

Relative size-at-sex-change in parrotfishes across the Caribbean: is there variance in a supposed life-history invariant?

Philip P. Molloy · Michelle J. Paddack · John D. Reynolds ·
Matthew J. G. Gage · Isabelle M. Côté

Received: 21 August 2009 / Accepted: 23 June 2010
© Springer Science+Business Media B.V. 2010

Abstract Invariant life-history theory has been used to identify parallels in life histories across diverse taxa. One important invariant life-history model predicts that, given simple assumptions and conditions, size-at-sex-change relative to maximum attainable body size (relative size-at-sex-change, RSSC) will be invariant across populations and species in sequential hermaphrodites. Even if there are broad species-wide limits to RSSC, populations could fine-tune RSSC to local conditions and, consequently, exhibit subtle but important differences in timing of sex change. Previous analyses of the invariant sex-change model have not explicitly considered the potential for meaningful differences in RSSC within the confines of a broader ‘invariance’. Furthermore, these tests differ in their geographical and taxonomic scope, which could account for their conflicting conclusions. We test the model using several populations of three female-first sex-changing Caribbean parrotfish species. We first test for species-wide invariance using traditional log–log regressions and randomisation analyses of population-specific point estimates of RSSC.

P. P. Molloy (✉)

Project Seahorse, University of British Columbia, 2202 Main Mall, Vancouver, BC V6T 1ZA, Canada
e-mail: philip.p.molloy@gmail.com

P. P. Molloy · M. J. Paddack · J. D. Reynolds · I. M. Côté
Department of Biological Sciences, Simon Fraser University,
8888 University Drive, Burnaby, BC V5A 1S6, Canada

J. D. Reynolds
e-mail: reynolds@sfu.ca

I. M. Côté
e-mail: imcote@sfu.ca

P. P. Molloy · M. J. Paddack · M. J. G. Gage
School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK

M. J. G. Gage
e-mail: m.gage@uea.ac.uk

M. J. Paddack
Santa Barbara City College, Santa Barbara, CA 93109, USA
e-mail: mjpaddack@sbcc.edu

We then consider error around these point estimates, which is rarely incorporated into invariant analyses, to test for differences among populations in RSSC. Log–log regressions could not unequivocally diagnose invariance in RSSC across populations; randomisation tests identified an invariant RSSC in redband parrotfish only. Analyses that incorporated within-population variability in RSSC revealed differences among populations in timing of sex change, which were independent of geography for all species. While RSSC may be evolutionarily constrained (as in redband parrotfish), within these bounds the timing of sex change may vary among populations. This variability is overlooked by traditional invariant analyses and not predicted by the existing invariant model.

Keywords Hermaphroditism · Invariant life-history analysis · Protandry · Protogyny · Sex allocation theory · Sex change

Introduction

Sex change occurs in a wide range of taxa, including many plants, invertebrates and fishes (Policansky 1982). It is expected to evolve when potential reproductive output is greater for one sex at small sizes and for the other sex at large sizes (Ghiselin 1969; Warner 1975; Leigh et al. 1976; Charnov 1993; Charnov and Skúladóttir 2000; Munday et al. 2006). An important goal in the study of the evolution of sex change is to understand similarities among species and/or populations in the trade-offs that produce this phenomenon. Particular attention has been paid to the timing of sex change. Sex allocation theory predicts that sex change should occur at the size at which reproductive gain is equal between the sexes (Charnov 1993). A key question is how the optimal timing of sex change differs across species or populations and whether there are commonalities in these optima (Charnov and Skúladóttir 2000; Allsop and West 2003a).

Recently, questions regarding the timing of sex change have been tackled using invariant life-history theory (Charnov 1993), which is based on sex-allocation theory. The strength of invariant life-history modelling is that life-history parameters are measured on relative scales, which facilitate comparisons across taxa, thereby allowing taxonomically general adaptive benefits to be easily tested. In particular, this approach has played a major role in generating testable predictions regarding sex change and of the timing of sex change (Charnov and Skúladóttir 2000). The invariant sex-change (ISC) model predicts an optimal size-at-sex-change (L_{50}), which yields the highest lifetime fitness. When this size is expressed *relative* to maximum size (L_{max}), comparisons of this optimum can be made easily across species or populations. Specifically, the model predicts that relative size-at-sex-change (L_{50}/L_{max} , ‘RSSC’) will be invariant across species/populations when three fitness-related parameters are constant: the exponent relating male reproductive output to body size (δ), the product of age-at-maturity and instantaneous mortality rate (αM), and the ratio of the Von Bertalanffy growth coefficient to instantaneous mortality rate (k/M). Further, ‘built in’ to the model structure are the assumptions that growth and mortality rates are similar across the sexes and that the relationship between female size and reproductive success is constant among populations/species.

The invariant sex-change (ISC) model has received considerable attention recently, due to the ease with which its predictions can be tested and its potential insights into broad evolutionary constraints on sex change. Allsop and West (2003a) reported invariance in RSSC and age-at-sex-change across a diverse array of animals. Similar analyses across fish species also revealed an invariant RSSC, although this value was slightly higher than that

reported across more taxonomically varied sex-changers (Allsop and West 2003b). However, the methods traditionally used to identify invariance have been heavily criticized (Buston et al. 2004; Cipriani and Collin 2005; Nee et al. 2005; Collin 2006). Until recently, invariance has been inferred using log–log regressions of two parameters of interest, e.g. \log_{10} size-at-sex-change versus \log_{10} maximum body size. A slope not significantly different from 1 was believed to demonstrate a proportional scaling of the two parameters, i.e. an invariant relative size-at-sex-change (Charnov 1993; Charnov and Skúladóttir 2000; Allsop and West 2003a, b). However, when y is bound by x (e.g. size-at-sex-change cannot exceed maximum body size), random data can also generate a slope of 1 when regressed on log–log axes (Buston et al. 2004; Cipriani and Collin 2005; Nee et al. 2005). In other words, an invariant relationship between two variables will yield a log–log slope of 1, but a log–log slope of 1 does not necessarily indicate an invariant relationship (Linde and Palmer 2008).

More recent methods for testing for invariance have relied on randomisation procedures to sidestep the limitations of log–log regressions (Gardner et al. 2005; Collin 2006; Linde and Palmer 2008). These studies have yielded conflicting results. Relative size-at-sex-change was found to be highly variable across species of male-first sex-changing slipper limpets (Gastropoda: Calyptraeidae) (Collin 2006). However, eight Mediterranean populations of a female-first sex-changing wrasse (Teleostei: Labridae: *Xyrichthys novacula*) showed invariance in RSSC: populations changed sex at approximately 79% of the population-specific maximum body size (Linde and Palmer 2008).

These seemingly incompatible results may be reconciled by considering the assumptions of the ISC model. It is not clear a priori why δ , αM and k/M should not vary, but the implication is that the trade-offs among life-history traits that generate such relationships are similar among populations and species. However, one might expect variation in size-dependent mortality, growth or mating success to preclude invariance in RSSC by changing δ , αM and/or k/M and other assumptions that are implicit in the model formulae. These differences are likely to be larger among species than among localised conspecific populations. This disparity might account for the different conclusions drawn by Collin (2006), who studied slipper-limpet species that originated from three continents, and Linde and Palmer (2008), who studied conspecific wrasse populations around the Balearic Islands.

