Article type : Articles

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Bottom-up processes mediated by social systems drive demographic traits of coral-reef fishes

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Type of article: Article

Abstract. Ectotherms exhibit considerable plasticity in their life-history traits. This plasticity can reflect variability in environmental and social factors, but the causes of observed patterns are often obscured with increasing spatial scales. We surveyed dichromatic parrotfishes across the northern Great Barrier Reef to examine variation in body size distributions and concomitant size at sex change ($L_{\Delta 50}$) against hypotheses of directional influence from biotic and abiotic factors known to affect demography. By integrating top-down, horizontal, and bottom-up processes, we demonstrate a strong association between exposure regimes (which are known to influence nutritional ecology and mating systems) and both body size distribution and $L_{\Delta 50}$ (median length at female-to-male sex change), with an accompanying lack of strong empirical support for other biotic drivers previously hypothesized to affect body size distributions. Across sites, body size was predictably linked to variation in temperature and productivity, but the strongest predictor was whether subpopulations occurred at sheltered mid and inner shelf reefs or at wave-exposed outer shelf reef systems. Upon accounting for the underlying influence of body size distribution, this habitat-exposure gradient was highly associated with further $L_{\Delta 50}$ variation across species, demonstrating that differences in mating systems across exposure gradients affect the timing of sex change beyond variation concomitant with differing overall body sizes. We posit that exposure-driven differences in habitat disturbance regimes have marked effects on the nutritional ecology of parrotfishes, leading to size-related variation in mating systems, which underpin the observed patterns. Our results call for better integration of life-history, social factors, and ecosystem processes to foster an improved understanding of complex ecosystems such as coral reefs.

Keywords: life-history variation, reaction norm, sex allocation, resource variability, parrotfishes, structural equation model, sex change

INTRODUCTION

Phenotypic traits in organisms often show considerable variability across space or time, representing adaptive responses to changes in the surrounding environment (Fagen 1987). The response capacity of a genotype to external conditions, manifested as phenotypic plasticity, allows individuals or populations to persist within a range of environments by optimizing regional fitness to maximize survival (Bradshaw 1965, Schichting and Pagliucci 1998). The resulting patterns of phenotypic variability can be measured as reaction norms across environmental or anthropogenic gradients and are observed across a variety of spatial and temporal scales (Schmalhausen 1949, Schlichting and Pigliucci 1998). A species' inherent capacity to adapt to local conditions by altering its physiological rates helps explain species-specific distributions on both regional (10–100s km) and biogeographic scales (1000s km) and can facilitate predictions of population and ecosystem dynamics under changing environmental conditions (Munday et al. 2008). Life-history traits, such as growth rate or age at maturity, are the embodiment of physiological processes in organisms. Understanding how and why such traits vary provides a link between ecological and evolutionary mechanisms, their response to prevailing biotic and environmental conditions, and biogeochemical pathways within ecosystems (Warner 1991, Agrawal 2001, Hutchings 2011). Thus, examination of trait variability can provide a powerful path to understanding spatio-temporal variation in fundamental ecosystem processes.

Sex allocation theory (Charnov 1982) provides a framework for understanding the advantage of resource distribution among males and females in a population. Stemming from this framework, the size-advantage hypothesis (Ghiselin 1969) predicts that protogynous hermaphroditism will be favored when size-mediated reproductive value increases at a greater rate in males than females (Warner 1975), with the male-female intercept of reproductive value representing the optimal size at which to change sex in a population. Hence, within a species, variability in the size of sex change is strongly linked to extant body size distributions (Allsop and West 2003, Gardner et al. 2005), but is also influenced by social factors such as mating system. Features of the surrounding environment can affect population dynamics within a species, leading to alternative mating behaviors across space (Henson and Warner 1997). These alternative mating behaviors, such as territorial haremic behaviors versus group spawning, can modify the reproductive values of males and females across size or age classes within a species (Warner 1975), thus influencing the timing of sex change or even the decision of whether to change sex. However, because of the interrelated nature of life-history processes, teasing apart the factors regulating such processes is challenging (Schaffer 2004). Accomplishing this in a holistic manner requires a study system spanning a spatial scale encompassing a broad spectrum of environmental variability.

Coral reefs represent one of the most diverse and dynamic ecosystems on Earth. Coral reef fishes are known to display a wide range of social and reproductive systems and are subject to a multitude of environmental and biological factors, including small-scale variability in water quality, wave exposure, ambient temperature, habitat complexity, resource availability, competitive interactions, and lethal and sub-lethal effects of predation (Sale 2002, Mora 2015). A substantial body of literature suggests that these factors yield adaptive responses in life-history traits such as growth rate, body size, mortality, life span, and reproductive dynamics (Warner and Hoffman 1980, Robertson et al. 2005, Ruttenberg et al. 2005, Munday et al. 2006, Taylor 2014). To date, one of the most conspicuous and consistent patterns of variation in life-history traits has been observed over small scales (≤ 20 km) between sheltered and exposed reefs on a longitudinal gradient (Gust et al. 2002, Gust 2004). This pattern revealed higher mortality, smaller size-at-age, shorter life spans, earlier reproductive development, and greater proportions of initial phase primary males (a male alternative reproductive behavior determined prematurationally and with implications to the mating system) on exposed outer shelf reefs versus the sheltered mid shelf reefs, and this outcome was linked to differences in competition and predation. These patterns provided a rationale for identifying biotic top-down and horizontal processes as primary drivers of demographic variation (Gust et al. 2002). However, reef ecosystems are also subject to markedly different environmental conditions at large spatial scales. This variation is reflected in differing patterns of reef configuration, hydrodynamics, or history and frequency of disturbance, and is especially relevant to reef systems that span latitudinal gradients sufficient to reflect changes in sea surface temperature. Yet, the relative extent to which biological factors are pertinent drivers of demography over a gradient extensive enough to reflect geographic-scale environmental variation is unknown.

