

RESEARCH ARTICLE

Integrating physiological and biomechanical drivers of population growth over environmental gradients on coral reefs

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Summary

Coral reefs exhibit marked spatial and temporal variability, and coral reef organisms exhibit trade-offs in functional traits that influence demographic performance under different combinations of abiotic environmental conditions. In many systems, trait trade-offs are modelled using an energy and/or nutrient allocation framework. However, on coral reefs, differences in biomechanical vulnerability have major demographic implications, and indeed are believed to play an essential role in mediating species coexistence because highly competitive growth forms are vulnerable to physical dislodgment events that occur with high frequency (e.g. annual summer storms). Therefore, an integrated energy allocation and biomechanics framework is required to understand the effect of physical environmental gradients on species' demographic performance. However, on coral reefs, as in most ecosystems, the effects of environmental conditions on organisms are measured in different currencies (e.g. lipid accumulation, survival and number of gametes), and thus the relative contributions of these effects to overall capacity for population growth are not readily apparent. A comprehensive assessment of links between the environment and the organism, including those mediated by biomechanical processes, must convert environmental effects on individual-level performance (e.g. survival, growth and reproduction) into a common currency that is relevant to the capacity to contribute to population growth. We outline such an approach by considering the population-level performance of scleractinian reef corals over a hydrodynamic gradient, with a focus on the integrating the biomechanical determinants of size-dependent coral colony dislodgment as a function of flow, with the effects of flow on photosynthetic energy acquisition and respiration.

Key words: population dynamics, mechanistic model, environmental gradient, reef corals, biomechanics.

Introduction

Coral reef research has a rich history of exploring the physical constraints on organism performance across environmental gradients (Rosen, 1975; Connell, 1978; Done, 1983; Massel and Done, 1993; Fulton et al., 2005; Madin and Connolly, 2006). One reason for this large body of work is the biogenic nature of the reef framework: for reef-building organisms, physical effects on individual-level performance have important ecosystem-level effects, including implications for the physical structure of the habitat itself. For example, for most coral species, recruitment requires space on a substratum that is relatively free of sediment and fleshy macroalgae, and subsequent survival and growth requires warm temperatures, sufficiently high aragonite saturation states, adequate light and substratum integrity. For reefs to form and be maintained, settlement and growth rates of calcifying organisms, particularly corals, must be high enough to outweigh calcium carbonate dissolution due to chemical processes, and bio-erosion caused by the activity of boring worms, sponges and other infauna, and feeding by reef fishes.

In addition, several important environmental gradients occur over relatively small temporal and spatial scales within reefs. For instance, solar irradiance attenuates at scales of centimetres to metres with depth and turbidity, resulting in marked changes in the composition of reef-builders and reef-associated species along such gradients (Done, 1983; Anthony and Fabricius, 2000). This

dependence of coral growth on irradiance, as well as sensitivity to exposure at high tide, results in the development of shallow, sub-tidal platforms that give rise to dramatic gradients in water motion with distance from the reef crest and with depth (Madin et al., 2006). Flow affects boundary layer width, and thus gas exchange and photosynthesis (Nobel, 1983). At the whole-reef scale, flow influences flushing times on reefs, and thus mediates diurnal swings in pH due to photosynthesis, calcification and respiration. Moreover, wave energy on reef platforms can intensify by orders of magnitude in a matter of hours as tropical storms pass (Massel and Done, 1993). These rapid temporal changes leave physical damage across relatively broad regions, although such damage can be patchy because of local variability in reef structure and disturbance history (Fabricius et al., 2008). Such distinct local-scale environmental transitions, and the trade-offs that organisms must make to live upon them, appear to be a primary driver of high diversity in coral reef systems (Connell, 1978; Chesson, 2000; Dornelas et al., 2006).

The interaction of an organism with its environment can be quantified through suitably chosen phenotypic and/or functional traits that strongly influence performance (Westoby et al., 2002). This approach has been successfully used in the study of plant communities to understand ecological distributions in relation to environmental resources (Wright et al., 2004), but has not yet been widely applied in the coral reef literature. The interaction of

functional traits and the dynamics of ambient physical and chemical conditions results in phenotypic trade-offs that differentiate individual-level success over environmental gradients. For instance, for corals and some other sessile organisms, there is a trade-off between competitive ability and mechanical stability (Jackson, 1979; Denny, 1988). Adopting an arborescent growth form to extend rapidly into the water column, overtop neighbours and maximise resource acquisition (e.g. photosynthesis and particle capture), also increases vulnerability to breakage and dislodgement in wave-exposed locations and, particularly, during hydrodynamic disturbances (e.g. storms).

There is a continuum of approaches to understanding the performance of organisms in their environment. One end of this continuum involves the application of first principles from geometry, chemistry, physics and engineering in order to quantitatively predict some aspect of individual-level performance. An example of this approach is the use of engineering theory to understand the dislodgement (whole-colony mortality) of reef corals based on their shape and their hydrodynamic environment (Madin and Connolly, 2006). At the other extreme, large numbers of variables are measured, and exploratory data analysis is used to identify environmental variables that correlate with organism performance (Baird et al., 2009; Díaz and Madin, 2011). In between these extremes are studies that utilise mechanistic reasoning to predict how organism performance will change qualitatively along environmental gradients. Sometimes, the mechanistic reasoning that underpins these hypotheses is experimentally calibrated or tested (Hoogenboom and Connolly, 2009), but this is not always so (Bosscher and Meesters, 1993). When adequately validated, first principle approaches have the benefit of constraining the functional form and magnitude of the relationship, whereas correlative approaches run a greater risk of mistakenly attributing observed relationships to the particular causal pathways under consideration. Consequently, mechanistic responses of organisms that have been captured with theory, and calibrated empirically, can provide scaffolding on which to understand ecological-level phenomena, such as population performance.

