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Searching for the best bet in life-strategy: A quantitative approach to individual performance and population dynamics in reef-building corals

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ABSTRACT

Ecological signs of Earth's biosphere forewarn an alarming trajectory towards a global mass-extinction. Assessing species performance and susceptibilities to decline is essential to comprehend and reverse this trend. Yet it is challenging, given difficulties associated with quantifying individual and population processes that are variable across time, space, and life-stages. We describe a new approach to estimating and comparing species performances that combines empirical data, a novel theoretical consideration of population dynamics, and modern statistics. Our approach allows for a more realistic continuous representation of individual performances along development stages while taking into account non-linearity, and natural variability as captured by spatio-temporally replicated observations. We illustrate its application in a coral meta-assemblage composed of populations of the three major reef-building taxa *Acropora*, *Pocillopora*, *Porites*. Using a unique set of highly replicated observations of individual coral dynamics under various environmental conditions, we show how taxa differ in their investment in recruitment and size-specific aptitude for growth and survival, notably through different use of clonal shrinkage, fragmentation, fission, and fusion processes. Our results reveal contrasting life-history trade-offs among taxa which, along with differing patterns of density-dependent recruitment, modulate species responses to decline. These differences in coral life history traits reflect opposing life-strategies, imply regulation at differing life-stages, and explain divergence in species trajectories. Our findings indicate a high potential for resilience in *Pocillopora* and *Porites* populations, thanks respectively to a sustained recruitment that promotes demographic elasticity through replacement of individuals, and a steady resistance to mortality which confers persistence through lingering of individuals. Resilience in *Acropora* appears more arbitrary, given high susceptibility to perturbations and dependency of recruitment on presence of established local populations. We identify management actions that can complement *Acropora*'s life history and benefit recovery of its populations following mortality events. Our regression-modelling approach to quantifying and comparing species performances in different population processes is applicable to all taxa, as illustrated even those with complex clonal life histories, and can be implemented at wide spatio-temporal and taxonomic coverage. It can promote more accurate representation of species dynamics in both descriptive and predictive modelling approaches. The semi-parametric contrast curve method we develop facilitates comparing response variables along continuous explicative metrics while accounting for multiple sources of complexity in empirical data. It should widely benefit investigations in ecology and quantitative science.

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1. Introduction

As global indicators of Earth's biosphere show inexorable signs of erosion, localized examples of successful ecosystem management attest to the potential for sustainable development (Butchart et al., 2010; Lotze et al., 2011; Barnosky et al., 2012). Yet practical opportunities for establishing conservation plans remain limited mainly due to a lack of political prioritization (Christensen et al., 1996). In this context, improving ecological understanding of the underlying drivers of species dynamics can help refine management efficiency (Mumby et al., 2014; Anthony et al., 2014; Vercelloni et al., 2014). In particular, quantitative assessments of species performance and susceptibilities are essential in allowing us to recognize where and why species fail to maintain their populations (Winemiller, 2005; McGill et al., 2006; Foden et al., 2013).

Investigations of species performances are not new. However, comprehensive performance-based approaches to population dynamics, those studies specifically designed to identify the most vulnerable stages in species lives, have been hampered by multiple limitations. These include complexity of species' life-cycles, diversity of life-strategies, variability in organism performances among observations, and a lack of advanced statistical and analytical tools (Jopp et al., 2011). Ecological investigations have especially suffered from difficulties associated with quantifying individual and population processes that are variable in nature, and comparing such empirical measurements across multiple explicative factors such as taxonomic identity, development stage, and environmental condition (Menge, 2000; McGill et al., 2006). These limitations have restricted most studies on species performances to mono-specific investigations, and inter-species comparisons to single population processes or life-stages. As a result, the prevalence of different population processes and their contributions to population maintenance remain unknown in many species groups. Therefore, a better quantitative knowledge of the mechanistic drivers of species dynamics can benefit our understanding of community trajectory, and improve our ability to identify species vulnerable to decline. For example, the importance of life-strategies, i.e. how species allocate energy to survival, growth, and reproduction, to ecological success needs to be evaluated (Winemiller, 2005; van Woesik et al., 2012; Foden et al., 2013; Rees et al., 2014). Similarly, species' abilities to resist and respond to various sources of stress and disturbance need to be quantified to improve our comprehension of ecosystem resilience (Lotze et al., 2011; Anthony et al., 2014; Mumby et al., 2014). Moreover, the importance of recruitment and individual performance across life-stages in population maintenance remains to be assessed (Caley et al., 1996; Menge, 2000). In general, our qualitative understanding of species dynamics lacks quantitative evaluation, which in turn limits our ability to achieve accurate predictions and efficient management of ecosystems.

We addressed these issues relating to ecological knowledge on the underlying drivers of species dynamics in a French Polynesian reef-building coral meta-assemblage composed of populations from the three major genera dominating tropical reefs: *Acropora*, *Pocillopora*, *Porites*. Because of their crucial role as foundation species in reef ecosystems and their high vulnerability, improving knowledge of coral dynamics can benefit both their conservation and management of marine resources in the tropics (see Box 1). The three taxa we studied exhibit different life forms that contribute differently to reef accretion and habitat structure (Veron, 2000). Their co-occurrence contributes to generating diverse refuges that are essential to host prolific reef communities (Appendix A). Yet, ecological mechanisms leading to their co-existence are not understood, particularly as recent research suggests these taxa rely on opposite life-strategies (Darling et al., 2012; Hughes et al., 2012; van Woesik et al., 2012; Riegl et al., 2013). Branching *Acropora* often grows fast, but is more susceptible to predation and disturbance. Massive *Porites* typically grows slowly yet resists diverse sources of stress. Sub-branching *Pocillopora* usually shows intermediate levels in growth and survival. Given such differences in life history traits, one expects populations from these taxa to show differing degrees of persistence on reefs and different rates of individual turnover. However, our understanding of coral life-strategies comes mainly from observations from disparate sources, as the complexity of the coral study model has limited most empirical studies of coral performance as mono-specific, restricted in time and space, or limited to single traits (see Box 1). As a result, a quantitative comparison of coral performance in different life history traits and the mechanisms supporting population maintenance had remained impossible.

Here we provide comprehensive measurements of population dynamics that are complementary to existing data on corals, resulting mostly from large-scale surveys of reef communities and short-term experiments. Based on a thorough in situ survey of populations exposed to various levels in environmental gradients and natural disturbances, we tested how individual coral performance varied as a function of size and taxonomic identity, and how populations responded to disturbance-driven alteration of communities. Our results show that taxonomic differences in coral performance are highly stage-dependent, and that each taxon relies on a different mechanism for population maintenance. We discuss the implications of the antagonistic life-strategies observed in coral protagonists for the mechanisms supporting population resilience and in the light of the community regulation literature. Our quantitative approach to life history traits and population dynamics is fully empirical and based on an analysis of species performance in different population processes as observed in nature (Hughes and Jackson, 1985; Darling et al., 2012). It differs from other methods using simulations and predictive modelling (e.g. Easterling et al., 2000; Kayal, 2011; Riegl et al., 2013; Rees et al., 2014), although more accurate demographic information obtained from real-life data can highly benefit such purpose. Our approach is applicable to any species, underpinned by modern non-linear modelling statistics, and can be implemented at differing geographical and taxonomic resolution while accounting for variability among observation units. We introduce the application of semi-parametric contrast curves in ecology, and show how their use facilitates comparing ecological responses (e.g. individual growth, species abundance) along continuous covariates (e.g. size, time, environmental stress) while accounting for natural variability and statistical complexity (e.g. non-linearity, spatio-temporally structured observations), thus promoting more accurate estimation of ecological thresholds (see Box 2). We further extend the advancement of this tool by developing a statistical method for calculating contrasts for binomial-distribution data (e.g. survival rates; Appendix B). Our study should thus benefit quantitative investigations in ecology, and the ability to build powerful data-based models in different fields of science.

2. Methods

2.1. Sampling design

We considered a French Polynesian coral meta-assemblage composed of populations from the locally most abundant species within each of the three major genera: branching *Acropora globiceps*, sub-branching *Pocillopora meandrina*, and the massive *Porites* spp. complex *P. lobata*, *P. lutea*, *P. australiensis* (Appendix A). To capture natural variability in coral performances, sympatric populations of the three taxa were surveyed through time and

Box 1. The coral study model.

