

Constant relative age and size at sex change for sequentially hermaphroditic fish

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Abstract

A general problem in evolutionary biology is that quantitative tests of theory usually require a detailed knowledge of the underlying trade-offs, which can be very hard to measure. Consequently, tests of theory are often constrained to be qualitative and not quantitative. A solution to this problem can arise when life histories are viewed in a dimensionless way. Recently, dimensionless theory has been developed to predict the size and age at which individuals should change sex. This theory predicts that the size at sex change/maximum size (L_{50}/L_{\max}), and the age at sex change/age at first breeding (τ/α) should both be invariant. We found support for these two predictions across 52 species of fish. Fish change sex when they are 80% of their maximum body size, and 2.5 times their age at maturity. This invariant result holds despite a 60 and 25 fold difference across species in maximum size and age at sex change. These results suggest that, despite ignoring many biological complexities, relatively simple evolutionary theory is able to explain quantitatively at what point sex change occurs across fish species. Furthermore, our results suggest some very broad generalities in how male fitness varies with size and age across fish species with different mating systems.

Introduction

Sex change occurs in a variety of fish, invertebrates and plants (Charnov, 1982; Policansky, 1982; also termed sex reversal or sequential hermaphroditism). Sex allocation theory provides an explanation for sex change, in terms of which species should do it, and in what direction it should be (i.e. male to female or vice versa: Warner *et al.*, 1975; Charnov, 1982). The general idea is that sex change is favoured when: (a) the reproductive value of an individual is closely related to its age or size, and (b) the relationship is different for the sexes. In this case, selection favours genes that cause an individual to first be the sex whose reproductive value increases more slowly with age, and then change to the other sex at a later stage. Although this theory has been quite successful,

tests of at what point sex change should occur, and the consequences for population sex ratios have generally been qualitative and not quantitative (Charnov, 1982; Policansky, 1982; Charnov & Bull, 1989). The reason for this is that quantitative tests require reliable estimates of the underlying trade-offs, which can be difficult to obtain (Charnov, 1982; Frank, 1987; Frank & Swingland, 1988).

Charnov & Skuladottir (2000) have recently shown that a solution to this problem lies in dimensionless life history theory (Charnov, 1993). They developed an optimization model to predict at what point sex change should occur, and then expressed the predictions dependent upon several dimensionless quantities – k/M , αM and δ . These parameters represent the relative growth rates (k , the Bertalanffy coefficient), the adult instantaneous mortality rate (M), the age at first breeding (α), and the coefficient in the equation relating male fertility to size (δ ; where male fertility is proportional to L^δ , and L is size). Charnov & Skuladottir showed that populations/species with the same values of these dimensionless quantities are predicted to have the same: (1) size at sex

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change/maximum size (L_{50}/L_{\max}); (2) age at sex change/age at first breeding (τ/α); (3) breeding sex ratio, defined as the proportion of breeders that are male. Several comparative studies have suggested that k/M and αM are invariant within taxa (reviewed by Charnov, 1993). Consequently, Charnov & Skuladottir's three predictions will hold whenever δ is similarly invariant. Importantly, the predictions can be tested quantitatively without a detailed knowledge of the relationship between size and male fertility (δ) – all that is required is that the relationship is approximately the same shape across the populations studied (e.g. squared or cubed). They provided support for their first prediction, by showing that across populations of a single shrimp species, the size at sex change/maximum size was invariant (Skuladottir & Petursson, 1999; Charnov & Skuladottir, 2000).