The fundamental niche concept is most useful when based on the underlying mechanisms that determine how specific environmental conditions influence organism performance (Chase and Leibold, 2003; Kearney, 2006; McGill et al., 2006; Kearney et al., 2012). However, environmental gradients may influence different aspects of organism performance in different ways. For example, for reef corals, living in a wave-exposed, high flow location may facilitate high net photosynthesis, but may also be associated with increased vulnerability to colony mortality. To understand how the fitness of different species is influenced by wave exposure, it is necessary to translate these different kinds of effects into a common currency (McGill et al., 2006). We propose that particularly good candidates for such a currency are measures of an individual's contribution to future population growth, such as its lifetime reproductive output, or the intrinsic population growth rate, under a particular set of environmental conditions. Lifetime reproductive output is a measure of total fecundity over the mean lifespan of individuals in a cohort. This measure may be especially useful for marine populations with planktonic dispersal phases, because knowledge of larval survival and settlement is not required. However, if recruitment feedback into the population can be estimated, and is a function of local reproductive output, then intrinsic population growth rate is likely to be another useful currency of ecological performance.

In shallow, wave-exposed habitats, flow is a major force influencing community structure (e.g. community composition and relative abundances change substantially along gradients of flow). Flow influences organisms through both biomechanical and physiological pathways. Therefore, to understand the trade-offs that underlie ecological responses to flow, we need to understand how these biomechanical and physiological effects interact to influence organism performance. Therefore, in this paper, we propose a modelling framework that explicitly integrates two field-validated mechanistic models to consider the effects of wave exposure on colony growth and reproduction, *via* the influence of flow on photosynthesis and respiration (Hoogenboom and Connolly, 2009), and also on the risk of colony dislodgement during severe storms (Madin and Connolly, 2006). We then translate this integrated model of individual-level performance into a population-level currency, lifetime reproductive output, to explore the shape of the fundamental niche of a reef coral species commonly found over a hydrodynamic gradient.

Materials and methods

Modelling approach

Corals are a symbiosis between photosynthetic algal symbionts known as zooxanthellae, and a colonial animal host that grows by producing an aragonite skeleton. In the case of reef-building corals, reproduction occurs both *via* colony growth (which is asexual) and by the establishment of new colonies (which occurs mainly *via* larval production and settlement). (Additional complications to coral reproduction, such as colony fission and fragmentation, are not considered here.) The ecological performance of corals is highly size-dependent, as colony size influences the acquisition of energy and its expenditure on maintenance and growth (Anthony et al., 2002; Sebens et al., 2003; Hoogenboom and Connolly, 2009), fecundity (Hall and Hughes, 1996; Baird et al., 2009) and susceptibility to mechanical mortality (Massel and Done, 1993; Madin and Connolly, 2006). Because of the sedentary nature of juvenile and adult corals, these demographic rates are relatively easy to quantify, at least once recruits are large enough to be identified. In contrast, most corals broadcast-spawn gametes that develop into larvae that settle onto reefs after what can be an extended period of time in the plankton (Connolly and Baird, 2010). Therefore, the proportion of a coral's offspring that survive and successfully recruit to a reef somewhere within the species dispersal range cannot, at present, be measured directly. The inability to quantify recruit production per coral colony means that it is difficult to estimate population growth rate. To avoid this problem, we focus here on lifetime reproductive output of gametes, which can be quantified from observations on individuals after settlement. We assume that this quantity is approximately proportional to the production of successful recruits, and thus is a reasonable surrogate for individual performance, because reef hydrodynamic gradients are apparent over small scales compared with the scale of coral larval dispersal (at least for the majority of coral species, which broadcast-spawn gametes), and thus offspring produced in different habitats are likely to have similar dispersal kernels, and thus similar post-settlement fates.

To illustrate our approach, we modelled the lifetime reproductive output of an ecologically important and widespread reef-building coral, *Acropora hyacinthus*, along a hydrodynamic gradient. Environmental variation is incorporated into this model based on existing data describing variation in the flow regime between the exposed reef crest to a distance of 120 m over the reef flat on the southeast reef at Lizard Island (Great Barrier Reef, Australia). This

location is especially suitable because the relationships between colony size and key individual-level characteristics (e.g. mechanical vulnerability) have been quantified locally for the study species. The new model developed here combines an existing mechanistic model of colony survival based on hydrodynamic thresholds for colony dislodgement (Madin and Connolly, 2006) with a model of colony growth and reproduction that is based on an existing model of photosynthetic energy acquisition (Hoogenboom and Connolly, 2009) in combination with a simple energy allocation model.

For a given position d over the hydrodynamic gradient, the expected reproductive output of a new recruit a years in the future is the product of the probability of surviving to age a (l_d) and the reproductive output of the colony (r_d), both of which are dependent on colony size x , which is, in turn, dependent on age. The lifetime reproductive output (or net reproductive rate) of the average individual is the sum of this product over the lifespan of a colony, which can be represented as (Gotelli, 2001):

$$L_d = \sum_{a=1}^t l_d(x_d(a)) r_d(x_d(a)). \quad (1)$$

Survivorship

We calculated the proportion of survivors l_d iteratively through years by tracking growth (see the next section) and calculating the probability of surviving based on colony size for a given time step, $s_d(x(a))$. Because of our focus on the direct effects of flow, we separated out mortality due to dislodgement from mortality due to other factors using the following equation:

$$s_d(x(a)) = (1 - b)\gamma_d(x(a)), \quad (2)$$

where b is a constant, size-independent background mortality probability and $\gamma_d(x(a))$ is the probability that a colony of size x at position d is not dislodged that year (hereafter ‘dislodgement survival’).

