

# Rapid human-induced divergence of life-history strategies in Bahamian livebearing fishes (family Poeciliidae)

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## Summary

1. Human-induced rapid environmental change (HIREC) can have dramatic impacts on ecosystems, leading to rapid trait changes in some organisms and extinction in others. Such changes in traits signify that human actions can lead to cases of increased phenotypic diversity and consequently can strongly impact population-, community- and ecosystem-level dynamics.

2. Here, we examine whether the ecological consequences of habitat fragmentation have led to changes in the life histories of three native species of mosquitofish (*Gambusia* spp.) inhabiting tidal creeks on six different Bahamian islands. We address two important questions: (i) How predictable and parallel are life-history changes in response to HIREC across islands and species, and (ii) what is the relative importance of shared (i.e. parallel) responses to fragmentation, differences between species or islands and species- or island-specific responses to fragmentation?

3. Phenotypic differences between fragmentation regimes were as great or greater than differences between species or islands. While some adult life histories (lean weight and fat content) showed strong, shared responses to fragmentation, offspring-related life histories (embryo fat and fecundity) exhibited idiosyncratic, island-specific responses. While shared responses to fragmentation appeared largely driven by a reduction in piscivorous fish density, increased conspecific density and changes in salinity, we found some evidence that among-population variation in male reproductive investment and embryo fat content may have arisen via variation in conspecific density.

4. Our results suggest that phenotypic responses to HIREC can be complex, with the predictability of response varying across traits. We therefore emphasize the need for more theoretical and empirical work to better understand the predictability of phenotypic responses to human-induced disturbances.

**Key-words:** anthropogenic habitat modification, biodiversity, competition, conservation, *Gambusia*, habitat fragmentation, population density, predation

## Introduction

Negative impacts of human activities on biodiversity and ecosystem functioning are widespread and well documented (Vitousek *et al.* 1997; Brooks *et al.* 2006; Barnosky *et al.* 2011). While we have made considerable

advances in our understanding of the ecological consequences of human-induced rapid environmental change (HIREC) during the past decades, we still have much to learn about the phenotypic consequences of HIREC (Stockwell, Hendry & Kinnison 2003; Hendry, Farrugia & Kinnison 2008). Because ecological processes are directly influenced by organismal phenotypes, we need to better understand impacts of human actions on the

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phenotypes of organisms living in human-altered environments. Only armed with this understanding can we better mitigate unwanted consequences of human activities (Carroll, Kinnison & Bernatchez 2011; Carroll *et al.* 2014; Smith *et al.* 2014).

The fact that HIREC can drive rapid trait changes in many organisms is now well recognized; however, two important questions stemming from this observation have so far received little attention: (i) How often does HIREC facilitate phenotypic diversification and speciation, and (ii) how predictably do organisms respond adaptively to HIREC? In the initial steps towards answering these questions, we need studies that investigate the predictability with which certain human activities drive rapid phenotypic divergence.

Habitat fragmentation represents one of the strongest and most pervasive anthropogenic environmental impacts, affecting both terrestrial and aquatic habitats, and generally leads to decreased biodiversity due to disruptions of species' behaviours, life histories, physiology or interactions with other species (Fahrig 2003; Ewers & Didham 2006; Fischer & Lindenmayer 2007). However, not all species suffer population declines or extirpations in the face of fragmentation; some resilient species actually increase in abundance in disturbed habitats, because they can tolerate or adapt to new environmental conditions (Fahrig 2003; Layman *et al.* 2004; Devictor, Julliard & Jiguet 2008). Thus, conditions that comprise an ecological catastrophe for one species might represent ecological opportunity for another, setting the stage for phenotypic diversification (Wellborn & Langerhans 2015). Resilient species that persist in degraded environments can experience altered abiotic conditions, predation pressures, parasite communities, interspecific competition and increased intraspecific competition owing to elevated population densities – these ecological changes likely result in markedly different selection regimes. Thus, resilient species should exhibit phenotypic shifts within fragmented areas, potentially including changes in life history, which in turn can strongly impact population dynamics (Fahrig 2003; Fischer & Lindenmayer 2007; Rypel & Layman 2008; Ozgul *et al.* 2010).

To better understand how resilient organisms cope, and even thrive, in the face of anthropogenic disturbances, we need to uncover the predictability and generality of rapid phenotypic responses to human activities. Employing an explicitly predictive approach – where one predicts phenotypic responses to anthropogenic habitat change using ecological and evolutionary theory, functional understanding of organismal traits and natural-history knowledge of a study system – allows us to gauge the predictability of trait changes (Langerhans 2008; Langerhans & Reznick 2010). We further need to understand the generality, or frequency, with which organisms exhibit certain patterns of phenotypic responses to human-induced environmental change. Rather than simply cataloguing a list of taxa that show human-induced trait changes, we

instead wish to uncover how multiple populations and species exhibit similar (parallel) and unique (non-parallel) phenotypic shifts subsequent to anthropogenic impacts (Franssen *et al.* 2013; Heinen-Kay *et al.* 2014; Merila & Hendry 2014; Giery, Layman & Langerhans 2015). This type of knowledge can aid in restoration and conservation efforts and also help mitigate the negative impacts of HIREC on human health and economies (Pimentel *et al.* 2000; Carroll *et al.* 2007).

Aquatic ecosystem fragmentation (i.e. interruption of hydrologic connectivity) is widespread and results in considerably altered ecological conditions (e.g. March *et al.* 2003; Cooney & Kwak 2013). Here, we use Bahamian tidal creeks to investigate impacts of human-induced fragmentation on the life histories of three native species of mosquitofish from six different islands. More specifically, we asked two questions: (i) How predictable and parallel are life-history changes in response to human-induced habitat fragmentation across islands and species, and (ii) what is the relative importance of shared (i.e. parallel) responses to fragmentation, differences among species or islands and species- or island-specific responses to fragmentation in explaining life-history variation? Based on changes in extrinsic mortality rate (i.e. the reduction of piscivorous fish density), combined with increased resource competition due to elevated conspecific density (Layman *et al.* 2004; Valentine-Rose *et al.* 2007a; Araújo *et al.* 2014; Heinen-Kay *et al.* 2014; see 'Materials and methods' section below), we formulated a set of specific *a priori* predictions for life-history shifts in fragmented systems (Table 1). We use comparative analyses to address our two primary questions and test our *a priori* predictions.

