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ORIGINAL PAPER

## Life-stage specific environments in a cichlid fish: implications for inducible maternal effects

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**Abstract** Through environmentally induced maternal effects females may fine-tune their offspring's phenotype to the conditions offspring will encounter after birth. If juvenile and adult ecologies differ, the conditions mothers experienced as juveniles may better predict their offspring's environment than the adult females' conditions. Maternal effects induced by the environment experienced by females during their early ontogeny should evolve when three ecological conditions are met: (1) Adult ecology does not predict the postnatal environmental conditions of offspring; (2) Environmental conditions for juveniles are correlated across successive generations; and (3) Juveniles occasionally settle in conditions that differ from the juvenile habitat of their mothers. By combining size-structured population counts, ecological surveys and a genetic analysis of population structure we provide evidence that all three conditions hold for *Simochromis pleurospilus*, a cichlid fish in which mothers adjust offspring quality to their own juvenile ecology. In particular we show (1) that the spatial niches and the habitat quality differ between juveniles and adults, and we provide genetic evidence (2) that usually fish of successive generations grow up in similar

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habitats, and (3) that occasional dispersal in populations with a different habitat quality is likely to occur. As adults of many species cannot predict their offspring's environment from ambient cues, life-stage specific maternal effects are likely to be common in animals. It will therefore be necessary to incorporate parental ontogeny in the study of parental effects when juveniles and adults inhabit different environments.

**Keywords** Maternal effect · Life-stage specific · Juvenile and adult environment · Cichlid fish

## Introduction

Environmentally induced parental effects represent a form of phenotypic plasticity spanning generations (Uller 2008) and appear to occur ubiquitously across all major taxa (Lacey et al. 1998; Mousseau and Fox 1998; Räsänen et al. 2008). Adaptive transgenerational plasticity is expected to be favoured when environments across generations are heterogeneous in space or time (Uller 2008). In the presence of reliable environmental cues, non-genetic maternal effects allow females to fine-tune the offspring's phenotype to the expected environmental conditions, which can confer fitness advantages for both generations (Galloway and Etterson 2007).

When maternal and offspring ecologies are correlated the environment can often provide reliable cues about the postnatal conditions offspring will experience (e.g. Bashey 2006; Galloway and Etterson 2007; Räsänen and Kruuk 2007; Badyaev 2009). In many species, however, juvenile and adult ecologies differ greatly because animals undergo ontogenetic shifts in feeding niche (reptiles: Clark and Gibbons 1969, Pough 1973, Ballinger et al. 1977; fish: Werner and Gilliam 1984; annelids: Davies et al. 1981; insects: Johannsson 1978, Amarillo-Suarez and Fox 2006; echinoderms: Town 1981; spiders: Turner 1979). Juveniles may occupy a different, often much narrower niche than adults in a common habitat (e.g. crustaceans: Lind and Welsh 1994; Dionne et al. 2003) or juveniles and adults may even be separated spatially (e.g. birds: Gillanders et al. 2003; fish: Mumby et al. 2004). In these cases, precise forecasting of offspring conditions from the ambient environment is often difficult or even impossible, whereas the conditions females experienced themselves in early life might predict their offspring's future environment quite reliably (Jonsson et al. 1996; Rotem et al. 2003; Taborsky 2006a). This situation can give rise to 'life-stage specific maternal effects', where the environmental conditions experienced by females during a certain life stage (e.g. the early juvenile stage) induce a maternal effect that affects the *same* life stage in the offspring generation. To date, no study has: (a) Identified which ecological cues experienced by females during their own early life are more reliable than cues experienced during reproduction; or (b) Tested whether these conditions hold true in the natural habitat of animals known to have life-stage specific maternal effects.

In a laboratory experiment, females of the mouthbrooding cichlid *Simochromis pleurospilus* were shown to adjust egg size to the experimental environment they experienced as juveniles, and not those that they experienced during egg production. Irrespective of current food availability, females reared under reduced access to food produced larger offspring (Taborsky 2006a). Further experiments suggest that this maternal effect prepares young for harsh post-natal conditions, as larger *S. pleurospilus* young grew faster than smaller conspecific competitors when food was scarce, whereas larger body size did not yield benefits when food was abundant (Segers and Taborsky, in revision). Thus,

*S. pleurospilus* exhibits a life-stage specific maternal effect and represents a suitable model to test whether the three ecological conditions outlined above apply to this species.