Here we test the first two of Charnov & Skuladottir's invariance predictions in a comparative study across 52 sex changing fish species. The extent to which these predictions are expected to hold across species depends upon variation in δ , the coefficient in the equation relating male size to fertility. We know that δ will vary between species in which sex change occurs from male to female (protogynous) to those in which it is female to male (protandry). The reason for this is that the exponent in the female fitness function is approximately 3 for fish (Charnov, 1993), and so for sex change to be favoured, $\delta < 3$ for protandrous species and $\delta > 3$ for protogynous species. However, δ may also vary within species that change sex in the same direction, due to factors such as variation in the mating system, or the occurrence of individuals that mature early into the second sex (diandry). For example, in systems where mating opportunities can be monopolized by a few large males, such as harems and leks, we might expect relatively large values of δ compared to species with more open mating systems, such as in nonterritorial schooling species or those where large aggregations are formed (Young & Martin, 1982; Warner, 1984; Coleman *et al.*, 1996). Consequently, we also test the extent to which the relationships predicted by Charnov & Skuladottir (2000) are influenced by the direction of sex change, mating system and presence of diandry.

Materials and methods

Data collection

We collected data on the sex-size frequency distribution and the ages at sex change and maturity for 61 populations from 52 different species of sex changing fish (See Table A1 in supplementary material appendix). Importantly, there is sufficient data to ensure at least one or two representative species for most of the major taxonomic groups containing sex changers (Fig. 1). We obtained these data from the literature, and by donation from currently active projects in fisheries management. We located relevant studies by: (1) searching the ISI Web of

Science database, using the key words 'sex change' + 'fish' + 'population' + 'size'; (2) searching citations in all papers found as well as reviews on the topic; (3) directly contacting researchers. The original authors collected their data by a variety of methods, including the use of traps, hook and line fishing, anaesthetic with nets, and trawls. Further details on the methodology used in different studies can be found in the relevant articles (see references to Table A1).

Our criteria for inclusion of a species in the study were that: (i) it should be a unidirectional sex changer, and (ii) if it is diandric (having a proportion of animals maturing directly or early into the second sex – which for convenience we shall term 'Early Maturers' or EM's), the dataset should either distinguish between the EM's and the true sex changers, or the population should have a minimal amount of EM's (i.e. sex change is the predominant strategy – e.g. Warner & Hoffman, 1980). These criteria were necessary to fit the assumptions of the theoretical model that we are testing (Charnov & Skuladottir, 2000), and to allow the required data to be calculated. The model does not make predictions for simultaneous hermaphrodites with sequential allocation patterns (bi-directional sex changers – Kobayashi & Suzuki, 1992; Sunobe & Nakazono, 1993; St Mary, 1997; Munday *et al.*, 1998; St Mary, 2000; Munday, 2002; Munday & Molony, 2002) and so we were unable to include them. The only exception to this is that we have included data for the cleaner wrasse *Labroides dimidiatus* despite the fact that it has recently been demonstrated to have the ability of bi-directional sex change (Kuwamura *et al.*, 2002). We include it on the basis that its normal mode of sequential hermaphroditism is unidirectional, and it would appear that it is rare and difficult for it to go the other way. We would add that this appears to be usual for the reported cases of bi-directional sex change, and that it may well be that many more instances of its occurrence will become apparent with further studies.

The size at sex change [L_{50} = size at which 50% are the second sex (male for protogynous fish, female for protandrous fish)] was calculated for each population using the logistic regression of the proportion of second sex breeders against the population body size distribution. Previous work investigating variation in size at sex change within a species has used the size of the smallest second sex individual as the 'size at sex change' (Shapiro, 1981). We chose to use the sigmoidal logistic regression curve, consistent with the method used to develop the theory that we are testing, on the basis that it provides a more statistically rigorous and quantitatively consistent estimation of the population average size at sex change. Several populations were extremely clear outliers, with an L_{50} well out of the range of the natural size distributions – for example, populations of the Lethrinid *Lethrinus lentjan* from the Seychelles (Grandcourt, 2002) have overlapping sex size distributions, which we