We contend that a species' RSSC may be bound by selection to a limited range (which statistical analyses would reveal as an “invariance”), but that this does not preclude the possibility of observing meaningful variation among populations. Current tests of the ISC model typically use point estimates of population- or species-specific RSSC to test for invariance in RSSC. However, local conditions can hone the timing of sex change in each population even when, across populations, RSSC appears to be limited to a narrow window beyond which sex change is not advantageous. Such subtle variability among populations, which may be the consequence of socially controlled phenotypic plasticity or genetic differences, can only be detected by considering within-population variances in timing of sex change (Collin 2006). Within- and among-population variability in RSSC have not been explicitly integrated to test for the counter-intuitive situation of meaningful differences among populations within the confines of a broad (species-wide) invariance.

The possibility that RSSC may be fine-tuned to local conditions independently from any species-wide variability gives rise to four mutually exclusive hypotheses (Table 1). (A) There is species-wide variance in RSSC and no local fine-tuning (Fig. 1a). (B) There is species-wide invariance in RSSC and no further fine-tuning to local conditions (Fig. 1b). (C) There is species-wide variance in RSSC but RSSC is fine-tuned to local conditions (Fig. 1c). (D) There is species wide invariance in RSSC with further fine-tuning to local

Table 1 Four hypotheses regarding variation in relative size-at-sex-change (RSSC) and the predicted result under each hypothesis for the three analyses used here

Test	Hypothesis			
	(A) Species-wide variance in RSSC with no local fine-tuning	(B) Species-wide invariance in RSSC with no further local fine-tuning	(C) Species-wide variance in RSSC with local fine-tuning	(D) Species-wide invariance in RSSC with further local fine-tuning
Log–log regressions	Slope ≈ 1 ; low r^2	Slope ≈ 1 ; high r^2	Slope ≈ 1 ; low r^2	Slope ≈ 1 ; high r^2
Comparison of variance across observed point estimates to random RSSC	Variance across observed point estimates same as across random RSSC	Variance across observed point estimates less than across random data	Variance across observed point estimates same as across random RSSC	Variance across observed point estimates less than across random data
Comparison of 95% CIs	All CIs overlap hence no differences among populations	All CIs overlap hence no differences among populations	Some CIs do not overlap hence differences among populations	Some CIs do not overlap hence differences among populations

Hypotheses are depicted graphically in Fig. 1

conditions (Fig. 1d). These hypotheses are best tested using an analysis of widely distributed conspecific populations, which will also fill the gap between localised within-species analyses and global among-species tests. Detection of species-wide variance in RSSC would indicate that the ISC model lacks universality in depicting broad evolutionary trade-offs in sex-changing species; detection of species-wide invariance in conjunction with locally fine-tuned strategies would indicate that the ISC model captures broad trade-offs driving sex-change but overlooks subtle but potentially important variability.

The goal of this study was to test for variance in RSSC (Table 1) across a broad geographic scale using multiple populations of three Caribbean species of female-first sex-changing parrotfish (Teleostei: Scaridae, recently placed within Labridae, Westneat and Alfaro 2005). Caribbean parrotfishes provide a convenient system with which to study within-species variance in RSSC. First, they exhibit two colour morphs that are easily distinguishable and serve as a useful proxy for gender (van Rooij and Videler 1997; DeMartini et al. 2005). Second, many species have wide geographical distributions that encompass a range of environmental conditions and habitat differences. Third, several species are well studied, providing thorough ecological and life-history knowledge against which to interpret results. We do not test the mechanisms driving variance in RSSC but focus instead on emergent patterns and their implications regarding generalities in the evolution of sex-change strategies and the validity of the ISC model.

Materials and methods

Study species and data collection

Three species of parrotfish from two subfamilies were considered: striped parrotfish (*Scarus iserti*, formerly, *S. croicensis*; subfamily Scarinae) and redband (*Sparisoma aurofrenatum*) and stoplight parrotfish (*Sparisoma viride*) in the subfamily Sparisomatinae. Size-at-sex-change was inferred from size-at-colour-change (van Rooij and Videler 1997;

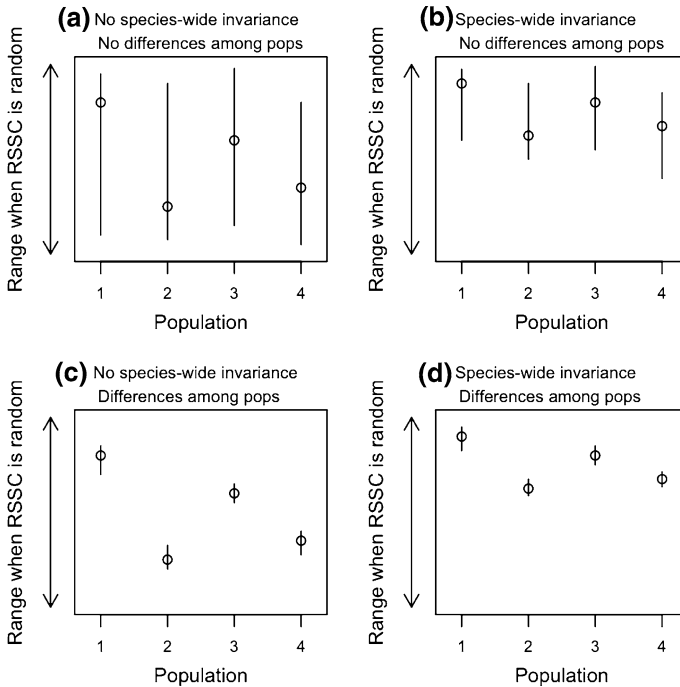


Fig. 1 Four hypothetical scenarios for variability in relative size-at-sex-change (RSSC). **a** RSSC point estimates are distributed widely across the theoretical range in RSSC, suggesting no species-wide invariance, and there are no differences in RSSC among populations owing to overlapping *error bars*. **b** RSSC point estimates are restricted to a small portion of the theoretical range in RSSC, suggesting a species-wide invariance, and there are no differences in RSSC among populations. **c** RSSC point estimates suggest no species-wide invariance but *error bars* reveal differences among populations, indicating local fine-tuning in RSSC. **d** RSSC point estimates indicate species-wide invariance in RSSC, but significant differences among populations also indicate local fine-tuning in RSSC

DeMartini et al. 2005). Typically, females exhibit a drab ‘initial-phase’ colour and sex-changed males exhibit a gaudier ‘terminal-phase’ colour. This distinction is blurred somewhat by the presence of non-sex-changed (primary) and sex-changed (secondary) males with initial-phase colouration (Robertson and Warner 1978). Primary males are absent in sparismatine parrotfishes (Robertson and Warner 1978). In striped parrotfish, these males also change colour to terminal phase at approximately the same size at which females undergo sex and phase change (Robertson and Warner 1978). Among sparismatine fishes, IP (and secondary) males are less common than initial-phase females (ratio of IP secondary males to IP females: redband = 1:47; stoplight = 1:9; Robertson and Warner 1978) and change phase at slightly smaller sizes than IP females change sex. Thus, using phase change as a proxy for sex change in these species may lead to small overestimates of true size-at-sex-change by overestimating the size at which the relatively few IP individuals became male without changing phase. However, it is unclear whether IP males ever function as females in these species. Because size-at-phase-change is likely to be highly correlated to size-at-sex-change and phase is easily assessed non-lethally, we follow van Rooij and Videler (1997) and DeMartini et al. (2005) and use size-at-phase-change to approximate size-at-sex-change.