We modelled changes in dislodgement survival along the reef gradient using a previously developed, field-validated model of mechanical dislodgement (Madin and Connolly, 2006):

$$\frac{\sigma_d}{u_{d,\max}^2 \rho} \leq \frac{16}{d_{\parallel}^2 d_{\perp} \pi} \int_{y=0}^h y w(y) dy, \quad (3)$$

where the left-hand side of the inequality, the dislodgement mechanical threshold (H), is related to three environmental variables that vary over the gradient – substrate tensile strength (σ), maximum water velocity (u_{\max}) and water density (ρ , assumed to be constant). The right-hand side of the inequality – a functional trait called the colony shape factor (C) – is a dimensionless measure of mechanical vulnerability that relates the distribution of colony volume above the substrate to the attachment dimensions (i.e. top heaviness), where d_{\parallel} is the diameter of the colony basal attachment in the direction of flow, d_{\perp} is the basal diameter perpendicular to flow, y is the distance above the substrate, h is the height of the colony and $w(y)$ is the projected cross-sectional width (that is, excluding interstitial space between branches) of the colony perpendicular to water flow as a function of distance y above the substrate.

When C is greater than H , colony dislodgement is predicted to occur. Using estimates of C for *A. hyacinthus* colonies as a function of planar area (Madin and Connolly, 2006), substrate strength over the reef gradient (Madin, 2005) (J.S.M., unpublished data) and maximum yearly water velocities over the gradient for 1967 to

2003 (Madin et al., 2006), we calculated expected yearly dislodgement survivorship probability across the reef gradient based on position d and colony size x (Fig. 2G,H) as:

$$\gamma_d(x) = \int [1 - H_d(C)] f(C | x(a)) dC, \quad (4)$$

where $f(C|x(a))$ is the probability density of having C , given age-dependent colony size $x(a)$, and $H_d(C)$ is the Gumbel cumulative probability distribution of minimum yearly H from 1967 to 2003 for a given position d on the gradient.

Reproduction and growth

Colony reproduction depends upon colony energy acquisition and the way in which colonies apportion energy between metabolic costs of tissue maintenance, growth of new tissue and skeleton, and production of gametes (e.g. Anthony et al., 2002). Corals acquire energy through two processes: symbiont photosynthesis and heterotrophic feeding. Here, we consider only photosynthetic energy acquisition because, for healthy corals in shallow habitats with oligotrophic waters (like those at Lizard Island), heterotrophic feeding generally makes a small contribution to the total energy budget (e.g. Muscatine et al., 1989). We note, however, that nutrient acquisition through feeding is particularly important for production of new tissue (Ferrier-Pages et al., 2003), and discuss this potential effect of flow-enhanced particle feeding on energy allocation in the Discussion.

Photosynthetic energy acquisition, E_P , is a function of colony size, water flow velocity and light intensity. Flow influences coral energy acquisition because it mediates the delivery of gases required for photosynthesis and respiration. To model changes in growth and fecundity of *A. hyacinthus* over a hydrodynamic reef gradient [i.e. the colony size and reproductive functions, $x_d(a)$ and $r_d(x_d(a))$, respectively], we first model yearly photosynthetic energy acquisition for this species based on the relationships calibrated by Hoogenboom and Connolly (Hoogenboom and Connolly, 2009). The model explicitly incorporates gas exchange into the photosynthesis–irradiance relationship, and indicates that photosynthetic energy acquisition is lower where flow is weaker (because thicker boundary layers inhibit gas exchange), but it asymptotes relatively quickly as flow increases and processes other than gas exchange become limiting.

Daily photosynthetic energy acquisition at positions (d) along the hydrodynamic gradient was modelled as a function of colony size (x) using the equations from Hoogenboom and Connolly (Hoogenboom and Connolly, 2009):

$$E_P(x|d) = \int_{t=0}^{12} h_m(u_d, x) \{P_{vs}[E(t), u_d] - P_{vf}\} dt \quad (5)$$

$$E_R(x|d) = 12 [h_m(u_d, x) \{R_{vs}[u_d] - P_{rf}\}],$$

where $h_m(u_d, x)$ is the mass transfer coefficient – a function of mean water velocity at position d along the gradient (u_d) and colony size, x – which was experimentally calibrated for a congener of our study species (*Acropora nasuta*), $P_{vs}[E(t), u_d]$ is the oxygen concentration at tissue surface during photosynthesis as a function of irradiance throughout the daylight period, $R_{vs}[u_d]$ is the oxygen concentration at the tissue surface during respiration in darkness as a function of mean water velocity, and P_{vf} is the oxygen concentration of seawater (estimated at $280.5 \mu\text{mol l}^{-1}$ based on data from One Tree Island, Great Barrier Reef). In this model, $P_{vs}[E(t), u_d]$ follows a typical photosynthesis–irradiance curve where oxygen at the tissue

surface rises from R_{vs} (where light=0) asymptotically to a maximum value, P_x , with a sub-saturation irradiance value equal to $100 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ as in Hoogenboom and Connolly (Hoogenboom and Connolly, 2009). Here we assume that irradiance varies sinusoidally with time of day, over a 12 h daylight period, with a maximum (midday) irradiance set equal to the yearly mean irradiance modelled as for a shallow non-turbid reef [$1800 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Hoogenboom and Connolly, 2009)], and was assumed to be similar across the hydrodynamic gradient, where water depth is approximately constant and water turbidity is generally low (Fig. 1A). Yearly mean water velocity over the reef gradient was estimated using a wave model for the Great Barrier Reef, forced by a 37-year historical wind database, and validated with *in situ* measurements from Lizard Island (Madin et al., 2006) (Fig. 1D).

E_P , measured in units of oxygen produced ($\mu\text{mol O}_2 \text{ cm}^{-2} \text{ d}^{-1}$), was converted into units of $\text{J cm}^{-2} \text{ d}^{-1}$ by multiplying by the oxyjoule equivalent [$21.83 \text{ J ml}^{-1} \text{ O}_2$ released during fixation of carbon into lipids *via* glycerol (Davies, 1991)] after first converting oxygen units from μmol to ml O_2 produced (using a conversion factor of 44.61). The same unit conversion was applied for E_R , except using an oxyjoule equivalent value of $21 \text{ J ml}^{-1} \text{ O}_2$ consumed during metabolism (Davies, 1991). After maintenance metabolism costs have been subtracted, total (net) energy available for use in growth and reproduction, E_U , in units of $\text{J cm}^{-2} \text{ d}^{-1}$, is given by:

$$E_U = E_P - E_R \quad (6)$$

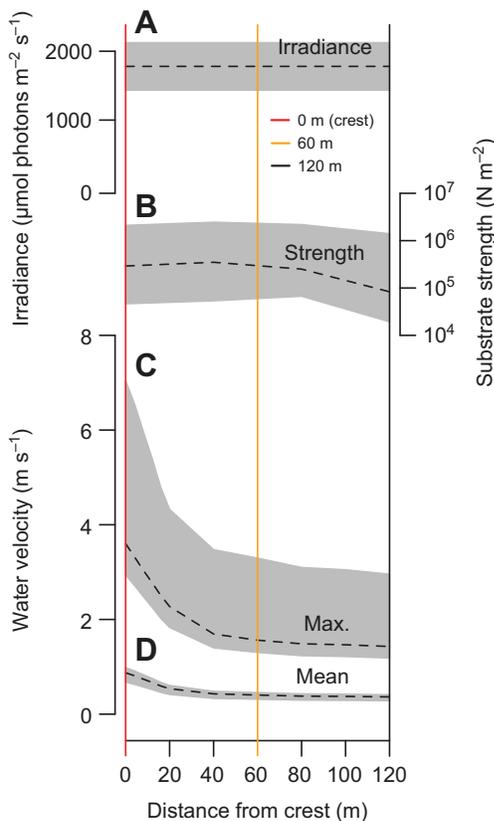


Fig. 1. The reef environmental gradient from the reef crest to 120 m over the reef flat at the southeast reef, Lizard Island: (A) mean solar irradiance, (B) mean substrate tensile strength, (C) mean yearly maximum water velocity and (D) mean yearly mean water velocity. Grey areas capture 95% confidence intervals. Coloured vertical lines represent the three focal reef positions for which population model outputs are presented in other figures.

Experimental data describing variation in energy allocation strategies along environmental gradients are virtually non-existent for corals. However, the modular growth of corals means that energy allocation rules for other organisms, such as the kappa (κ) rule in dynamic energy budget theory (Nisbet et al., 2000; Nisbet et al. 2012), may not be suitable for corals. In particular, each polyp needs its own reproductive tissues, so any cost of ‘maturation’ should be proportional to the number of new polyps added. A fixed energy allocation rule, where energy is apportioned between maturation and growth (prior to puberty) and between reproduction and growth (for mature individuals), cannot be reconciled with the fact that small coral colonies do not reproduce. Instead, it appears for coral that there is a genuine shifting of energy towards reproduction as colonies pass a certain size threshold (Hall and Hughes, 1996). In the absence of specific data regarding patterns of energy allocation for our study species, we here assume that energy (E_U) is allocated between growth (E_G) and reproduction (E_R) as follows:

$$E_G = \begin{cases} E_U & x < 7 \\ \kappa E_U & x \geq 7 \end{cases} \quad (7)$$

$$E_R = \begin{cases} 0 & x < 7 \\ (1 - \kappa) E_U & x \geq 7 \end{cases},$$

where κ is a proportional energy allocation constant and 7 (cm) is the approximate size of first reproduction for *A. hyacinthus* (from Wallace, 1985).

Finally, we converted energy available for growth (E_G) and reproduction (E_R) into actual predicted growth and actual predicted reproductive output based on the energy costs of building tissue and skeleton, and the energy costs of producing eggs. The energy cost of growth was calculated based on estimates of the surface area (tissue) and volume (skeleton) added during growth. To do this we analysed photographs of *A. hyacinthus* at Lizard Island to determine branch diameter, height and density per unit colony area, and used geometric formulae for the area and volume of a cylinder to estimate the amount of material required to be synthesised during branch growth. These analyses indicated that colonies have 3.9 branchlets per square centimeter of colony area and that branchlets are 0.4 cm in diameter and 1.75 cm high, yielding a branchlet surface area of 2.1 cm^2 and a volume of 0.2 cm^3 . Assuming a tissue biomass of 9 mg cm^2 with a composition of 52% lipid, 43% protein and 5% carbohydrate [based on data for *Acropora tenuis* (Leuzinger et al., 2003)], and enthalpies of combustion of 23.9 kJ g^{-1} protein, 17.5 kJ g^{-1} carbohydrate and 39.5 kJ g^{-1} lipid (Anthony et al., 2002; Gnaiger and Bitterlich, 1984) results in tissue energy content of $610 \text{ J branchlet}^{-1}$. Assuming a skeletal density of 1.44 g cm^{-3} and an energy cost of calcification equal to 0.152 J mg^{-1} (Anthony et al., 2002) returns an energy cost of building skeleton of $41 \text{ J branchlet}^{-1}$. Correspondingly, growth of an additional unit area of coral colony requires an energy investment of 2.56 kJ . Energy investment in reproduction was calculated similarly, based on an egg diameter of $622 \mu\text{m}$ ($\sim 41 \mu\text{g}$) (Wallace, 1985) and a composition of 80% lipid (Harri et al., 2002) and an assumed remaining composition of 18% protein and 2% carbohydrate. These values yield an energy cost per egg of 1.85 J .

Model analyses and outputs

The model equations described above were first used to calculate survival probability, energy surplus and the allocation of this surplus

into fecundity and growth of *A. hyacinthus* colonies each as a function of position over the reef gradient and colony size. We then modelled the cohort dynamics for 50 time steps (years), recording (1) the proportion of survivors, (2) the mean colony size of survivors and (3) the fecundity of survivors. These dynamics were calculated at a series of positions over the 120m hydrodynamic gradient and using different values for the energy allocation constant κ . Illustrative time series are presented for values of d equal to 0, 60 and 120m along the hydrodynamic gradient, given $\kappa=0.5$. Lifetime reproductive output was calculated as per Eqn 1, which sums the area under mean cohort fecundity curves. Note that value of $\kappa=0.5$ was used for calculations in Fig. 2C,D, representing a 50% split of energy surplus between colony growth and egg production. This value was chosen arbitrarily because data on proportional allocation of acquired energy between growth and reproduction are unavailable. To test whether the value of κ substantively influenced variation in cohort lifetime reproductive output along the reef hydrodynamic gradient, we re-ran the model simulations using κ ranging between 0.05 and 0.95. Finally, we conducted additional analyses to separate the effects of the different model components (mechanical vulnerability and energy acquisition) and to detect which component has the strongest effect on lifetime reproductive output. We considered four different models in this analysis: (1) the full model described previously; (2) the mechanical dislodgement component only, assuming that energy acquisition is equal to that at the reef crest for the whole gradient; (3) the mechanical dislodgement component only, assuming that substratum strength is constant over the gradient; and (4) the energy acquisition component only, assuming that mechanical dislodgement is equal to that at the reef crest for the whole gradient.