## Materials and methods

### STUDY SYSTEM AND ECOLOGICAL MEASUREMENTS

Tidal creeks in The Bahamas typically comprise small watersheds and are characterized by shallow, tidally influenced estuaries with a relatively narrow creek mouth that broadens landward. The dominant emergent vegetation is red mangrove (*Rhizophora mangle*). Most of the water flux in these systems arises from tidal exchange (freshwater input only provided via rainfall and aquifer percolation), so salinities are typically around 30–35, with marine taxa comprising the biotic communities (Layman *et al.* 2004; Valentine-Rose *et al.* 2007a,b). From the late 1950s through the early 1970s, a large number of roads were constructed throughout The Bahamas, many of which fragmented tidal creeks. This dramatically reduced tidal exchange (tidal amplitude ~0–5 cm vs. ~50–80 cm in unfragmented creeks), typically leading to greater extremes in dissolved oxygen and temperature, increased sedimentation rates, reduced animal biomass and changes in community composition of fishes, macroinvertebrates, and plants and macroalgae (Valentine-Rose *et al.* 2007a,b; Valentine-Rose & Layman 2011; Valentine-Rose, Rypel & Layman 2011). Congruent with patterns observed in other fragmented ecosystems (e.g. Devictor, Julliard & Jiguet 2008), fragmented Bahamian tidal creeks are usually dominated by small, generalist species such as

**Table 1.** Predicted and observed life-history shifts in response to tidal-creek fragmentation in mosquitofishes from The Bahamas (see main text for details). Predictions were derived from life-history theory (e.g. Gadgil & Bossert 1970; Jørgensen, Auer & Reznick 2011) and previous studies on the effects of differential predation and competition (including changes in resource availability) on life histories and body morphology in poeciliid fishes

Trait	Prediction	Selective/ Inducing agent	Supported by this study (Y) or not (N)
Body size	Larger*	Predation, Competition	Predation: N, Competition: Y
Adult lean weight	Smaller*	Predation, Competition	Predation: Y, Competition: Y
Adult body fat	Greater	Predation	Predation: Y
Female reproductive investment (RA)	Reduced Reduced*	Competition Predation	Competition: N Predation: N
Male reproductive investment (GSI)	Greater*	Competition (Sperm Competition)	Competition: N
Fecundity	Reduced* Reduced*	Predation Predation, Competition	Predation: N Predation: N, Competition: N
Embryo lean weight	Larger*	Predation, Competition	Predation: N, Competition: N
Embryo fat content	Greater	Competition	Competition: Suggestive

\*Predicted trait shifts that most likely could reflect evolutionary (i.e. heritable) responses rather than solely ecological responses (i.e. phenotypic plasticity; e.g. Reznick & Bryga 1987; Reznick, Bryga & Endler 1990; Reznick, Butler & Rodd 2001; Johnson 2002; Langerhans *et al.* 2004; Langerhans, Gifford & Joseph 2007; Bashey 2008; Riesch, Martin & Langerhans 2013).

mosquitofishes (genus *Gambusia*) and sheepshead minnow (*Cyprinodon variegatus*), while the density of top predators (e.g. piscivorous fishes) is severely decreased or predators are absent (Layman *et al.* 2004; Valentine-Rose *et al.* 2007a). Although piscivorous fishes represent the primary predators of Bahamian mosquitofish in these systems, avian predators also occur, but do not differ in abundance or composition between fragmented and unfragmented sections of tidal creeks (Chacin *et al.* 2015).

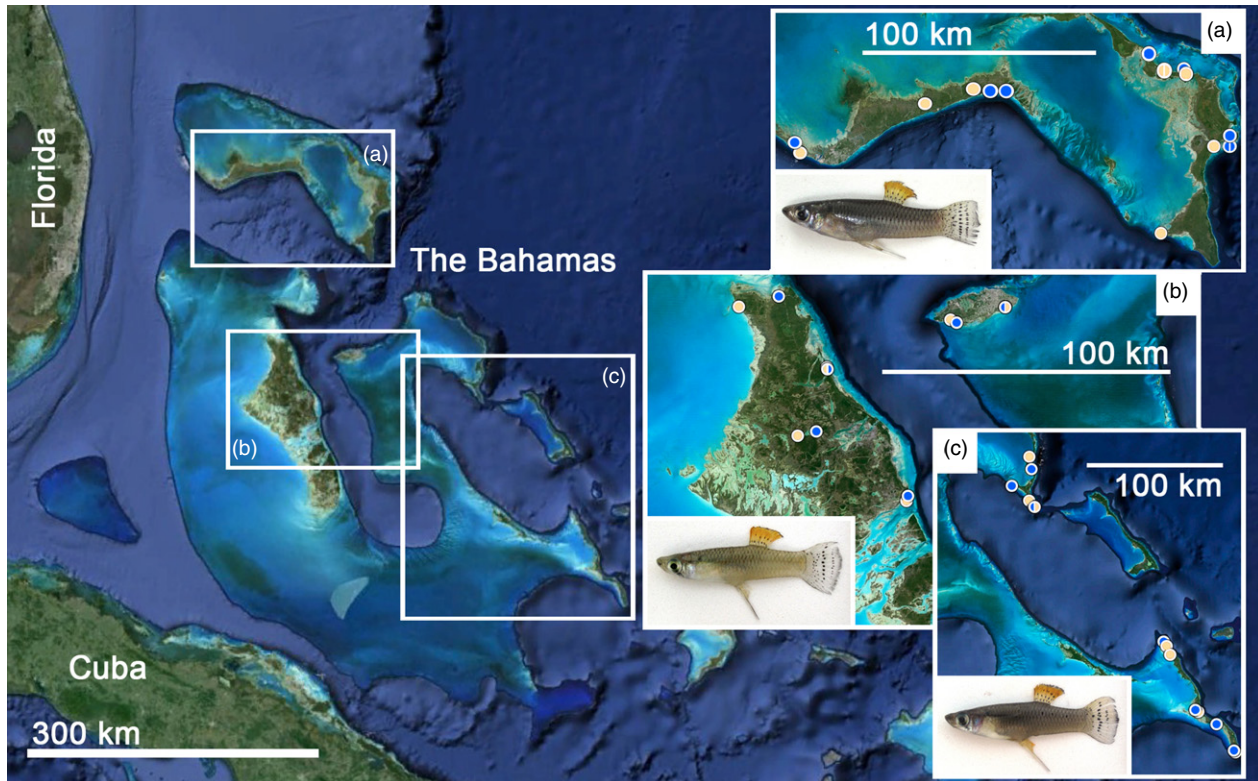
Mosquitofish and other livebearing fishes of the family Poeciliidae serve as classical models for studying how ecological factors shape life histories (e.g. Reznick & Endler 1982; Johnson 2002; Reznick, Bryant & Bashey 2002; Riesch, Martin & Langerhans 2013). The Bahama Archipelago harbours three endemic species of *Gambusia* that form a monophyletic clade of closely related species (originating ~1.7–4.8 million years ago), all of which are allopatric within tidal creeks: *Gambusia hubbsi* inhabits north-western islands of the Great Bahama Bank, *G. manni* inhabits eastern and southern islands of the Great Bahama Bank, and a yet unnamed species, *G. sp.*, inhabits the islands of the Little Bahama Bank (Heinen-Kay *et al.* 2014). We collected Bahamas *Gambusia* from 42 tidal creek populations (21 fragmented and 21 unfragmented) across six islands in The Bahamas in March–April 2010 using dip nets and minnow traps (Table S1, Supporting information). For each of the three species, we collected multiple populations from both fragmented and unfragmented tidal creeks