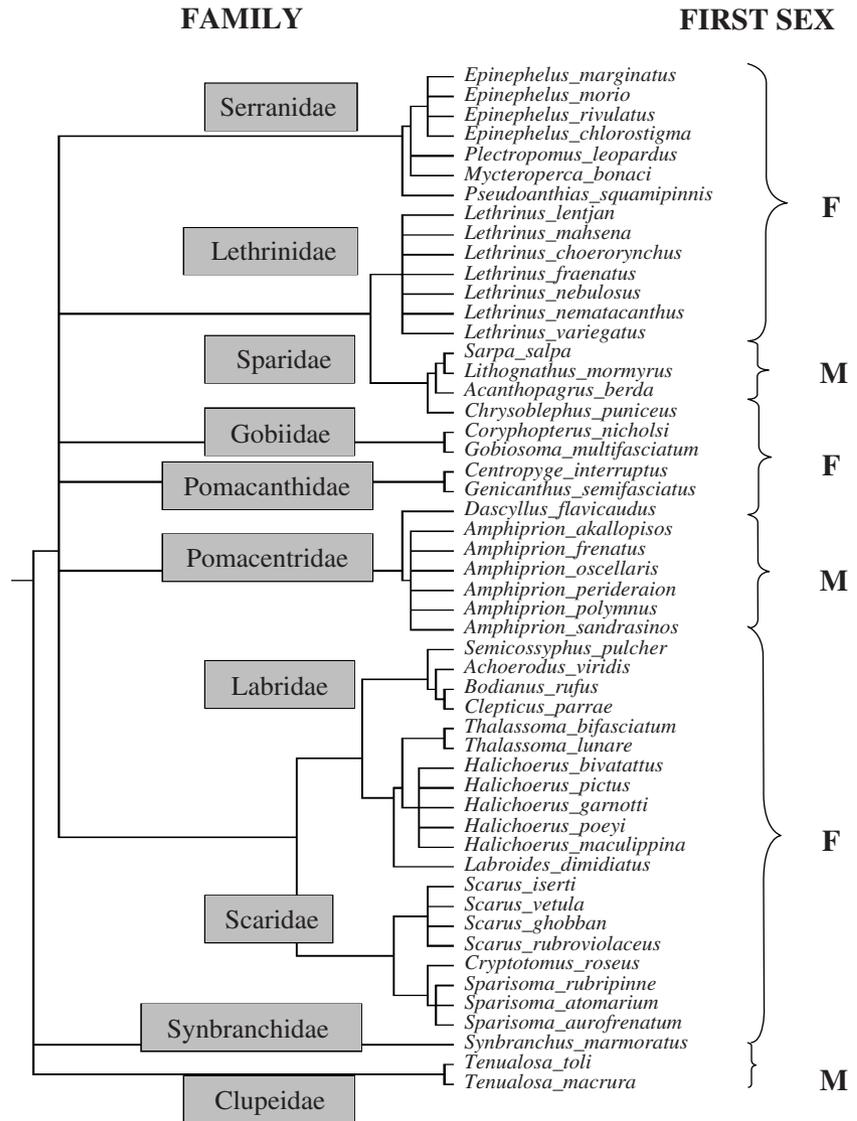


Fig. 1 The phylogeny used in our formal comparative analyses, constructed based upon molecular and morphological phylogenies (see methodology for details).

interpret to mean that very little sex change is occurring. In contrast, populations of the same species from the North West shelf of Australia (Young & Martin, 1982), show clear evidence of sex change occurring. These 'non sex-changing' populations are not suitable for testing Charnov & Skuladotir's predictions, and so were eliminated from our analysis (although this variation across populations is obviously very interesting from the perspective of why sex change is favoured).

The maximum size, L_{max} , was recorded for each population. Testing the age invariant predictions required knowledge of the age at maturity (α) and the age at sex change (τ). Fish age is calculated by rearing fish from egg, or more commonly by extracting the otoliths (ear bones) and counting the daily or annual rings therein (Jones, 1992). We were able to find adequate age

data for 15 species of sex changing fish. We were also able to obtain information on the type of mating system for five of those species.