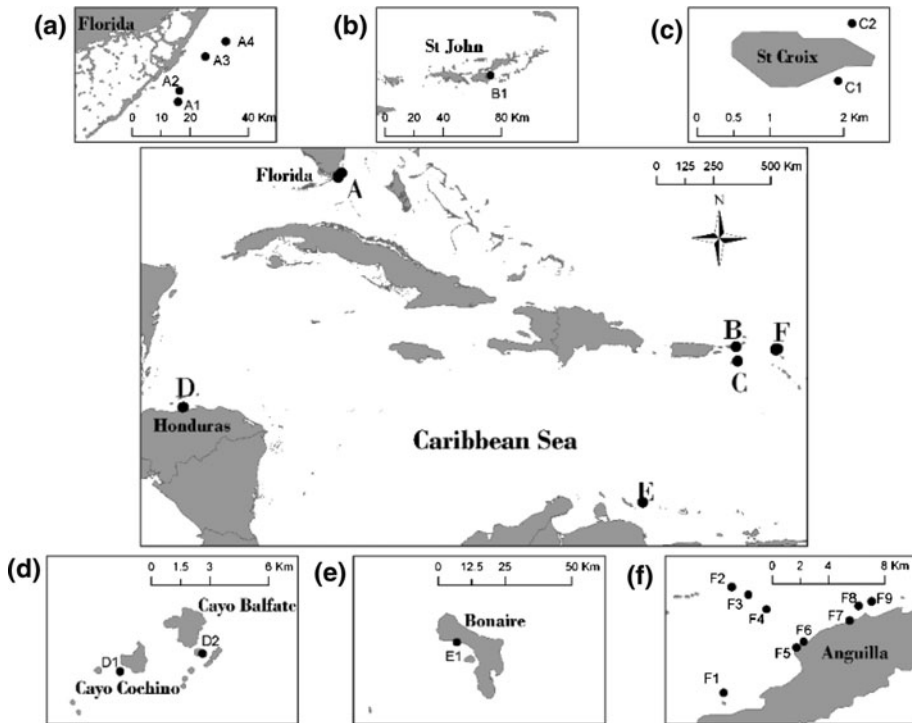


Fig. 2 Location of study sites across the Caribbean and Florida Keys. *A1* Key Largo, Molasses; *A2* Key Largo, White Banks; *A3* Key Largo, Algae; *A4* Key Largo, Ogden 4; *B1* St. John, Haulover; *C1* St. Croix, FR2; *C2* St. Croix, Boatcut; *D1* Honduras, Cayo Cochino; *D2* Honduras, Cayo Balfate; *E1* Bonaire, Karpata; *F1* Anguilla, Sandy Island North; *F2* Anguilla, Seal Island North 2; *F3* Anguilla, The Reef 2; *F4* Anguilla, The Reef East; *F5* Anguilla, Limestone Bay; *F6* Anguilla, Black Garden; *F7* Anguilla, Shoal Bay; *F8* Anguilla, Madeirman West; *F9* Anguilla, Madeirman North

Data on size and phase were recorded for these parrotfishes from 55 sites throughout Florida and the Caribbean using SCUBA. At 22 of these sites, size-at-sex-change could be determined (see below) for at least one species (Fig. 2; Table 2). Ultimately, we considered 488 size estimates from seven populations of striped parrotfishes (at least 38 per site) spanning 5–33 cm, 451 size estimates from 12 populations of redband parrotfish (at least 21 per site) spanning 7–31 cm, and 395 size estimates from 10 populations of stoplight parrotfish (at least 22 per site) spanning 7–47 cm (Table 2).

Populations around Anguilla (Fig. 2f) were surveyed by P.P.M. using five haphazardly located transects (6 m wide \times 30 m long) at 5 and 10 m depths. Size (total length, TL) was visually estimated to the nearest cm and colour phase was recorded for each parrotfish observed. All other populations were surveyed by M.J.P. using 10 transects (2 m wide \times 25 m long) per site, recording colour phase and fork length (FL) of all parrotfish with transects. Total lengths of Anguillian stoplight parrotfish were converted to FL using the equation $FL = 0.93 \times TL$ (regression through origin, $n = 31$, $r^2 = 0.97$, $P < 0.0001$; size range: 21.0–36.5 cm) for initial-phase fish, and $FL = 0.89 \times TL$ (regression through origin, $n = 25$, $r^2 = 0.96$, $P < 0.0001$; size range: 24.0–42.5 cm) for terminal-phase fish; these relationships were based on locally caught specimens. No conversions were necessary for striped and redband parrotfish, since tail shape in these species means that TL and

Table 2 Absolute size-at-sex-change (L_{50}), size of largest observed fish (L_{max}), relative size-at-sex-change ($RSSC = L_{50}/L_{max}$) with associated 95% confidence intervals in parentheses, and number of fish observed (n) for striped, redband and stoplight parrotfishes at 19 sites around the Caribbean (see Fig. 2 for locations of sites)

Site	Striped parrotfish			Redband parrotfish			Stoplight parrotfish				
	L_{50} (cm)	L_{max} (cm)	RSSC (95% CI) n	L_{50} (cm)	L_{max} (cm)	RSSC (95% CI) n	L_{50} (cm)	L_{max} (cm)	RSSC (95% CI) n		
A1. Key Largo, Fl: Molasses							30.5	47	0.65 (0.58–0.72)	39	
A2. Key Largo, Fl: White Banks				23.6	26	0.91 (0.88–0.94)				21	
A3. Key Largo, Fl: Algae				24.7	26	0.95 (0.91–0.99)				29	
A4. Key Largo, Fl: Ogdén 4				22.4	26	0.86 (0.83–0.89)				28	
B1. St. John: Haulover	12.8	17	0.76 (0.73–0.78)				24.7	29	0.85 (0.78–0.93)	39	
C1. St. Croix: FR2				19.1	25	0.77 (0.7–0.83)	35	31.3	44	0.71 (0.6–0.83)	24
C2. St. Croix: Boatcut											
D1. Honduras: Cayo Cochino				23	27	0.85 (0.81–0.89)	45				
D2. Honduras: Cayo Balfate				23.5	27	0.87 (0.84–0.91)	50	23.5	27	0.87 (0.84–0.91)	50
E1. Bonaire: Karpata				17.3	20	0.87 (0.78–0.96)	22	17.3	20	0.87 (0.78–0.96)	22
F1. Anguilla: Sandy Island North	21.4	25	0.86 (0.67–1)								
F1. Anguilla: Seal Island North 2											
F3. Anguilla: The Reef 2				23.6	26	0.91 (0.88–0.94)	26	23.6	26	0.91 (0.88–0.94)	26
F4. Anguilla: The Reef East	24.1	33	0.73 (0.66–0.81)	74	24.4	0.79 (0.76–0.81)	38	24.4	31	0.79 (0.76–0.81)	38
F5. Anguilla: Limestone Bay				25.3	30	0.84 (0.82–0.87)	53	25.3	30	0.84 (0.82–0.87)	53
F6. Anguilla: Black Garden				24.5	29	0.84 (0.83–0.86)	59	24.5	29	0.84 (0.83–0.86)	59
F7. Anguilla: Shoal Bay Reef	16.1	20	0.8 (0.78–0.83)	51							
F8. Anguilla: Madeirman West	19.7	24	0.82 (0.69–0.95)	61							
F9. Anguilla: Madeirman North	16.2	22	0.74 (0.72–0.75)	105	22.3	0.74 (0.68–0.81)	45	22.3	30	0.74 (0.68–0.81)	45

Empty cells represent sites where either no fish of that species were seen or where size-at-sex-change could not be calculated. Abbreviations of site names correspond to those given in Fig. 2

FL are comparable. Since all species were observed to move freely between the depths sampled, data from different depths were pooled within sites. Because fish were not marked, it is possible that some individuals were counted more than once. However, the abundance of each species was such that the effect of any double counts would be negligible and unlikely to have been biased with respect to fish size or phase.