Results

Survivorship

Over the hydrodynamic gradient, colony survivorship showed a hump-shaped pattern, where survivorship was greater for a colony of a given size at intermediate positions between the reef crest and

flat (Fig. 2A). This pattern occurs because substrate strength and maximum water velocity differ distinctly in how they attenuate over the gradient (Fig. 1B,C). Large waves responsible for maximum water velocity attenuate rapidly over the first 50m of reef (Madin et al., 2006), whereas substrate strength, which is more closely related to mean water flux (Rasser and Riegl, 2002), remains high until approximately 80m along the gradient before decreasing. These patterns combine to generate an area in the middle of the hydrodynamic gradient (between approximately 40 and 80m) that has relatively strong substrate and relatively low maximal velocities in which the dislodgement mechanical threshold (Eqn 3) is high.

Reproduction and growth

The decrease in water flow between the reef crest to the back reef caused a decline in annual energy surplus (Fig. 2B) that was most pronounced over the first 20m of the gradient. Energy surplus, summed over the entire colony, increased with colony size because of the multiplicative effect of obtaining a positive energy balance per unit surface area summed over the entire colony surface area (Fig. 2B). In the model, energy allocation to reproduction (Fig. 2C) and energy allocation to growth (Fig. 2D) are both proportional to total energy acquisition and therefore follow identical variation in response to colony size and position along the gradient. For direct comparison between the model predictions and data for *A. hyacinthus* reported in the literature, we plotted the relationships between colony growth and reproduction *versus* colony diameter for a range of κ values at the reef crest (0m). On a log scale, colony radial expansion (Fig. 3A) and total colony fecundity (Fig. 3B) increased linearly with colony size for colonies above the reproductive threshold. The magnitude of predicted colony growth is of an order similar to that reported by Stimson (Stimson, 1985) for this species on Enewetak Atoll (Marshall Islands); however, the increasing radial expansion with colony size (which follows from the assumption of a constant κ value) differs qualitatively from the statistically non-significant increase in growth with colony size

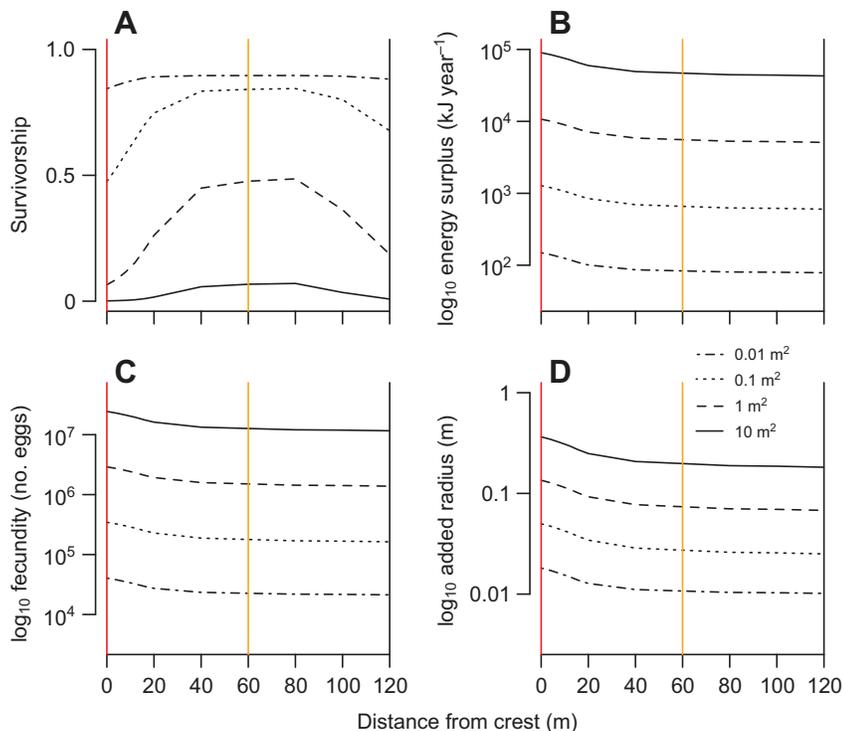


Fig. 2. Individual-level estimates of yearly demographic rates for different sized colonies of *Acropora hyacinthus* living across the hydrodynamic reef gradient: (A) yearly survival probability, (B) daily energy acquisition, (C) colony fecundity and (D) radial growth. Coloured vertical lines represent the three focal reef positions.