Data on the breeding sex ratio would require detailed information on the breeding condition of all fish in the population, which ultimately can only be obtained through histological analysis of the gonads of all fish. Hence we were not able to collect this data, and so could not test Charnov & Skuladotir's third invariant prediction.

We classified mating systems on the basis of the potential for mate monopolization, where information was available. In instances where there is good opportunity for permanent mate monopolization (e.g. resource or female defence polygyny), we grouped them under the umbrella term Harem (H). If mate monopolization

occurs temporarily (at a certain time each day for instance) we term these species lekking (L). Monogamous species are termed so (M) and more open mating systems (with potentially less opportunity for mate monopolization) are termed aggregation spawners (A). The mating system is unknown for many species (U).

Statistical analyses

We tested whether the relative size (L_{50}/L_{\max}) and age (τ/α) at sex change are invariant. If these relationships are invariant then a log-log regression of the numerator against the denominator, would give a slope of 1.0. For example, a regression of $\ln(L_{50})$ against $\ln(L_{\max})$ would give a slope of 1.0. We carried out these regressions in three ways. First we carried out regressions using each sample as an independent data point. Second we averaged multiple samples from the same species, and carried out a regression using species as independent data points.

Third, we carried out an independent contrasts analysis across species. Species may not be independent data points because they are phylogenetically related (Felsenstein, 1985). This leads to problems if a trait is evolutionarily conserved or highly correlated with an unknown phylogenetically inert third variable. A formal method to control for this is to carry out an analysis with independent contrasts. Independent contrasts are derived by calculating the difference in the response and explanatory variables across pairs of species or higher nodes that share a common ancestor (Felsenstein, 1985; Harvey & Pagel, 1991). These contrasts can then be analysed by a regression through the origin; the expected value of the slope through the origin equals the true relationship between the variables in the absence of phylogenetic effects (Pagel, 1993). We carried out such an analysis with the CAIC statistical package (Purvis & Rambaut, 1995), assuming equal branch lengths.

The phylogeny for the species that we examined was constructed based upon molecular and morphological phylogenies (Fig. 1). Westneat *et al.*, pers. comm. provided detailed information for the Labridae family, which they obtained using traditional morphological techniques as well as molecular analysis of both mitochondrial and nuclear DNA. Relationships amongst the Sparidae were taken from De la Herran *et al.* (2001) and Day (2002) who used centromeric *Eco* RI and subtelomeric *Dra*I satellite DNA families and traditional morphological techniques. Lethrinid relations were obtained from Lo Galbo *et al.* (2002) who used cytochrome b gene sequence variation, and Scarid relations were taken from Streelman *et al.* (2002) using nearly 2 kb of nuclear and mitochondrial DNA sequence. We obtained higher order relationships and that of any groups for which we could not readily locate information from Nelson (1994).

We carried out regression analyses using two methods. The use of standard Ordinary Least Squares (OLS)

regression is based upon the assumption that the x variable is fixed or controlled by the observer (i.e. no error in the x term). This is the most commonly used method of estimating the functional relationship between biological variables, and yet its assumptions are often violated, leading to a biased slope estimate. Although we may often be more confident of our estimates of the x variables in our analyses, they are clearly subject to measurement error. A possible solution to this problem is to carry out a Major Axis (MA) regression. MA (or Model II) regression is used when there may be no causal structure between the y and the x variable and they are both measured with equal error. The MA produces a line that minimizes the sum of the squared deviations perpendicular to itself. In order to examine any effect of error assumptions, we repeated all analyses using both OLS and MA regression (Gemmell *et al.*, 1999), using SYSTAT 10.2.

Results

The species presented here span a size range from 27 mm maximum length for the Caribbean goby *Gobiosoma multifasciatum* to 1500 mm maximum length for the Western Atlantic serranid *Mycteroperca bonaci*. The fish range in age at sex change from 9 months for the tropical shad *Tenuulosa macrura* to 18 years for the wrasse *Achoerodus viridis*. The analysis contains 52 species representing three orders within the class Actinopterygii, and ten families (see Fig. 1). Of the 52 species, 11 are protandric (change sex from male to female) (see Table A1 and Fig. 1). The remaining 41 species are protogynous (change sex from female to male), and of those, ten species are definitely known to have early maturing fish (EM's) of the second sex.