Reef-building corals are representative foundation species characterized by sessility, slow growth, and longevity, features that make them particularly susceptible to sources of regulation (e.g. predation, competition, abiotic stress) and alteration of their environment. The tropical reefs they build are among the most productive, diversified, and socio-economically valuable ecosystems on Earth, but also one of the most threatened (Riegl et al., 2009; Butchart et al., 2010; de Groot et al., 2012; Anthony et al., 2014). Because coral growth designs the physical structure of reef habitats, reef characteristics and health are directly related to coral performance and the size and structure of coral assemblages (Appendix A).

Despite their ecological importance and fragility, quantitative investigations to coral performance and population dynamics have remained relatively rudimentary, given difficulties associated with the consideration of the various population processes that corals exhibit in nature (Fig. I a–h). This is due to the clonal life-form of most species, which in addition of the typical recruitment, growth, and mortality processes observed in other organisms, also undergo shrinkage, fragmentation, fission, and fusion. These clonal processes are thought to significantly contribute to population maintenance; yet quantitative case-studies to coral dynamics have remained too limited to evaluate the prevalence of each population process, and implications of life-strategy trade-offs in species ecological success (Hughes et al., 1992).

Because individual corals can grow and shrink, split apart and fusion several times during their life span, coral size and age often do not show a direct relationship (Hughes and Jackson, 1985; Babcock, 1991). Here as in other studies on corals, colony size was used as a proxy for coral condition and major driver of individual performance, as colony dimensions are easily measurable in situ, and because most demographic responses of corals such as survival, growth, and fecundity are related to colony size rather than age (Hughes et al., 1992). Similarly, coral recruitment (a) was defined as observation of a new small colony visibly resulting from larval settlement (Hughes and Jackson, 1985; Babcock, 1991); i.e. obviously not resulting from fragmentation (e), fission (f), or immigration (h). Growth (b) and shrinkage (c) were associated with changes in colony live-tissue surface, mortality (d) being defined as the loss of a formerly-established live colony. Observed live corals unattached to the substrate were considered as immigrants (h) or fragments (e), depending on if they consisted of dislodged entire colonies or dismantled colony pieces. Fission (f) was defined as production of separate colonies through isolation of potions of coral live-tissue via partial-mortality. Inversely, fusion (g) corresponded to the inclusion of neighbour corals into the colony surface, usually following fission or fragmentation.

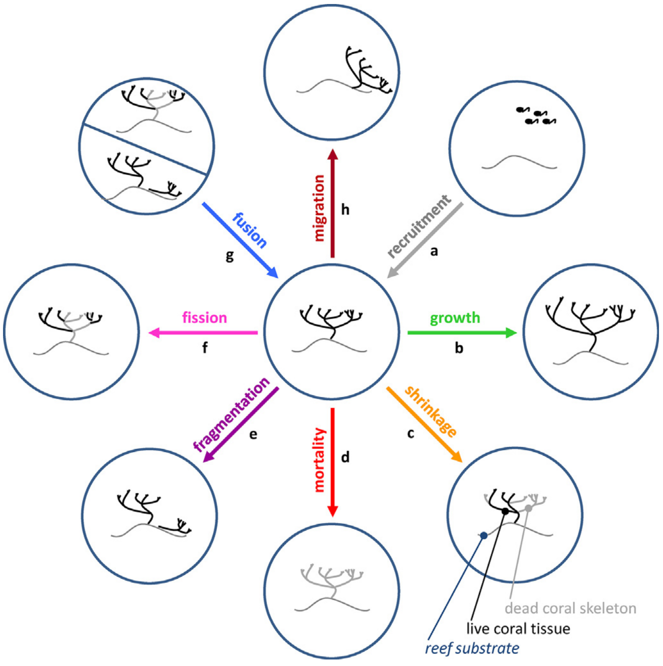

Fig. I.

space at seven outer-reef locations in Moorea and Raiatea. These seven coral assemblages are situated at 50 m–200 km from each other, and were exposed to differing levels in environmental gradients and natural disturbances (Appendix C; Kayal et al., 2012). Surveys were performed by mapping and measuring individual corals in 3–4 replicate 10 m × 1 m permanent-transects positioned along constant depth contours. All corals visible to the naked eye and belonging to the focal taxa were considered, as long as at least half of the colony fell within transects. Coral centroids were mapped at the centimetre level within the permanent-transects using two-dimensional x–y coordinates (Kayal, 2011). This fine-scale mapping system allowed identification of individual corals across consecutive sampling and required no additional tagging. Colony size was measured in three dimensions at the millimetre scale, and the surface was estimated by using geometric formulae corresponding to the general morphology of each species (Appendix D). Sampling was repeated every six months between March 2008 and March 2010 to capture population dynamics, allowing (1) characterization of population size and structure at each observation, and (2) estimation of individual coral performance in different population processes between consecutive sampling (Box 1). A total of 16,910 coral mapping and measurements were performed, including 1460 *Acropora*, 8380 *Pocillopora*, 7070 *Porites*. All sampling was performed by the same observer using SCUBA.

2.2. Theoretical and statistical approach

Population and assemblage trajectories were modelled using a semi-parametric approach combining Generalized Linear Mixed-effect Models (GLMMs) and penalized splines (Ruppert et al., 2003). GLMMs allow consideration of correlated data resulting from longitudinal observations (e.g. temporal trends), and random effects resulting from consideration of multiple subjects and scales (e.g. spatial replicates and hierarchical designs). Penalized splines account for deviations from linearity in an optimal fashion considering model accuracy and complexity (Durbán et al., 2005).

In a novel approach to consider the underlying drivers of population dynamics, we quantified the prevalence and intensity of each type of transition that individual corals undergo on the reef (Box 1), and related these measurements to coral taxonomic identity and size. Prevalence is a measurement of the preponderance of each event, i.e. frequency of occurrence, and was coded by a binary variable. Intensity is a measurement of the amplitude of each event, i.e. rate of change at occurrence, and was coded by a continuous variable. Such discriminative consideration of population processes by prevalence and intensity constitutes an efficient way to quantify the dynamics of species in which the number of possible transitions is higher than the simple binary alternative 'mortality versus growth', and where statistical implementation is otherwise difficult (Kayal et al., 2011). For each type of transition (Box 1), size-dependent prevalence and intensity profiles were calculated per taxa using GLMMs, and compared among taxa using a semi-parametric contrast approach (Durbán et al., 2005).

Box 2. Introduction to the use of contrast curves in ecology.

Ecological metrics typically vary with gradients in intrinsic biological characteristics of the study systems and extrinsic environmental conditions. Accounting for such gradients in comparisons of ecological data can help identify sources of divergence and thresholds, and reduce analytical error. Yet conventional statistics do not allow for comparing empirical responses along continuous covariates. The contrast curve technique combines Generalized Linear Mixed-effect Modelling technology (GLMM) and a semi-parametric regression approach using penalized splines to compare response variables along continuous explicative gradients while accounting for multiple sources of complexity. It can benefit investigations on a broad range of ecological data.

The contrast curve approach calculates the difference between two curves and identifies specific regions of the covariable x where difference in response variable y is significant (Durbán et al., 2005). Calculations use GLMM software to account for a longitudinal design of observations on multiple subjects, unbalanced designs, and other characteristics in data (Ruppert et al., 2003; Bolker et al., 2009). The penalized splines component is an optimized approach to smoothing given model accuracy and complexity. Penalized splines represent a trade-off between the spline regression approach which is highly dependent on the number and position of knots, and smoothing splines which are highly computationally intensive with large datasets (Durbán et al., 2005). Here, penalized splines complement GLMMs to account for deviations from linearity at the different levels of estimations, both in subject-specific responses within groups, and in calculations of group-average curves and their difference (Ruppert et al., 2003).