Scaling up analyses of life-history features to allow investigation over an appropriate geographic scale is important to investigate the extent to which small- and broad-scale processes contribute to the demographic patterns we find today. We examine drivers of trait variability using a multi-scale design across 6° of latitude spanning the northern half of the Australian Great

Barrier Reef (GBR). This system includes significant environmental variation on both longitudinal (wave exposure gradient of 40–100 km) and latitudinal (≤1000 km) axes. In recognizing that various environmental and biotic factors in complex natural systems are interdependent and hierarchically structured, we use a structural equation modelling framework to test hypothesized pathways that yield striking differences in body size distributions observed between shelf environments. We then focus on variability in the relationship between body size and length of female-to-male sex change in parrotfishes, traits that are heavily linked to physiological processes of growth and maturity, as well as with social demography and surrounding environment (Shapiro 1991). By examining covariance among environmental gradients and reaction norms of trait variability, the present study represents the first rigorous holistic test of multiple, hierarchical drivers of life-history variation in reef fishes in the absence of direct human exploitation on the study species.

METHODS

We surveyed 82 sites within 31 reefs along 6° of latitude on the northern GBR, Australia (Fig. 1A), where parrotfishes are not exploited by humans. Surveys were conducted during Sep-Oct 2014, using diver-operated stereo-video along 40-min timed swims (5 m wide), with a towed GPS on a surface buoy showing an average speed of 20.3 m min^{-1} (±3.98 m min^{-1} S.D.). Surveys were conducted on the outer reef slopes at 6–10 m depth and were stratified across two shelf positions (exposed and sheltered) and three management zones (no entry, no fishing, and fishing allowed; Appendix S1: Table S1). All surveys were conducted on seaward (east-facing) reef slopes of sheltered (inner and mid shelf) and exposed (outer shelf) reefs. Parrotfish surveyed by stereo-video were measured to the nearest mm fork length and recorded by color phase (initial or terminal phase) using the EventMeasure software (seagis.com.au). A second diver visually surveyed all sharks, carangids, and other large mobile piscivores along a wider transect (20 m wide), and lengths and abundances of smaller predators were determined from video analysis.

We estimated the median length at female-to-male sex change ($L_{\Delta 50}$) by site of the four most common parrotfish species with dichromatic coloration on video surveys (*Chlorurus spilurus*, *Scarus frenatus*, *S. psittacus*, and *S. schlegeli*) at both exposed and sheltered habitats (Fig. 1B). Either a logistic model (see *Data Analysis* section) fitted to relative proportions of initial and terminal phase individuals across the various length classes, or the midpoint between the largest initial phase and smallest terminal phase individual (when lengths of color phases did not overlap) was used to estimate $L_{\Delta 50}$ by species and site. The use of color phase is a highly robust proxy for estimating functional sex change in parrotfishes, and the potentially confounding presence of initial phase primary males has a minor effect on $L_{\Delta 50}$ estimates (Taylor 2014). We further estimated a proxy to represent the high-range of the length frequency distribution for each species by site using the 95th quantile of length (L_{max}). This approach provided a 'buffered' estimate of maximum length because actual observed maximum length can vary by breadth of exposure to the population.

Environmental data

We measured a range of environmental factors known or hypothesized to influence life-history variation either directly or indirectly (Appendix S1: Table S2). Species-specific densities (individuals ha^{-1}) were estimated from standardized video surveys and represented the intensity of intraspecific competition. Species richness was treated as the total number of parrotfish species observed at a site and was highly correlated with more complex diversity measures. Predator biomass (as a proxy for the prevailing level of predation) represented the mean biomass density of all species (using appropriate size classes) known or highly suspected to prey upon parrotfish species based on an exhaustive literature search regarding diets and length-weight ratios of piscivores surveyed. Reef area (in hectares), reef slope (0–90°; mean of ten measurements per site from random video frames), habitat rugosity, and coral cover (1–5 scale; mean of ten estimates per site from random video frames) were measured to represent potential features of the environment influencing carrying capacity or spawning dynamics across reefs. Metabolic rates of ectothermic primary consumers are also influenced by sea surface temperature (SST) and primary production; hence, we acquired remotely-sensed SST as well as chlorophyll-A (Chl-A) data as a proxy for benthic productivity (Appendix S1: Table S2). Importantly, while satellite-derived SST can be a high-quality reflection of ambient SST (Kilpatrick et al. 2015), the relationship between satellite-derived pelagic Chl-A and benthic productivity can be highly tenuous (Gove et al. 2013), especially for complex ecosystems such as the GBR. However, the relative differences in estimated productivity values across regions and shelf positions were broadly similar to those of *in-situ* measurements of chlorophyll sampling stations across geographically comparable locations of the GBR (Brodie et al. 2007). Nevertheless, with such a coarse measure of primary productivity, the relative effects here should be interpreted with caution.

A primary determinant of sex change dynamics is the prevailing type of mating system. While it was not feasible to collect empirical data on mating systems across the scale of the study, Gust (2004) found pronounced differences in the reproductive biology of *C. spilurus* populations, implying sheltered populations had almost exclusively haremic territorial systems, whereas territoriality was less pronounced (suggesting increased rates of group spawning) at exposed outer shelf reefs. In the absence of this information for our sites, we used shelf position to represent variation in exposure as well as a proxy for concomitant differences in mating systems, as it relates to timing of sex change.

Data Analysis

We first examined the consistency and ubiquity of trends in $L_{\Delta 50}$ across exposure levels. Relative proportions of initial and terminal phase individuals across length classes were pooled by exposure regimes and fitted with logistic models for each species following $P_L = \{1 + e^{-\ln(19)(L-L_{\Delta50})/(L_{\Delta95}-L_{\Delta50})}\}^{-1}$, where P_L is the estimated proportion of terminal phase individuals at a given length (L), 19 represents the number of breakpoints to the 95th quantile in a cumulative density function (19/20 = 0.95; Haddon 2001), and $L_{\Delta50}$ and $L_{\Delta95}$ are the length at 50% and 95% sex change, respectively. We generated corresponding 95% confidence ellipses surrounding $L_{\Delta50}$ and $L_{\Delta95}$ estimates for comparison by bootstrap resampling through 1000 iterations.