on two separate islands (Fig. 1). Immediately after collection, we euthanized all fish in an aqueous solution of tricane methanesulfonate (MS 222) and preserved them in 95% ethanol.

Simultaneous with fish collections, we measured three abiotic variables and three biotic variables: salinity, pH, dissolved oxygen, *Gambusia* density, piscivorous fish density and number of piscine competitor species. We chose these variables in an effort to capture some of the major factors that vary among tidal creeks and could influence life-history traits for reasons including metabolic constraints, intraspecific resource competition, extrinsic mortality regime and interspecific resource competition. We focus on predation and competition as major agents of phenotypic change for our *a priori* predictions (see Table 1), but included the abiotic variables to additionally control for their potential influence on life histories. We measured salinity and dissolved oxygen ( $\text{mg L}^{-1}$ ) using a YSI 85 (Yellow Springs, OH, USA), and pH using a Hanna HI 98128 hand-held meter. We measured conspecific *Gambusia* density using quadrat surveys, in which we counted all *Gambusia* individuals within 20 0.25-m<sup>2</sup> quadrats randomly selected across the microhabitats where *Gambusia* were observed within each creek (all quadrats > 2 m apart). The observer approached each pre-designated quadrat, stood still 1 m from the quadrat and waited 1 min prior to counting fish. We used the average of these 20 quadrat counts to calculate our estimate of *Gambusia* density ( $\# \text{m}^{-2}$ ) for each site. This method proved effective due to water clarity and these fishes' tendency to be unaffected by our presence (see also Araújo *et al.* 2014).

We measured density of piscivorous fish using underwater visual census (UVC) methods (Nagelkerken *et al.* 2000; Layman *et al.* 2004), which provides reliable estimates of relative predator densities of Bahamian tidal creeks (Layman *et al.* 2004; Valentine-Rose *et al.* 2007a; Valentine-Rose, Rypel & Layman 2011). In sites with water depths too shallow for UVC, we conducted predator surveys from above water by slowly walking the survey areas (all piscivores readily visible from above in these clear waters). We conducted roving-diver visual surveys covering c. 3000 m<sup>2</sup> within each creek, encompassing the region where we collected *Gambusia*. We included the following piscivorous fish species in our counts: barracuda (*Sphyraena barracuda*), needlefish (*Strongylura notata*), snappers (*Lutjanus* spp.), tarpon (*Megalops atlanticus*), Nassau grouper (*Epinephelus striatus*), jacks (*Caranx* spp.) and lionfish (*Pterois* spp.). Nearly all of the predators encountered in our surveys comprised known predators of *Gambusia* – barracuda, needlefish and snappers (>99%) – with other potential predators rarely observed. We used our survey counts to calculate piscivore density ( $\# \text{m}^{-2}$ ) for each site. We measured the number of potential competitor fish species by recording, during our UVC surveys, the presence/absence of species from a fairly broad list of potential competitors according to prior diet studies: sheepshead minnow (*Cyprinodon variegatus*), crested goby (*Lophogobius cyprinoides*), yellow fin mojarra (*Gerres cinereus*), mojarra (*Eucinostomus* spp.), redear herring (*Harengula humeralis*), hardhead silverside (*Atherinomorus stipes*), sergeant major (*Abudefduf saxatilis*) and beaugregory (*Stegastes leucostictus*). Our snapshot estimates of these ecological variables provide meaningful values for comparison among tidal creeks, as variables exhibit significant repeatability based on multiple measurements across multiple years within a subset of 12–24 tidal creeks (see Heinen-Kay *et al.* 2014 for repeatability of five factors examined here; repeatability of competitor species richness based on surveys for 20 tidal creeks across 2–5 years: intraclass correlation coefficient  $r = 0.85$ ,  $P < 0.0001$ ).





**Fig. 1.** Map of sampling localities of three different *Gambusia* species in The Bahamas. Blue (dark grey) circles indicate the location of unfragmented tidal creeks; beige (light grey) circles indicate the location of fragmented tidal creeks. (a) Islands of Grand Bahama (left) and Abaco (right): male *Gambusia* sp. depicted; (b) islands of Andros (left) and New Providence (right): male *G. hubbsi* depicted; (c) islands of Eleuthera (left) and Long Island (right): male *G. manni* depicted. Maps created with GOOGLE EARTH VS. 7.1.2.2041 (Google Inc., Mountain View, CA, USA).