In this example (Fig. II), probability of growth is compared across colony sizes between the two coral taxa, *Acropora* and *Pocillopora*, based on replicated observations on individual coral dynamics performed at multiple points in time and space (random effects accounted for in the calculation of the probability profiles). Plot (a) illustrates empirical observations (dots, binary data) along with the size-dependent probability profiles of the two species as estimated by GLMM (curves, equations provided on plot). Plot (b) illustrates the difference between the two probability profiles and the associated 95% confidence intervals as estimated by the semi-parametric contrast curve approach. This curve also accounts for non-linear deviations that are not represented in the GLMM estimates. Domains of significant difference are identified on this plot as portions of the covariable where the contrast curve and corresponding confidence intervals do not cross the no-difference threshold (grey line). Here, *Acropora* and *Pocillopora* show equivalent probabilities of growth at colony log-sizes in the range 1.2–2.4, with *Acropora* colonies having lower chances of growing below and above this size range. Note that different conclusions could have been drawn if growth probability was compared among these two taxa only on a narrow range in colony size, or if individual size was not taken into account.

Programming syntax for implementing semi-parametric contrast curve for normal-distribution data can be found in Durbán et al. (2005). The code for calculating contrast curves for binomial data is provided in Appendix B.

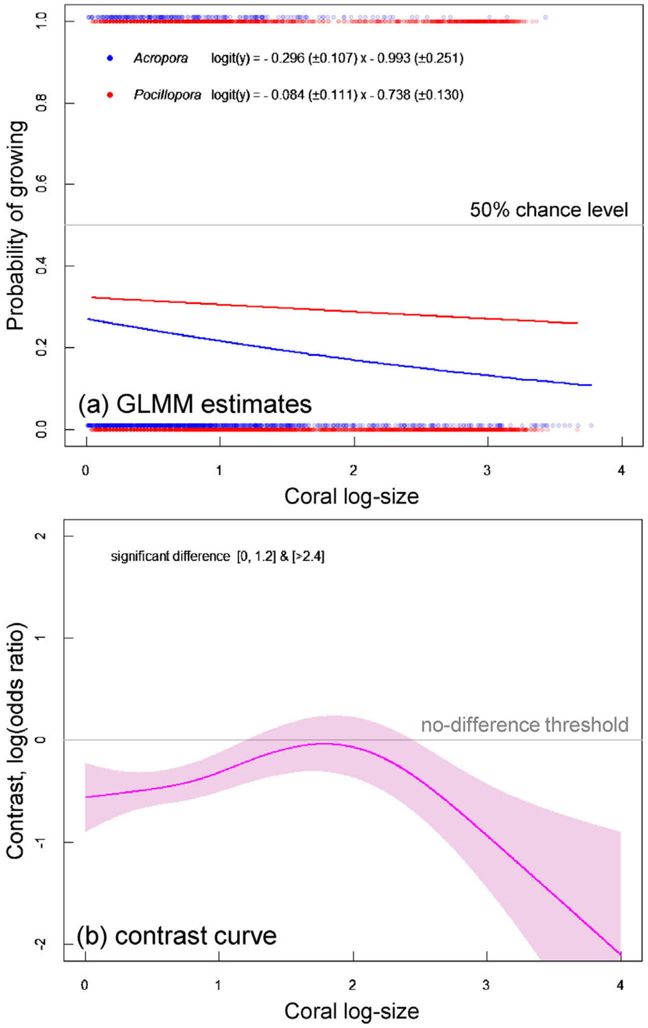

Fig. II.

Contrasts calculate the difference between two curves and allow for identifying specific regions of the covariable x (e.g. size) where difference in response variable y (e.g. growth) among two groups is significant (Box 2). This continuous consideration of the covariable confers a considerable advantage compared to prior methods used in ecology, as it allows a smooth calculation of the difference in response variable y without the need to partition the predictor x into a subjective number of classes. Associated with GLMMs and penalized splines, contrast curves also account for different sources of complexity often associated with ecological data, such as random effects resulting from longitudinal observations on multiple subjects, non-linearity in the x–y relationship, and unbalanced designs (Ruppert et al., 2003; Bolker et al., 2009). Contrasts for continuous data (intensity of transitions) were calculated using statistics based on normal distribution theory, as described in Durbán et al. (2005). We developed new statistics allowing calculation of contrasts for binomial-distribution data (e.g. frequency of occurrence; see Appendix B).

We also used GLMMs to model temporal variation in recruitment, and to investigate the relationship between the size of local populations and the abundance of coral recruits and fragments. Similarly, the prevalence of fission and fusion was related to coral size. As coral size was log-transformed to homogenize data distribution, and to facilitate realistic representation of coral dimensions from results provided in log-sizes, we refer to the equivalent diameter $\varnothing_{\mathrm{E}}$, which is the diameter of a hypothetical coral with an equivalent surface and a spherical shape (Appendix D). Similarly, to ease interpretation of results, we report the major patterns in size-dependent transition-profiles of corals, and compare taxa performances at the specific sizes of $\varnothing_{\mathrm{E}} = 1.7$ cm (log-size = 1), $\varnothing_{\mathrm{E}} = 30$ cm (log-size = 3.45), and $\varnothing_{\mathrm{E}} = 180$ cm (log-size = 5, observed in *Porites* only), corresponding respectively to the dimensions of a young juvenile, a well-developed adult, and a massive elderly coral (Appendix D). All statistics were performed in R (R Development Core Team) complemented by packages NLME

(Pinheiro et al., 2008) and BRugs (Ruppert et al., 2003) at a risk level of 5%.

2.3. Ecological context

We conducted our study in French Polynesia, in a period of strong influence by two natural disturbances, an outbreak of the coral-predator crown-of-thorns starfish (COTS, *Acanthaster planci*) from 2002 to 2010, and a tropical cyclone in February 2010. These disturbances differed in their development and had complementary impacts on reef habitats and communities (Kayal et al., 2012). Biological disturbance by COTS was slow-paced, diffusive, and selective, following COTS propagation and feeding preference: high selectivity for *Acropora*, intermediate preference for *Pocillopora*, neutrality for *Porites* (Kayal et al., 2011). The cyclone constituted a pulse physical disturbance that mostly affected north-exposed reefs. Disturbances accentuated regulation processes on corals, hastening population dynamics and amplifying differences in species performances and susceptibilities. This facilitated characterization of life-strategies and the evaluation of the repercussions of life history trade-offs in population trajectories.

Our study was conducted at the meta-assemblage scale by considering sympatric populations facing various levels and timing of exposure to environmental stress (see Kayal et al., 2012 for details on disturbance dynamics and how the different reef locations were affected). This allowed a fair representation of the natural variability as observed in our study system. To account for this environmental heterogeneity in the calculation of coral performances, random effects associated with the consideration of observations from multiple islands, sites, depths, and seasons (Appendix C) were taken into account in the parameterization of GLMMs (Bolker et al., 2009). Similarly, because the cyclone severely affected corals and habitat-structure on several reefs (Kayal et al., 2012), it potentially disrupted a possible general relationship between local population sizes and abundance of coral recruits and fragments. The statistical effects of the cyclonic period on these two specific relationships were thus tested a priori using χ^2, and where significant, corresponding data were removed from the corresponding GLMMs (Pinheiro et al., 2008).

3. Results

3.1. Population and assemblage trajectories

Coral populations showed differing trajectories, depending on their exposure to disturbances and their taxonomic identity (Fig. 1, Appendix E; see Kayal et al., 2012 for a broader account of disturbance dynamics and impacts on the studied reefs).

