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Body size and mortality rates in coral reef fishes: a three-phase relationship

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Body size is closely linked to mortality rates in many animals, although the overarching patterns in this relationship have rarely been considered for multiple species. A meta-analysis of published size-specific mortality rates for coral reef fishes revealed an exponential decline in mortality rate with increasing body size, however, within this broad relationship there are three distinct phases. Phase one is characterized by naive fishes recruiting to reefs, which suffer extremely high mortality rates. In this well-studied phase, fishes must learn quickly to survive the many predation risks. After just a few days, the surviving fishes enter phase two, in which small increases in body size result in pronounced increases in lifespan (estimated 11 d mm^{-1}). Remarkably, approximately 50% of reef fish individuals remain in phase two throughout their lives. Once fishes reach a size threshold of about 43 mm total length (TL) they enter phase three, where mortality rates are relatively low and the pressure to grow is presumably, significantly reduced. These phases provide a clearer understanding of the impact of body size on mortality rates in coral reef fishes and begin to reveal critical insights into the energetic and trophic dynamics of coral reefs.

1. Introduction

Body size is one of the most fundamental characteristics of any organism. With its direct impact upon factors such as energetic requirements [1–3], abundance [4,5], susceptibility to extinction [6,7], reproductive modes [8–10], home range size [11–13], and functional capabilities [14,15], body size has played a critical role in the evolutionary history of entire ecosystems. While shaped by evolutionary history, body size has more immediate impacts on the life of organisms. All animals must cope with the day-to-day consequences of their body size.

For vertebrates, one of the most pressing consequences of body size is the risk of predation. Smaller animals dominate most communities as they have disproportionately small energy requirements [4,16,17], develop and reproduce quickly [10,18], and can occupy niches unavailable to larger organisms [19–21]. However, small animals can quite literally fit in more mouths, and as such, may suffer a greater risk of predation. While this pattern is well accepted and supported by evidence from a number of taxa [21–24], there are very few multi-species assessments of the relationship between body size and predation risk (but see [22]). Relatively little is known about the nature of this relationship and the potential driving forces behind it [10,25].

Ray-finned fishes account for approximately half of all vertebrate species, with the highest diversity fish assemblages found on coral reefs [26,27]. Most coral reef fishes are broadcast spawners with planktonic larval stages [28]. On their return to coral reefs, recruiting fishes are generally very small (most are only 7–12 mm long [21]), however, they have well developed sensory and locomotory systems [29–32]. While these small fishes have the ability to detect and avoid predators, recently settled recruits are naive to the environment and potential risks, and therefore suffer extremely high mortality rates [33]. Through a combination of learning to recognize predators [34–36], growth, and extreme consequences of failure, these mortality rates appear to decline rapidly [23,37]. However, the interactions

between size, experience, and mortality rates remain poorly studied outside a few single species assessments.

While almost all coral reef fishes spend some time as small juveniles on reefs, many species remain small throughout their lives. The average length of all reef fishes is just 45 mm [38]. These small fishes have relatively high mortality rates, and short lifespans [18,39]. How the mortality rates of these small experienced fishes differs from naive recruits of similar size has received relatively little attention, and the relative impact of growth on mortality rates across whole coral reef fish assemblages remains largely unknown.

To reveal how predation influences fishes on coral reefs our goal is to assess the relationship between body size, experience, and mortality rates in coral reef fishes using a meta-analysis of published evidence. The results of this analysis will identify any marked differences in mortality rates between naive recruits and experienced small fishes, and also reveal any overarching patterns in the relationship between predation rates and prey fish size. By exploring the impact of predation-based mortality on fishes across different sizes and growth stages these results will allow a greater understanding of the processes controlling populations and energy transfer on coral reefs.

2. Material and methods

A meta-analysis was conducted to assess the effect of body size on mortality rates of coral reef fishes. Publications were chosen which provided estimates of natural mortality rates (whether based on growth calculations or observational data), focusing on those papers which gave size estimates of the fishes for which mortality rates were estimated. For three studies of adult individuals where sizes were not specified, we used 50% of L_{∞} if provided in the same study, or 50% of published maximum lengths [40,41]. Where multiple models were used to calculate mortality rates, we included all published rates. In total, 322 data points, for 156 species were collected from 25 published sources (electronic supplementary material, table S1).