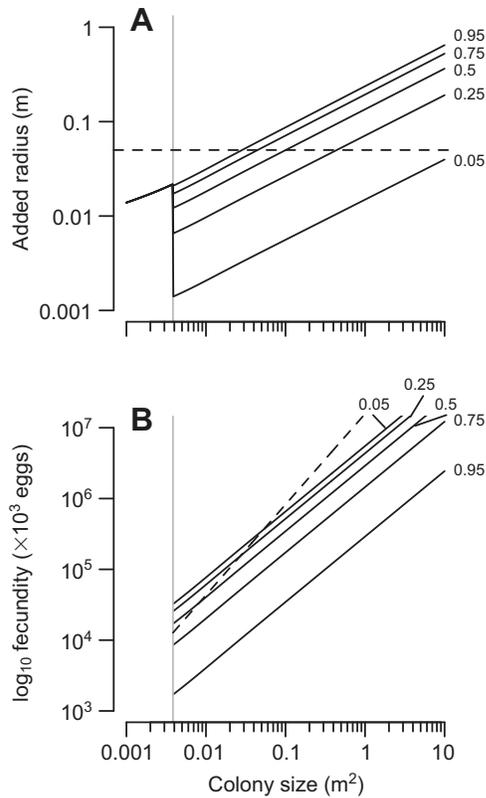


Fig. 3. Individual-level estimates of yearly (A) growth and (B) reproduction for *A. hyacinthus* colonies as a function of colony size (planar area). Solid lines represent estimates for different energy allocation scenarios ($\kappa=0.05, 0.25, 0.5, 0.75, 0.95$). Grey vertical lines represent size at first reproduction (Eqn 7). The dashed line in A is the best-fit line for the empirical relationship found for *A. hyacinthus* growth from Stimson (Stimson, 1985). The dashed line in B is the best-fit line for the empirical relationship found for reproduction in Hall and Hughes (Hall and Hughes, 1996).

reported by Stimson (Stimson, 1985) for colonies between 0.1 and 2 m² in size (dashed line in Fig. 3A). With respect to reproduction, the positive relationship between fecundity and colony size is also similar in magnitude to empirical data from the same reef (Hall and Hughes, 1996) (dashed line in Fig. 3B), although for most of the range of energy allocation values (κ) our model tends to underestimate the fecundity of large colonies or overestimate the fecundity of small colonies of *A. hyacinthus* at the study site (i.e. reproduction increases with colony size faster in nature than predicted by the model).

Population-level performance

The proportion of individuals remaining in a cohort declined fastest with age at the reef crest (because of high maximal water velocities; red line, Fig. 4A), at an intermediate rate 120 m from the reef crest (due to decreased substrate strength, orange line) and slowest midway over the gradient (black line). Consequently, colonies tend to live longest at an intermediate position over the reef (an average of approximately 7 years; Fig. 4A, lower panel). Faster cohort decline at the reef crest is the result of greater energy acquisition and faster growth, such that colonies reach sizes that are vulnerable to mechanical dislodgment at a younger age (Fig. 4B). Colonies grow faster initially up to a size (7 cm in diameter) where they become reproductive, resulting in a subtle inflection point in the time series after 1 to 2 years depending on

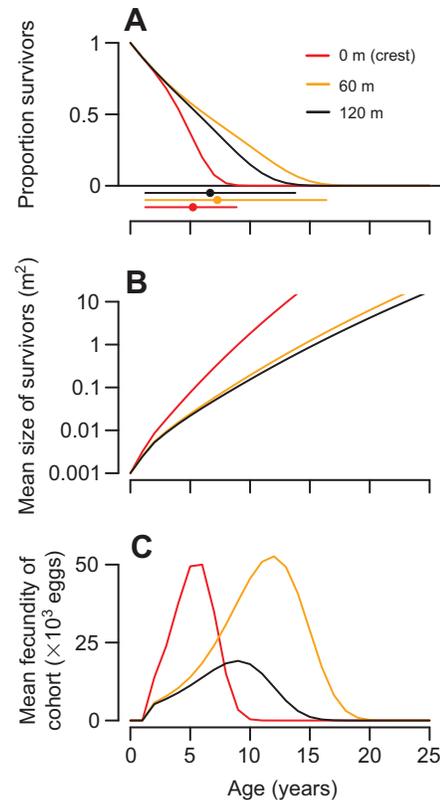


Fig. 4. Population model results through time for an *A. hyacinthus* cohort living at three focal positions over the hydrodynamic gradient showing the relationship between age and: (A) the proportion of the cohort remaining, (B) the mean size of a survivor (planar area) and (C) the expected cohort fecundity. Points and lines in A correspond to mean colony lifespan and 95% confidence intervals. Predicted lifetime reproductive output (Figs 5 and 6) is the area under the fecundity–time curve, which captures the growth of colonies and the mortality of individuals.

position along the gradient. Faster growth at the reef crest also results in higher reproductive output earlier in the cohort's life, but low survivorship results in low reproductive output overall (Fig. 4C). (Note that lifetime output is the area under the curves in Fig. 4C.) Conversely, at the reef back, energy acquisition is lowest, but survivorship is still relatively low because of weaker substrate, resulting in the slowest accumulation of reproductive output through time and lowest overall lifetime output (Fig. 4C, black line). High survivorship at 60 m over the gradient, and intermediate levels of energy acquisition, result in the largest colony sizes (Fig. 4B) and a prolonged period of relatively high reproductive output (Fig. 4C).

In general, our model predicts that lifetime reproductive output is highest at an intermediate point on the gradient for the majority of κ values (Fig. 5), where energy is sufficiently high for growth and reproduction (Fig. 4C) and mechanical thresholds are high enough to allow survival of older, larger colonies (Fig. 4A,B). Lifetime reproductive output decreases dramatically away from the crest because of both increasing mechanical vulnerability associated with reduced substrate strength and reduced energy available for reproduction due to low flow rates and thus gas exchange for photosynthesis. Empirical measurements of *A. hyacinthus* cover and colony size at the study site tend to reflect this hump-shaped pattern, peaking between approximately 10 and 40 m over the gradient. The model most

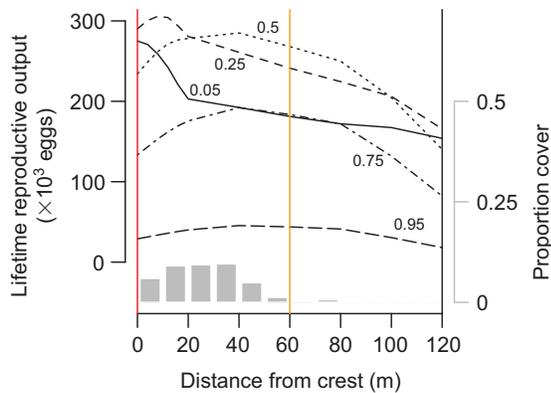


Fig. 5. Estimated lifetime reproductive output for colonies of *A. hyacinthus* living at different positions over the reef gradient for a range of energy allocation scenarios ($\kappa=0.05, 0.25, 0.5, 0.75, 0.95$). Grey bars represent empirical proportion cover data over the study reef at Lizard Island.

closely represents this empirical peak in ecological dominance where yearly energy surplus is allocated equally to growth and reproduction ($\kappa=0.5$).