Size invariant

The relationship between L_{50} and L_{\max} shows a slope not significantly different from 1 (Fig. 2). This suggests that the ratio of L_{50}/L_{\max} is invariant across species, and that fish are changing sex at a constant proportion of their maximum size. This result holds when the data are analysed with populations as data points [OLS: intercept = -0.22 ($\pm 95\%$ C.I.) ± 0.24 , slope = 0.99 ± 0.04 , $r^2 = 0.971$, $n = 61$; MA: intercept = -0.29 ± 0.24 , slope = 1 ± 0.05], species as data points (OLS: intercept = -0.25 ± 0.28 , slope = 0.99 ± 0.28 , $r^2 = 0.967$, $n = 52$; MA: intercept = -0.33 ± 0.28 , slope = 1 ± 0.06), or the method of independent contrasts (OLS: slope = 0.98 ± 0.098 , $r^2 = 0.982$, $n = 25$; MA: slope = 0.98 ± 0.08). Figure 2 shows the OLS regression with species as independent data points. The average value across species of L_{50}/L_{\max} was 0.79.

When comparing across species, the relationship between L_{50} and L_{\max} is not influenced significantly by: (1) the mating system, comparing species that are

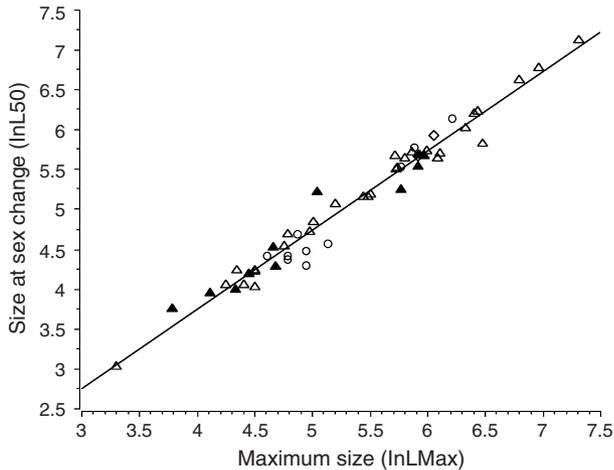


Fig. 2 A logarithmic plot of the size at sex change (L_{50}) vs. maximum size (L_{max}) for 52 species of sex changing fish (species as independent data points). The slope of the relationship (0.99) is not significantly different from 1.0 (95% C.I. ± 0.28 ; $r^2 = 0.967$), suggesting that fish change sex at a constant proportion (0.79) of their maximum size. Filled symbols are for protandrous fish (change sex from male to female), open symbols for protogynous fish (change sex from female to male). The presence or absence of Early Maturing fish of the second sex is shown by the shape of the symbols. A circle represents Diandric species (with EM's present), a triangle represents Monandric species (EM's absent) and a diamond represents fish for which we are unsure of the status for EM's.

monogamous, lekking, form harems, or aggregations (ANCOVA, Intercept: $F_{3,25} = 0.63$, n.s.; Slope: $F_{3,25} = 0.55$, n.s.); or (2) comparing species in which the first sex is male (protandry) or female (protogyny) (ANCOVA, Intercept $F_{1,48} = 3.27$, n.s.; Slope $F_{1,48} = 3.03$, n.s.), although these values are close to significance. However, when we looked at the effects of the presence of early maturing individuals of the second sex (i.e. whether a species is monandric or diandric) we did see a significant difference in both the slope and the intercept (ANCOVA, Intercept: $F_{1,46} = 5.2$, $P < 0.05$; Slope: $F_{1,46} = 4.5$, $P < 0.05$, $r^2 = 0.971$). However, the separate regression models are still showing a positive relationship between L_{50} and L_{max} , and the slopes of the respective relationships are still not significantly different from 1 (monandrics: Intercept: -0.12 ± 0.28 , Slope: 0.98 ± 0.046 , $n = 40$, Diandrics: Intercept: -1.3 ± 1.3 , Slope: 1.2 ± 0.25 , $n = 10$). Adding in the presence of EM's as an explanatory variable increases r^2 by 0.004, from 0.967 to 0.971.