#### LIFE-HISTORY MEASUREMENTS

Samples of a maximum of 10 mature male and 10 pregnant female Bahamian *Gambusia* were randomly selected from collections made at each site (total of 637 individuals; Table S1); however, for several sites we were not able to collect enough pregnant females for reliable analyses, resulting in a lower number of population replicates for females ( $N = 24$  tidal creek populations). Following the protocol of Reznick & Endler (1982), all preserved fish were weighed and measured for standard length. In the case of females, the reproductive tissue and all developing offspring were removed. Offspring were counted and their stage of development determined (Riesch *et al.* 2011). Somatic tissues, reproductive tissues and embryos were then dried for 24 h at 55 °C and weighed again. To assess female and embryo condition, somatic tissues and embryos were rinsed up to six times for at least 6 h in petroleum ether to extract soluble non-structural fats (Heulett, Weeks & Meffe 1995; Riesch, Martin & Langerhans 2013) and were then redried and reweighed. Furthermore, we calculated reproductive allocation (RA) by dividing offspring weight by the sum of offspring weight plus somatic dry weight (Reznick & Endler 1982; Riesch, Martin & Langerhans 2013). In the case of males, we calculated the gonadosomatic index (GSI) by dividing a male's reproductive tissue dry weight by the sum of reproductive tissue dry weight and somatic dry weight (Riesch, Martin & Langerhans 2013). Males were classified as mature based on

the complete development of the terminal structures of their modified anal fin (i.e. gonopodium; Heinen-Kay *et al.* 2014), following methods similar to those described by Turner (1941).

In total, we measured seven life-history traits. For both males and females, we measured standard length [SL (mm)], lean weight (g; a good proxy for muscle mass), fat content (%) and investment into reproduction [males: GSI (%), females: RA (%)]. For females, we also measured the offspring-related traits fecundity (no. developing offspring), offspring lean weight (mg) and offspring fat content (%).

We then  $\log_{10}$ -transformed (male/female SL, male/female lean weight and embryo dry/lean weight), square-root-transformed (fecundity) or arcsine (square root)-transformed (male/female fat content, embryo fat content, female RA and male GSI) all life-history variables to meet assumptions of statistical analyses (i.e. these transformations greatly facilitated normality of model residuals). To remove size/allometry effects on life-history traits other than SL, we regressed these variables against SL (and for females also embryonic stage of development) separately for each sex, and used residuals from these models in all subsequent analyses. We first tested for heterogeneity of slopes among fragmentation regimes and only found two cases of heterogeneity of slopes, female lean weight ( $P = 0.0130$ ) and male fat content ( $P = 0.0108$ ). Because slopes were only moderately different (virtually identical for female lean weight), and because differences in intercept were far greater than differences in slope, we pooled individuals within sexes to calculate all residuals for analysis.

## STATISTICAL ANALYSES

We calculated population averages for each life-history variable and used these mean values in analyses ( $n = 42$  for males,  $n = 24$  for females; Table S1). To examine shared responses to fragmentation across all species and islands, differences between species, differences between islands for each species, species-specific responses to fragmentation and island-specific responses to fragmentation, we conducted three different multivariate analysis of variance (MANOVA) models, one for adult male life histories (male SL, male lean weight, male fat content and GSI), one for adult female life histories (female SL, female lean weight, female fat content and RA) and one for offspring-related life histories (fecundity, offspring lean weight and offspring fat content). In each case, the life-history variables served as dependent variables, and fragmentation regime, species, island nested within species, interaction between fragmentation and species and interaction between fragmentation and island nested within species served as independent variables. However, because the interaction between fragmentation and species was consistently non-significant in all models (all  $P > 0.41$ ), indicating that species did not exhibit differential responses to fragmentation, we excluded that term from all final models. We evaluated the relative importance of model terms by calculating the multivariate effect size using Wilks's partial  $\eta^2$  (measure of partial variance explained by a particular term, see Langerhans & DeWitt 2004). To interpret MANOVA results, we examined standardized canonical coefficients for the major canonical axes derived from each model term and conducted *post hoc* univariate analyses. In so doing, we can uncover which life-history traits were most influential in driving effects of each model term.

To evaluate which particular abiotic and biotic variables might underlie inter-population variation in life-history traits, we used a backward-elimination stepwise regression model selection approach for each trait. In each case, we forced the inclusion of model terms for species and island nested within species so that we could more directly examine causal mechanisms explaining among-population variation within islands. We then performed backward stepwise regression using general linear models with possible model terms for salinity, pH, dissolved oxygen (residuals from linear regression on time of day), log-transformed *Gambusia* density, log-transformed piscivore density and log-transformed competitor species richness. The latter transformations were made to facilitate normality of residuals. We removed one model term at a time with  $P > 0.2$  until no remaining terms met that criterion. In this way, we could identify any statistical associations between life-history traits and a given environmental factor, while statistically controlling for other potentially important environmental factors. Among-population variation exists for all six of these

variables; however, consistent differences between fragmentation regimes across all islands only occur for three of them: fragmented sites exhibit much higher *Gambusia* density, much lower piscivore density and fewer competitor species (Table S2). All analyses were conducted in JMP PRO 10.0 (SAS Institute, Inc., Cary, NC, USA).

## Results

## MALE LIFE HISTORIES

Descriptive statistics for life histories of 414 adult males from 42 populations (21 fragmented and 21 unfragmented) can be found in Table S3. MANOVA revealed that all three main effects of 'fragmentation', 'species' and 'island(species)' had significant effects on male Bahamian mosquitofish life histories, while the interactions were not significant (Table 2). This indicates a surprising level of replicated responses to fragmentation across the different species and islands for males. Based on our measure of effect size (partial  $\eta^2$ ), shared responses to human-induced fragmentation and long-term historical effects (differences between species and islands) exhibited similar magnitudes of effects (Table 2). Evaluation of the canonical axes derived from the significant model terms, coupled with *post hoc* univariate analyses, revealed that the fragmentation effect mainly resulted from differences in lean weight and fat content, with males in fragmented tidal creeks tending to have smaller lean weights but greater body fat compared to males from unfragmented tidal creeks (Table 3, Fig. 2a,c). Species differences reflected that *G. manni* exhibits a larger body size, greater relative lean weight and greater relative fat content than *G. hubbsi*, while *G. sp.* tended to be intermediate. Males from different islands also differed from one another (island effect) in all traits except fat content, with lean weight showing strongest differences among islands (Table 3; Fig. 2a,c, and e).