We then devised an integrated set of hypotheses to explain patterns in L_{max} (penultimate response variable) and $L_{\Delta 50}$ (ultimate response variable) across all sites surveyed in the study (Fig. 1C). We included three exogenous variables (*Shelf position* [ordinal; 0 = sheltered, 1 = exposed], *Protection zone* [ordinal; 0 = fishing allowed, 1 = no fishing zone, 2 = no-entry zone)], and *Latitude* [absolute degrees latitude South]) and nine endogenous variables (Sea Surface Temperature [*SST*], *Productivity* [Chl-A], *Coral cover*, *Rugosity*, *Predator biomass*, *Intraspecific density*, *Species richness* [of parrotfish], L_{max}, and $L_{\Delta 50}$). Habitat variables *Coral cover*, *Rugosity*, *Reef area*, and *Slope* were assessed independently before full model construction and non-significant variables *Reef area* and *Slope* were eliminated to avoid over-parameterization of the resultant models and to improve clarity of the path diagram. We analyzed all specified paths as linked equations using a structural equation modeling approach (SEM) based on d-separation tests (Shipley 2009), which permits the rigorous quantification of indirect effects in a causal network and provides an overall goodness-of-fit measure for an *a priori* model through the statistical evaluation of a series of independence claims. Given the hierarchical nature of our data, we used a piecewise SEM approach (Lefcheck 2015), which allows the specification of models that can accommodate random effects. We formulated the following linkages: 1) *Productivity* and *SST* are affected by *Shelf position* and *Latitude* and are subject to unquantified common sources of variation (requiring the inclusion of a correlated error structure between *Productivity* and *SST*); 2) *Coral cover* is affected by *Shelf position*, *Productivity*, and *SST*; 3) *Rugosity* is affected by *Shelf position, Coral cover*, and *Latitude*; 4) *Predator biomass* is affected by *Protection zone*, *Latitude*, and *Shelf position*; 5) *Species richness* is affected by *Coral cover*, *Rugosity*, *Latitude*, and *SST*; 6) *Intraspecific density* is affected by *Productivity*, *Species richness*, *Latitude*, *Coral cover*, *Rugosity*, and *Shelf position*; 7) L_{max} is affected by *Shelf Position*, *Latitude*, *SST*, *Productivity*, *Intraspecific density*, *Rugosity*, and *Predator biomass*; and 8) $L_{\Delta 50}$ is affected by *Shelf position* (interpreted here as alternative mating systems), L_{max}, *Predator biomass*, *Intraspecific density*, and *Rugosity*. For models 1) through 5), a random intercept was specified for each surveyed reef. For models 6), 7), and 8) (which included species-specific estimates of density, L_{max}, and $L_{\Delta 50}$), the random intercept for reefs was nested within species. Estimates of L_{max} and $L_{\Delta 50}$ for all species were scaled and centered prior to the analyses to eliminate biases linked to differences in body size among species, while *Latitude*, *SST*, *Predator biomass*, *Species richness*, and *Intraspecific density* were log-transformed to satisfy assumptions of normality and homogeneity of variance. The goodness-of-fit of the devised model was evaluated using Fisher's C statistic on the cumulative results of the d-separation tests (Shipley 2009). Model coefficients were standardized by their mean and variance to facilitate comparison. For all significant pathways (and all pathways leading into L_{max} and $L_{\Delta 50}$), we visualized relationships using partial regression plots. In addition, goodness-of-fit values (R^2) were extracted for each component model. Homogeneity of variance was visually verified for each component model using residual plots. All analyses were performed using R version 3.2.3.

RESULTS

Across 82 sites spanning the northern GBR, the median fork length at sex change ($L_{\Delta 50}$) ranged from 165 to 266 mm for *C. spilurus*, 181 to 313 mm for *S. frenatus*, 166 to 245 mm for *S. psittacus*, and 156 to 332 mm for *S. schlegeli*. All four species had larger collective $L_{\Delta 50}$ values at sheltered versus exposed reefs (Fig. 1). This difference was highly pronounced for *C. spilurus* and *S. frenatus*, resulting in non-overlapping 95% confidence ellipses surrounding sex change parameters, while a similar suggestive trend for *S. psittacus* and *S. schlegeli* was present (Appendix S1; Fig. S1).