Sex-change data

Size-at-sex change for each population was calculated using a logistic regression model relating body size to colour phase (Eq. 1):

$$p_{tp} = \frac{1}{1 + \exp^{-\frac{(L-L_{50})}{s}}} \quad (1)$$

where p_{tp} is the probability of being terminal phase, L is fork length, L_{50} is fork length at which there is a 50% probability of being terminal phase (location parameter), and s is the scale parameter, which controls slope (Schafer and Sheffield 1973). Size-at-sex-change for each species at each site was taken as the best-fitting L_{50} value. L_{50} could not be determined for populations where the logistic regression model did not converge (usually due to a scarcity of a species at that site), and these populations were not considered further. For each population, size-at-sex-change relative to the size of the largest individual in the population (L_{\max}) was calculated as L_{50}/L_{\max} (Gardner et al. 2005; RSSC). L_{\max} was assumed to approximate the asymptotic length for that species at that site, although the sensitivity of our results to this assumption (including dependence between L_{\max} and population density) was explored (see below). Ultimately, RSSC data were available for at least seven populations for each species (Table 2). A feature of Eq. 1 is that L_{50} is not bound by observed length range; as such, the best-fitting L_{50} may exceed L_{\max} . This only occurred for one population of striped parrotfish (Table 2). Since size-at-sex-change cannot exceed maximum body size, we interpreted this as indicative of a population where comparatively few females change sex and, when sex change does occur, it only happens at very large body sizes.

Analysis of variance in relative size-at-sex-change

We tested the four hypotheses regarding RSSC (Table 1) using three analytical approaches.

Log–log regressions

Traditionally, a regression of two log-transformed life-history traits that yields high r^2 and a slope not significantly different from unity has been interpreted as indicative of proportionality and hence invariance (Charnov 1993; Allsop and West 2003a, b). We tested whether the slope of the relationship between $\ln L_{50}$ and $\ln L_{\max}$ significantly differed from 1 using major-axis regression (Warton et al. 2006) and estimated r^2 using standard least-squares regression.

Comparison to null data

Since log–log plots of bounded variables may give misleading results (Buston et al. 2004; Cipriani and Collin 2005; Nee et al. 2005; Munday et al. 2006) we supplemented

regression analyses with a randomisation procedure. Such methods provide a more robust test of whether the observed covariance between L_{50} and L_{\max} is less than expected by chance, given the biological constraints on the timing of sex change. Specifically, observed variance in point estimates of RSSC was compared to variance of 10,000 random RSSC datasets (Gardner et al. 2005; Collin 2006; Linde and Palmer 2008). Since sex change must occur after maturity, we first generated a null relative size-at-maturity (nRSM) from a uniform distribution between a biologically relevant minimum bound (RM_{\min}) and 1. We set RM_{\min} for each species as the relative size-at-maturity observed for that species: $RM_{\min i} = \min(L_{\text{mat } i,j}/L_{\text{max } i,j})$ where $L_{\text{mat } i,j}$ and $L_{\text{max } i,j}$ are, respectively, the size of the smallest and largest observed individuals of species i at site j . A null relative size at sex-change (nRSSC) was then allowed to take any value between the nRSM and 1 with equal probability, i.e. $\text{nRSSC} \sim \text{U}(\text{nRSM}, 1)$. The standard deviation of these 10,000 nRSSC data was calculated for each species and compared to the observed value. We report the percentage of null datasets that had a larger standard deviation than that of observed data. We conclude that a species showed less variation in RSSC than predicted by our null model if the standard deviation of more than 95% of random datasets exceeded that of observed data. Such a result would indicate a species-wide invariance in RSSC (Table 1; Fig. 1). We repeated analyses using another null model in which nRSM was uniformly distributed between 0.4 and 0.8 and nRSSC was uniformly distributed between nRSM and 1 (sensu Buston et al. 2004). These results (not shown) supported the same hypotheses as those obtained using the first null model described above.

Comparison of 95% confidence intervals

Even if there is a species-wide invariance in RSSC, there may be biologically meaningful differences in RSSC among populations in timing of sex change (Fig. 1c or d). We therefore tested for differences in RSSC among populations by considering within-population variability in timing of sex change. We did not explore differences among populations in RSSC using standard analysis of variance (ANOVA) because, for a given population, all simulated RSSC estimates were based on a common population-specific L_{\max} estimate. As such, the ANOVA assumption of independent data is violated. Instead, we compared 95% confidence intervals around population-specific estimates of RSSC to test for among-population differences. Error around RSSCs comes from inaccuracy associated with estimates of L_{50} and L_{\max} . Initially, we focussed solely on error around L_{50} (see below for tests of sensitivity to error around L_{\max}). Ninety-five percent CI around observed size-at-sex-change was calculated as $L_{50 i,j} \pm 1.96\sigma_{L_{50 i,j}}$ (Zar 1999), where $L_{50 i,j}$ and $\sigma_{L_{50 i,j}}$ are the logistic-model estimates of L_{50} and the associated standard error for species i at site j . Normal distributions closely approximate error around location parameters in logistic regression (Antle et al. 1970). L_{50} CIs were converted to RSSC CIs by dividing the upper and lower L_{50} 95% confidence limits by the relevant L_{\max} . We counted the number of significant pairwise differences in RSSC among populations of the same species as indicated by non-overlapping 95% CIs. To standardize across species, we report these counts as the proportion of sites that differed in RSSC. Significant differences among populations would indicate local fine-tuning in RSSC (Fig. 1c, d).

In order to calculate unbiased 95% CIs around population RSSC values, we allowed simulated size-at-sex-change values to exceed simulated maximum body sizes. As above, this situation can be interpreted as representing a population where few females change sex. When the upper 95% confidence limit exceeded 1, we took 1 as the upper 95% confidence limit for that population's RSSC. The populations for which this situation arose

always had higher RSSCs than other populations. Therefore, capping the upper 95% limit to 1 did not affect the result of pairwise comparisons. To test the sensitivity of pairwise differences to the presence of a single anomalous population, we repeated our comparison of 95% confidence intervals while sequentially excluding each population.

Populations that are close to one-another may be exposed to similar trade-offs determining optimal sex-change strategy. More distant populations are therefore more likely to differ in RSSC than close populations. We tested for spatial autocorrelation among populations using normalised Mantel tests.

Ostensibly, population RSSC data have a nested structure: sites within region. Since traditional ANOVAs (including nested-ANOVAs) were not appropriate and nesting could not be incorporated into our comparisons of confidence intervals, we could not explicitly account for such structuring. However, the lack of spatial structuring in RSSC values (see “Results”) implies that incorporating nesting into our statistical framework would not have improved our analyses.