After detecting that cues perceived by females early in life can induce a maternal effect on offspring performance in the same life stage, Taborsky (2006a) proposed two necessary conditions for the evolution of this life-stage specific maternal effect: (1) Ecologies across *different* life stages must differ such that adults cannot predict their offspring's environment during early ontogeny; and (2) Conditions for *juveniles* are correlated across successive generations. Here we add a third condition, necessary for *plastic* offspring adjustment via maternal effects to evolve: (3) Offspring must occasionally end up in a non-matching environment, for example, due to moderate rates of dispersal to divergent habitats or because of temporal fluctuations. This additional condition is important, because if the correlation between the early environment of mothers and that of offspring were perfect, juveniles would always grow up in the same habitat type as their mothers. In this case, a fixed egg size would perform equally well as an environmentally induced anticipatory maternal effect to prepare offspring for post-natal conditions.

## Materials and methods

### Study rationale

Condition 1 demands that adults are not able to predict their offspring's post-natal environment. This is relevant if adult and juvenile habitats differ or are spatially segregated. To assess spatial segregation and differences in habitat we combined size-structured population counts and habitat surveys of five neighbouring *S. pleurospilus* populations in Lake Tanganyika. Condition 2 demands that juvenile environments are correlated across successive generations. The natural habitat of *S. pleurospilus* is stable over time. Thus, a correlation between the juvenile habitat of females and offspring is expected if juveniles of successive generations of the same population grow up in the same area. We tested for this by applying a population genetics approach predicting that genetic differentiation among neighbouring populations should occur, but not genetic differentiation between adult and juvenile habitats of the same population. Finally, condition 3 demands that occasional mismatch between the juvenile environment of a mother and her offspring occurs, for example, as a result of dispersal. To test for this, we applied a combined population genetics approach with a habitat quality survey in five neighbouring populations along a continuous 20 km stretch of Lake Tanganyika shoreline. We investigated the genetic data for signals of weak gene flow between neighbouring populations, and we tested for habitat quality differences between neighbouring populations.

### Study species

*Simochromis pleurospilus* is a maternally mouthbrooding cichlid of the tribe *Tropheini* endemic to Lake Tanganyika, East Africa. It inhabits the rocky shoreline between 0 and 12 m depth (depending on study site; pers. obs.), where it feeds exclusively on epilithic turf algae. These algae constitute the sole food source of *S. pleurospilus* and their productivity declines exponentially with depth, differing by two orders of magnitude within the first 2 m (Taborsky 1999). The observed reduction in algal productivity with depth correlates with a declining biomass of algae-grazing cichlids (B. Taborsky, unpub. data; this study). *S. pleurospilus* reproduces year-round, with adult males defending small, adjoining

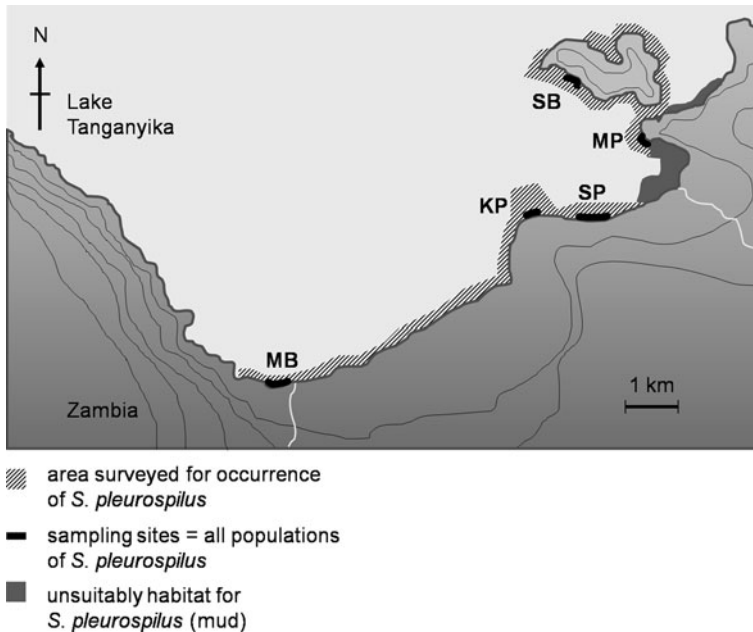
territories of 2–4 m<sup>2</sup> which females visit to spawn. Juveniles and females are non-territorial, but inhabit large home ranges (Kotrschal and Taborsky 2010a). After spawning, females leave the male territory immediately and care for the clutch on their own. The young are independent after 4 weeks (Taborsky 2006b). The environmental conditions juveniles are exposed to after independence until they reach maturity are known to strongly influence their adult body composition (Kotrschal et al. 2011), metabolic rate and digestive efficiency (Kotrschal 2010), behaviour (Kotrschal and Taborsky 2010b) and life history (Taborsky 2006a, b; Segers and Taborsky 2011; Segers and Taborsky in revision).