In the structural equation model (SEM), *Shelf position*, *Latitude*, *SST*, *Rugosity*, and *Productivity* exhibited significant effects on L_{max} (Fig. 2; Appendix S1: Figure S2), with more sheltered reefs, lower *Latitude*, lower *SST*, lower *Rugosity,* and higher *Productivity* associated with larger body size distributions (*standardized parameter estimate: Exposed* = -1.212 ± 0.184 SE; $P < 0.0001$; Fig. 2I; *Latitude* = -0.365 ± 0.118 SE; $P = 0.0029$; Fig. 2J; *SST* = -0.315 ± 0.123 SE; $P = 0.0126$; *Rugosity* = -0.0172 ± 0.072 SE; $P = 0.0189$; *Productivity* = 0.169 ± 0.075 SE; $P = 0.0271$). The negative relationship between L_{max} and *Latitude* was unpredicted, but appears to be an artefact of the spatial distribution of sheltered and exposed sites in our survey. In contrast, *Intraspecific density* and *Predator biomass* had no effect on L_{max}. As predicted, $L_{\Delta 50}$ was significantly and positively associated with L_{max} (L_{max} = 0.392 ± 0.065 SE; $P < 0.0001$; Fig. 2K), but was most strongly associated with *Shelf position* (*Exposed* = -0.875 ± 0.156; $P < 0.0001$; Fig. 2L). This result suggests that a large portion of the influence of *Shelf position* on $L_{\Delta 50}$ was not transferred through shelf-associated differences in body size distribution, but instead directly and independently related to shelf-associated alternative mating systems. No other factors included in the model significantly affected estimates of $L_{\Delta 50}$ across sites (Appendix S1: Figure S2). The marginal model fit for the L_{max}-model was 0.352 (*marginal* R^2), while the conditional model fit was 0.556 (*conditional* R^2). For the $L_{\Delta 50}$-model, these values were 0.522 (*marginal* R^2) and 0.556 (*conditional* R^2). Other significant pathways in the model included an effect of *Shelf position* and *Latitude* on *SST* (*Exposed* = -0.608 ± 0.255 SE; $P = 0.0241$; *Latitude* = -0.709 ± 0.118 SE; $P < 0.0001$; Fig. 2A; Appendix S1: Figure S2), an effect of *Protection zone, Shelf position*, and *Latitude* on *Predator biomass* (*No-entry* = 0.559 ± 0.140 SE; $P = 0.0001$; *Exposed* = 0.824 ± 0.171 SE; $P = 0.0001$; *Latitude* = -0.166 ± 0.078 SE; $P = 0.0348$; Fig. 2B-C; Appendix S1: Figure S2), an effect of *Species richness* and *Latitude* on *Intraspecific density* (*Species richness* = 0.218 ± 0.068 SE; $P = 0.0022$; *Latitude* = 0.293 ± 0.091 SE; $P = 0.0020$; Fig. 2D-E), an effect of *SST* and *Shelf position* on *Coral cover* (*SST* = 0.384 ± 0.147 SE; P = 0.0102; *Exposed* = 0.738 ± 0.347 SE; P = 0.0426; Appendix S1: Figure S2), an effect of *Coral cover*, *Latitude*, and *Shelf position* on *Rugosity* (*Coral cover* = 0.631 ± 0.080 SE; $P < 0.0001$; *Latitude* = 0.527 ± 0.095 SE; $P < 0.0001$; *Exposed* = -0.978 ± 0.200 SE; $P < 0.0001$; Fig. 2F-H), and contrasting effects of *Coral cover* and *Rugosity* on *Species richness* (*Coral cover* = 0.203 ± 0.100 SE; P = 0.0455; *Rugosity* = -0.173 ± 0.082 SE; P = 0.0367; Appendix S1: Figure S2).

Overall, results of the SEM supported the *a priori* specified pathways. Specifically, Fisher's C statistic revealed that p-values obtained through d-separation tests of independence claims were likely to occur by chance ($C = 63.93$, $df = 54$, $P = 0.167$), suggesting no important pathways among the specified variables were omitted from the hypothesized model. Summaries of the coefficients and component model fits are provided in Appendix S1: Tables S3-4.

The interplay between *Shelf position*, L_{max}, and $L_{\Delta 50}$ is visualized in Fig. 3. Linear regressions between L_{max} and $L_{\Delta 50}$ demonstrate, as predicted, a positive relationship between these factors. However, the residuals of this relationship are separated by *Shelf position* for all four species, whereby sex change occurs on average at larger than expected body sizes (relative to underlying body size distributions) at sheltered sites. This pattern was highly pronounced for *C. spilurus* and *S. frenatus*, but less conclusive for the more data-limited species *S. psittacus* and *S. schlegeli*.

DISCUSSION

Despite a number of causal links between shelf position and biophysical factors, our results demonstrate the overwhelming significance and generality of shelf position mediating parrotfish body size and associated length at sex change. This conclusion is accompanied by a lack of direct support for the roles of some previously hypothesized biotic interactions, specifically predator-induced mortality estimated as predator biomass (DeMartini et al. 2005, 2008, Hall and Kingsford 2016) and intraspecific competition estimated as density (Gust 2004), in driving variation in body size distributions. The timing of sex change is heavily influenced by features of the social system (Ross 1990), and our results demonstrate that length at sex change is linked to local size distribution. However, for at least two of our study species, an additional directional response in $L_{\Delta 50}$ beyond that explained by underlying size distributions was linked with a common source of variation associated with exposure regime alone, presumably consistent with alternative mating systems between shelf positions. Below, we frame our interpretations of these observed spatial patterns of trait variation in light of nutritional ecology, sex allocation theory, and mating systems across complex and variable ecosystems.

Drivers of parrotfish size distributions

Our results suggest that parrotfish body size distributions are weakly influenced by ambient temperature and productivity, but are highly influenced by biophysical features associated with shelf positions along the northern GBR. Temperature and productivity (estimates of food quality and availability) are strongly linked to metabolic processes in ectotherms (Atkinson 1994, Anguilleta et al. 2004). In contrast, underlying drivers of variation between exposed and sheltered reefs remain much less clear and, to date, have not been explicitly linked to changes in reef fish life-history traits. A major difference between these systems is the intensity of perpetual hydrodynamic forces that influence benthic structure (Done 1982). Parrotfishes are nutritionally reliant on benthic resources; specifically, they target endolithic and epilithic microbes, and, to a lesser extent, detrital material (Clements et al. 2017). There is evidence that the distribution and productivity of such nutritional resources varies along exposure gradients (Crossman et al. 2001, Tribollet and Golubic 2005, Tribollet 2008), with epilithic resources increasing in sheltered environments and endolithic resources increasing in exposed environments. This variation likely facilitates different growth rates and resultant size distributions of the consumers who differentially target both resources. Further refinement of productivity estimates beyond satellite-derived Chl-A may strengthen the link between shelf position, benthic productivity, and body size distributions. Gust et al. (2002), while examining life-history traits of fishes from an overlapping subset of the reefs surveyed here, demonstrated a general pattern of faster initial growth leading to larger body sizes at sheltered mid shelf reefs for three parrotfishes (including *C. spilurus* and *S. frenatus*) and a surgeonfish. Further, higher adult mortality rates were linked to shorter life spans on the exposed outer shelf reefs.