## FEMALE LIFE HISTORIES

Descriptive statistics for life histories of 223 pregnant females from 24 populations (12 fragmented and 12 unfragmented) can be found in Table S4. MANOVA revealed that shared responses to fragmentation clearly represented the most important factor explaining female

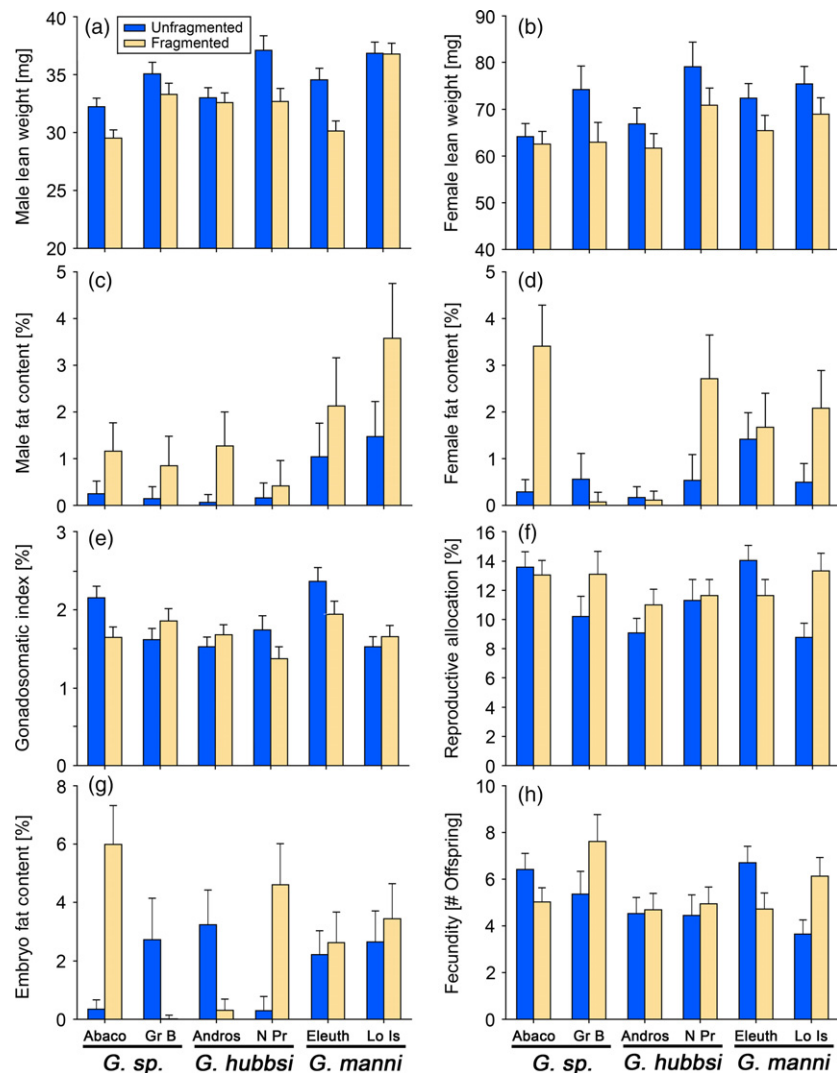
**Table 2.** Results of MANOVA examining variation in adult life-history traits. *F*-ratios were approximated using Wilk's  $\lambda$  values, and partial variance was estimated using Wilk's partial  $\eta^2$

Test for	Males				Females			
	<i>F</i>	d.f.	<i>P</i>	Partial variance	<i>F</i>	d.f.	<i>P</i>	Partial variance
Shared response to fragmentation (Frag)	5.15	4, 29	0.0029	0.42	4.10	4, 11	0.0284	0.60
Species histories (Species)	4.52	8, 58	0.0003	0.38	1.22	8, 22	0.3312	0.31
Island histories (Island[Species])	4.89	12, 77.0	<0.0001	0.39	1.91	12, 29.4	0.0751	0.40
Island-specific responses to fragmentation (Frag $\times$ Island[Species])	1.25	12, 77.0	0.2665	0.15	1.88	12, 29.4	0.0803	0.39

**Table 3.** Standardized canonical coefficients describing variation in adult life-history traits associated with the relevant terms of the MANOVA

Trait	Males			Females		
	Frag CV1	Species CV1	Island CV1	Frag CV1	Island CV1	F × I CV1
Body size	-0.02	<b>0.17</b>	<b>0.10</b>	-0.08	-0.05	-0.13
Relative lean weight	<b>0.21</b>	<b>0.13</b>	<b>0.27</b>	<b>0.22</b>	0.07	0.11
Relative fat content	<b>-0.12</b>	<b>0.15</b>	0.04	<b>-0.21</b>	<b>0.38</b>	<b>0.40</b>
Investment into reproduction	0.03	0.05	<b>-0.13</b>	-0.23	0.24	<b>0.08</b>

Note: Bold:  $P < 0.05$  in *post hoc* univariate analysis, and F × I indicates the Fragmentation × Island(Species) term.



**Fig. 2.** Differences between unfragmented and fragmented populations on each island for the life-history traits exhibiting the strongest responses to human-induced fragmentation: lean weight for (a) males and (b) females; fat content for (c) males and (d) females; (e) gonadosomatic index for males and (f) reproductive allocation for females; (g) embryo fat content; and (h) fecundity. All values represent back-transformed least-squares means  $\pm 1$  SE (all values adjusted for mean body size). Gr B: Grand Bahama; N Pr: New Providence; Eleuth: Eleuthera; Lo Is: Long Island.

life-history phenotypes (based on significance and partial  $\eta^2$ , Table 2). Both island effects and island-specific responses to fragmentation had suggestive, marginally non-significant, effects – because we did not have especially high statistical power for females ( $n = 24$ ), and because we wished to evaluate any potential factor influencing female life histories, we cautiously interpret underlying causes of these suggestive effects. We found no evidence for species-level differences in female life