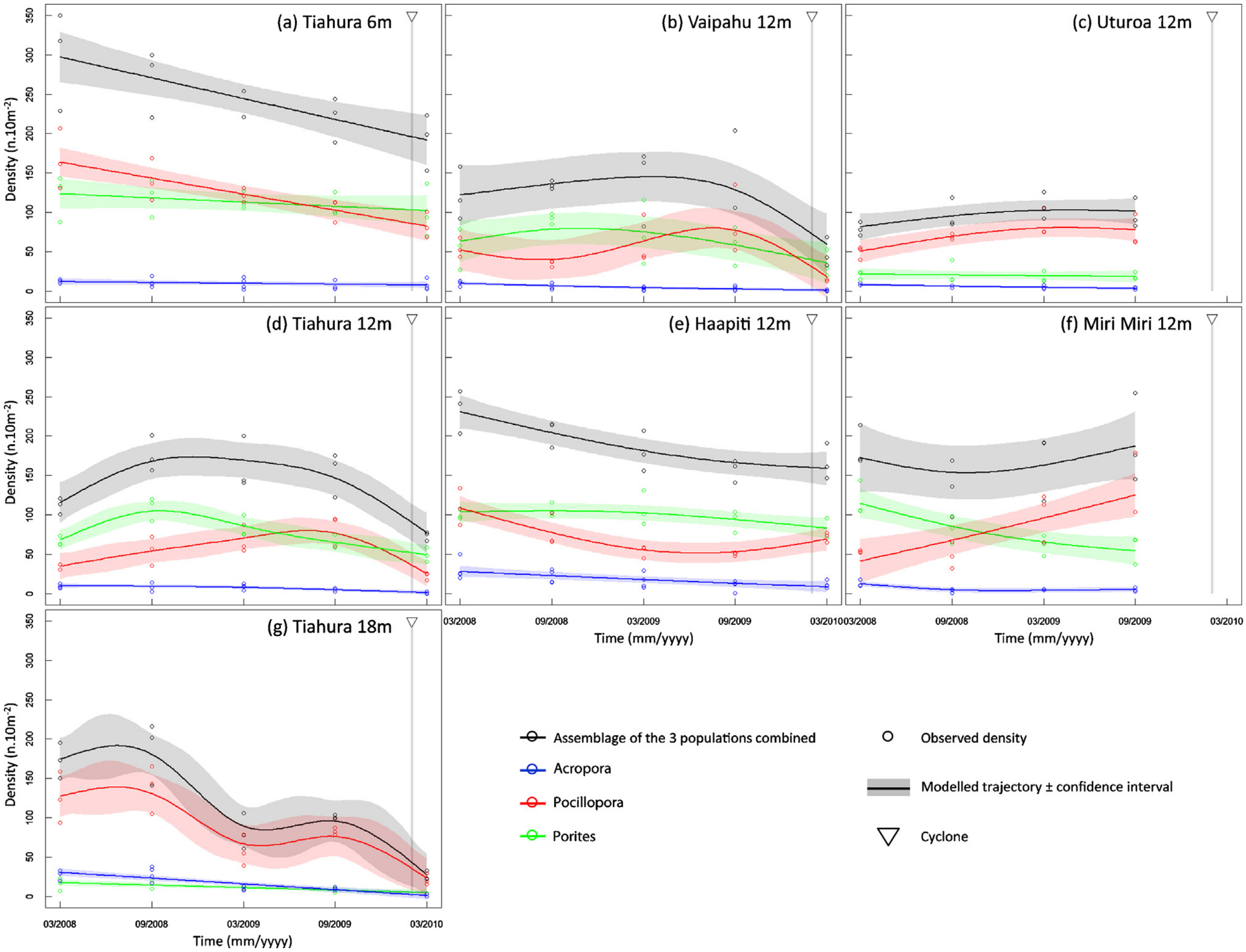

Fig. 1. Coral density through time (x-axis) and space (different sites and depths). Trajectories were modelled using a semi-parametric regression approach associating Generalized Linear Mixed-effect Models and penalized splines (Ruppert et al., 2003). Coral decline was driven by predation by COTS (crown-of-thorns starfish, *Acanthaster planci*) over the process of the study, and a cyclone occurring by the end of our survey. Note that coral assemblages were facing differing intensity and timing of exposure to disturbances (Kayal et al., 2012). See Appendix E for an analogue representation of population and assemblage overall surfaces (as a proxy for coral biomass and cover).

Assemblage dynamics were locally driven by population declines, and increases with the subsequent initiation of recovery. The structure of assemblages was altered during both decline and recovery phases due to taxonomic differences in population responses. Most susceptible *Acropora* populations were always kept at smaller sizes independently of disturbance phases (densities ranging 1–30.3 n.10 m^{-2} ±0.4–6.7 SE). *Pocillopora* populations were most dynamic and showed the highest rates of decline (e.g. Fig. 1a) and the only signs of post-disturbance increases observed (e.g. Fig. 1f). *Pocillopora* dominated assemblages at the earlier stages of disturbance (max pre-disturbance density of 166.7 n.10 m^{-2} ±22.1 SE) and after initiation of the recovery process (max post-disturbance density of 129 n.10 m^{-2} ±25 SE). *Porites* populations showed slower declines and predominated when other populations were depleted (densities ranging 3.7–121.3 n.10 m^{-2} ±0.3–16.9 SE). Analogous trajectory patterns were observed in terms of population surface (Appendix E), although population declines were accompanied by a loss of bigger corals and a shift towards higher proportions of smaller colonies (Appendix F).

3.2. *Probability of growth, shrinkage, mortality*

Coral aptitude for survival and growth varied as a function of taxonomic identity, size, and their interaction. Coral size had a stronger and more consistent effect among taxa on probabilities of mortality and shrinkage than on growth (Fig. 2a–c). Mortality was maximal for smaller corals, approximating 75–80% for the three taxa, and dropped <40% with size. Size-mediated decreases in probability of death differed among taxa, and was most pronounced in *Porites* which had significantly lower rates of mortality than *Acropora* and *Pocillopora* above a size of $Ø_{E} = 0.4$ cm and 0.8 cm respectively: these ranges are identified in Fig. 2f as portions of the *x*-axis (colony size in log-scale) where contrast curves and corresponding confidence intervals (CI) do not cross the non-difference threshold $y = 0$. In opposition, *Acropora* had the highest rates of mortality, which contrasted with *Pocillopora* at sizes below $Ø_{E} = 2.3$ cm. *Acropora* had to reach a size of $Ø_{E} = 12.2$ cm to reduce its probability of mortality to a level below 50%, against a size of $Ø_{E} = 5.9$ cm in *Pocillopora* and $Ø_{E} = 1.8$ cm in *Porites* (Fig. 2c).

Probability of shrinkage showed an opposite pattern, with lowest values of 0–10% at smallest coral sizes and an increase to 60–90% with colony dimensions (Fig. 2b). Shrinkage was more frequent in *Porites*, with a probability-to-size profile higher than *Acropora* at colony sizes below $Ø_{E} = 13.7$ cm, and than *Pocillopora* on the entire size-range (illustrated in Fig. 2e by the *Poc*/*Por* contrast curve ±CI never crossing the $y = 0$ threshold). *Acropora* had a lower probability of shrinkage than *Pocillopora* at colony sizes below $Ø_{E} = 2.1$ cm and a higher one above $Ø_{E} = 6.8$ cm (see inversion in the sign of the *Acr*/*Poc* contrast curve in Fig. 2e).

Probability of growth increased from 25% to 40% with colony dimensions in *Porites*, approximated 30% over the entire size-range in *Pocillopora*, and decreased from 30% to 10% in *Acropora* (Fig. 2a). *Acropora* had a significantly lower probability of growth than *Pocillopora* at colony sizes below $Ø_{E} = 2.2$ cm and above $Ø_{E} = 9.5$ cm, and than *Porites* at sizes above $Ø_{E} = 0.7$ cm (see domains of significant difference as revealed by contrast curves in Fig. 2d). *Pocillopora*'s chances of growth were higher than *Porites* at sizes below $Ø_{E} = 1.0$ cm, lower in the size-range $2.0 < Ø_{E} < 13.4$ cm, and equivalent at larger dimensions.