The consistent shelf-related variability in body size and concomitant life-history traits observed by Gust et al. (2002) and Gust (2004) was attributed to differences in food levels, predation rates, and [intraspecific] competition, all of which contribute to mortality rates. We extended the scope across a greater diversity of environments spanning the northern half of the GBR, and, based on our holistic analytical framework, posit that, among these variables, resource distribution and quality across exposure gradients have by far the greatest effect, while the previously reported effects of predation and competition are likely by-products of the observed variation. Food availability is often a limiting factor in animal growth and has produced similar demographic differences in a variety of marine and terrestrial ectotherms (e.g., Clifton 1995, Hjelm et al. 2000, Madsen and Shine 2000), including reef fishes (Bonin et al. 2015), sometimes over small spatial scales. We found no relationship in our model between intraspecific density and body size distributions within or across shelf positions, suggesting that competition was not a major factor. We recognize that this analysis was not corrected for underlying resource levels and acknowledge that competition may be demographically important. However, our results suggest it is not the primary driver of the demographic variation observed. We also found no relationship between predator biomass and body size distributions. This result implies either (1) that variation in predation-induced mortality does not account for observed demographic variation or (2) that predator biomass may not be an appropriate indicator of predator-induced mortality in the study system. Greater adult mortality rates observed on exposed reefs (Gust et al. 2002) correspond with life-history theory predicting greater reproductive allocation associated with shorter life spans (Stearns 1976). It is not entirely clear whether the source of greater mortality on exposed shelves is extrinsic (e.g., predation) or intrinsic (i.e., linked to rate of metabolic processes; see Brown et al. 2004), but our results suggest the latter.

The effect of size distributions and mating systems on length at sex change

A defining feature of social control is that the length at sex change tends to be a function of the local size distribution (Warner 1984). This pattern was demonstrated in the present study, but for at least two species there was remarkable additional variation (after normalizing for underlying size distribution) associated with shelf position. This result suggests that changes in social demography associated with different environments elicits further control on sexual selection (Warner and Hoffman 1980). Gust (2004) found large differences in the proportion of initial phase primary males between mid and outer shelf populations of *C. spilurus* (i.e., more initial phase males at outer shelf reefs). This pattern strongly implies that haremic territoriality among males was the predominant mating system at sheltered mid shelf reefs where primary males were rare, and that group spawning emerged to some degree at exposed outer shelf reefs.

Such changes in mating strategies can influence the size-related reproductive value of males (Warner 1984), and potentially explains the differences we observe after correcting for underlying body size distributions between exposure regimes. For example, conceptual application of the size-advantage hypothesis implies that, if male and female reproductive values are stable, the shifts in body size distribution observed between habitats would yield proportional shifts in $L_{\Delta 50}$ (orange arrow in Fig. 4a). However, if larger body size distributions select for greater prevalence of haremic territoriality, and haremic male reproductive values favor the largest males, then the optimal $L_{\Delta 50}$ would be higher than expected based on body size distributions alone (blue arrow in Fig. 4b) compared to a less haremic system. A related scenario was observed by Bruggeman et al. (1994) for *Sparisoma viride* (Bonaire, Caribbean) between depth zones. In that study, disparity in substrate densities led to different nutritional yields, which were linked to changes in mean body size and associated variability in mating systems. Deriving a better understanding of the mechanisms for how environmental features can affect mating systems is an important objective for future research.

Linking ecosystem processes and demographic patterns across spatial scales

Despite the influence of social factors described above, we found only weak evidence of consistent relationships among body size distributions, population density, and sex ratio across species (Appendix S1: Fig. S3). This result is somewhat in contrast with patterns for *C. spilurus* from Micronesia (using an identical survey strategy), where strong relationships among these three factors were discovered at spatial scales matching those of the present study (Taylor 2014). We reconcile these perceived differences based on the spatial distribution of the observed systems. In Micronesia, variability was measured within and among highly isolated island systems, where the influence of social structure was much easier to quantify in the absence of extreme habitat variability. In contrast, on the GBR social groups and subpopulations at close proximity reefs are subject to extremely high among-reef variability, thereby obscuring our ability to easily identify such relationships.

The major similarity among cosmopolitan species across both the northern GBR (present study) and oligotrophic islands of Micronesia (Taylor 2014) is that, at relatively large spatial scales (>100–1000 km), geomorphological features appear highly influential of observed patterns of variation in length at sex change for dichromatic parrotfishes. The categorical distinction between shelf positions (GBR) and between island types (Micronesia) consistently explained the majority of the response variance despite considerable gradients of latitude (GBR) and fishery exploitation (Micronesia), suggesting that geomorphological features influence variation in demographic traits through their hierarchical effect on biotic factors directly affecting life-history variation. Although we were not able to determine mating systems at the site level across the scale of our study, prior biological sampling and decades of research on the dynamics of sex change suggest that the variation observed among distinct environments was driven by shelf-associated alternative mating systems. Broadening observations and analyses of life-history variation to mesoscales, as done here, is an important research objective. In particular, given the direct link between variation in life-history traits (such as growth rate) and ecosystem-level parameters that indicate overall ecosystem functioning (such as secondary biomass production), identifying the hierarchy of underlying drivers of demographic variation represents a paramount objective in the study of coral-reef ecosystems.

Broad-scale investigations of life-history variation help identify the capacity of populations to achieve local adaptation, thereby linking ecological and evolutionary processes (Petersen and Warner 2002). This study and others have demonstrated the high magnitude of life-history variation across multiple spatial scales in sex changing reef fishes, as well as the hierarchical and context-specific nature of relationships between life-history traits and influential factors. We expect that environmental perturbations concomitant with climate change will have major impacts on the persistence of coral-reef fish species (Munday et al. 2008), and the ability to modify demographic profiles to optimize survivability will be critical to population persistence.

ACKNOWLEDGMENTS

This project was made possible by the Khaled Bin Sultan Living Oceans Foundation and was supported by a James Cook University Graduate Research grant to B.M.T. We thank P. Chops for gear maintenance and F. Carvalho, K. Clements, A. Heenan, B. Langseth, and J. O’Malley for helpful discussions. Comments by three anonymous reviewers greatly improved the framework and direction of the manuscript.