To assess which component of the model (mechanical thresholds *versus* energy acquisition) had the greatest effect on lifetime reproductive output along the flow gradient, and to better depict how biomechanical and physiological pathways trade off to determine demographic performance, we repeated the simulations under a range of scenarios where we set the values of different components of the model to a constant along the flow gradient. First, to illustrate the influence of the photosynthetic energy acquisition model component, we reran the model with all colonies receiving the same amount of energy as those living in the reef crest environment (Fig. 6B). (We assumed $\kappa=0.5$ for all scenarios in Fig. 6.) Here, a hump-shaped pattern is much more pronounced (note the log scale), where colonies living in the middle of the gradient are predicted to have an order of magnitude greater output than colonies living at the reef crest or back. We then removed the influence of substrate strength by assuming that strength was constant over the gradient and equal to that of the reef crest (Fig. 6C). Here, we see colonies further from the crest living for longer and producing an order of magnitude more gametes during their lifetime than at the reef crest, emphasizing the importance of including the substratum environmental variable in the model. Finally, to explore the influence of the mechanical vulnerability model component, we reran the model with all colonies on the gradient experiencing maximum wave forces as if living at the reef crest (Fig. 6D). Higher mean water velocities at the crest resulted in faster growth and greater reproductive outputs compared with further back over the gradient.

Discussion

The model presented above highlights how the effects of two flow-mediated processes – dislodgement and photosynthesis – interact to influence population-level performance of a reef coral species over a ubiquitous environmental gradient on coral reefs. However, by using a common population-level currency as a proxy for fitness – in this case lifetime reproductive output – we are able to delineate the shape of the fundamental niche and assess how the performance of an individual depends upon the location it chooses (or finds itself in) at the time of recruitment into the population. There is a long history of considering trade-offs in energy and nutrient allocation (especially for plants) and how these trade-offs influence

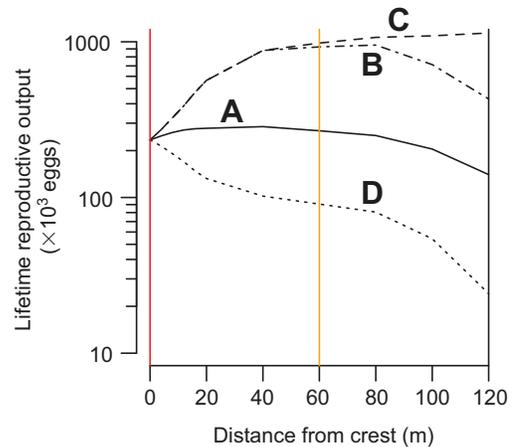


Fig. 6. Estimated lifetime reproductive output for colonies of *A. hyacinthus* living at different positions over the reef gradient for: (A) the integrated model (energy acquisition and mechanical vulnerability), (B) the mechanical vulnerability component only, (C) the mechanical vulnerability component with constant substrate strength and (D) the energy acquisition component only.

demographic performance, fitness and species coexistence across different environments (e.g. Westoby et al., 2002), but a quantitative theory of such tradeoffs has yet to be developed for corals. For biomechanics, there is strong evidence for biomechanical effects on individual survival (e.g. Denny, 1995; Madin and Connolly, 2006) and on population and community dynamics (e.g. Pascual et al., 2002; Van de Koppel et al. 2012). For example, for scleractinian reef corals in particular, the importance of trade-offs involving colony dislodgment has been recognized for decades (Jackson, 1979; Connell, 1978). Despite this, mechanical vulnerability has yet to be incorporated into trade-off theory with anything like the same quantitative rigor as physiological trade-offs. Such an integration of biomechanical and physiological constraints is especially important for coral reefs because flow imposes biomechanical constraints on organisms with relatively high frequency (e.g. annual severe storms), limiting the possible sizes and shapes of coral colonies in different reef habitats. At the same time, flow is a major determinant of variation in the rates of physiological processes, which has implications for growth and reproduction. Our results reveal a complex, nonlinear interaction between biomechanical and physiological effects along a gradient of flow for a dominant species in exposed reef coral communities. Because mechanical stability, as well as boundary layer dynamics, are highly dependent upon colony shape, these relationships are likely to differ in important ways among species with different growth forms and physiologies.

In general, the integrated biomechanical and physiological model shows that *A. hyacinthus* is expected to do better closer to the reef crest, but not right at the crest, which is consistent with their observed distribution on exposed reefs throughout the Indo-Pacific region, including the Lizard Island study site (Fig. 5). This pattern is most apparent when both the biomechanical and physiological effects of flow are included in the model (Fig. 6), highlighting the benefit of mechanistically integrating both processes for understanding population-level performance over environmental gradients. The qualitative shape of performance over the gradient changes depending on how energy is allocated to growth and reproduction (Fig. 5). Investing only a small proportion

of energy surplus in growth (small κ) increases the benefits of high flow because colonies grow slowly, the positive effects of flow on energy balance lead to higher reproductive output over time and mechanical dislodgement is delayed until later in life. As energy allocation to growth (κ) increases, colonies reach the dislodgement threshold sooner, so being closer to the crest becomes comparatively more costly, and thus peak reproductive output occurs further back. If κ is too high, though, colony performance drops substantially. We suspect that this change in the qualitative shape of performance with κ is mediated by the change in the relative importance of background *versus* dislodgement mortality as a function of growth rate. When κ is small, background mortality dominates for a longer period of time, and thus a smaller proportion of any given cohort ultimately dies from dislodgement. Conversely, if κ is large, dislodgement mortality becomes significant much earlier in colony life, and a larger proportion of mortality events will be directly due to the negative effects of flow.