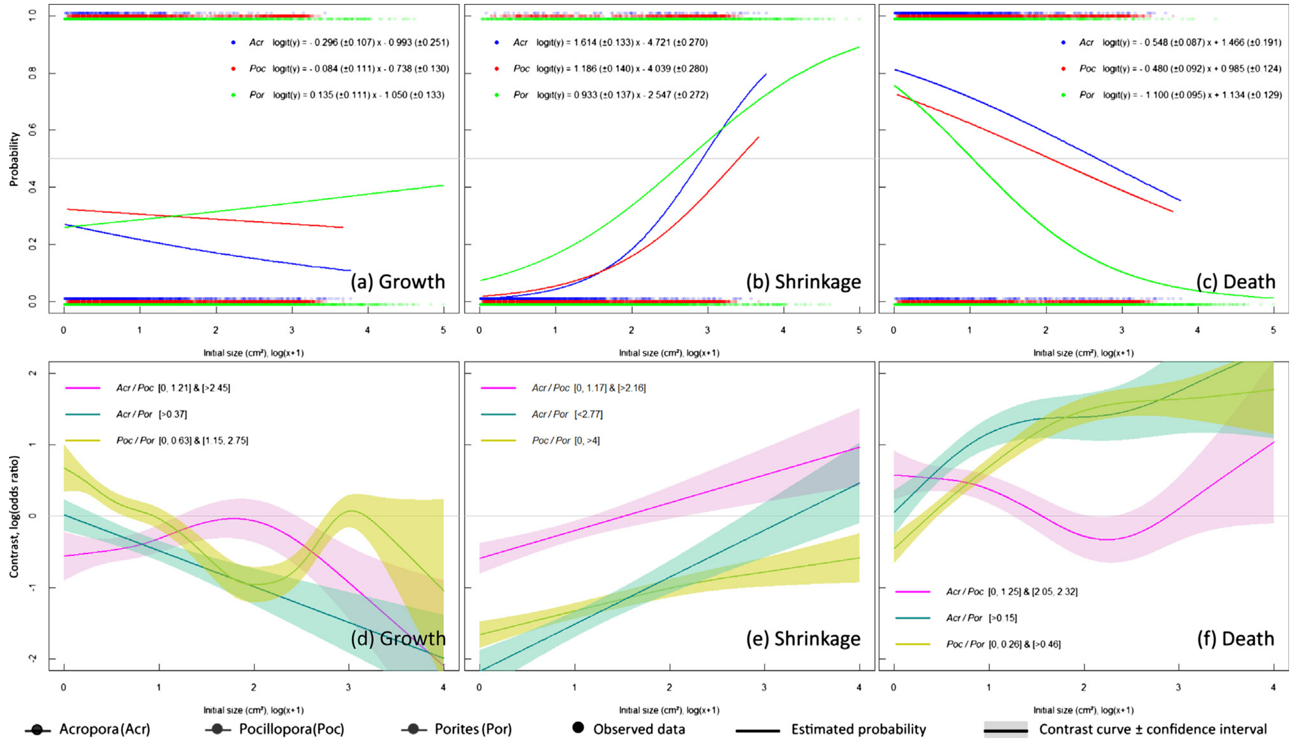

Fig. 2. Taxonomic differences in probability-to-size profiles of corals for growth, shrinkage and mortality. Probability profiles (a–c) were calculated using Generalized Linear Mixed-effect Models based on binomial probability distribution. Domains of significant difference between probability profiles of taxa were calculated in a pairwise fashion using semi-parametric contrast curves for binomial-distribution data (d–f) based on log(odds ratio) in response variable; see programming script detailed in Appendix B. Grey lines on probability profiles (a–c) indicate the 50%-chance level; and the no-difference threshold for contrast curves (d–f): differences in probabilities are significant when contrast curves and corresponding confidence intervals do not cross this line; e.g. cyan *Acr*/*Por* curve in (f) indicates that mortality in *Acropora* is significantly higher than in *Porites* at colony log-sizes >0.15 ($Ø_{E} > 0.4$ cm). Equations of probability profiles (a–c) and domains of significance in contrasts (d–f) are given on graphics. See Appendix D for the relation between coral log-size and equivalent diameter $Ø_{E}$. Note the jittering of the response values in (a–c) for clarity.

3.3. Size variation in growth and shrinkage

Coral relative-growth was highest and more contrasted among taxa at smaller sizes, and decreased with colony dimension (estimated relative-growth ranged 126–132% among taxa at a size of $Ø_{\mathrm{E}} = 1.7$ cm, against 100–104% at a size of $Ø_{\mathrm{E}} = 30$ cm; Fig. 3a). *Acropora* had the fastest growth, which significantly differed from *Pocillopora* in the size-range $0.6 < Ø_{\mathrm{E}} < 7$ cm, and from *Porites* at sizes below $Ø_{\mathrm{E}} = 2.1$ cm (see contrast curves in Fig. 3b). *Pocillopora* grew faster than *Porites* below a size of $Ø_{\mathrm{E}} = 1.0$ cm, and slower in the size-range $1.3 < Ø_{\mathrm{E}} < 25.8$ cm (inversion in the sign of the contrast curve).

Size variations were less consistent during shrinkage than growth, as changes in coral dimensions ranged from small losses relative to colony dimensions to high proportions of partial-mortality (Fig. 3a). Overall, shrinkage was more intense in smaller corals relative to colony dimensions, and its severity decreased with size (estimated relative-growth increased from 59–79% among taxa at a size of $Ø_{\mathrm{E}} = 1.7$ cm, to 78–87% at a size of $Ø_{\mathrm{E}} = 30$ cm). Shrinkage was more pronounced in *Porites*, and significantly differed from *Acropora* in the size-range $1.9 < Ø_{\mathrm{E}} < 23.5$ cm, and from *Pocillopora* for $Ø_{\mathrm{E}} > 0.7$ cm (Fig. 3c). *Acropora* colonies shrank more intensely than *Pocillopora* above a size of $Ø_{\mathrm{E}} = 20.2$ cm.

3.4. Recruitment

Coral recruitment was variable across time, space, and taxa (Appendix G). The density of new recruits observed per semi-annual survey ranged 12–109.3 n.10 m^{-2} ±0–28.7 SE, and was dominated at 81% by *Pocillopora* (9.7–85 n.10 m^{-2} ±0.3–21.9 SE, $N_{\mathrm{recruit}} = 2834$), against 9% of *Acropora* (0.5–18 n.10 m^{-2} ±0.5–4.9 SE, $N_{\mathrm{recruit}} = 332$) and 10% of *Porites* (1–19 n.10 m^{-2} ±1–3.8 SE, $N_{\mathrm{recruit}} = 338$). Coral recruitment was negatively correlated with the size of resident assemblages, both when expressed in terms of density and overall surface of the three taxa combined (Fig. 4a and d). This pattern was driven by *Pocillopora*, as *Acropora* and *Porites* showed recruitment rates independent of assemblage sizes. Such a negative relationship between coral recruitment and local crowdedness was also observed at the population level for *Pocillopora* (Fig. 4e). In contrast, *Acropora* recruitment was positively related to the density of its local populations (Fig. 4b), a pattern however not observed with population surfaces (Fig. 4e). In *Porites*, recruitment was not correlated with the size of local populations. New coral recruits measured $Ø_{\mathrm{E}} = 0.8$–0.9 cm (Appendix H).

3.5. Fragmentation, fission, fusion, immigration

Fragmentation was occasional, the density of fragments ranging 0–17 n.10 m^{-2} ±0–1 SE per assemblage, and was dominated at 92% by *Pocillopora* ($N_{\mathrm{fragment}} = 143$) against 6% for *Acropora* ($N_{\mathrm{fragment}} = 10$) and 1% for *Porites* ($N_{\mathrm{fragment}} = 2$). Fragment density showed an exponential relationship with population size in branching *Acropora* and *Pocillopora*, and was observed only during the cyclonic period for massive *Porites* (Fig. 4c and f). Coral fragments measured $Ø_{\mathrm{E}} = 2.5$–2.7 cm (Appendix H). Fragment survival and reattachment was low ($N_{\mathrm{reattachment}} = 10$), ranging 0–2 n.10 m^{-2} ±0–1.5 SE per assemblage, and was dominated at 90% by *Acropora* against 10% for *Pocillopora* and 0% for *Porites*. Based on these statistics, i.e. the number of successful reattachment observed relative to the abundance of fragments produced, *Acropora* fragments had a 90% rate of survival and reattachment (9/10), against 0.7% in *Pocillopora* (1/143). Observed reattached fragments measured $Ø_{\mathrm{E}} = 2.4$–3.1 cm (Appendix H).

Fission was mostly observed in *Porites*, with some occurrences in larger ($Ø_{\mathrm{E}} > 7$ cm) colonies of *Acropora* and *Pocillopora* undergoing shrinkage (Appendix H). In *Porites*, fission was also more frequent during shrinkage than growth, and increased with size. The number of sister colonies generated through fission was positively correlated with coral size in *Porites*, particularly in shrinking colonies. Similarly, a positive relationship was found between the size of sister colonies generated by fission and the initial size of corals.