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FIGURE LEGENDS

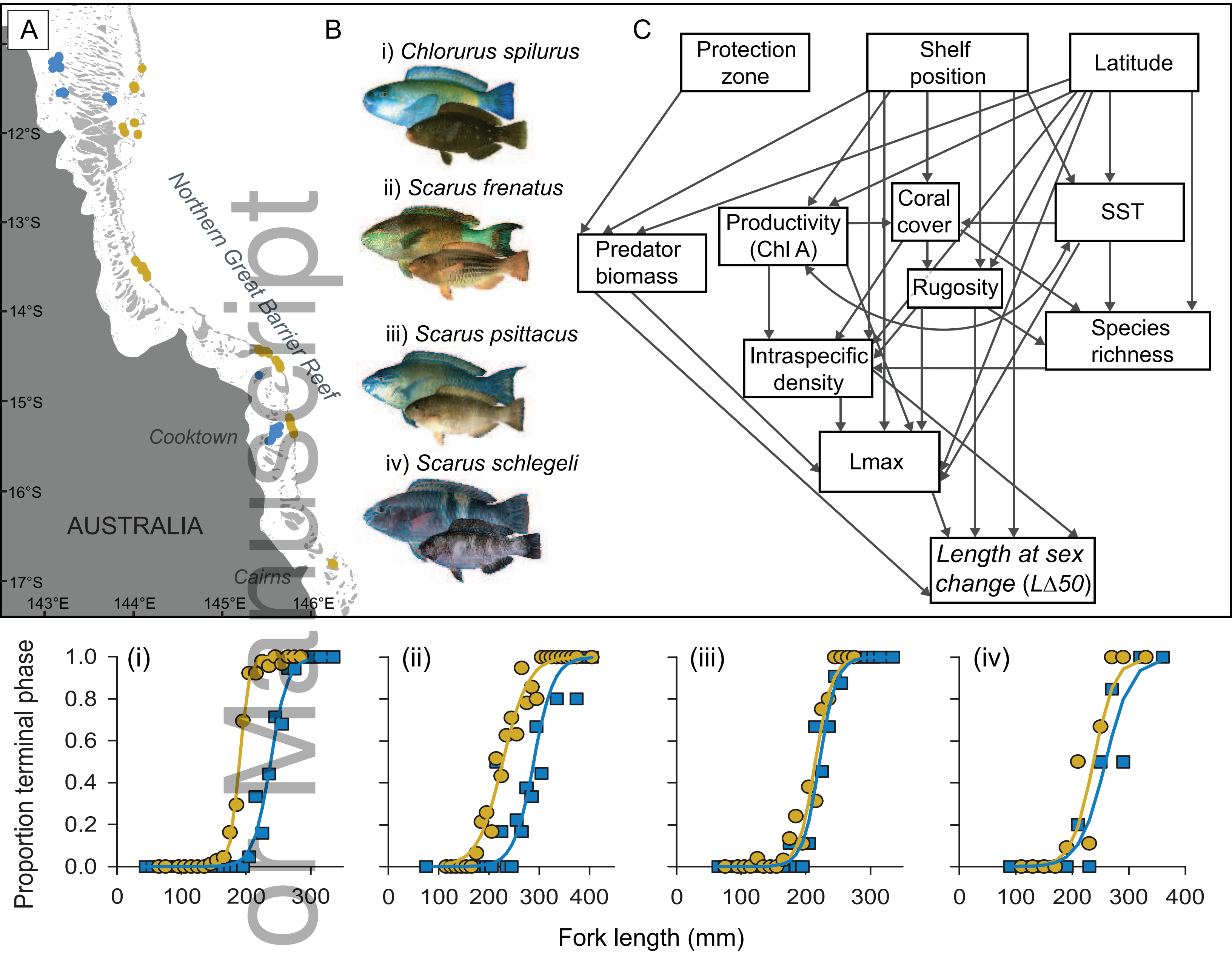
Fig. 1. (A) Map of 82 sites across the northern Great Barrier Reef. Exposed sites in yellow, sheltered sites in blue. (B) Species with associated color phases of initial (lower, front) and terminal (above, behind) broadly representing females and males, respectively. (C) Hypothesized pathways of influence from exogenous to endogenous biotic and abiotic factors ultimately affecting maximum length and length at sex change. Curved, double-headed arrows indicate correlated error structure. (i-iv) Comparison of sex change schedules for species in (B) pooled across exposed (yellow) and sheltered (blue) sites. Confidence ellipses surrounding $L_{\Delta 50}$ and $L_{\Delta 95}$ estimates are displayed in Appendix S1: Fig. S1.

Fig. 2. Directed acyclic graph displaying standardized regression coefficients for highly significant ($P < 0.01$) hypothesized pathways. Solid black and red arrows represent pathways with positive and negative coefficients, respectively. Line thickness reflects coefficient values. Subplots (A-H) represent the effects plots for significant pathways between explanatory factors. Plots (I-L) represent effects plots for significant pathways to the primary response variables, maximum length and length at sex change. Additional effects plots are presented in Appendix S1: Figure S2.

Fig. 3. Relationships between maximum length (represented here as the 95th quantile of the body size distribution) and length at sex change across sheltered mid and inner shelf reefs (blue) and exposed outer shelf reefs (yellow) of the Great Barrier Reef (n_{max} = 82 sites) for four parrotfish species: (A) *Chlorurus spilurus*, (B) *Scarus frenatus*, (C) *S. psittacus*, and (D) *S. schlegeli*. Shaded regions represent 95% confidence limits surrounding linear regression fits to each exposure regime.

Fig. 4. Conceptual diagram depicting potential change in the optimal size at sex change ($L_{\Delta 50}$ [dotted line]; intercept of male and female reproductive values following the size-advantage hypothesis) across populations with different body sizes and alternative mating systems. In (A), the orange arrow represents the expected change in $L_{\Delta 50}$ based only on proportional shifts in body size distribution, with mating system remaining unchanged. In (B), the blue arrow

represents expected change in $L_{\Delta 50}$ based on shifts in body size distribution coupled with changes in the rate of male reproductive value as the prevalence of haremic territoriality changes. Note that reproductive value is an age-related value, but for parrotfishes with only moderately determinant growth, the curves presented across body size should be approximately correct.