Currently, patterns of energy allocation for corals are poorly understood. Specifically, there are very few data comparing *in situ* energy acquisition by colonies with energy allocation to tissue growth, skeletal growth and reproduction. Experimental studies have demonstrated among-species and among-environment variation in production of lipid, protein and skeleton depending upon the availability of carbon from photosynthesis, and carbon and nutrients from heterotrophic feeding (Anthony and Fabricius, 2000; Hoogenboom et al., 2010). However, complex variation in light and food regimes in the field presents challenges for monitoring proportional energy allocation (as a function of acquired energy) under natural conditions. Although energy acquisition was not monitored directly, Villinski (Villinski, 2003) showed that energy allocation to reproduction was constant along a depth gradient (over which energy acquisition almost certainly decreased) whereas growth decreased. This pattern indicates a shift in proportional energy acquisition (i.e. a change in the value of κ) towards reproduction as total energy acquisition decreases, and implies that the value of κ is not a constant independent of environmental conditions. Coral energy allocation is further complicated by potential changes in energy allocation to different structural materials (skeleton *versus* tissue) (e.g. Anthony et al., 2002) depending on environmental variation in light and flow regimes. Our model indeed demonstrates that a fixed value for proportional energy allocation (κ) is unlikely to be valid for corals, and that small changes in energy allocation can have profound implications for lifetime reproductive output (Fig. 3). Qualitative differences between the model run for a given κ value and the empirical growth and fecundity relationships from the literature can only be explained if the value of κ changes with colony size. That is, the fit between our model and empirical data (Fig. 3) would only improve if energy allocation were to shift from growth while colonies are small to reproduction as they grow [i.e. the intercept between the model (solid) and empirical (dashed) lines, Fig. 3]. Field-based measurements of energy allocation to calcification, tissue growth and reproduction, in combination with measurement of energy acquisition, are crucial for an improved understanding of variation in coral demographic parameters, and associated fitness, along environmental gradients.

The integration of biomechanics and physiology allows a bottom-up, mechanistic approach to population ecology. One strength of this approach is that environment-specific measures of demographic performance can help to quantify source and sink structures across

meta-populations in which patches have different combinations of environmental variables. However, this approach does not account for community-level processes, such as species interactions, that may diminish (e.g. aggressive interactions) or augment (e.g. facilitatory interactions) demographic performance. For example, the intensity of competitive interactions can increase further from the wave-exposed reef crest (Lang and Chornesky, 1990), and corallivorous fishes, for whom *A. hyacinthus* is a preferred prey, tend to be most active near the reef crest (Pratchett et al., 2008). We have focused here on just one biomechanical and one physiological effect of flow, because it is sufficient to explore the utility of a framework that integrates these two pathways by which flow influences demography. However, conceptually, the incorporation of additional effects of flow, including those involving species interactions, is straightforward (although obtaining the data necessary to calibrate such relationships may be challenging). Two additional processes are likely to be critically important for the performance of coral populations in the long term: (1) large-scale dispersal processes, which would allow the quantification of adult feedback into the population and currently limits the application of the model for assessing population viability over the reef gradient (Connolly and Baird, 2010); and (2) small-scale settlement processes, which are expected to concentrate recruitment closer to the reef crest at the point where larvae enter the reef system or perhaps due to the higher cover of crustose coralline algae – a potential coral settlement cue (Morse et al., 1988) – in this area.

Hydrodynamic dislodgement is, of course, not the only source of coral mortality. In this study we have focused explicitly on mortality associated with hydrodynamic disturbance and assumed a constant background mortality rate ($\sim 0.1 \text{ year}^{-1}$) based on a previous long-term study at our study location (Wakeford et al., 2008). Moreover, we assume that background mortality acts independently of colony size and applies equally over the entire hydrodynamic gradient. Some mortality processes (e.g. sedimentation and disease) are expected to be more significant either near the reef crest or further back on the reef. For example, coral bleaching can be significantly more prevalent where flow is minimal and mixing is reduced, because these conditions lead to increased warming or decreased salinity [e.g. shallow lagoons during neap tides (Baker et al., 2008; Maina et al., 2011)]. Bleaching susceptibility also varies substantially among species (e.g. McClanahan et al., 2004). In some cases, bleaching can cause mortality (Anthony et al., 2008), and non-lethal bleaching can lead to reduced growth and reproduction (Baird et al., 2009). However, in very few cases do taxonomically resolved data exist that allow us to calibrate how a species' bleaching severity varies as a function of the severity of the thermal stress event (but see Yee et al., 2008). To our knowledge, no studies allow quantitative estimates of how mortality rate, growth rate or fecundity vary as a function of bleaching susceptibility. This type of information is crucial, however, in order to project community change as a function of changes in the distribution of summer maximum temperatures associated with global warming. How various mortality sources depend on environmental conditions in general, and on flow in particular, requires additional research.

More broadly, the approach presented here provides a quantitative basis for incorporating mechanical vulnerability into theory for life history and demographic trade-offs, a trait that is likely to be an important determinant of species coexistence in coral reefs and other environments subject to frequent extreme biomechanical stress events. It can also help us begin to understand and predict how population performance is likely to vary across spatial and temporal gradients of environmental variables at a range of different scales.

The present model focused on changes in population performance mediated by the effects of flow on physical dislodgement, and net photosynthetic energy acquisition, and could be readily incorporated to consider the consequences of changes in flow regime. For instance, increases in the intensity of tropical storm activity (Elsner et al., 2008; Young et al., 2011) will increase maximum yearly water velocities on the hydrodynamic gradient (Madin et al., 2008), but is unlikely to materially change the day-to-day flow rates that influence photosynthesis and respiration. This is likely to change the shape of the demographic response along gradients of wave exposure in ways that can be expected to differ among species, with implications for community dynamics. We hope that the framework outlined here can form the foundation of a more comprehensive theory that integrates the effects of biomechanical and physiological pathways on ecological responses to the physical environment.

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