Sensitivity analysis

To determine whether our results could have been affected by under-estimation of L_{\max} , we explored the sensitivity of between-site differences in RSSC to simulated error in L_{\max} . We assumed that error on L_{\max} is solely due to overlooking a larger individual and only modeled upper error on L_{\max} . We generated 10,000 size-at-sex-change values for species i at site j from a normal distribution with a mean of $L_{50\ i,j}$ and standard deviation of $\sigma_{L_{50\ i,j}}$. We also verified that error on L_{50} is independent of error on L_{\max} . For species i at site j , we generated 10,000 random L_{\max} values ($rL_{\max\ i,j}$) using Eq. 2:

$$rL_{\max\ i,j} = L_{\max\ i,j} + |L_{\max\ i,j} - N(L_{\max\ i,j}, \sigma_{L_{\max\ i,j}})| \quad (2)$$

where $N(L_{\max\ i,j}, \sigma_{L_{\max\ i,j}})$ is a normal distribution with a mean of L_{\max} and standard deviation of $\sigma_{L_{\max}}$ specific to species i at site j .

We controlled the amount of simulated error in L_{\max} by using a range of values for $\sigma_{L_{\max\ i,j}}$. Initially, we assumed that the accuracy of our L_{\max} estimate was independent of the population being surveyed but was a function of $L_{\max\ i,j}$ itself; thus, $\sigma_{L_{\max\ i,j}} = p \times L_{\max\ i,j}$ where p is a scaling parameter, which we allowed to range from 0 to 0.3: $p = 0$ represents no error; $p = 0.3$ represents a scenario where 95% of simulated values were between $L_{\max\ i,j}$ and $\sim 1.6 \times L_{\max\ i,j}$ (0.95 quantile = $L_{\max\ i,j} (1 + [1.96 \times 0.3])$; Zar 1999). The resulting $rL_{\max\ i,j}$ values were paired with $L_{50\ i,j}$ values yielding 10,000 randomised RSSCs for each population, for which associated 95% CIs were calculated. As before, the number of pairwise differences in RSSC among populations was determined by the number of non-overlapping 95% CIs.

Subsequently, we performed the same procedure but assumed that $\sigma_{L_{\max\ i,j}}$ depended on site-specific sampling effort (i.e., total area surveyed) or, separately, on population density. Thus, $\sigma_{L_{\max\ i,j}} = p \times L_{\max\ i,j} \times w_{i,j}$ where $w_{i,j}$ is either:

$$w_{i,j} = \sqrt{\left(\frac{\bar{S}_i}{S_{i,j}}\right)} \quad (3a)$$

$$w_{i,j} = \sqrt{\left(\frac{\bar{D}_i}{D_{i,j}}\right)} \quad (3b)$$

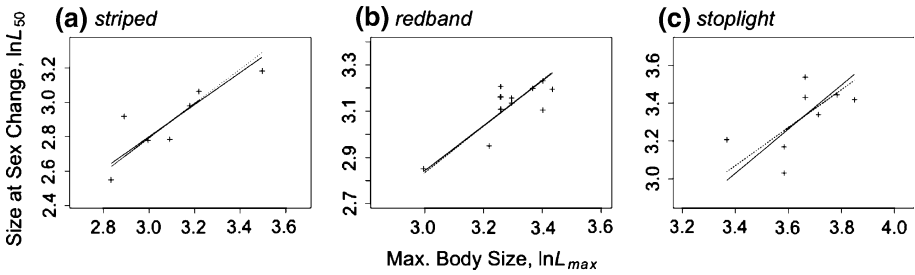


Fig. 3 Log–log relationships between maximum body size ($\ln L_{\max}$) and size at sex change ($\ln L_{50}$) for **a** striped, **b** redband and, **c** stoplight parrotfishes. *Solid and dotted lines* indicate, respectively, the best-fitting major-axis regression model and models with slopes constrained to 1

where $S_{i,j}$ and $D_{i,j}$ are, respectively, sampling effort and fish density for species i at site j , and S_i and D_i are, respectively, average sampling effort and fish density for species i . We show how the proportion of sites that differed in RSSC declines with increasing error on L_{\max} when $\sigma_{L_{\max} i,j}$ was and was not weighted. The amount of error required before all significant pairwise differences are lost provides a measure of robustness of inter-population differences in RSSC. The sensitivity to simulated error in L_{\max} increased slightly when L_{\max} error was weighted by area surveyed and decreased when L_{\max} error was weighted by fish density (results not shown).

Results

Log–log regressions

Slope estimates from major-axis regressions of *lnsize-at-sex-change* against *lnmaximum body size* did not differ from 1 in any species (striped: slope (95% CI) = 0.93 (0.53–1.65), $p = 0.76$; redband: slope (95% CI) = 0.97 (0.64–1.46), $p = 0.88$; stoplight: slope (95% CI) = 1.16 (0.55–2.43), $p = 0.66$; Fig. 3). Model r^2 were high for striped and redband parrotfish, but not stoplight parrotfish (striped: 0.73; redband: 0.64; stoplight: 0.34).

Comparison of observed variance to random RSSC data

Observed variance among point estimates of relative size-at-sex-change (RSSC) was significantly smaller than among random data (in which sex change occurs at a random size between a nominal size-at-maturity and maximum size) only in redband parrotfish. For this species, 99.6% of random RSSC datasets showed more variance than observed data (Fig. 4). Striped and stoplight parrotfish RSSC point estimates were not significantly less varied than null data (% of null datasets with greater variance than observed: striped = 84.1%, stoplight = 89.2%; Fig. 4).

Comparison of 95% confidence intervals

Comparison of 95% confidence intervals around population-specific point estimates of RSSC revealed differences among populations in all species (proportion of significantly different 95% CIs: striped = 0.24 (5 of 21 pairwise comparisons); redband = 0.45 (30 of

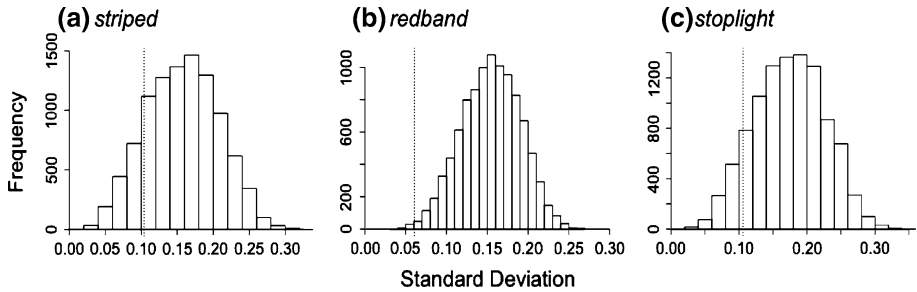


Fig. 4 Distributions of variance (standard deviation, SD) in 10,000 null relative size-at-sex-change (L_{50}/L_{max}) datasets for **a** striped, **b** redband and, **c** stoplight parrotfishes. Vertical dotted lines show SD in observed data

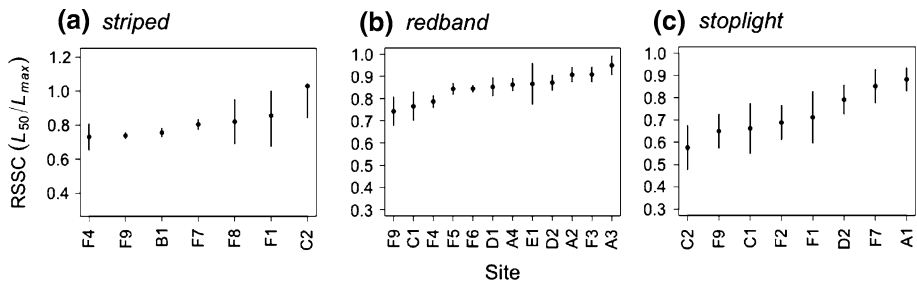


Fig. 5 Relative size-at-sex-change (RSSC, L_{50}/L_{max}) \pm 95% confidence intervals in populations of **a** striped, **b** redband and, **c** stoplight parrotfishes. See Fig. 2 for explanation of sites codes

66 comparisons); stoplight = 0.39 (11 of 28 comparisons); Fig. 5). Inspection of Fig. 5 reveals that, for all three species, differences were observed between both geographically close and distant populations. Differences between pairs of sites were not significantly related to geographic distance between sites for all species (all normalised Mantel $r < 0.40$, all $p > 0.14$). For all three species, differences among populations remained when individual populations were removed from pairwise comparisons of 95% CIs. Differences among striped parrotfish populations were most sensitive to the inclusion of population C2, which had the highest RSSC for this species (Fig. 5a). Only one difference (7% of comparisons) remained when this population was removed. Differences among populations of redband and stoplight parrotfishes were less sensitive to the removal of individual populations with at least 22 (40% of comparisons) and six (29% of comparisons) differences remaining, respectively.