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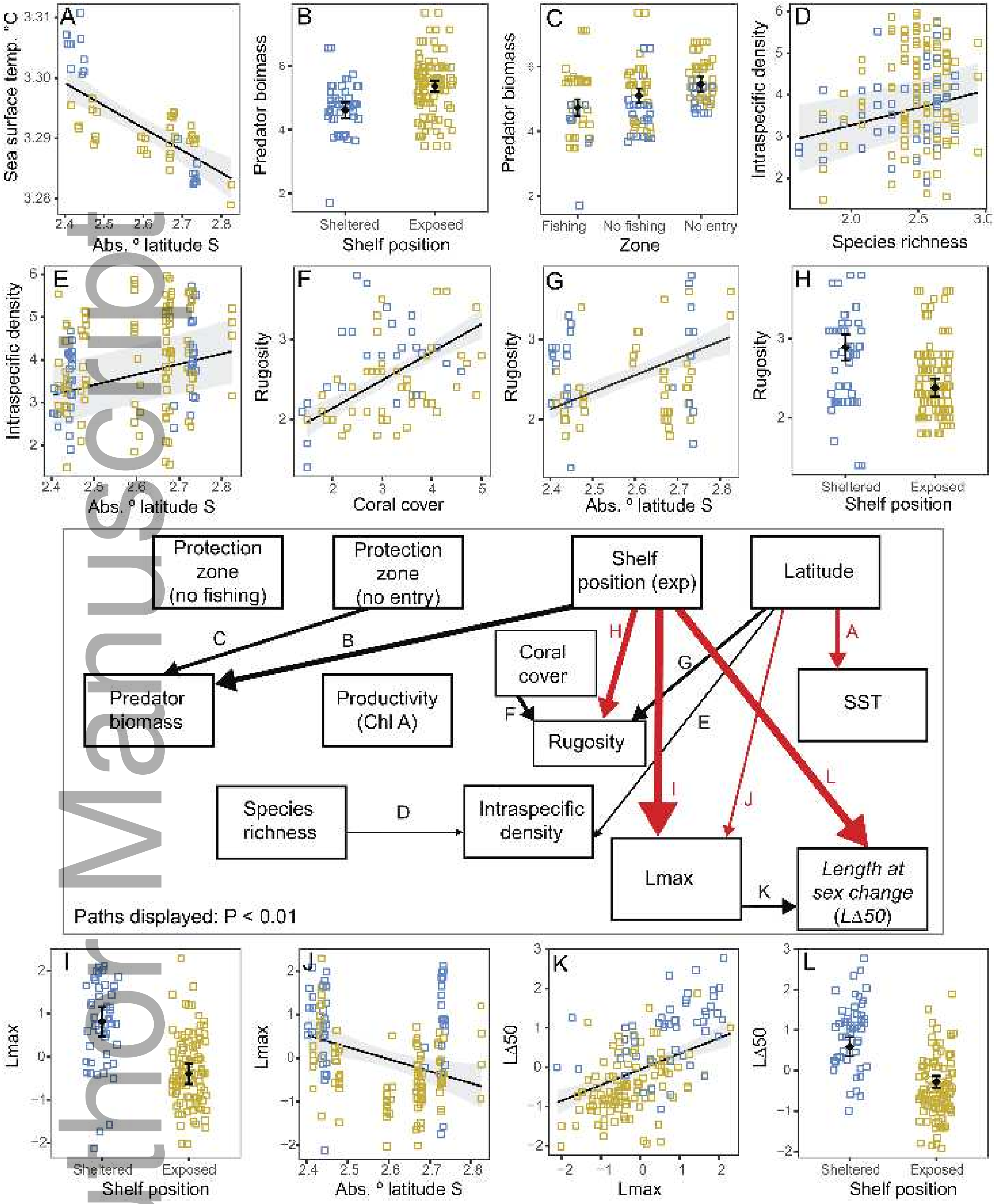

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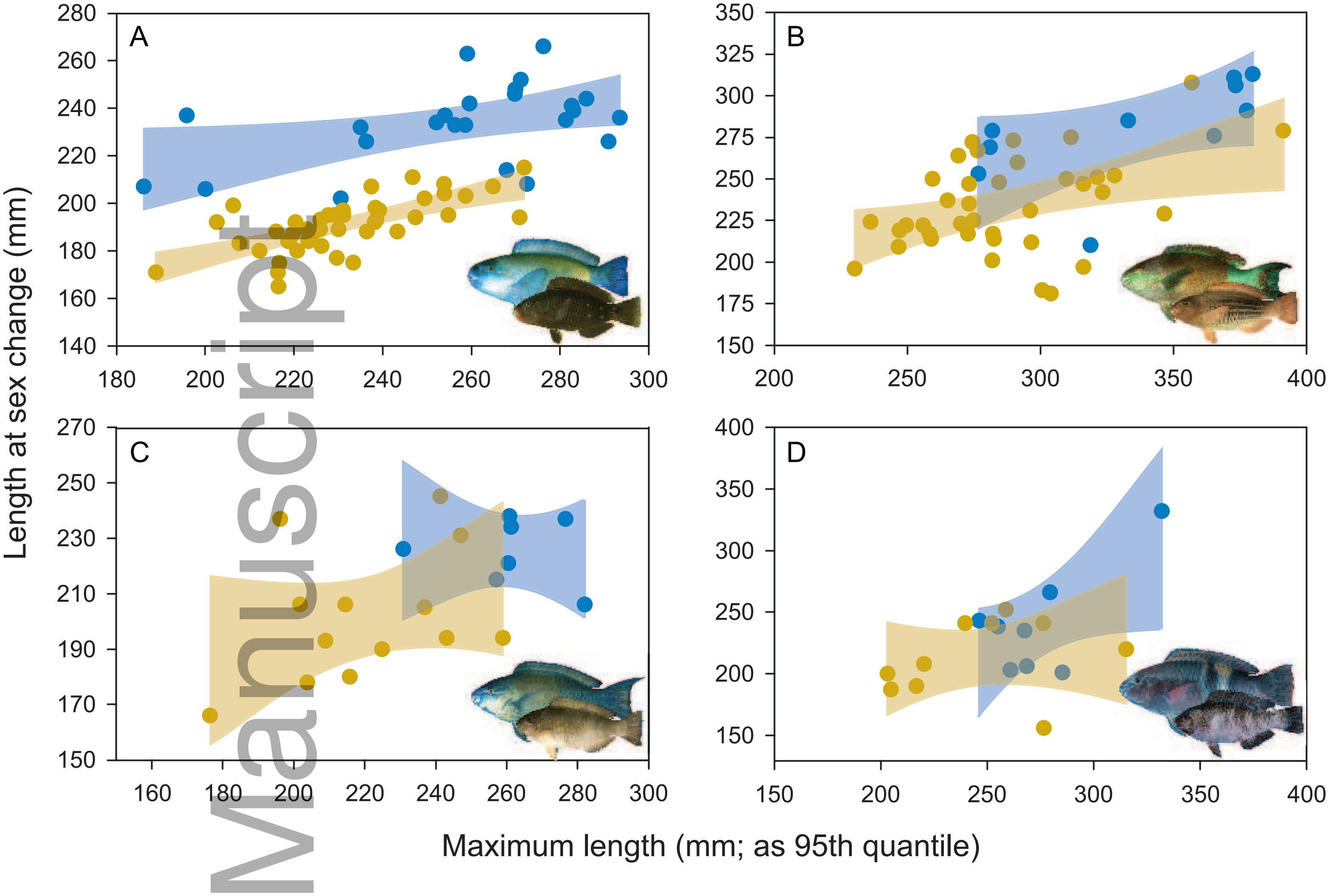