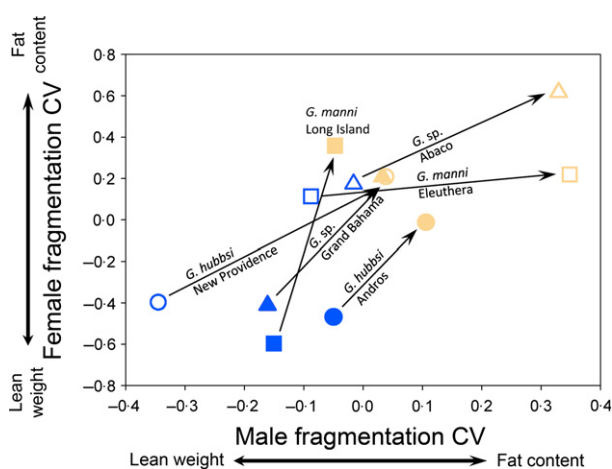
histories. Evaluation of the canonical axes from the three relevant model terms and *post hoc* univariate analyses revealed that the fragmentation effect again resulted from differences in lean weight and fat content, with females in fragmented tidal creeks also tending to have smaller lean weights and greater body fat compared to females from unfragmented tidal creeks (Table 3, Fig. 2b,d). However, the effects of fragmentation on fat content and RA depended on the island of origin ('fragmentation-by-



island(species) effect): fat content was elevated in fragmented tidal creeks on four islands, but Grand Bahama and Andros exhibited a trend in the opposite direction; RA was greater in fragmented tidal creeks on three islands, exhibited only a weak trend on a fourth island (New Providence) and the opposite trend on two islands (Abaco and Eleuthera; Table 3, Fig. 2d,f). Only fat content differed across islands, with Andros having less fat content than most other islands (especially compared to Abaco and Eleuthera; Table 3, Fig. 2d). Figure 3 summarizes the overall shared responses to fragmentation for both males and females.

#### OFFSPRING-RELATED LIFE HISTORIES

Descriptive statistics for offspring-related life histories of 223 pregnant females from 24 populations (12 fragmented and 12 unfragmented) can be found in Table S5. MANOVA revealed that island-specific responses to fragmentation clearly represented the most important factor explaining offspring-related life-history patterns (Table 4). We also uncovered marginally non-significant differences between islands, suggestive of island effects for at least some offspring-related trait. We found no evidence for shared responses to fragmentation or differences between species in offspring-related life histories. Evaluation of the canonical axes for the two relevant model terms and *post hoc* univariate analyses revealed that the fragmentation-by-island(species) effect resulted from two patterns: (i) greater embryo fat content in fragmented tidal creeks on four islands, but the opposite trend on Grand Bahama and Andros, and (ii) reduced fecundity in fragmented tidal creeks on two islands (Abaco and Eleuthera), greater fecundity in fragmented tidal creeks on another two



**Fig. 3.** Shared life-history responses to fragmentation within each sex visualized by the canonical axes derived from the fragmentation term of the sex-specific MANOVAs. Unfragmented sites in blue (dark grey), fragmented sites in beige (light grey). Congruent with our *a priori* predictions, males and females had higher fat content and reduced lean weight in fragmented compared to unfragmented sites.

islands (Grand Bahama and Long Island) and a weak trend for greater fecundity in fragmented tidal creeks on the remaining two islands (Andros and New Providence) (Table 5, Fig. 2g,h). Suggestive island effects arose because embryo lean weight was greatest on New Providence and smallest on Andros (Tables 5 and S5).

#### PUTATIVE SELECTIVE AGENTS

Five of the six putative environmental factors had a significant influence on at least one life-history trait in our backward stepwise regression approach (Table 6). In populations with a greater *Gambusia* density (as occurs in fragmented sites), female Bahamian mosquitofish exhibited a larger body size and tended to produce embryos with greater fat content, while males invested less into their testes and exhibited reduced lean weight. In tidal creeks with greater piscivore density (as occurs in unfragmented sites), both male fat content and female fat content were lower (no other factor influenced adult fat content), female lean weight and body size were greater, and males tended to exhibit increased body size. In sites with a greater number of piscine competitor species (as occurs in unfragmented sites), both sexes exhibited smaller body size. In sites with increased salinities, males had greater lean weight. Females exhibited reduced lean weight, tended to exhibit reduced body size and had a suggestive trend towards reduced fecundity in tidal creeks with higher pH. Females showed a suggestive tendency towards higher fecundity in tidal creeks with greater dissolved oxygen content. We found that no measured environmental variable influenced embryo lean weight (Table 6).

#### Discussion

Investigating the effects of human-induced habitat fragmentation on three species of mosquitofish from six Bahamian islands, we found that some adult life histories showed strong shared responses to fragmentation (lean weight and fat content; see Fig. 3), but that offspring-related life histories exhibited idiosyncratic island-specific

**Table 4.** Results of MANOVA examining variation in offspring-related life-history traits. *F*-ratios were approximated using Wilk's  $\lambda$  values and partial variance was estimated using Wilk's partial  $\eta^2$

Test for	<i>F</i>	d.f.	<i>P</i>	Partial variance
Shared response to fragmentation (Frag)	0.26	3, 12	0.8536	0.06
Species histories (Species)	1.49	6, 24	0.2225	0.27
Island histories [Island(Species)]	2.14	9, 29.4	0.0586	0.34
Island-specific responses to fragmentation [Frag × Island(Species)]	4.74	9, 29.4	0.0006	0.52

responses (embryo fat and fecundity). Overall, magnitudes of differences between fragmentation regimes were as large or larger than differences between species and islands. Shared responses to fragmentation appeared largely driven by a reduction in piscivorous fish density (male and female fat content, female lean weight), increased *Gambusia* density (male lean weight) and changes in salinity (male lean weight). Also, male investment into reproduction (testes size) decreased consistently with increasing *Gambusia* density, irrespective of fragmentation status; body size of both males and females exhibited comparatively complex associations with environmental factors, resulting in no overall differences between fragmentation regimes. We further found some weak support, indicating that among-population variation in offspring-related life histories may have arisen via variation in *Gambusia* density, pH and dissolved oxygen.

#### CONSISTENT AND PREDICTABLE EFFECTS OF FRAGMENTATION ON MOSQUITOFISH LIFE HISTORIES

Because the ability to accurately predict phenotypic consequences of human activities can improve the effectiveness of conservation, restoration and management (Ashley *et al.* 2003; Stockwell, Hendry & Kinnison 2003; Carroll, Kinnison & Bernatchez 2011), we set out to test a series

**Table 5.** Standardized canonical coefficients describing variation in offspring-related life-history traits associated with the two relevant terms of the MANOVA

Trait	Island CV1	F × I CV1
Relative embryo fat content	-0.06	<b>-0.42</b>
Relative fecundity	0.19	<b>0.26</b>
Relative embryo lean weight	<b>0.35</b>	0.13

Bold:  $P < 0.05$  in *post hoc* univariate analysis, and F × I indicates the Fragmentation × Island(Species) term.