### Study sites

Data were collected at the southern tip of Lake Tanganyika, Zambia; we surveyed 20 km of Lake Tanganyika coastline and found populations of *S. pleurospilus* at five sites (Fig. 1) further referred to as: ‘Mbete’ (8°48′41.74″S, 31°02′08.56″E); ‘Kasakalawe Point’ (8°46′48.05″S, 31°04′58.60″E); ‘Simo Paradise’ (west of the town Mpulungu, 8°46′46.05″S, 31°05′47.48″E); ‘Mpulungu’ (near Fisheries Department, Mpulungu, 8°45′55.04″S, 31°06′10.56″E); and, ‘Simo Bay’ (at Nkumbula Island; 8°45′16.40″S, 31°5′28.81″E).

### Population size structure along depth gradient

Previously, the size structure—depth gradient correlation was known for only one of the study populations (Kasakalawe Point, KP; Taborsky 2006a). To investigate whether the



**Fig. 1** Study sites at the southern tip of Lake Tanganyika, Zambia. Shaded areas indicate the area surveyed for the occurrence of *Simochromis pleurospilus*, thick black lines mark the range along the shoreline inhabited by the five study populations and dark grey areas indicate habitats that are a priori unsuitable for *S. pleurospilus*. MB, Mbete; KP, Kasakalawe Point; SP, Simo Paradise; MU, Mpulungu; SB, Simo Bay

correlation applies to *S. pleurospilus* populations in general, we determined the size-frequency distribution in a second population (Simo Bay, SB), which differs most strongly from KP with regard to habitat and climate. In contrast to KP, SB is largely protected from waves (see Fig. 1) and strongly affected by sedimentation, and consequently has reduced algae growth.

We conducted 100-m transect counts in parallel to the shore every 0.5 depth-meter between 0.5 and 12 m depth. We repeated these transect counts three times during a 10 h period (7.00–17.00), during daylight (which was from 6.00 to 18.00), on three different days, adding up to a total of 720 ( $3 \times 10 \times 24$ ) 100-m transects. During each transect count, we dived approximately 1 m above the lake bottom along the transect line and estimated the size (to the nearest 0.5 cm) of each male, female and juvenile *S. pleurospilus* occurring 2 m to the left and to the right of the transect line. In the lab, *S. pleurospilus* females start to reproduce at a minimal size of 5.7 cm total length (TL) (Taborsky 2006b). Therefore, we considered individuals  $<5.5$  cm as ‘juveniles’ and individuals  $\geq 5.5$  cm as ‘adults’. The transects were carried out by two observers (AK and MJ). To minimize bias both observers sampled all depths. Furthermore, when the observer was included as a factor in the statistical analyses, it was non-significant ( $P > 0.7$ ).

### Ecological parameters

To measure habitat parameters, we conducted transects in parallel to the shore every 0.5 m between 0.5 and 3 m depth except at Mbete and Simo Paradise, where the habitat for *S. pleurospilus* extends only down to 1.5 and 2.5 m, respectively (only sandy bottom below these depths). We distinguished between ‘shallow’ (0.5, 1.0 and 1.5 m) and ‘deep’ (2.0, 2.5 and 3.0 m) habitats. Since the sandy bottom began at 1.5 m at Mbete, we numbered the 1.5 m transect among the ‘deep’ habitats.

### Algal cover

At our study sites four distinct categories of substrate occurred: solid rock (the lakebed consists of a flat surface of solid rock); stones (large pebbles and rounded rocks); sand; and plants. We placed a weighted 2-m yardstick on the lakebed and measured the distance  $d$  covered by the different classes of substrate. Starting each transect at the western edge of a population and proceeding eastwards, we sampled the substrate at every second 2 m-section and repeated this 10 times for each depth, yielding 60 samples per population (except Mbete and Simo Paradise, for which there are only 30 and 50 samples, respectively). Data points of equal depth were entered into the statistical analysis as independent values, since the sample sizes per depth are equal, which allows for data pooling without biasing the results (Leger and Didrichsons 1994). We calculated an index of algal cover by assuming that rocks have a flat surface and stones are spherical. Since only the top half of a stone is exposed to sunlight and can hence be colonised by turf algae we multiplied the distances covered by stones by  $\frac{\pi}{2}$ . For each 2 m section we calculated an index for algal cover as:  $A = \frac{d_{\text{rock}} + d_{\text{stones}} \times \frac{\pi}{2}}{200}$  with  $A \leq \frac{\pi}{2}$  cm. As the turf algae used as food by *S. pleurospilus* only grow on hard surfaces, plants and sand are not included in the equation. Note that  $A$  represents an index of the area available for feeding only and does not incorporate depth-specific algal productivity (see “Discussion”).