Cases of fusion were rare and almost-exclusively restricted to *Porites* (Appendix H). The probability of fusion in this taxon increased with colony dimensions, representing approximately 0–10% of growing colonies. Fusion-mediated size-increment was highest for smaller corals and decreased with colony size (estimated relative-growth of 197% at a size of $Ø_{\mathrm{E}} = 1.7$ cm, against 131% at a size of $Ø_{\mathrm{E}} = 30$ cm).

Coral immigration was relatively low, ranging 0–3.7 n.10 m^{-2} ±0–0.7 SE per semi-annual observation. Overall, immigrant assemblages were dominated at 71% by *Porites* ($N_{\mathrm{immigrant}} = 67$, representing 1% of censused colonies in this taxon) against 27% of *Pocillopora* ($N_{\mathrm{immigrant}} = 26$, 3‰ of encounters) and 2% of *Acropora* ($N_{\mathrm{immigrant}} = 2$, 2‰ of encounters). Immigrant corals measured $Ø_{\mathrm{E}} = 2.6$–5.2 cm (Appendix H).

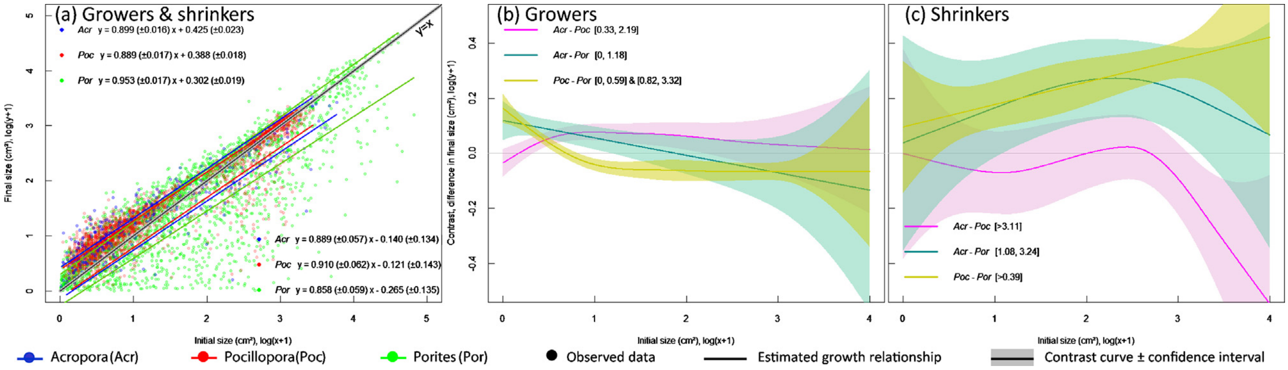

Fig. 3. Taxonomic differences in size-dependent relative-growth profiles of corals. Relative-growth (a) is expressed as the relationship between initial and final colony sizes, and was calculated separately for growing (relative-growth >100%) and shrinking (relative-growth <100%) corals using Generalized Linear Mixed-effect Models based on normal probability distribution. Domains of significant difference between relative-growth profiles of taxa were calculated in a pairwise fashion using semi-parametric contrast curves for normal-distribution data (b–c) based on difference in response variable; see programming script detailed in Durbán et al. (2005). Grey line on relative-growth plot (a) indicates the zero-growth threshold (relative-growth = 100%); and the no-difference threshold for contrast curves: differences in relative-growth are significant when contrast curves and corresponding confidence intervals do not cross this line; e.g. purple *Acr-Poc* curve in (b) indicates growth in *Acropora* is significantly higher than in *Pocillopora* at colony log-sizes in the range 0.33–2.19 ($0.6 < Ø_{\mathrm{E}} < 7$ cm). Equations of relative-growth profiles (a) and domains of significance in contrasts (b–c) are given on graphics. See Appendix D for the relation between coral log-size and equivalent diameter $Ø_{\mathrm{E}}$.

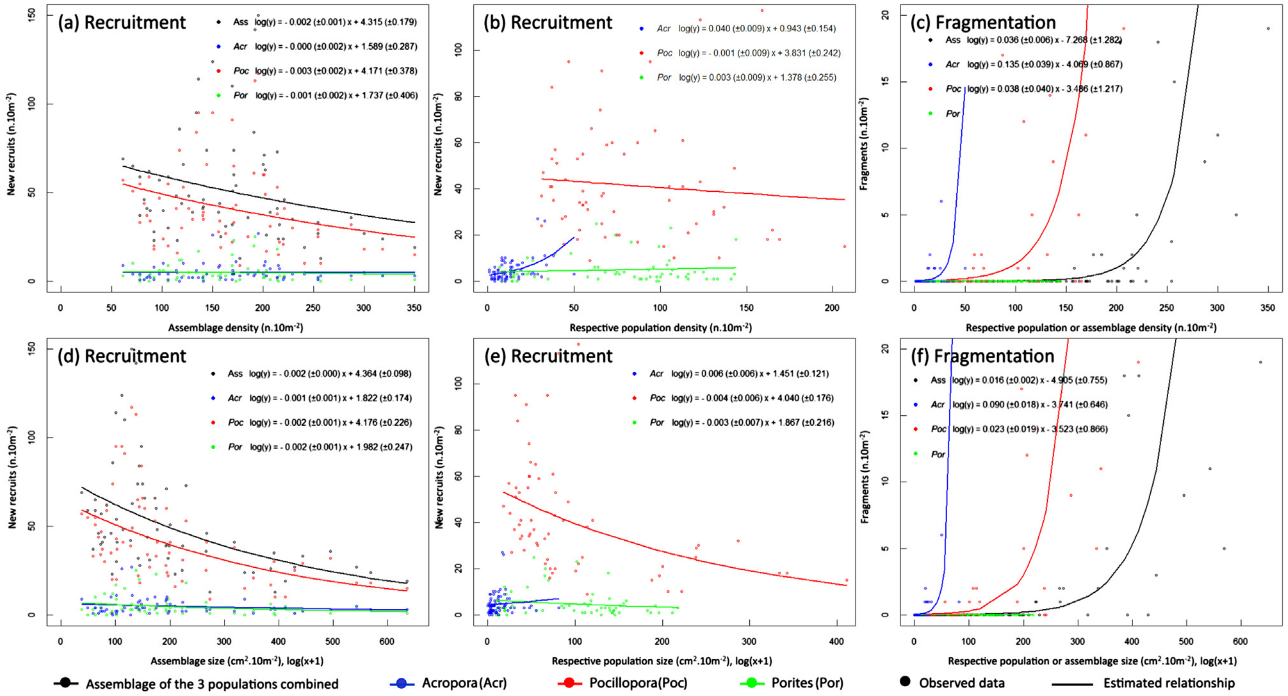

Fig. 4. Relationships between the abundance of new coral recruits and fragments observed per semi-annual survey, and the size of local populations and assemblages as expressed as density (a–c) or overall surface (as a proxy for coral biomass and cover, d–f). Relations were calculated using Generalized Linear Mixed-effect Models. Equations of regressions are given on graphics.

3.6. Synthesis on species life history traits

Coral taxa showed opposing life-strategies, with differing levels of recruitment and size-specific individual performances (Fig. 5). In *Acropora*, recruitment was low and proportional to population density. Survival was minimal, and growth was the fastest at smaller sizes. Fragment production was high relative to population sizes, and fragments had a high rate of survival and reattachment. *Pocillopora* showed the highest recruitment, which was inversely proportional to local coral abundances. Survival and growth were intermediate. Fragment production increased with population size, yet fragment survival and reattachment were rare. Recruitment was low in *Porites*, and independent of population size. Colonies had a high aptitude for growth and survival through shrinkage rather than death, even at smaller sizes. Growth was maintained at bigger sizes, leading to larger colony dimensions; yet shrinkage was also more intense. Fission was common, particularly during shrinkage and at bigger sizes, and fusion was occasionally observed.