Sensitivity to error in L_{max}

For all species, the proportion of sites that differed significantly in RSSC fell with increasing simulated error in L_{max} (Fig. 6). All among-site differences in RSSC were lost when the upper L_{max} error limit was 150% of observed L_{max} . Redband parrotfish was most sensitive to L_{max} error and stoplight parrotfish was least sensitive.

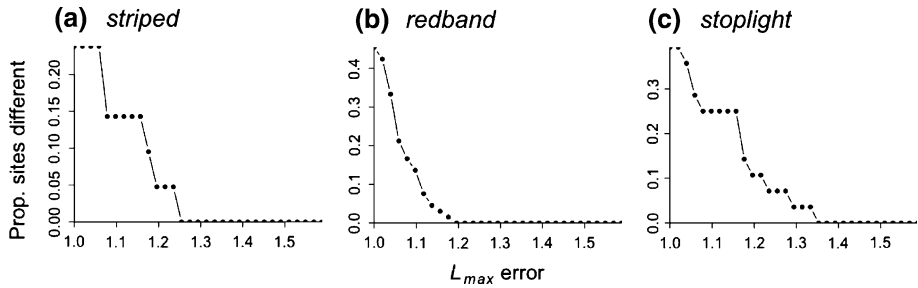


Fig. 6 Proportion of sites that differ in relative size-at-sex-change (L_{50}/L_{\max}) when varying amounts of error above L_{\max} are simulated for **a** striped, **b** redband and **c** stoplight parrotfish. Differences were identified by non-overlapping 95% confidence intervals in pairwise comparisons (Fig. 4). The amount of error simulated on L_{\max} was drawn from a one-sided normal distribution bound at L_{\max} error with an upper 95% quantile of $L_{\max} \times L_{\max}$ error (see “Sensitivity analysis” in Materials and Methods); hence, greater L_{\max} error values indicate greater error

Discussion

The goal of invariant life-history analyses is to test for broad constraints on life-history traits across populations or species. We did not find universal invariance in relative size-at-sex-change (RSSC) in parrotfishes: only one of three species, the redband parrotfish, showed such invariance. However, in all species populations differed in RSSCs, indicating locally fine-tuned sex-change strategies. Our results indicate that the invariant sex change (ISC) model does not always accurately predict patterns in timing of sex change. Further, even when species-wide invariance exists, the model does not capture subtle, but potentially important variability within species.

Measuring invariance

Our study highlights the difficulties associated with testing for life-history invariances. For redband and stoplight parrotfishes, the log–log regression and randomisation analyses lead to congruent conclusions (species-wide invariance in RSSC for redband but not stoplight parrotfish; Table 3). However, for striped parrotfish, log–log regressions yielded high r^2 values (higher than those of the 10,000 random datasets simulated by Linde and Palmer 2008), and slopes closely approximating 1 (in support of hypothesis B or D, Table 3). In contrast, randomisation analyses suggested high variability in RSSC (in support of hypotheses A or C, Table 3). This conflict should not occur (Table 1) and further highlights the danger of relying on log–log regressions to test for life-history invariances (Buston et al. 2004; Cipriani and Collin 2005; Nee et al. 2005; Munday et al. 2006). We have more confidence in the randomisation analyses and, therefore, in a conclusion of variance in RSSC in striped parrotfish.

In all species, even the redband parrotfish, variance in sex-change strategy was revealed by cross-population comparisons of RSSC confidence intervals (CIs). This variance is not identified by log–log regressions or randomisation analyses since they only consider population-specific point estimates of RSSC and overlook within-population variability around these values. Consequently, these tests give no insight into whether differences among sites are real or random. The existence of a species-wide invariance concurrent with subtle but potentially meaningful differences among populations, as was detected for the

Table 3 Observed results of the three main tests for variance in relative size-at-sex-change, and the hypothesis supported by each test (in parentheses—refer to Table 1) and the overall conclusion for each parrotfish species

Species test	Striped	Redband	Stoplight
Log-log regression	Slope ≈ 1 ; high r^2 (B or D)	Slope ≈ 1 ; high r^2 (B or D)	Slope ≈ 1 ; low r^2 (A or C)
Comparison to random RSSC	Similar variance between observed and random RSSC (A or C)	Significantly lower variance in observed than random RSSC (B or D)	Similar variance between observed and random RSSC (A or C)
Comparison of CIs	Differences among sites (C or D)	Differences among sites (C or D)	Differences among sites (C or D)
Conclusion	C, based on comparison to random data: Species-wide variance in RSSC with local fine-tuning	D: Species-wide invariance in RSSC with further local fine-tuning	C: Species-wide variance in RSSC with local fine-tuning

redband parrotfish, was also reported for male-first sex-changing slipper limpets (Collin 2006).

Comparisons of RSSC CIs may overestimate differences among sites because they do not consider error on L_{\max} . Simulating error on L_{\max} and recalculating confidence intervals provided insight into how sensitive these comparisons are to unmeasured error on L_{\max} . This sensitivity was greatest for redband parrotfish and least for stoplight parrotfish. Figure 5 shows that this was because species-wide variance in RSSC is lowest for redband. As a result, error around RSSC estimates needs to be increased by a comparatively small amount before CIs overlap. Generally, our sensitivity analyses support the conclusion that, although there may be constraints to RSSC in parrotfish (e.g. redband parrotfish), within these constraints populations have the plasticity to fine-tune their sex-change strategy to local conditions.

Theoretically, variance across or around point estimates of RSSC could be caused by measurement error (Charnov 1993) arising, for example, by inaccuracies in estimating body size and/or by different observers collecting data at different sites. Inaccuracy in estimates of body sizes would have increased the confidence limits around population RSSC estimates; thus our observation of differences among populations would be conservative. Differences among observers could have led to systematic error either causing Anguillian populations (surveyed by P.P.M.) to have consistently higher or lower RSSCs compared to other populations (surveyed by M.J.P.), or to have different within-population estimates of error in RSSC (Fig. 5). Neither of these possibilities is supported by our results. Therefore, it seems likely that differences among populations in RSSC represent real differences in sex-change strategies.

Why does parrotfish RSSC vary?

Species-wide variance in RSSC may be accounted for by two potentially interacting explanations. First, the invariant sex-change (ISC) model only predicts invariant RSSC when αM , k/M and δ are constant (see “Introduction”, Charnov and Skúladóttir 2000; Gardner et al. 2005); if these parameters vary, RSSC should vary (Gardner et al. 2005). We were unable to quantify α , k , M and δ and therefore cannot assess whether or how the observed variance in RSSC was specifically driven by differences in αM , k/M and δ .