### Food competition

After determining algal cover, we rested motionless near the 2-m yardstick placed at the lake bottom for 5 min. During this period the fish habituated to the yardstick and to our presence and resumed feeding. We noted species, size (estimated by eye to the nearest 1.0 cm) and number of all food competitors (algae grazers) within 2 m of both sides of the stick (8 m<sup>2</sup>). We converted length to mass using allometric relationships of all algae eating species, established during previous field studies (see Appendix 1. Finally, we converted total algae eater biomass into total metabolic rate  $MR_{\text{total}}$  (in g  $\times$  m<sup>-2</sup>) by  $MR_{\text{total}} = \text{body mass}^{0.79}$ , which is the typical allometric relationship in teleost fish (Clarke and Johnston 1999).  $MR_{\text{total}}$  best reflects the amount of algae removed by food competitors.

### Food availability

To obtain an estimate of food availability we built a model with log-transformed  $A$  as the dependent variable and study site and habitat (shallow or deep) as fixed factors. Because we wanted to test for potential differences in food availability, which must also take the presence of food competitors into account, we controlled for the effect of  $MR_{\text{total}}$  on  $A$  by including it as a covariate. We first tested for significant interactions between  $MR_{\text{total}}$  and the fixed factors in our model. All interaction terms with  $MR_{\text{total}}$  were non-significant ( $P > 0.3$ ) and were therefore excluded from our final model.

We log-transformed the data or used non-parametric statistics whenever the distributions violated the assumptions of parametric testing. All analyses were conducted in SPSS 17.0 (SPSS Inc., Chicago, IL, USA).

### DNA sampling and microsatellite analysis

In total, we collected 550 tissue samples from shallow (<1 m) and deep (>1.5 m depth) water habitats. Sample sizes per population ranged between 85 and 146 individuals (Mbate: shallow (s) 47, deep (d) 45; Kasakalawe Point: s 44, d 41; Simo Paradise: s 55, d 40, Mpulungu: s 83, d 49, Simo Bay: s 54, d 92). Using hand nets each fish was driven slowly towards a fence net, where the fish's fins were caught and it could be removed quickly and without damage. Supported by local professional fish catchers, we managed to sample most individuals of a population during a 2 h session. However, in the case of very large populations, we obtained only a representative subsample. Fish caught in shallow habitats were found to be mostly juveniles, whereas those caught in deep habitats were exclusively adults. Fish of a specific population were kept in two tanks of 200 litres separated according to habitat type (shallow or deep) for up to 3 h with frequent water exchanges. All fish survived and were released after sampling. Fin clips were taken from the tip of the anal fin, and stored in 98% ethanol for later processing (see Appendix 2 for details on sample collection and processing).

We used fourteen polymorphic microsatellite loci with protocols specifically adapted for *S. pleurospilus* (loci NP007 (=UME002), NP773 (=US-758/773), NP781 (=US-781/784): (Schliewen et al. 2009); Pzeb2, Pzeb3, Pzeb4: (Van Oppen et al. 1997); TmoM5, TmoM13, TmoM25: (Zardoya et al. 1996); UME003: (Parker and Kornfield 1996); UNH106, UNH130, UNH154: (Lee and Kocher 1995) and UNH1009 (Carlton et al. 2002); see Appendix 2 for details on DNA extraction and microsatellite analysis).

## Statistical analyses of microsatellite data

We computed estimates of genetic diversity including allelic richness and heterozygosity, as well as tests for departure from Hardy–Weinberg proportions and linkage equilibrium for each sampling locality and depth separately in Arlequin 3.1 (Excoffier and Laval 2005). Overall and sample-specific inbreeding coefficients ( $F_{IS}$ ) were used to assess *S. pleurospilus* samples for internal kin structure or evidence of inbreeding (Schweizer et al. 2007). The nominal significance level of 0.05 was corrected with the sequential Bonferroni procedure whenever applicable (Holm 1979).

