mortality estimate of 0.97.
3. **Size-based mortality**

**Fitted parameters:** Our third IBM modelled as a function of size (Fig. 3, third row) using a quadratic equation for which the best fitting parameter values were $m_1 = 9 \times 10^{-6}$, $L^* = 240$ mm and $m_2 = 0.005$. The model predicted a settlement flux of 80 individuals ha$^{-1}$ mo$^{-1}$, which was an order of magnitude higher than the flux predicted by the two models that did not incorporate size. The simulated population stabilised around the empirical density (dashed line, Fig. 3G).

**Model validation:** (1) **Size class structure:** For four out of the eight size classes, the size-based model predicted densities to within the 95% confidence intervals of the field data but failed to accurately predict the other four, including the two largest classes that contain most of the territorial males (Fig. 3I). The class densities produced are unlikely to be from the same distribution as the field data ($\chi^2_7 = 48.19; P < 0.001$). (2) **Maximum lifespan:** The size-based model overestimated lifespan, predicting a maximum of 16 years, or 1.78 times the observed lifespan (Fig. 3H). (3) **Juvenile mortality:** the size-based model predicted that 0.78 (± 0.07 S.D.) of settlers would have died by the third month, compared to the empirical mortality estimate of 0.97.

4. **Multi-trait model**

**Fitted parameters:** Our fourth IBM (Fig. 3, bottom row) modelled mortality using two exponential, ontologically opposing functions of size and age (Fig. 2). The optimised parameter values for the size-based function were $a = 0.75$ (the vertical scaling factor) and $f = -0.015$ (the exponential rate of decay in the probability of size-based mortality). The values for the age-based function were $r = 0.19$ (the growth rate of the function) and $d = 21$ (the horizontal displacement of the function). The model predicted a flux of 96 settlers ha$^{-1}$ mo$^{-1}$. The simulated population stabilised around the mean empirical population density (Fig. 3J). **Model validation:**
(1) Size class structure: the multi-trait IBM predicted densities of all eight *S. viride* size classes that were within the 95% confidence intervals of the field data (Fig. 3L), accurately replicating the bimodal size structure of the Bonaire population. A two-sample chi-square suggests that the simulated class densities fit the same distribution as the field data ($\chi^2 = 5.14; P = 0.642$). 

(2) Maximum lifespan: The multi-trait model estimated lifespan at nine years (Fig. 3K), accurately matching the empirical maximum value. 

(3) Juvenile mortality: the multi-trait model predicted that 0.87 (± 0.06 S.D.) of settling juveniles would not survive beyond their third month, compared to the empirical estimate of 0.97.

SENSITIVITY ANALYSIS

A sensitivity analysis of the fitted parameters (Fig. 4) showed that the multi-trait model was most sensitive to $a$, the parameter that controls the vertical range of the size-based mortality function, such that greater fitted values of $a$ define a higher initial probability of mortality at the first time step of the model. The remaining parameters, including the flux of settlers each month, had less influence on the model output.

DISCUSSION

The decoupling of individual size and age is commonplace, and has been observed in organisms as diverse as plants (Salguero-Gómez and Casper 2010), reptiles (Wikelski and Thom 2000) and even astronauts on extended space missions (Grigoriev et al. 1998). Such size-age decoupling may result from a wide-range of biological processes, including fission or fusion of colonies in sessile marine invertebrates (Hughes and Connell 1987), density-specific resource competition in plants (Wiener and Thomas 1986) and somatic shrinking in vertebrates as a response to environmental conditions (Wikelski and Thom 2000). In those cases where the vital rates of survival, growth and reproduction may vary independently with size (Hughes 1984) and age
(Deevey 1947), the decoupling can have non-trivial consequences for population dynamics and evolution. In these common situations, we demonstrate that model predictions can be improved when mortality \((i.e., \ 1 - \text{survival})\) is implemented as a function with independent size-based and age-based terms that are allowed to act in ontogenetic opposition within an individual-based modeling (IBM) environment. The multi-trait IBM allows us to make reasonably robust inferences about the biology of the stoplight parrotfish \((Sparisoma viride)\) population at Bonaire because the model was: (1) process-based, (2) constructed using empirical growth rates, (3) implemented with a size-based mortality function based on empirical knowledge of reef fish mortality processes, and (4) found to perform well when validated against empirical data for size structure, maximum lifespan and juvenile mortality rate.