Second, irrespective of αM , k/M and δ , several basic assumptions are ‘built-in’ to the model formula: (1) constant growth (k) and mortality (M) rates across sexes, (2) female reproductive success follows a cubic relationship with length and (3) is constant among populations/species (Charnov and Skúladóttir 2000). Violation of these assumptions could lead to unpredictable variance in RSSC, indicating that the ISC model over-simplifies the ecology and life history of sex-changers (Collin 2006).

Generally, there is evidence that the assumptions of the ISC model are not valid. Growth rates differ between the sexes in many sex-changers (Jones 1980; Garratt et al. 1993; Chen and Soong 2002; Munday et al. 2004; Choat et al. 2006; Gavio et al. 2006; Fairhurst et al. 2007), including parrotfish (Choat et al. 1996). Such differences may be driven by a growth spurt immediately following sex change, as is often observed in sex-changing fishes (e.g. Walker and McCormick 2004; Fairhurst et al. 2007). Sex-specific natural mortality estimates are rarely available but it is likely that, in female-first sex-changing species at least, the more gaudy colour and/or more aggressive behaviour of males predisposes them to higher natural mortality rates than females. Indeed, on inshore reefs along the Florida Keys, initial phase and terminal phase stoplight parrotfish differ in mortality rates (Paddack et al. 2009). In addition, larger individuals are often disproportionately removed by fisheries (Bannerot et al. 1987; Punt et al. 1993; Vincent and Sadovy 1998; Alonzo and Mangel 2004; Molloy et al. 2007), which, in the case of sex-changers, equates to substantially increased relative mortality on the second sex (Hamilton et al. 2007). Relationships between female reproductive success and size/age are also likely to vary widely across populations. Female reproductive output is affected by resource availability (Clifton 1995; van Rooij et al. 1995), which varies spatially (Crossman et al. 2001; Gust et al. 2002; Paddack 2005). In some species, females are able to adjust current reproductive output in response to expected future reproductive output (Heubel et al. 2008), which will affect size-reproduction relationships. Without site-specific information on life-history parameters or habitat we are unable to distinguish the cause (or causes) of among-population differences in RSSC. Nevertheless, our results imply that “the breeding tactics [...] adopted by individuals often appear to be adaptive responses to their own social–ecological context and variation in these conditions results in significant differences in the timing of sex change” (Munday et al. 2006). These observations support Collin’s (2006) assertion that the ISC model “does not accurately capture what is going on in nature”.

A natural next-step would be to address the drivers of variation in RSSC. It is not clear if differences among populations in RSSC are genetically based or the consequence of phenotypic plasticity. Although timing of sex change is flexible and socially mediated (Shapiro 1981; Nemtsov 1985; Warner and Swearer 1991; Mackie 2003), it is unclear if this translates into socially controlled RSSC. It is also unclear if the forces controlling species-wide variance in RSSC differ to those controlling local-scale differences; species-wide constraints to RSSC in redband parrotfishes may limit the range of habitats in which this species can thrive. Alternatively, broad-scale patterns may be simply the net consequence of population-level differences in RSSC; redband parrotfish may show such low species-wide variance in RSSC compared to stoplight and striped parrotfish because the local-scale conditions affecting RSSC are less variable across redband populations than across those of the other two species. Translocations experiments or controlled manipulations of social conditions may help to disentangle the importance of genetic and phenotypic differences in RSSC and to reveal whether redband parrotfish truly show little capacity for flexibility in RSSC.

Our results shed some light on the discrepancy between previous tests for invariance in RSSC that have used robust randomisation analyses. Specifically, variance in RSSC was detected in a broad-scale cross-species comparisons of male-first sex-changing slipper limpets (Collin 2006) but not in a within-species, small-scale comparison of female-first sex-changing Mediterranean wrasses (Linde and Palmer 2008). One possible explanation for this discrepancy is the difference in scale. Widely dispersed populations may be particularly likely to differ in their sex-change strategies since they span a wider range of environmental and, potentially, selection pressures. Our results do not support this hypothesis. Firstly, for all three species of parrotfish, differences in RSSC between neighbouring populations were as large as differences between more distant populations. Furthermore, although populations from all three species were widely distributed across the Caribbean, variance in RSSC was not universally observed—redband parrotfish showed a species-wide invariance in RSSC. Additional explanations include differences between studies in the direction of sex change and the taxonomic scope. Our study suggests that neither provides a full explanation since we obtained mixed results using a taxonomically narrow group of species that all change from female to male.

The ISC model has spurred a wealth of research into the evolutionary optimality of sex change (Allsop and West 2003a, b; Collin 2006; Linde and Palmer 2008). The model may occasionally be useful to identify broad constraints on timing of sex change, as was the case for redband parrotfish. However, our results suggest that the assumptions of the ISC model are too simple to universally and accurately represent natural situations. It is unlikely that such universality can be acquired without incorporating further complexities such as sex-specific growth and mortality; doing so would undermine the alluring simplicity of the life-history invariant approach. Instead, a more productive avenue may be to refocus on other well-supported sex-change models, such as those based on the size-advantage model (Warner 1975; Leigh et al. 1976; Muñoz and Warner 2003).

Acknowledgments Thanks to Fab* and Earth2Ocean labs at Simon Fraser University, Jenn Sunday, Maria José Juan Jorda, Arne Mooers, Wendy Palen, Nick Dulvy, Stuart West, Nick Colegrave, Wolf Blanckenhorn, Martin Reichard and two anonymous reviewers for helpful feedback on earlier versions of this manuscript, Alex Chubaty for help with R coding, and Marianne Fish for help creating Fig. 2. Particular thanks to Pete Buston for his suggestions regarding the framework of this manuscript, Table 1 and other useful comments. This is a contribution from the Earth2Ocean Group and Project Seahorse. P.P.M. was supported by the John and Pamela Salter Charitable Trust, a BBSRC studentship 02/A1/S/08113, a Leverhulme studentship # SAS/30146, a Government of Canada post-doctoral research fellowship and Conservation International's Marine Management Area Science program. M.J.P. was supported by the National Center for Caribbean Coral Reef Research (NCORE) through EPA grant #R828020. I.M.C. and J.D.R. were supported by NSERC of Canada Discovery Grants.

References

- Allsop DJ, West SA (2003a) Changing sex at the same relative body size. *Nature* 425:783–784
- Allsop DJ, West SA (2003b) Constant relative age and size at sex change for sequentially hermaphroditic fishes. *J Evol Biol* 16:921–929
- Alonzo SH, Mangel M (2004) The effects of size-selective fisheries on the stock dynamics of and sperm limitation in sex-changing fish. *Fish Bull* 102:1–13
- Antle CE, Klimko L, Harkness W (1970) Confidence intervals for parameters of the logistic distribution. *Biometrika* 57:397–402
- Bannerot S, Fox WWJ, Powers JE (1987) Reproductive strategies and the management of snappers and groupers in the Gulf of Mexico and Caribbean. In: Polovina JJ, Ralston S (eds) *Tropical snappers and groupers: biology and fisheries management*. Westview Press, Boulder, pp 561–604