The level of genetic differentiation among *S. pleurospilus* from different sampling depths and localities was quantified separately by pairwise and overall  $F_{ST}$ -values (Weir and Cockerham 1984), and statistically tested with 10,000 permutations using Arlequin 3.1. Analyses of molecular variance (AMOVA) (Excoffier et al. 1992) were performed to assess the amount of genetic variation explained by differences between the two sampling depths relative to differences between sampling localities. Furthermore, we used Mantel tests (Smouse et al. 1986) implemented in Arlequin 3.1 to test the relationship between spatial and genetic distances ( $F_{ST}$ ) among sites as expected under isolation by distance. We tested both the logarithm of Euclidean distances and the logarithm of distances along the coastline against  $F_{ST}$ . A linear relationship between  $F_{ST}$  and the logarithm of distance is expected under short-distance dispersal among neighbouring populations (Rousset 1997).

## Ethical note

Animal care procedures during genetic sampling are in accordance with the ‘Memorandum of Understanding’ between the Fisheries Department of the Ministry of Agriculture and Cooperatives, Mpulungu, Zambia, and the Universities of Lusaka (Zambia), Bern and Basel (Switzerland) and Graz (Austria). We adhered to the “Guidelines for the treatment of animals in behavioural research and teaching” published in ‘Animal Behaviour’ 2006, 71, 245–253.

## Results

### Differences between juvenile and adult habitats

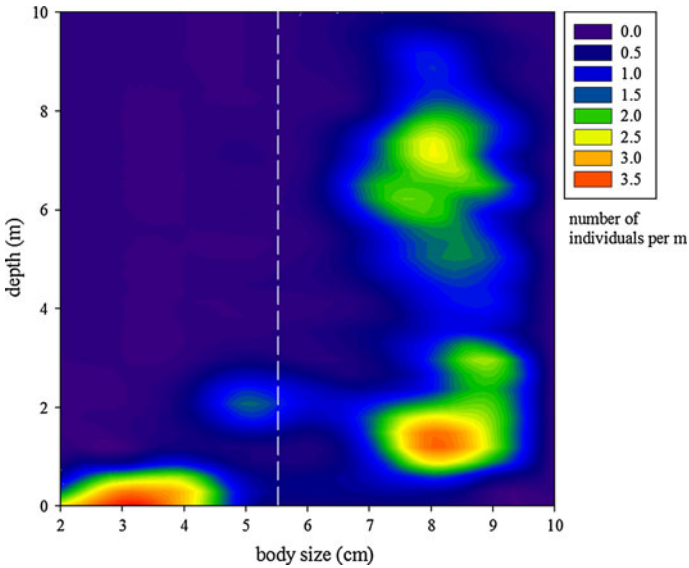
#### *Spatial segregation*

At Simo Bay the depth distributions of juveniles and adults differed significantly (Chi-square test,  $\chi^2_{24} = 66.66$ ,  $P < 0.001$ ). Juveniles occurred exclusively at depths  $\leq 1.5$  m, whereas adults were found regularly at all depths between 1.0 and 10.0 m (Fig. 2).

#### *Habitat differences*

Algal cover (controlled for the effect of food competition) was higher in shallow than in deep habitats ( $P < 0.001$ ; Table 1; Fig. 3). Additionally, the variances of algal cover and food competition were greater in deep habitats (Levene’s test for equality of variances: algal cover,  $F = 51.9$ ; food competitor metabolic requirement  $F = 42.3$ ; both  $N = 130$  and  $P < 0.001$ ).





**Fig. 2** Size-depth distribution of *Simochromis pleurospilus*. Colours indicate frequencies of fish recorded for each size class and depth (mean of 30 surveys). Dashed line indicates size at maturity

**Table 1** Potential food availability (algae cover, controlled for the effect of food competition) compared between water depths study sites

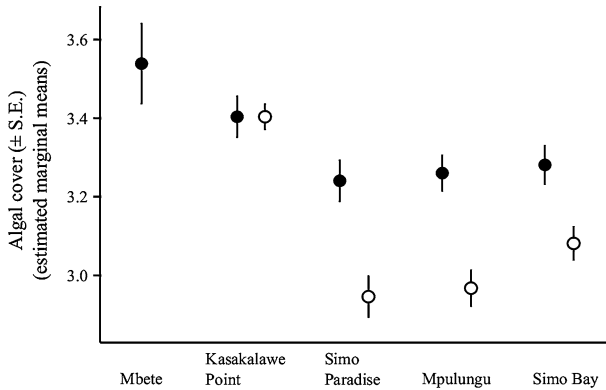
	<i>df</i>	Food availability	
		<i>F</i>	Sig.
Corrected model	8	16.511	<0.001
Water depth	1	26.761	<0.001
Study site	4	10.589	<0.001
Depth * site	3	4.747	0.004
Competitors <i>MR</i> <sub>total</sub>		0.664	0.42