4. Discussion

4.1. Size-dependency in individual performance

Coral performance was revealed to be highly size-dependent. Size-increment benefitted survival and the chances of partial-mortality rather than death. A larger size also promoted asexual propagation through fragmentation and fission. In contrast, coral relative-growth and benefits of colony fusion decreased with size. Smaller corals thus had higher chances of changing condition, either through mortality or relatively higher size-variations, than did bigger corals, which were more stable through time. Much inter-specific difference in coral performance was also size-dependent. For example, mortality decreased faster with size in *Porites* where colonies suffered <50% mortality beyond a size of 2 cm. Comparatively, *Pocillopora* and *Acropora* had to reach a size-refuge of respectively 6 cm and 12 cm to lower mortality to an equivalent rate. Similarly, both the probability and kinetics of growth were inhibited with increasing colony size in *Acropora* and *Pocillopora*, while large *Porites* preserved a high potential for growth. These differences in the size-specific aptitude of corals for growth explain dissimilarities observed in the size-range of colonies among populations of these taxa, and why only massive *Porites* reaches larger dimensions of several metres (Veron, 2000; Adjeroud et al., 2007b; Kayal, 2011).

Previous studies identified the importance of colony size in coral dynamics (Hughes and Jackson, 1985; Babcock, 1991), yet statistical limitations had restricted accurate estimations of how individual performance varied with size-increment, and how size-specific performances differed among species. The contrast curve technique allows recognition of such stage-dependent divergence in species traits (see Box 2). For example, differences in growth between *Acropora* and *Pocillopora* were restricted to colonies smaller than 7 cm, suggesting similar levels of energy allocation and/or success in growth at bigger stages. Similarly, contrasts exposed size-driven inversions in inter-taxa divergences, as *Pocillopora* grew faster than *Porites* at smaller sizes, and slower at bigger stages. Limited information is presently available on fecundity and other metabolic investment of French Polynesian corals to ascertain in which processes these taxa allocate energy at specific sizes, and to identify size-specific trade-offs in individual performances (Carroll et al., 2006; Hédouin and Berteaux-Lecellier, 2014). Corals usually reach maturity at an age of 3 years (colonies about 5 cm), and fecundity thereafter increases with size (Babcock, 1991; Hughes et al., 1992). Our quantification of coral dynamics indicate that *Pocillopora* invests highly in sexual reproduction, that fragmentation plays a major role in population maintenance of *Acropora*, and that sustained growth and fission and fusion processes predominate in *Porites* (Fig. 5). Complementary investigations are needed to elucidate whether taxonomic differences in size-specific allocation to growth are indeed related to differing levels of investment in fecundity and other processes such as

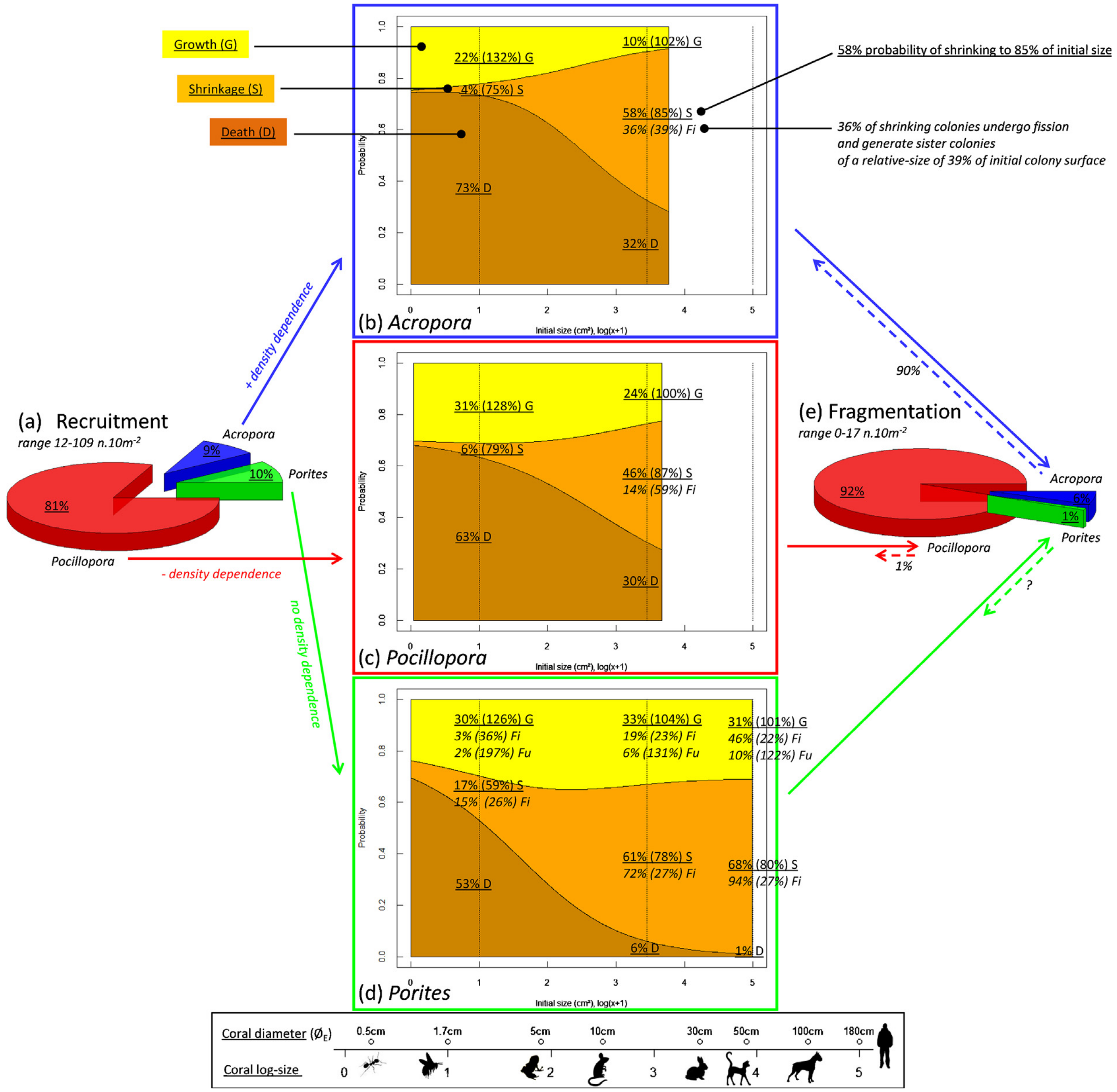

Fig. 5. Synthesis on coral life history traits as quantified based on our survey of population dynamics. Information on recruitment (a) and fragmentation (e) is provided as taxonomic contributions to the overall density of coral recruits/fragments observed in assemblages. Detection of density-dependent relationships in recruitment, and relative proportion of successful fragment reattachment (dashed return arrows) are indicated. Individual coral performances are summarized per taxon by illustrating how probabilities of growth, shrinkage, and death vary with colony size (b–d). These probability regions were drawn by cumulating the probability curves estimated in Fig. 2 and standardizing their sum in order to keep a constant total probability of 100%. For comparison, the probability of occurrence (prevalence of each event) and intensity at occurrence (amplitude of each event) of these transitions are indicated on graphs at the reference log-sizes of 1 ($Ø_E$ = 1.7 cm), 3.45 ($Ø_E$ = 30 cm), and 5 ($Ø_E$ = 180 cm; *Porites* only) in the form probability (intensity). Similarly, prevalence and intensity of fission (*Fi*) and fusion (*Fu*) in growing and shrinking colonies are indicated in the form *probability (intensity)*. Bottom scale gives size-references (see Appendix D).

colony maintenance and fragmentation (Hall, 1997; Smith and Hughes, 1999).