We defined naive fishes (new recruits) as those individuals that were within 48 h of settlement. This time was chosen following numerous studies which have revealed considerable changes in the mortality rates of fishes within this time period [33,37,42,43]. To assess whether the relationship between mortality rates and body size differed between naive recruits (less than 48 h after settlement) and experienced fishes (experienced juveniles and small adults; e.g. gobies and other cryptobenthic reef fishes [27]) we applied a two-way beta regression model with body size (total length) and experience as factors. This analysis was selected as it best accounted for the proportional and heteroscedastic nature of the data. To prevent any bias from differences in sample sizes and body sizes between naive and experienced fishes, we conducted the analyses on fishes with total lengths equal to, or smaller than, the largest naive recruit in the dataset (54 mm TL).

To assess the relationship between mortality rates and body size for the experienced fishes only, and to identify any transitions in this relationship, we conducted a segmental linear regression leaving x_0 (the break between segments) unconstrained, to allow the model to determine the most robust split. To conduct this analysis, we used a robust regression approach with outlier removal (with $Q = 1\%$) following [44].

Finally, a series of analyses were conducted to determine whether the observed relationships are robust to taxonomic differences across the size range of study organisms. To look for family effects, a multidimensional scaling (MDS) plot was

Figure 1. The relationship between body size (TL) and mortality rates ($\% \text{ day}^{-1}$) for 322 individual estimates from 156 coral reef fish species. Red points represent naive coral reef fishes (less than 48 h post-settlement), while blue points represent experienced fishes (more than 48 h post-settlement). The overall relationship appears to follow an exponential decline ($r^2 = 0.36$). (Online version in colour.)

created, followed by a two-way permutational analysis of variance (PERMANOVA) using size/experience category (naive, small experienced, and large fishes) and family as factors. Both multidimensional analyses were based on a Bray–Curtis matrix of untransformed data, using the size and mortality rates of fishes as variables. Vectors were plotted using multiple correlations in the software PRIMER 7, PERMANOVA+. These analyses were designed as a post hoc test to examine the findings of the previous univariate analyses and to test for differences in the relationships between the factors among families. To account for the impact of differences in body size and sample sizes among families, the mean mortality rates and mean total lengths of each family were also calculated and plotted as per the initial individual-based analyses. Finally, for those four families with sufficient data in both small experienced and large individual categories, segmental linear regressions were conducted. This enabled us to compare the relationships within families to the overall relationship established among all individuals.

3. Results

Mortality rates in coral reef fishes appeared to decline exponentially with increasing body size (figure 1). However, on closer examination, there is relatively high variance associated with the overall relationship ($r^2 = 0.36$). The underlying nature of the relationship can be better understood by dividing the relationship into three phases. The first phase appears to be restricted to the period shortly after recruitment. In the smallest fishes, i.e. those below 54 mm TL (the maximum size of a naive fish), there was a clear separation between the mortality rates in naive recruits and in more experienced fishes (i.e. fishes settled for more than 48 h, cf. [37]; figure 2a). The beta regression model revealed that the relationships between mortality and length differed between naive recruits and experienced small fishes (Pseudo- $r^2 = 0.75$, length $\times$ experience interaction: $z = 5.65$, $p \leq 0.0001$; electronic supplementary material, table S2). Naive recruits had considerably higher mortality

Figure 2. (a) The results of a two-way beta regression model revealed differences in the relationship between body size (TL) and mortality rates in naive recruits (red points and upper trend line) in phase one, and experienced fishes of comparable size (less than or equal to 54 mm TL; blue points and lower trend line; model interaction term $p < 0.0001$; electronic supplementary material, table S2). (b) During phase two, experienced fishes display a rapid decline in mortality rates with increasing size (solid blue points; slope = -0.10). An unconstrained segmental linear regression ($r^2 = 0.80$) identified the transition to phase three (open blue points) at $x_0 = 43.12 \pm 0.66$ mm. (Online version in colour.)

rates than experienced fishes at all sizes. The predicted daily mortality rates in naive recruits varied considerably, however, they were on average $30\% \text{ day}^{-1}$; approximately 20 times higher than in similarly sized experienced fishes ($1.5\% \text{ day}^{-1}$). Furthermore, naive recruits displayed a slight positive relationship between size and mortality rates (however, this did not differ from 0 in a linear regression; $p = 0.30$), while the mortality rates of experienced fishes reduced rapidly with increasing size (figure 2).