Age invariant

Similarly the relationship between τ/α (age at sex change/age at maturity) shows a slope not significantly different from 1 (Fig. 3). This suggests that the ratio of τ/α (relative age of sex change) is invariant across species,

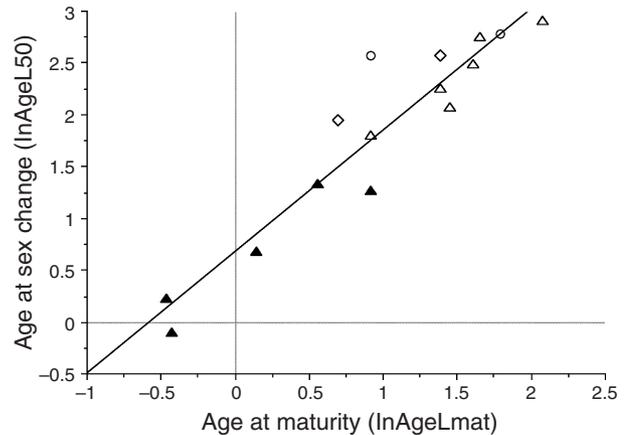


Fig. 3 A logarithmic plot of the age at sex change (τ) vs. the age at maturity (α) for 15 species of sex changing fish (species as independent data points). The slope of the relationship (1.17) is not significantly different from 1.0 (95% C.I. ± 0.25 ; $r^2 = 0.885$), suggesting that fish change sex at a constant ratio (2.5) to their age at maturity. Filled symbols are for protandrous fish (change sex from male to female), open symbols for protogynous fish (change sex from female to male). The presence or absence of Early Maturing fish of the second sex is shown by the shape of the symbols. A circle represents Diandric species (with EM's present), a triangle represents Monandric species (EM's absent) and a diamond represents fish for which we are unsure of the status for EM's.

and that fish are changing sex at a constant multiplier of their age at maturity. This result holds when the data are analysed with populations as data points [OLS: intercept = $0.66 (\pm 95\% \text{ C.I.}) \pm 0.27$], slope = 1.12 ± 0.21 , $r^2 = 0.872$, $n = 21$; MA: intercept = 0.56 ± 0.28 , slope = 1.22 ± 0.23], species as data points (OLS: intercept = 0.69 ± 0.3 , slope = 1.17 ± 0.25 , $r^2 = 0.885$, $n = 15$; MA: intercept = 0.59 ± 0.33 , slope = 1.26 ± 0.27) or independent contrasts (OLS: slope = 0.99 ± 0.48 , $r^2 = 0.753$, $n = 11$; MA: slope = 1.3 ± 0.69). Figure 3 shows the OLS regression with species as independent data points. The average value across species of τ/α was 2.5.

As with the size invariant analysis, when comparing across species, the relationship between τ and α is significantly influenced by the occurrence of EM's (ANCOVA, Intercept: $F_{1,9} = 14.5$, $P < 0.01$; Slope: $F_{1,9} = 7.8$, $P < 0.05$, $n = 13$, $r^2 = 0.943$). However this analysis is limited as there are only two samples for diandric species within the age data. Our dataset on mating systems for fish where we have age information was also too small to make meaningful inference ($n = 5$), although a nonsignificant ANCOVA is suggestive that the type of mating system has no effect on the relationship between τ and α . Comparing species in which the first sex is male (protandry) or female (protogyny), there was a significant difference on the intercept (ANCOVA,

$F_{1,11} = 10.2$, $P < 0.01$), but not the slope (ANCOVA, $F_{1,11} = 1.35$, n.s.) of the relationship between τ and α ($n = 15$, $r^2 = 0.940$). This means that fish are changing sex at a constant ratio of their age at maturity, but that this proportion differs between protandrous and protogynous species – protogynous species change sex at a higher ratio of their age at maturity. Adding in ‘first sex’ as an explanatory variable increased r^2 by 0.055, from 0.885 to 0.940.