Arguably the most striking differences among the four models we tested were in the settler densities they predicted, and the related rates of juvenile mortality. The prediction of 0.87 \((\pm 0.06 \text{ S.D.})\) juvenile mortality after three months made by the multi-trait IBM was lower than the empirical estimate of 0.97 reported by Vallès \textit{et al.} (2008) from Barbados, although the empirical estimate does lie within two standard deviations of our modelled mean. That settler mortality would be lower at our study site in Bonaire than in Barbados may be expected given that, during the data-gathering period, coral cover in Bonaire was almost double that in Barbados \((\text{Jackson \textit{et al.} 2014})\), potentially increasing refuge availability in Bonaire and consequently decreasing predation mortality on settlers.

A notable prediction of the multi-trait IBM is the existence of a late-life change in the way mortality acts on the \(S. \ viride\) population in Bonaire (Fig. 2B), which supports our overarching hypothesis that size-based and age-based mortality act in ontogenetically opposing directions in our study animal. Although molecular and/or physiological evidence would be required to
corroborate our modelling results, we speculate that this prediction of late-stage and rapid age-
based mortality in *S. viride* may be driven by an acute change in the way males invest energy
when they acquire a territory. The Disposable Soma Theory (*DST*, Kirkwood 1977) predicts that
senescence may result from the diversion of limited energy resources that were previously used
for somatic maintenance. Although *S. viride* females maintain a relatively constant investment in
growth and reproduction as long as they remain female (vanRooij *et al.* 1996b), changing sex
may entail dramatic changes in energy investment. When a *S. viride* female transitions to
become a bachelor male, the individual increases its investment in growth. Although this change
may divert energy from somatic maintenance, the energy available for somatic maintenance will
be bolstered by the benefit accrued by abstinence from reproduction (vanRooij *et al.* 1996b).
However, if a bachelor male becomes a territorial male, he will commence mating with multiple
partners up to 13 times a day (vanRooij *et al.* 1996b), representing a substantial change in energy
investment.

The benefits afforded by territoriality come at a cost (Clifton 1990). Although the elevated
reproductive output of a territorial male compensates the individual for the spawning foregone
during the ‘bachelor years’, energetic expenditure is extremely high and the spawning rate of
territorial males in Bonaire was negatively correlated with growth rate (vanRooij *et al.* 1996b).
Based on our model prediction that *S. viride* is subject to late-stage mortality, bachelor males and
territorial males of the same age in the same population (same energy resources, same extrinsic
mortality etc.) may be expected to exhibit different rates of mortality. The *S. viride* population in
Bonaire may thus be an ideal study system for DST investigations in a wild population.

A limitation of our study is that our models unavoidably lack a fecundity relationship that
numerically couples the densities of breeding adults and juveniles. Unfortunately, quantifying
stock-recruitment relationships has proven as elusive in *S. viride* (Vallès *et al*. 2008) as it has in most other reef fishes (e.g., Hixon and Carr 1997). Although our sensitivity analysis indicated that the best-fitting IBM (the multi-trait model) is not strongly influenced by settler density, simulation performance would probably be improved by supplying an empirical estimate for this parameter.

Multi-trait IBMs can capture systematic differences in traits among individuals within a population, creating a rich modeling environment for ecological and evolutionary research and complementing existing approaches such as population matrix models (Leslie 1945; Lefkovitch 1965), integral projection models (Easterling *et al*. 2000; Coulson 2012) and ontogenetic population models (De Roos and Persson 2013). As a result, we encourage population ecologists and formal demographers to consider whether a potential decoupling of size and age would impact on the population dynamics and/or evolutionary ecology of their study organisms, and to take this into account when selecting models for their research.

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**DATA ACCESSIBILITY**

Full Matlab code for the IBMs is available in Online Supporting Information.

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Table 1  Parameter values for the von Bertalanffy growth function (VBGF) estimated from empirical data for the protogynous hermaphrodite, *Sparisoma viride*. $L_\infty$ is the asymptotic size and $K$ is the growth rate of the function. The VBGF was used in our model to define the growth rates of each individual. Gaussian distributions of $L_\infty$ were fitted to mark-recapture size data (vanRooij *et al.* 1995). The relationship between the parameters is negatively linear, and was quantified here by regressing size (fork length, mm) on age (years) from otolith data (Bozec *et al.* 2014).