When considering experienced fishes only, we see an initial rapid decline in mortality rates with increasing size (figure 2b). The unconstrained segmental linear regression offered a good explanation of the observed patterns ($r^2 = 0.80$) and identified a change in the rate of decline at $x_0 = 43.12 \pm 0.66$ mm ($\pm$ standard error (s.e.)). The second phase of mortality relates to fishes smaller than this threshold, which display rapidly decreasing mortality rates (slope = -0.10), from a y -intercept of $4.69 \pm 0.16\%$ ($\pm$ s.e.) mortality per day, down to just 0.20% per day at x_0 (43.12 mm). Assuming that populations are stable and consistently recover following predation, and that predation pressure is constant (i.e. estimating lifespans using the formula: $\text{lifespan}_{[\text{days}]} = 100 \div \text{daily mortality}_{[\%]}$), this difference in mortality rates equates to an 11.10 day increase in lifespan for every millimetre increase in length. Phase three of the relationship is beyond this size threshold of 43.12 mm. The slope is much shallower (-0.0003) but still

exhibits a negative relationship, with mortality rates slowly decreasing with increasing body length ($p < 0.0001$).

The MDS supports these findings, clearly identifying separations among the three size/experience categories (electronic supplementary material, figure S1). However, the PERMANOVA identified a significant interaction between size/experience (naive, small experienced, and large fishes) and families (Pseudo- $F_{10,286} = 5.22$, $p_{(\text{perm})} = 0.001$). This interaction was probably driven by the general relationship between size and mortality rates, but it may also be affected by different families occupying different size ranges. To correct for this potential family-level taxonomic bias, we plotted the mean sizes and mean mortality rates ($\pm$ s.e.) of each family for naive fishes, then for 'small experienced' and 'large' fishes combined (electronic supplementary material, figure S2); both plots revealed strikingly similar patterns to those seen in the overall analyses (cf. figure 2), but x_0 , the threshold between phases two and three was larger, at 91.51 ± 13.62 mm. For those families with multiple individuals in both the 'small experienced' and 'large' size categories, we found remarkably similar patterns within families to those seen in the overall analysis, with x_0 values ranging from 30.35 ± 3.53 mm in the Gobiidae to 43.02 ± 0.29 mm in the Apogonidae (electronic supplementary material, table S3; cf. 43.12 ± 0.66 mm for the general relationship).

4. Discussion

Both size and experience appear to be critical factors in determining the mortality rates of coral reef fishes. The results of our meta-analysis indicated that coral reef fishes display a three-phase relationship between body size and mortality rates. Naive recruits, small experienced fishes, and large experienced fishes display markedly different relationships between body size and mortality rates.

Shortly after settlement, naive recruits are exceptionally prone to predation, with the largest recruiting fishes suffering particularly high mortality rates of over 60% per day. While the susceptibility of naive recruits has been well studied [33,45,46], this phase in the mortality of coral reef fishes lasts for only a very short time. With such high predation pressure fishes that lack the traits and abilities to avoid predation are unlikely to survive.

There is a considerable body of literature on the behavioural and physiological traits that facilitate survivorship in small coral reef fishes. Variation in personality traits (e.g. boldness) or physiological traits (e.g. sensory abilities) can be of considerable importance in determining susceptibility to predation [46–49]. Likewise, associative learning, where fishes associate a conspecific's predation with the predator responsible using visual or olfactory cues, can allow fishes to rapidly identify multiple predators, and thus reduce the predation risk of an individual [34,35,50–52]. Learning appears to benefit fishes quickly [37]. After only a day or two, the remaining fishes—which may be just a fraction of those originally settling—have learned to identify and respond to the presence of predators. On successfully running, this predation gauntlet (*sensu* [33]) it appears that gaining further experience, while possible [53], is of less importance. On entering phase two, the most important aspect relating to a fish's mortality appears to be its size.

While mortality rates of small experienced fishes may be considerably lower than their naive predecessors, their life expectancies are still relatively short, with mortality rates in

the region of 3–8% per day [18,39,54,55]. Remarkably, these small fishes are the most abundant size class on coral reefs [27]. Reef fishes have a mean length of just 45 mm and approximately half of all reef fishes may remain under this size threshold for their entire lives [27,38]. Growth appears to be critical for fishes in this mortality regime. Each millimetre of growth may potentially result in a significant increase in life expectancy. Our simple calculations suggested that for fishes smaller than 43.1 mm TL, a 1 mm increase in length is roughly equivalent to an 11.1 day increase in life expectancy. While these calculations may be affected by pulses in recruitment, e.g. [42,56] and density-dependent mortality effects [45,57], small fish communities are often remarkably stable [58–61] with the dominant species on coral reefs (e.g. gobies, acanthurids, chaetodontids [27,42]) often displaying continual recruitment [56]. Regardless, these results clearly reveal the importance of growth for small fishes. This imperative to grow to avoid predation pressure highlights the potential role of mesopredators on coral reefs [62–64] and supports the findings of previous studies that have identified the importance of cryptobenthic fishes in underpinning productivity in coral reef ecosystems through growth [17,65].