**Table 6.** Results of backward stepwise regression examining putative importance of six explanatory environmental factors on life-history trait variation. Standardized partial regression coefficients presented for males (M), females (F) and offspring-related life histories for all terms retained in each model

Model term	<i>Gambusia</i> density	Piscivore density	# Competitors	Salinity	pH	Dissolved oxygen
body size	F: <b>0.93**</b>	M: <b>0.34</b> , F: <b>0.87*</b>	M: <b>-0.53**</b> , F: <b>-0.51*</b>		F: <b>-0.38</b>	
Relative lean weight	M: <b>-0.22*</b>	F: <b>0.34*</b>		M: <b>0.60**</b>	F: <b>-0.45*</b>	
Relative fat content		M: <b>-0.42**</b> , F: <b>-0.55**</b>				
Investment into reproduction	M: <b>-0.47**</b>					
Relative embryo fat content	<b>0.43</b>					
Relative fecundity					-0.33	0.37
Relative embryo lean weight						

Bold:  $P \leq 0.1$ , \* $P \leq 0.05$ , \*\* $P \leq 0.01$ .

All models included terms for Species and Island(Species).

of *a priori* predictions for changes in life-history traits in *Gambusia* species subsequent to human-induced habitat fragmentation (Table 1). Understanding the magnitude, nature and predictability of human-induced trait changes can aid conservation in several ways, for example by facilitating prioritization of restoration efforts in the particular case studied here. We uncovered strong evidence for predictable and parallel responses to fragmentation between the three different *Gambusia* species from six different islands; however, only two of the seven measured life-history traits exhibited such predictable patterns, male and female lean weight and fat content. Within the context of recent findings for other traits in the same system, our results reinforce the complexity of human-induced phenotypic change in the wild, as some traits show strongly predictable divergence, some show consistent but unpredicted differences, some exhibit idiosyncratic responses to fragmentation across species or islands, and some show no differentiation at all (e.g. male and female life histories: this study; male genital morphology: Heinen-Kay *et al.* 2014; male coloration: Giery, Layman & Langerhans 2015).

First, congruent with our *a priori* prediction based on morphological divergence between predation regimes in *Gambusia* from other systems (e.g. Langerhans *et al.* 2004; Langerhans, Gifford & Joseph 2007; Langerhans 2009), as well as on life-history responses to differences in competition/resource availability (e.g. Mueller 1997), adult male and female Bahamian *Gambusia* consistently had greater lean weight in unfragmented tidal creeks, relatively high-predation/low-competition environments (Fig. 2a,b; see also Riesch, Martin & Langerhans 2013 for a similar pattern in *G. hubbsi* from Bahamian blue holes). Interestingly, while our backward stepwise regression approach confirmed that female lean weight indeed seems to have ultimately resulted from differences in piscivore density (pH also influenced this trait, but did not consistently differ between fragmentation regimes), male lean weight



seemed to primarily correspond to differences in conspecific density (salinity also influenced this trait, but did not consistently differ between fragmentation regimes). For females, the most likely explanation for consistent reductions in lean weight in fragmented tidal creeks involves relaxed selection for fast starts, combined with the need for streamlined bodies for enhanced cruising performance in the water column in systems with predatory fish (see Langerhans 2009; Riesch, Martin & Langerhans 2013). Reduced lean weight in males within fragmented tidal creeks appears to have resulted from increased intraspecific resource competition in the presence of elevated *Gambusia* densities. Previous work in Bahamian tidal creeks on one of the islands studied here demonstrated that increased conspecific densities results in reduced growth rates of Bahamian *Gambusia*, as measured by RNA : DNA ratios (Araújo *et al.* 2014), consistent with the notion that intensified levels of resource competition in fragmented sites lead to reduced lean weight.

Secondly, the vast majority of *Gambusia* of both sexes were characterized by elevated fat content in fragmented tidal creeks, matching our prediction based on differences in predation between fragmented and unfragmented tidal creeks, but contrary to predictions based on variation in resource competition (Table 1). Our model selection analyses revealed that piscivore density alone could explain this consistent change in fat content in both males and females. We suggest this reflects the premium for high muscle mass and low fat content to facilitate fast-start escape behaviours when coexisting with high densities of predatory fishes as described above, in combination with altered foraging behaviours that include additional microhabitats and diet items with higher fat content (e.g. cladocerans and insect larvae) in the presence of reduced predation threat in fragmented sites (Araújo *et al.* 2014).

#### IDIOSYNCRATIC EFFECTS OF FRAGMENTATION AND OTHER ENVIRONMENTAL INFLUENCES

The majority of life-history traits examined here either showed no differences or an irregular pattern of differentiation between fragmentation regimes. While we never observed any species-specific response to fragmentation, we did observe a range of island-specific effects of fragmentation on life-history traits. We found that body size, male GSI and embryo lean weight exhibited no significant association with fragmentation, while female RA, fecundity and embryo fat content showed island-specific patterns of differentiation between fragmented and unfragmented tidal creeks.

For the traits with no significant evidence for effects of fragmentation, we did uncover possible environmental drivers for among-population variation in two of the traits: body size and male GSI. For both males and females, body size increased in sites with fewer species of possible competitors, regardless of fragmentation status. This suggests that ecological release from competitors may allow

selection to favour larger body sizes to exploit previously unobtainable resources (e.g. Simberloff *et al.* 2000), and represents a clear hypothesis for future testing. For females, body size additionally increased with increasing conspecific density (matching predictions of traditional *K*-selection theory for strong intraspecific competition: Pianka 1970; Reznick, Bryant & Bashey 2002) and increasing piscivore density (contrary to traditional *r*-selection theory). Larger body size might be favoured in sites with higher densities of predatory fishes if larger size offers some sort of enhanced escape capabilities, but no prior work with *Gambusia* supports this claim – indeed, previous work suggests that if anything, smaller body size might enhance escape performance (Langerhans 2009), leaving the cause for this pattern unknown.