Genetic differentiation within and among populations

Genetic data from 550 individuals revealed very high levels of genetic diversity at the 14 microsatellite loci analyzed. The number of alleles per locus ranged from four for locus Pzeb3–43 for locus TmoM5 with a mean value of 25.2. The observed heterozygosity per locus and sampling locality ranged from 0.4 to 1 with a mean value of 0.84 over all sampling localities. After sequential Bonferroni correction, significant deviations from Hardy–Weinberg equilibrium were detected for 6/140 tests per locus and sampling locality. Locus UNH130 was affected three times, locus UNH1009 twice and locus NP-007 once, but this low number of significant tests suggests no overall departure from Hardy–Weinberg equilibrium. Tests for linkage disequilibrium provided no evidence for physical linkage among loci in the data set.

Estimates of the inbreeding coefficient  $F_{IS}$  per *S. pleurospilus* sample from different sampling depths and localities provided no evidence for extensive kin substructure or inbreeding. Neither the overall  $F_{IS}$ -value of 0.004 ( $P > 0.2$ ) nor sample-specific  $F_{IS}$ -values (range:  $-0.016$ – $0.029$ ;  $P > 0.05$ ) were significantly different from zero.





**Fig. 3** Potential food availability in juvenile and adult habitats of *Simochromis pleurospilus*. Filled and empty circles represent the estimated marginal means of shallow and deep habitats respectively ( $\pm$ S.E.). Values are derived from a model in which we used the surface area as dependent variable, study site and habitat (shallow or deep) as fixed factors and metabolic requirement of food competitors as a covariate (see main text). No data for deep habitat in Mbete (see main text)

Genetic differentiation between *S. pleurospilus* sampling localities and sampling depths was relatively low at this very fine geographical scale with an overall  $F_{ST}$ -value of 0.0158 ( $P < 0.0001$ ). There was no evidence for genetic structure between sampling depths within sampling localities. An AMOVA with each sampling locality defined as its own group consisting of deep and shallow samples revealed significant variation between sampling locality ( $F_{CT} = 0.0149$ ;  $P < 0.0001$ ) but not between deep and shallow samples ( $F_{SC} = 0.0008$ ;  $P = 0.11$ ). Pairwise  $F_{ST}$ -values between deep and shallow samples from a locality ranged between 0.0006 and 0.0019 and were all not significantly different from zero (all  $P \geq 0.1$ ).

*S. pleurospilus* from the five sampling locations were significantly genetically structured with an overall  $F_{ST}$ -value of 0.0154 ( $P < 0.0001$ ). Pairwise genetic distances between sampling locations ranged from 0.0011 for Kasakalawe Point—Simo Paradise (the only non-significant comparison;  $P = 0.081$ ) to 0.030 (Simo Bay—Mbete;  $P < 0.0001$ ; Table 2).

Mantel tests provided no evidence for a dependence of genetic structure among *S. pleurospilus* populations with either Euclidean distances between sampling localities ( $r = 0.13$ ,  $P \geq 0.2$ ) or distances measured along the shoreline ( $r = 0.45$ ,  $P \geq 0.2$ ).

**Table 2** Pairwise  $F_{ST}$ -values between different sampling localities of *Simochromis pleurospilus*

	Mpulungu	Simo paradise	Simo bay	Mbete
Simo paradise	<b>0.0077</b>			
Simo bay	<b>0.0193</b>	<b>0.0219</b>		
Mbete	<b>0.0135</b>	<b>0.0047</b>	<b>0.0301</b>	
Kasakalawe point	<b>0.0089</b>	0.0011	<b>0.0264</b>	<b>0.0030</b>

All comparisons were significantly different from zero ( $P < 0.002$ , highlighted in *bold*) except for fish from the geographically closest sites Simo Paradise and Kasakalawe Point ( $P = 0.081$ )