4.2. Recruitment limitation versus regulation

At our meta-assemblage scale of observation, coral recruitment was correlated to the size of resident populations in two of the three taxa. A positive relation was found in *Acropora*, suggesting a stock-recruitment supply of larvae, whereas a negative correlation indicated density-dependent regulation in *Pocillopora* (Hughes et al., 2000; Menge, 2000). The importance of density dependence in replenishment of open populations has generated a central debate in ecology, because in theory, local population density can both boost and inhibit recruitment, and as occurrences of both positive and negative density dependence have received empirical support (Caley et al., 1996). Ecological research advocates the importance of crowding and larval input in the preponderance of positive versus negative density dependence, as a growing density of adults is expected to promote provision of offspring in sparse populations, but inversely to limit chances of additional recruitment at higher abundances (Courchamp et al., 1999; Winemiller, 2005). Our findings support this pattern, given the positive relationship estimated in *Acropora* where populations were sparser and recruitment less frequent, and the negative relationship in *Pocillopora* where recruitment was high and restrained by the size of local populations and assemblages. Indeed, *Pocillopora* reproduces abundantly and dominates the pool of coral recruits in French Polynesia (Adjeroud et al., 2007a; Fig. 5). Our study shows that replenishment of its populations is not limited by supply of larvae, but inversely regulated by the presence of established corals that probably affect recruitment through direct predation and indirect competition (Caley et al., 1996; Fabricius and Metzner, 2004). The absence of a density-dependent relationship in *Porites* recruitment might reflect the equivalent strengths of recruitment limitation and regulation, a more stochastic reproduction success given its gonochorism, or divergence in other processes such as fertilization, dispersal, settlement, or facilitation (Courchamp et al., 1999; Baird et al., 2009; Appendix A). However, complementary investigations are required to test these mechanisms.

4.3. Recognition of species life-strategies

Identification of life-strategies constitutes a prerequisite to formulating expectations on species dynamics (Winemiller, 2005; McGill et al., 2006). It naturally represents a central step in conservation planning (Christensen et al., 1996; van Woesik et al., 2012; Foden et al., 2013). Studies on coral life-strategies have however resulted in contradictory affiliations of several major taxa, emphasizing the need for a standardized approach (Edinger and Risk, 2000; Darling et al., 2012; Hughes et al., 2012; Riegl et al., 2013). We advocate a more stringent classification of species strategies based on a quantitative and comprehensive approach to life history traits. Indeed, because species performances are stage-dependent and related to environmental conditions (e.g. see the strong effect of individual size on coral performance as discussed in section 4.1. and Box 2), characterization of life-strategies based on non-standardized data from various sources can lead to erroneous outcomes (Christensen et al., 1996; McGill et al., 2006). Similarly, as species pools and ecosystem characteristics are region-specific, and since single species can adopt divergent evolutionary pathways among geographical locations, a generalized classification of life-strategies not accounting for these sources of variability would be subjective, and an objective classification context-dependent (Veron, 2000; Baird et al., 2009; Riegl et al., 2009; van Woesik et al., 2012). Furthermore, because deficiency in one trait can be compensated for by higher performance in another, holistic considerations of population dynamics are recommended (Winemiller, 2005). Modern developments in statistical methods are improving our ability to account for diverse sources of variability in investigated data (Ruppert et al., 2003; Bolker et al., 2009; Jopp et al., 2011; Vercelloni et al., 2014). Our integrative approach to modelling and comparing species performances based on hierarchically organized observations of individual dynamics at a meta-assemblage scale can be scaled up to broader geographical and taxonomic coverage in an adaptive learning framework (Anthony et al., 2014).

In our study system, *Acropora* life history traits approached more a competitive strategy, based on the production of fewer offspring endowed with a high aptitude to preempt space and resources in optimal environments, but also a high susceptibility to being dislodged by perturbations (Grime, 1977; Connell, 1978). Indeed, this is not the first time that fragmentation has been identified as an evolutionary reproductive strategy in branching *Acropora*, which along with individual growth and stock-recruitment, tend to increase the size of local populations in an exponential manner (Hughes et al., 1992; Smith and Hughes, 1999). This life-strategy is well adapted for an effective occupation by selected genotypes of habitats that are suitable for the establishment of adult corals. Yet it can prove risky in unstable environments as rarefaction of reproduction success following mortality episodes can lead to local extinctions (Courchamp et al., 1999). *Pocillopora* exhibited a more opportunistic strategy, with intermediate levels in colony performances counterbalanced by a high investment in reproduction, to the extent that recruitment saturated habitats and was regulated by crowdedness (Caley et al., 1996). Indeed, *Pocillopora* populations in French Polynesia broadcast an elevated flux of larvae and are well mixed genetically within and among islands, implying a high capacity for dispersal (Magalon et al., 2005; Adjeroud et al., 2007a). These populations are composed of relatively small-sized colonies and characterized by high proportions of smaller individuals, suggesting fast turnover among generations (Adjeroud et al., 2007b; Kayal, 2011). These characteristics indicate a ruderal (also referred to as weedy) life-strategy of *Pocillopora*, relying on a sustained ability to colonize habitats over large spatial-scales, rather than an individual-colony aptitude to preempt resources (Grime, 1977; Connell, 1978). A low recruitment compensated by high survival and extended growth to proportionally more resistant larger dimensions confirm a stress-tolerant life-strategy for *Porites*, which is characterized by the production of fewer offspring with higher capacity for persistence (Grime, 1977). Shrinkage and fission have been recognized to play a central role in the life history of massive and encrusting corals (Hughes and Jackson, 1985; Hughes et al., 1992). In *Porites*, they promoted survival and, when followed by fusion, an accelerated recovery of colonies.

4.4. Life-strategies and mechanisms promoting population resilience

With life-strategies gambling on different mechanisms for population maintenance, coral taxa show differing potential for resilience in the face of disturbances. *Pocillopora* and *Porites* appear rather resilient, thanks respectively to a sustained recruitment that promotes demographic elasticity through a constant replacement of individuals, and a steady resistance to perturbations that confers persistence through lingering of individuals (Anthony et al., 2014; Mumby et al., 2014). Resilience in *Acropora* appears more arbitrary, given high susceptibility of individuals to mortality and dependency of recruitment on the presence of established populations. Indeed, declines in *Acropora* populations are often drastic, and have led to regional extirpations (Kayal et al., 2012; Alvarez-Filip et al., 2013; Riegl et al., 2013). Yet given the elevated aptitude of its fragments for survival and reattachment, *Acropora* also possesses a high potential for recovery following a physical disturbance (Smith and Hughes, 1999; Connell et al., 2004). Such latent resilience is corroborated by the fast recovery of *Acropora* observed following a cyclone that affected French Polynesia in 1991, even outpacing widespread colonization of habitats by opportunistic *Pocillopora* (Adjeroud et al., 2009). However, as in other ecosystems, global alterations of coral reefs are overwhelming the resilience of the most vulnerable taxa such as *Acropora*, and progressively pushing communities towards the predominance of opportunistic and stress-tolerant species (Riegl et al., 2009; Butchart et al., 2010; Barnosky et al., 2012; Darling et al., 2012; Alvarez-Filip et al., 2013). Such long-lasting decline in *Acropora* populations is already being observed in some lagoonal habitats of French Polynesia (Pratchett et al., 2011). In this context, the positive density-dependent recruitment and the high ability for asexual propagation identified for *Acropora* point towards the potential for using active management efforts to support its resilience, by preserving a portion of populations from the impacts of disturbances and using colony fragments to repopulate decimated reefs. Such efforts are already being implemented in some regions in order to favour maintenance of local *Acropora* populations (Young et al., 2012).

4.5. Final remarks

As many natural ecosystems keep vanishing at an accelerating pace (Butchart et al., 2010; Barnosky et al., 2012), conservation requires efficient tools to evaluate ecological trajectories and assess species abilities to sustain their populations. Based on non-linear regression models of spatio-temporally replicated observations, our approach facilitates quantifying species performances in different population processes with a more realistic account of natural variability and continuous organism progress along development stages. Complemented by the contrast curve technique (Box 2), our approach further allows for quantitative comparisons of species performances along continuous metrics (e.g. organism size or any ecological gradient), thus facilitating recognition of sources of divergence and ecological boundaries. Our study illustrates how application of this approach to comprehensive measurements of population dynamics can facilitate identifying those critical stages in species lives that undermine population maintenance, and help recognize species vulnerable to decline. In our reef-building coral meta-assemblage, it revealed several otherwise undetectable divergences in species life history traits, notably specific size-refuges, growth potentials, and mechanisms of population maintenance, thus allowing a finer recognition of life-strategies. We advocate the power of our approach to ameliorate estimates of species performances and their variability from real-life data, thus advancing quantitative models and predictions in a more realistic framework and improving species management in diverse ecosystems.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecocom.2015.07.003.

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