Discussion

Sex change invariants in fish

We have demonstrated two life history invariants for sex change across several fish species. First, fish change sex at a constant proportion of their maximum size – the size at sex change divided by the maximum size (L_{50}/L_{\max}) is 0.79. Second, fish change sex at a constant ratio of their age at maturity – the age at sex change divided by the age at maturity (τ/α) is 2.5. Given the differences across species in life history and method of data collection, the degree of invariance observed is striking, especially for the size at sex change invariant, where $r^2 = 0.967$. More noise is observed with the age at sex change invariant, where $r^2 = 0.885$, but this could be explained by the relative imprecision involved in estimating fish age (see materials and methods section and Bell, 2001). Of course, it is not surprising that individuals of larger fish species change sex when bigger and older. What is surprising is that when viewed dimensionlessly, they change sex at the same relative size and age.

Charnov & Skuladottir's (2000) model predicts these two invariants if δ , the exponent in the male fitness function is invariant. Although the two invariants hold very well across all species examined, as shown by the r^2 values, our data also suggest that slightly different invariants hold: (i) for the size at sex change depending upon whether EM's of the second sex occur (diandry); (ii) for the age at sex change invariant dependent upon the occurrence of diandry and the direction of sex change (male or female first). These effects could be expected as they are factors that may be expected to influence δ . However, their biological significance is not clear because: (i) they lead to a very small increase in the amount of variance explained (e.g. r^2 for size at sex change increases from 0.967 to 0.971), that is statistically significant because r^2 is extremely high and consequently the error (residual) variance is so low; (ii) they often rely on analyses with subsets of the data where we have the relevant information, and a small number of data points. Indeed, the most striking point is that these factors have very little explanatory power for the size and age of sex change. This suggests that the value of δ : (a) is approximately invariant across fish species that change sex in the same direction; (b) for protandrous and protogynous species is such that it favours sex change at the same

relative size and age. We are currently extending theory in order to address this, and to use the size at sex change data to indirectly estimate δ .

Our results suggest that Charnov & Skuladottir's (2000) model can quantitatively explain when sex change occurs across fish species. This is particularly remarkable because the model ignores many biological details in which there is variation, such as the mating system (from harems, leks and monandry to large temporary spawning aggregations), maximum size and age, the presence of early maturing individuals of the second sex, and the cues and mechanisms involved in determining when sex change occurs. Instead, their model approximates all sex changing species by a single life history, with fitness being related to size raised to the power δ in males, and size raised to the power three in females. The fact that the invariant occurs across fish species therefore suggests that their approximation captures the important points of the underlying biology extremely well for fish. To give a specific example, the cues/mechanisms involved in sex change have been the subject of much debate (Warner *et al.*, 1975; Shapiro, 1979; Shapiro & Lubbock, 1980; Shapiro & Boulon, 1982; Charnov, 1986; Warner, 1988a, b; Lutnesky, 1996; St Mary, 1997; Munday, 2002). Charnov & Skuladottir's (2000) model assumes that fitness depends primarily upon size (age), and so sex change occurs when individuals reach a certain size (age). However, it has been argued that in some species fitness depends upon the social environment, and that sex change occurs in response to the local ratio of females to males (Shapiro & Lubbock, 1980). Our empirical support for Charnov & Skuladottir's (2000) model suggests that assuming a fixed relationship between body size and fitness provides a very good approximation irrespective of the underlying mechanism controlling when sex change occurs.