The final phase in the relationship between mortality and body length, phase three, lies beyond a size threshold. Surprisingly, this threshold appears very small, at just 43.1 mm TL (with similar thresholds in single family analyses). Above this length, the mortality rate experienced by fishes is low (less than 0.2% day⁻¹) and changes little with increased size. Indeed, compared with small experienced fishes, the decrease in mortality rate per millimetre increase in body size is almost seven times lower. While predation still has effects on the behaviour and mortality of larger reef fishes [66,67], its role appears to be less important in structuring communities [68,69]. Smaller predators, preying upon small (and in particular, naive) prey may be the key force structuring coral reef fish communities [70]. While there is continual pressure to grow to avoid predation, it may be that larger sizes in fishes above 43.1 mm provide other advantages including reproductive benefits [71–73], and allow the exploitation of niches unavailable to smaller organisms, whether through strength benefits in prey handling [74–78], other physiological benefits such as swimming ability permitting larger home ranges [11,12,15], or even endothermy [79]. These patterns mirror those seen in savannah dwelling ungulates, which above body masses of 150 kg cease to be controlled by predator populations and start to become limited by food availability. Remarkably for fishes, the size at which we see this response is exceptionally small.

Given that more than half of the fishes on coral reefs live their entire lives below the 43.1 mm threshold, it appears that there must be a strong evolutionary incentive to remain small, even in the face of the increased risk of mortality [18,33] which may be further intensified by density-dependent mortality [57]. There are a range of potential explanations. Small fishes can reproduce quickly [10], have relatively low energy requirements [17], abundant food resources (e.g. crustaceans and detritus [38,80,81]), and shelter [19,82], and

lower chances of detection by predators [83,84]. The abundance of small fishes on coral reefs clearly highlights that mortality is just one component of a complex set of life-history trade-offs which shape body size–abundance relationships [5,85].

The three phases in the individual level relationship were mirrored in a family-level analysis (to allow for the impact of family-level size differences), and even within individual families. Clear transitions between phases two and three were revealed in the Gobiidae and Apogonidae, both abundant small-bodied reef fish families [27,38]. While only a small number of families occupied size ranges in both the ‘small experienced’ and ‘large’ size categories (necessary to conduct within family assessments) it would be valuable to conduct further studies of fishes that span these size ranges as they may reveal important ecological information about the drivers of body size in coral reef fishes.

While the patterns remained in the relationship between body size and mortality rates, there was some variation in the size threshold between phases two and three. In the family-level analysis, the threshold was 91.5 mm TL, whereas within families it was as small as 30.4 mm (Gobiidae). This variation in the thresholds between phases two and three is likely the result of differences in factors other than body size among and within families. Likely factors include prey biology (e.g. body shape, behaviour, etc.) and predator responses, such as the development of specific prey search images and/or density-dependent prey selection [86] (but see [87]). While some variation was observed, the results of the inter- and intra-familial analyses strongly support the patterns seen in the individual relationship and highlight the importance of body size in determining the mortality rates of coral reef fishes.

The three-phase relationship between body size and mortality rates in coral reef fishes emphasizes the importance of experience in shaping the early lives of fishes. Subsequently, size-dependent variation in predation may shape future energy allocations and life-history strategies of fishes. Once post-settlement fishes have learned to identify predators, growth is critical to avoid predation. Surprisingly, half of all reef fish individuals remain in this vulnerable phase two throughout their entire lives. This factor probably underlies the high productivity of cryptobenthic fish communities, driving the fast growth rates that fuel ecosystem processes [38]. By shaping population sizes and energetic and trophic connectivity in coral reef fishes, the relationship between body size and mortality rate appears to be a key factor in our understanding of the ecology of coral reef fishes.

Data accessibility. Supporting data for this manuscript are available in the electronic supplementary material, table S1.

Authors' contributions. C.H.R.G. and D.R.B. conceived the study, C.H.R.G. analysed the data, C.H.R.G. and D.R.B. wrote the manuscript.

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