- Buston PM, Munday PL, Warner RR (2004) Sex change and relative body size in animals. *Nature* 428(6983):U1
- Charnov EL (1993) *Life history invariants*. Oxford University Press, Oxford
- Charnov EL, Skúladóttir U (2000) Dimensionless invariants for the optimal size (age) of sex change. *Evol Ecol Res* 2:1067–1071
- Chen M-H, Soong K (2002) Estimation of age in the sex-changing, coral-inhibiting snail *Coralliophila violacea* from growth striae and a mark-recapture experiment. *Mar Biol* 140:337–342
- Choat JH, Axe LM, Lou DC (1996) Growth and longevity in fishes of the family Scaridae. *Mar Ecol Prog Ser* 145(1–3):33–41
- Choat JH, Davies CR, Ackerman JL et al (2006) Age structure and growth in a large teleost, *Cheilinus undulatus*, with a review of size distribution in labrid fishes. *Mar Ecol Prog Ser* 318:237–246
- Cipriani R, Collin R (2005) Life-history invariants with bounded variables cannot be distinguish from data generated by random processes using standard analyses. *J Evol Biol* 18:1613–1618
- Clifton KE (1995) Asynchronous food availability on neighboring Caribbean coral reefs determines seasonal patterns of growth and reproduction for the herbivorous parrotfish *Scarus iserti*. *Mar Ecol Prog Ser* 116(1):39–46
- Collin R (2006) Sex ratio, life-history invariants, and patterns of sex change in a family of protandrous gastropods. *Evolution* 60(4):735–745
- Crossman DJ, Choat JH, Clements KD et al (2001) Detritus as food for grazing fishes on coral reefs. *Limnol Oceanogr* 46(7):1596–1605
- DeMartini EE, Friedlander A, Holzwarth SR (2005) Size at sex change in protogynous labroids, prey body size distributions, and apex predator densities at NW Hawaii atolls. *Mar Ecol Prog Ser* 297:259–271
- Fairhurst L, Attwood CG, Durholtz MD et al (2007) Life history of the steentjie *Spondylisoma emarginatum* (Cuvier 1830) in Langebaan Lagoon, South Africa. *Afr J Mar Sci* 29(1):79–92
- Gardner A, Allsop DJ, Charnov EL et al (2005) A dimensionless invariant for relative size at sex change in animals: explanations and implications. *Am Nat* 165(5):551–566
- Garratt PA, Govender A, Punt AE (1993) Growth acceleration at sex change in the protogynous hermaphrodite *Chrysoblephus puniceus* (Pisces: Sparidae). *S Afr J Mar Sci* 13:187–193
- Gavio MA, Orensanz JML, Armstrong D (2006) Evaluation of alternative life history hypotheses for the sand shrimp *Crangon franciscorum* (Decapoda: Caridea). *J Crust Biol* 26(3):295–307
- Ghiselin MT (1969) The evolution of hermaphroditism among animals. *Q Rev Biol* 44:189–208
- Gust N, Choat JH, Ackerman JL (2002) Demographic plasticity in tropical reef fishes. *Mar Biol* 140(5):1039–1051
- Hamilton SL, Caselle JE, Standish JD et al (2007) Size-selective harvesting alters life histories of a temperate sex-changing fish. *Ecol Appl* 17(8):2268–2280
- Heubel KU, Lindstrom K, Kokko H (2008) Females increase current reproductive effort when future access to males is uncertain. *Biol Lett* 4(2):224–227
- Jones GP (1980) Growth and reproduction in the protogynous hermaphrodite *Pseudolabrus celidotus* (Pisces: Labridae) in New Zealand. *Copeia* 1980(4):660–675
- Leigh EGJ, Charnov EL, Warner RR (1976) Sex ratio, sex change and natural selection. *Proc Natl Acad Sci USA* 73(10):3656–3660
- Linde M, Palmer M (2008) Testing Allsop and West's size at sex change invariant within a fish species: a spurious ratio or a useful group descriptor? *J Evol Biol* 21(3):914–917
- Mackie M (2003) Socially controlled sex-change in the half-moon grouper, *Epinephelus rivulatus*, at Ningaloo Reef, Western Australia. *Coral Reefs* 22:133–142
- Molloy PP, Goodwin NB, Côté IM et al (2007) Predicting the effects of exploitation on male-first sex-changing fish. *Anim Conserv* 10(1):30–38
- Munday PL, Hodges AL, Choat JH et al (2004) Sex-specific growth effects in protogynous hermaphrodites. *Can J Fish Aquat Sci* 16:323–327
- Munday PL, Buston PM, Warner RR (2006) Diversity and flexibility of sex-change strategies in animals. *Trends Ecol Evol* 21(2):89–95
- Muñoz RC, Warner RR (2003) A new version of the size-advantage hypothesis for sex change: incorporating sperm competition and size-fecundity skew. *Am Nat* 161(5):749–761
- Nee S, Colegrave N, West SA et al (2005) The illusion of invariant quantities in life histories. *Science* 309:1236–1239
- Nemtsov SC (1985) Social control of sex change in the Red Sea razorfish *Xyrichtys pentadactylus* (Teleostei, Labridae). *Environ Biol Fishes* 14(2–3):199–211
- Paddock MJ (2005) *Herbivorous coral reef fishes in a changing ecosystem*. PhD Dissertation, University of Miami

- Paddock MJ, Sponaugle S, Cowen RK (2009) Small-scale demographic variation in the stoplight parrotfish *Sparisoma viride*. *J Fish Biol* 75:2509–2526
- Policansky D (1982) Sex change in plants and animals. *Annu Rev Ecol Syst* 13:471–495
- Punt AE, Garratt PA, Govender A (1993) On an approach for applying per-recruit methods to a protogynous hermaphrodite, with an illustration for the slinger *Chrysoblephus puniceus* (Pisces: Sparidae). *Afr J Mar Sci* 13:109–119
- Robertson DR, Warner RR (1978) Sexual patterns in the labroid fishes of the western Caribbean, II: the parrotfish (Scaridae). *Smithson Contrib Zool* 255:1–26
- Schafer RE, Sheffield TS (1973) Inferences on the parameters of the logistic distribution. *Biometrics* 29(3):449–455
- Shapiro DY (1981) Size, maturation and the social control of sex reversal in the coral reef fish *Anthias squamipinnis*. *J Zool* 193:105–128
- van Rooij JM, Videler JJ (1997) Mortality estimates from repeated visual censuses of a parrotfish (*Sparisoma viridae*) population: demographic implications. *Mar Biol* 128:385–396
- van Rooij JM, Bruggemann JH, Videler JJ et al (1995) Plastic growth of the herbivorous reef fish *Sparisoma viride*: field evidence for a trade-off between growth and reproduction. *Mar Ecol Prog Ser* 122:93–105
- Vincent ACJ, Sadovy Y (1998) Reproductive ecology and the conservation and management of fishes. In: Caro TM (ed) *Behavioral ecology and conservation biology*. Oxford University Press, Oxford, pp 209–245
- Walker SPW, McCormick MI (2004) Otolith-check formation and accelerated growth associated with sex change in an annual protogynous tropical fish. *Mar Ecol Prog Ser* 266:201–212
- Warner RR (1975) The adaptive significance of sequential hermaphroditism in animals. *Am Nat* 109:61–82
- Warner RR, Swearer SE (1991) Social control of sex change in Bluehead wrasse, *Thalassoma bifasciatum* (Pisces: Labridae). *Biol Bull* 181:199–294
- Warton DI, Wright IJ, Falster DS et al (2006) Bivariate line-fitting methods for allometry. *Biol Rev Camb Philos Soc* 81:259–291
- Westneat MW, Alfaro ME (2005) Phylogenetic relationships and evolutionary history of the reef fish family Labridae. *Mol Phylogen Evol* 36:370–390
- Zar JH (1999) *Biostatistical analysis*. Prentice Hall, Englewood Cliffs