<table>
<thead>
<tr>
<th>Life phase</th>
<th>Mean $L_\infty$ (S.D.), mm</th>
<th>Mean $K$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Females (incl. juveniles)</td>
<td>305 (16)</td>
<td>0.89</td>
</tr>
<tr>
<td>Bachelor male</td>
<td>378 (19)</td>
<td>0.59</td>
</tr>
<tr>
<td>Territorial male</td>
<td>439 (18)</td>
<td>0.45</td>
</tr>
</tbody>
</table>
Table 2 Proportions of *Sparisoma viride* life phases (or stages) within each 50 mm length class observed at the study site in Karpata, Bonaire.

<table>
<thead>
<tr>
<th>Length class</th>
<th>&lt;50</th>
<th>51–</th>
<th>101–</th>
<th>151–</th>
<th>201–</th>
<th>251–</th>
<th>301–</th>
<th>&gt;350</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>100</td>
<td>150</td>
<td>200</td>
<td>250</td>
<td>300</td>
<td>350</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juvenile</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Adult female</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0.96</td>
<td>0.84</td>
<td>0.58</td>
<td>0</td>
</tr>
<tr>
<td>Bachelor male</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.04</td>
<td>0.16</td>
<td>0.37</td>
<td>0.75</td>
</tr>
<tr>
<td>Territorial male</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.06</td>
<td>0.25</td>
</tr>
</tbody>
</table>
Figure legends

Figure 1. We validated our individual-based models against a five-year demographic dataset of the stoplight parrotfish (*Sparisoma viride*) at Bonaire, Netherlands Antilles. The data are represented by size class and life phase, averaged across all sampled depths and habitats. Error bars show 95% confidence intervals for each size class estimated from eight temporally replicated censuses.

Figure 2. To accommodate ontogenetically opposing mortality when modeling the population dynamics of *Sparisoma viride*, our individual-based model combines functions that model the mortality risk ($P$) as a function of body size and age, as described in equation 8. **A.** A size-based function negatively influences mortality risk as individuals grow larger. **B.** An aging function positively influences mortality risk as individuals become older. Functions were parameterized using empirical data from *S. viride* in Bonaire (Netherlands Antilles; Plate 1).

Figure 3. Results of individual-based model simulations incorporating four different mortality functions, displayed top to bottom, and parameterized with values optimized on field data. Quasi-continuous (mm scale at one-month increments) simulated data were classified into one-year bins for age and 50 mm bins for length and to allow simulated length-class densities to be compared against observed length-class densities when optimising parameters and assessing model fit and sensitivity. Panels in the left-hand column (A, D, G, J) represent population density at each time step, and the dashed lines indicate the observed mean population density in the field. Panels in the middle column (B, E, H, K) show the simulated population age structure in year classes (cohorts). Panels in the right-hand column (C, F, I, L) display the simulated population
size structure classified into 50 mm bins, and error bars represent the means (±95% C. I.) of field data, with shading by life phase as in Fig. 1.

**Figure 4.**

We assessed sensitivity by perturbing the model with a 10% increase in the value of each of the optimised parameters values in turn, while holding the other four parameters constant. Sensitivity is represented here as the percentage change in the value of the objective function that was induced by the 10% increase in the value of each parameter. To smooth stochastic noise, we assessed the model 100 times for each parameter change and the averaged values of δ were used. Error bars show standard deviations.
Figure 1

- Juveniles
- Mature females
- Bachelor males
- Territorial males

Density (individuals/hectare)

Size class (mm)

0-50
51-100
101-150
151-200
201-250
251-300
301-350
>350
Figure 2

(A) Relationship between size (mm) and probability of mortality.

(B) Relationship between age (months) and probability of mortality.
Figure 4.

Fitted parameters

settlers

Sensitivity of multi-trait ABM (% deviation)
Plate 1 The *Sparisoma viride* population in Bonaire exhibits four life phases: (A) juveniles; (B) initial phase mature females; and (C) two classes of terminal phase males which are socially sub-divided into non-territorial (*bachelor*) and territorial groups, but are visually indistinguishable. Scale bars are approximate. Image credits – G. Stoyle (A, C); P. Ryan (B).