**Table 3** Pairwise comparison of food availability in shallow habitats of five study populations

	MB Mean $\Delta$	<i>P</i>	KP Mean $\Delta$	<i>P</i>	SP Mean $\Delta$	<i>P</i>	MU Mean $\Delta$	<i>P</i>
KP	0.166	<b>0.036</b>						
SP	−0.341	<b>0.001</b>	−0.175	<b>0.003</b>				
MU	−0.319	<b>0.001</b>	−0.153	<b>0.009</b>	0.021	0.68		
SB	−0.307	<b>0.005</b>	−0.140	<b>0.030</b>	0.034	0.53	0.013	0.81

*MB* Mbete, *KP* Kasakalawe Point, *SP* Simo Paradise, *MU* Mpulungu, *SB* Simo Bay. Mean difference between study sites (mean  $\Delta$ ) and *p*-values (based on estimated marginal means) obtained from a general linear model with algae surface area as dependent variable, study site as factor and metabolic requirement of food competitors as covariate; significant *P*-values are highlighted in *bold*

### Heterogeneity of juvenile habitats

Food availability (algae cover controlled for competitor metabolic requirement) differed greatly across the shallow habitats (ANCOVA,  $F = 4.22$ ,  $df = 4$ ,  $N = 70$ ,  $P = 0.006$ , Fig. 3) and pairwise comparisons between study sites (based on estimated marginal means) revealed significant differences between most sites (Table 3). Moreover, study sites differed distinctly in several other features including shore orientation and wave impact, sedimentation, plant coverage and turbidity (A. Kotschal, pers. obs.).

### Discussion

In *Simochromis pleurospilus* egg size is influenced by cues mothers are exposed to during their juvenile period (Taborsky 2006a). We had proposed three general conditions that should favour the evolution of such a life-stage specific maternal effect. In the following sections we discuss our results in light of these proposed conditions.

Condition 1: juveniles and adults inhabit different ecological niches

We found that juvenile and adult *S. pleurospilus* inhabit different water depths with only a limited overlap. As observed also in other algae grazing species (Power 1984) the shallow areas were predominantly used by smaller, juvenile fish, whereas larger fish inhabited deeper areas. As *S. pleurospilus* follow a similar distribution, at Kasakalawe Point (Taborsky 2006a) and at Simo Bay (this study), we conclude that this pattern is typical for this species. In shallow depths algal cover controlled food competitor metabolic requirements were higher in all but one population. Shallow areas provide better feeding grounds than deep areas because a larger surface area of rocks and stone overgrown by algae is present, relative to the metabolic requirements of algae eaters. In addition, deeper habitats provide worse grazing grounds due to the exponential decline of sunlight with increasing depth, which corresponds to an exponential decline in algae productivity with depth (Taborsky 1999). Hence shallow and deep habitats usually differ with respect to the quality of feeding opportunities (cf. Fig. 3). Most likely the disparate distribution of juvenile and adult *S. pleurospilus* across the depth gradient is not solely explained by differences in feeding opportunities, but also by size-dependent predation risk. Wading and diving birds, which do not prey upon fish under a certain size threshold, hunt more effectively in shallow water

or near the surface (Whitfield and Blaber 1979; Kramer et al. 1983) whereas piscivorous fish that predate on juveniles of all sizes increase in number and size with increasing depth (Ruiz et al. 1993). Additionally, it may be risky for large fish to forage too close to the waterline because of the possibility of becoming beached, while small fish may use minute quantities of interstitial water to return to safer depths. In support of this consideration is the observation that the shoreline of Lake Tanganyika is frequently and heavily exposed to waves.

Overall, we can conclude that juvenile and adult habitats of *S. pleurospilus* differ with respect to several important ecological parameters. Here we compared only depths above 1.5 m with depths between 2.0 and 3.0 m. Adult *S. pleurospilus* use a much broader depth range than sampled by us, spanning over 9 or more meters in depth. The differences between shallow waters and a habitat at 10 m depth are likely to be even more pronounced. The larger variance in ecological parameters in the adult compared to the juvenile habitat indicates that adults occupy a much wider niche than juveniles. Females that solely rely on cues in their current (adult) habitat during egg production should therefore not be able to precisely predict juvenile conditions.

Condition 2: juveniles usually grow up under similar conditions as their parents

Life-stage specific maternal effects can occur when successive generations of juveniles usually grow up under similar ecological conditions. In the case of *S. pleurospilus*, where adults and juveniles occur at different depths, this can be checked by investigating genetic structure between depths of the same population and between fish of neighbouring populations. Our microsatellite analyses revealed that in all populations occurring along a 20-km stretch of shoreline shallow-water and deeper-water fish of the same study site were not genetically differentiated. In contrast, neighbouring populations were genetically differentiated as indicated by  $F_{ST}$  values significantly deviating from zero, except for the two closest populations ( $P = 0.081$ ). Kasakalawe Point and Simo Paradise are only 1,100 m apart and there is no obvious dispersal barrier for *S. pleurospilus* (sand, mud, or solid rock) between them, making gene flow between these populations more possible.