How do our results compare with previous research in this area? To our knowledge, this is the first comparative study across species on size and age at sex change. Previous empirical work has focused on either: (i) determining why and when sex change takes place in specific species (Shapiro, 1981; Cole, 1983; Hoffman *et al.* 1985; Lejeune, 1987; Warner & Swearer, 1991; Gillanders, 1995); (ii) descriptive work on if, in what direction and when sex change takes place for several species (Choat & Robertson, 1975; Robertson & Warner, 1978; Warner & Robertson, 1978; Kobayashi & Suzuki, 1992), or (iii) descriptive physiology of the gonads of several sex changing species (Cole, 1988; Cole & Shapiro, 1990; Cole *et al.* 1994). To an extent this has been because theoretical work prior to Charnov & Skuladottir (2000) has been phrased in terms of relatively hard to measure life history parameters, and so has been less useful for making testable quantitative predictions across species (Warner *et al.* 1975; Charnov *et al.*, 1976; Leigh *et al.* 1976; Charnov, 1979a). Although, there have been some related notable studies across populations of the same

species, on the amount of individuals that mature early as the second sex (Charnov, 1979b, 1982; Charnov & Andersson, 1989; Charnov & Hannah, 2002).

Future directions

As with other discoveries of dimensionless life history invariants, our results pose numerous questions, and suggest a number of future directions (Charnov, 1993). (1) Are Charnov & Skuladottir's (2000) invariant predictions model dependent, or can they be made with other approaches/assumptions? (2) Do the invariant rules that we have demonstrated across fish also hold within species (Charnov & Skuladottir, 2000)? This seems quite likely given that we would expect less variation in δ between populations of the same species than between species. (3) Do the invariant rules hold in other taxa where sex change occurs? If so, do they lie on the same slope as the fish? Differences within or between taxa would reflect fundamental differences in trade-offs linking growth, reproductive success and mortality, which in turn might be reflections of general differences in energetic/growth schedules (Charnov, 1993). (4) Is the breeding sex ratio invariant, within or across species? This invariant has yet to be tested because breeding sex ratios are difficult to estimate. (5) Is δ really invariant across species? If so, does this reflect some underlying fundamental constraint associated with sex change? (6) Several other areas of sex allocation, such as condition dependent sex ratio adjustment and environmental sex determination rely on the same underlying theory as sex change (Charnov, 1982; Frank & Swingland, 1988). Can similar invariant predictions be made for these areas?

Conclusions

Our results demonstrate the novel insights that may be gained with a dimensionless approach to evolutionary theory. A general problem in evolutionary biology is that quantitative tests of theory require a detailed knowledge of the underlying trade-offs, which can be very hard to measure (Stearns, 1992). The advantage of the invariant predictions that we have tested here is that they allow quantitative tests without a detailed knowledge of the underlying trade-off function – in this case, how male fertility changes with size or age. Within the field of sex change, it is no coincidence that the previously most striking quantitative success, predicting the proportion of individuals that mature as the second sex (Charnov, 1982), relied on theory that similarly finessed away this problem. Another advantage of this approach is that it may provide a useful indirect approach to understanding the more intractable breeding systems, such as the massive breeding aggregations observed in many of the commercially important grouper species (Shapiro *et al.*, 1993). To date the processes involved in sex ratio regulation of these large aggregations have remained

elusive, despite its possible importance for stock management (Tupper, 1999). If, as the theory suggests, the invariants demonstrate that the males of all of these species share similarly shaped trade-off curves linking size to reproductive value (δ), then we might reasonably assume that the unknown mating systems will turn out to approximate some form of mate monopolization (for protogynous species, *sensu* Robertson & Choat, 1974; Robertson & Warner, 1978; Warner & Robertson, 1978; Warner, 1988b).

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Supplementary material

The following material is available from:
<http://www.blackwellpublishing.com/products/journals/suppmat/JEB/JEB590/JEB590sm.htm>

Appendix S1. Species used in the current study.

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