Male GSI (i.e. relative testes size) decreased with increasing conspecific density. This trend runs counter to theory, as the hallmarks of sperm competition postulate that relative investment into testes size should generally *increase* with increasing conspecific density. This is because the threat (perceived or real) to successful fertilization increases with increasing numbers of competing males (e.g. Parker 1970; Wedell, Gage & Parker 2002). We can only speculate at this point, but future work could test whether tidal creeks with higher *Gambusia* population densities also tend to have more female-biased sex ratios, or changes in the mating system that provide greater female control over mating opportunities and reduced frequencies of multiple mating, which could lead to reduced sperm competition, and thus reduced testes size in these localities (e.g. Nandy *et al.* 2013).

Some of the classic examples of parallel evolution, especially related to predation environments in poeciliid fishes, involve the life-history traits of fecundity, offspring size and female investment into reproduction (e.g. *Poecilia reticulata*: Reznick, Butler & Rodd 2001; *Brachyrhaphis episcopi*: Jennions & Telford 2002; *G. hubbsi* from Bahamian blue holes: Riesch, Martin & Langerhans 2013), but we found that these traits did not consistently differ between fragmentation regimes. A previous study on *G. hubbsi* from seven high- and seven low-predation blue holes on Andros Island found strong convergence in offspring-related life histories in response to predation regime, with fish from low-predation blue holes exhibiting lower fecundity coupled with larger offspring size and greater embryo fat content (Riesch, Martin & Langerhans 2013). In the present study, offspring size (embryo lean weight) only differed between islands, while fecundity and embryo fat content showed inconsistent patterns of differentiation between fragmentation regimes across different islands. Given the strong and clear differences between fragmentation regimes in *Gambusia* population density and level of predation by piscivorous fish, why have these traits not predictably and consistently diverged? One explanation could be that not enough time has yet elapsed to permit strong evolutionary responses to selection ( $\leq 50$  years in most cases), given that these life-history

traits may have lower heritabilities than many other types of traits (Price and Schluter 1991). We find this explanation somewhat unlikely given that other studies have found strong phenotypic, and heritable, responses of poeciliid fishes to changes in predator regimes in these traits over shorter periods of time (e.g. *P. reticulata*: Reznick & Bryga 1987; Reznick, Bryga & Endler 1990). Nonetheless, embryo fat content did exhibit strong inter-population variation, just inconsistent differences with respect to fragmentation. In this case, we did uncover a suggestive trend where embryo fat content tended to increase with higher conspecific density. This is congruent with the idea that mothers should produce higher quality offspring in more competitive environments, and offspring born with larger fat reserves are expected to have a competitive advantage over similar-sized offspring with fewer fat reserves (e.g. Brockelman 1975; but see Anderbrant, Schlyter & Birgersson 1985). However, we currently do not know whether genetic (co)variance, the absence of hypothesized selection or other environmental agents might explain the lack of predictability in the effects of human-induced fragmentation on these traits.

We even found that one of the traits showing consistent and predictable differences between fragmentation regimes was additionally influenced by another environmental factor, independent of fragmentation. Greater lean weight in males found in sites with increased salinities could reflect physiological effects of salinity, such as increased ionoregulatory advantages of a larger body mass (e.g. Bilton *et al.* 1982; Mojazi Amiri *et al.* 2009). Because male *Gambusia* are smaller than females, these physiological effects might influence males more than females; however, effects of salinity on aspects of growth in teleost fishes are variable and require further study (e.g. Posey 2010; Enayat Gholampoor *et al.* 2011; Imanpoor, Najafi & Kabir 2012). Alternatively, the association between male lean weight and water salinity could reflect the correlation of salinity with an unmeasured factor. For instance, wetland-associated birds increase in abundance and species richness in Bahamian tidal creeks with increased salinities (but show no consistent differences between fragmentation regimes; Chacin *et al.* 2015), and thus perhaps increased lean weight in sites with elevated salinities reflects a response to an enhanced predation threat from avian predators.

Finally, future studies will have to investigate the extent to which the observed differences in life histories between fragmented and unfragmented sites, but also between sites differing in *Gambusia* density, piscivore density, the number of competitor species, salinity and pH, are purely ecological responses (i.e. phenotypic plasticity) or are indeed an indication of evolutionary responses (i.e. heritable differences). Given previous studies on life-history evolution in response to differences in predator regimes and competition, divergence in traits like male and female lean weight, body size, fecundity, GSI and RA could indicate evolved differences, while differences in other traits

(e.g. male, female, and offspring fat content) are likely to largely reflect phenotypic plasticity (Reznick & Bryga 1987; Reznick, Bryga & Endler 1990; Reznick, Butler & Rodd 2001; Johnson 2002; Langerhans *et al.* 2004; Langerhans, Gifford & Joseph 2007; Bashey 2008; Riesch *et al.* 2011; Riesch, Martin & Langerhans 2013).

## CONCLUSIONS

For conservation efforts to be effective, we need not only a proper understanding of the ecosystem- and community-level responses to human-induced disturbances but also of the phenotypic shifts they elicit in individual species. Our data clearly indicate that habitat fragmentation exerts multifarious selection on organisms, resulting in both shared and unique responses to habitat fragmentation. The same is likely also true for other forms of HIREC, which makes the formation of management and conservation plans much more difficult but also highlights the difficulty in correctly predicting the trajectory of many traits. Clearly, we need more theoretical and empirical work to better understand the predictability of phenotypic responses to HIREC.

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## Data accessibility

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.608d7> (Riesch *et al.* 2015).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Table S1.** Sample locations and sample sizes of sexually mature males and pregnant females used in analyses.

**Table S2.** Summary of results for separate general linear models testing for consistent differences in the six environmental factors between fragmentation regimes of Bahamian tidal creeks.

**Table S3.** Descriptive life histories (mean  $\pm$  SD) for 414 male mosquitofish (*Gambusia* spp.) from three different species and six islands (42 populations).

**Table S4.** Descriptive life histories (mean  $\pm$  SD) for 223 pregnant female mosquitofish (*Gambusia* spp.) from three different species and six islands (24 populations).

**Table S5.** Descriptive offspring-related life histories (mean  $\pm$  SD) for 223 pregnant female mosquitofish (*Gambusia* spp.) from three different species and six islands (24 populations).