The observed pattern of genetic differentiation between populations despite the very fine-grained, local scale of this study suggests that *S. pleurospilus* is mostly philopatric and gene flow rarely occurs over large distances. This observation differs clearly for the much larger congener, *S. diagramma*, which readily covers larger distances (Wagner and McCune 2009). Dedicated analyses including more populations covering larger geographical scales and several points in time will be necessary to provide a better understanding of dispersal patterns and frequency in *S. pleurospilus* (e.g. Hamilton et al. 2005; Heckel et al. 2005; Schweizer et al. 2007). This will also allow further assessment of the effects of distance and habitat structure on dispersal properties more specifically, as our analyses of isolation by distance do not detect significant patterns at this spatial scale.

Condition 3: occasional mismatches between maternal and offspring juvenile habitats occur

*Simochromis pleurospilus* occurred only along certain stretches of the lake's rocky shore, in discrete populations, separated by unoccupied habitat. We detected significant genetic differentiation between neighbouring populations, suggesting that there is limited gene flow between them. It is remarkable, however, that the observed  $F_{ST}$  values are very low. The high levels of genetic polymorphism present within populations together with the

relatively low levels of genetic differentiation between our five study populations are compatible with relatively large local populations with occasional dispersal between them. Occasional dispersal is crucial for a flexible egg size to be advantageous over a fixed egg size (e.g. Kinnison et al. 2001), but only if dispersing fish may encounter habitats different from their natal population. In the case of our study populations the latter is likely. Juvenile habitats of neighbouring populations differed significantly in algal cover controlled for food competitor metabolic requirement and in several other qualitative features. Remarkably, there was no gradual change of ecological parameters along the shore. Most pairwise comparisons between neighbouring populations revealed significant differences in the index of food availability. Hence, whenever fish disperse they are likely to encounter variable conditions, and so the ability of females to fine-tune offspring phenotype may therefore confer an advantage.

The environmental induction of a maternal effect during one life stage that takes effect at the same life stage of the following generation has so far only been demonstrated experimentally (Taborsky 2006a). Here we investigated under which conditions life-stage specific maternal effects induced during the juvenile period of mothers may evolve. In our study species, adult and juvenile ecologies differ only at a fine scale, and their habitats partially overlap. Life-stage specific maternal effects should be even more important when juveniles and adults have entirely different ecologies like in many metamorphosing animals or anadromous fishes. There is evidence that such species do indeed adjust offspring phenotype to their juvenile environment (Jonsson et al. 1996; Rotem et al. 2003; Amarillo-Suarez and Fox 2006). In salmonids, this can be beneficial as these fish occasionally end up in spawning habitats that differ substantially from their natal sites, despite high spawning site fidelity (reviewed in Quinn 1993). Also, in amphibians an occasional mismatch of early maternal and offspring environment is possible if females fail to return exactly to their own raising ponds (reviewed in Smith and Green 2005), since these can vary greatly in their climatic and ecological conditions even on small spatial scales (Van Buskirk and Arioli 2005; Räsänen et al. 2008). Even for species with pelagic larvae previously believed to have no opportunity to obtain information on their offspring's postnatal environment, evidence of a certain level of philopatry is accumulating (Gerlach et al. 2007). Hence, the early maternal environment may well predict the conditions experienced shortly after settlement, as many juveniles of reef fish grow up in nursery grounds entirely disparate from the adult habitat, such as mangroves or sea grass beds (Heck et al. 2003; Mumby et al. 2004).

In conclusion, we outlined the conditions when maternal adjustment of offspring phenotype to life-stage specific environmental differences should be beneficial, and showed that these conditions are fulfilled in the natural environment of a species where females do adjust the offspring phenotype to their own early environment. Females thus possess a mechanism that allows them, via maternal effects, to match the offspring phenotype to the postnatal environment, even if they are unable to obtain information about the environment that future offspring will experience while producing eggs. As many species occupy different ecological niches during different ontogenetic stages and thus life-stage specific maternal effects should be common in animals, it will often be inevitable to incorporate the parental ontogeny when aiming to understand the evolution of parental effects.

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