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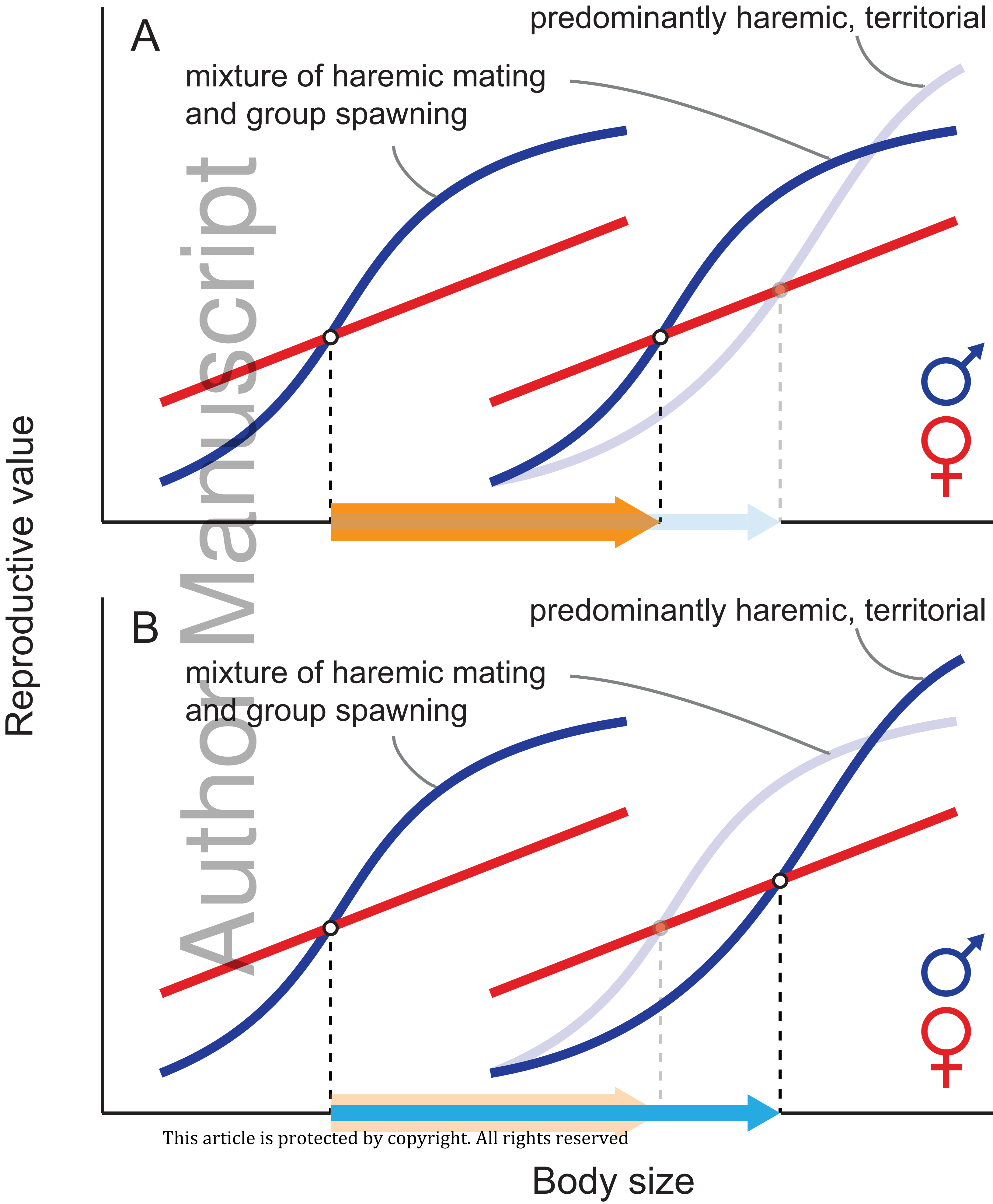
A
predominantly haremic, territorial
mixture of haremic mating
and group spawning
♂
♀
B
predominantly haremic, territorial
mixture of haremic mating
and group spawning
♂
♀
Reproductive value
Body size