# Ecological differences between hamlet (*Hypoplectrus*: Serranidae) colour morphs: between-morph variation in diet

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Dietary differences between hamlet *Hypoplectrus* spp. colour morphs were examined in fishes from Puerto Rico, U.S. Virgin Islands, Curacao, Honduras and Belize. Hamlet diet across all countries was characterized by large overlap between most colour morphs in both the proportion and numbers of dietary items consumed, although some differences between morphs were apparent. Indigo hamlets *Hypoplectrus indigo* were the only morph to consume fishes (blue chromis *Chromis cyanea* and sunshinefish *Chromis insolata*) almost exclusively. The sympatric occurrence of other ecologically indistinguishable colour morphs, however, suggests that divergent ecological selection alone cannot explain population divergence in hamlets. Geographical variation in diet was also observed within black *Hypoplectrus nigricans* and yellowtail *Hypoplectrus chlorurus* hamlets which may reflect geographical differences in prey availability or differences in prey choice.  © 2007 The Authors

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Key words: ecological specialization; morpho-species; niche partitioning; speciation; sympatry.

## INTRODUCTION

The past decade has seen a revival of the idea that speciation may arise from ecologically based divergent selection (Rundle & Nosil, 2005). In sympatric populations, frequency-dependent disruptive selection may induce intra-population polymorphism and, combined with assortative mating, lead to population divergence (Schluter, 2001). Alternative models suggest that the evolution of reproductive isolation arises primarily through sexual selection (Panhuis *et al.*, 2001; Turelli *et al.*, 2001). In freshwater taxa, mate choice based on colour patterns is believed to play a central role in initial species divergence (*e.g.* cichlids *Haplochromis* spp., Seehausen & van Alphen, 1998; Cumaná guppy *Poecilia* spp., Alexander & Breden, 2004). Many of these species also display differences in jaw morphology and diet partitioning which are likely to be important in

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species coexistence and population divergence (*e.g.* mbuna cichlids, Genner & Turner, 2005; whitefish *Coregonus* spp., Lu & Bernatchez, 1999). Ecology is therefore integral to speciation, whether as an ultimate or proximate cause of divergence. Understanding the ecologically based selective forces acting on populations is therefore critical to fully understand population divergence and speciation. This issue is highlighted in one of the most striking examples of a marine radiation: the complex of brightly coloured hamlets *Hypoplectrus* (Serranidae).

Hamlets are small, brightly coloured, coral reef fishes occurring throughout the Caribbean. The number of species recognized in the genus *Hypoplectrus* has been extensively debated, in large part due to the lack of obvious structural differences between species. Hamlets show little differentiation in morphometric measurements and historically have been distinguished only by colour patterns which vary strikingly. On this basis at least nine different types can be recognized which have been described either as separate species or, more commonly, as colour morphs (Domeier, 1994). Until recently, lack of allozyme differences between morphs was used to support a monotypic view of this group (Graves & Rosenblatt, 1980). Slight but significant mitochondrial DNA haplotype and microsatellite allele frequency differences have been observed, however, both between geographic regions and between colour morphs (McCartney *et al.*, 2003). Interestingly, genetic differences between colour morphs were observed in Puerto Rico but not Panama, suggesting that the processes creating or maintaining morph differences may vary geographically. These genetic differences between morphs have led to increasing interest in the mechanisms that may be creating and maintaining genetic differences between morphs.

Up to eight different morphs may co-occur on a single reef (pers. obs.) and hamlets display strong colour-assortative mating, both in the field (Fischer, 1980; Puebla *et al.*, 2007) and in aquaria (Domeier, 1994; unpubl. data). Mixed-pair matings between different colour morphs are rare [3·7% (Fischer, 1980) and <1% (unpubl. data) of observed spawns]. By comparison, there has been little conclusive evidence of ecological differences between hamlet colour morphs. Some broad habitat differences have previously been noted (Fischer, 1980), as well as slight differences in depth distributions of morphs in Puerto Rico (Aguilar-Perera, 2003) and Jamaica (Fischer, 1980) but these do not clearly separate colour morphs. Even without obvious differential habitat selection, however, hamlets may still show niche segregation by diet. There has also been little conclusive evidence of dietary differences between morphs. Most previous studies have been limited by small sample sizes and a small spatial scale of study. Stomach contents analysis of hamlets from Puerto Rico and the U.S. Virgin Islands showed large overlap in diet but also differences between morphs in the dominant food item consumed. Black hamlets *Hypoplectrus nigricans* (Poey) in this region consumed mostly fishes while yellowtail *Hypoplectrus chlorurus* (Cuvier), barred *Hypoplectrus puella* (Cuvier) and yellowbelly *Hypoplectrus aberrans* Poey hamlets consumed mostly shrimp (Randall, 1967). Similarly, Fischer (1980) noted that foraging behaviour was similar for all colour morphs in Jamaica, except for indigo hamlets *Hypoplectrus indigo* (Poey) which were observed to strike at and consume small fishes, mostly blue chromis *Chromis cyanea* (Poey). Dietary differences between

morphs may therefore exist but these differences have not yet been fully elucidated. In this study, dietary differences between morphs from five countries across the Caribbean were examined.

## MATERIALS AND METHODS

### FISH COLLECTION

Between November 2004 and August 2005, 226 hamlets were collected from shallow reefs at five locations in the Caribbean: (1) La Parguera, Puerto Rico ($n = 30$), (2) St Thomas, U.S. Virgin Islands (U.S.V.I., $n = 59$), (3) Curaçao ($n = 63$), (4) Belize ($n = 54$) and (5) Cayos Cochinos, Honduras ($n = 20$). Individuals for diet analysis were collected opportunistically as part of ongoing genetic sampling. Sample sizes for each colour morph therefore reflect the relative abundance of each morph at each site as well as the focus of the genetic studies (Table I). In addition, hamlets were collected as encountered and the size range of fish collected therefore reflects the size range of individuals on each reef. Depths of all collected fish ranged from 5 to 25 m.

Collections were made between 0700 and 1900 hours. All fishes used in this study were collected by colleagues as part of a genetic study, using a combination of net, hook and line fishing and spearing, all while scuba diving. Fishes were quickly placed in individual bags upon capture and killed by placing the bags in ice water immediately after each dive. In the laboratory, the total length ($L_T$) of each fish was measured to the nearest mm and fishes were dissected to obtain the gut samples. The stomach and intestines were preserved whole in 95% alcohol.

### DIET ANALYSIS

The entire gut was dissected and split into two sections: the stomach and the intestine. Initial trials revealed that little identifiable material could be found in the intestine and results are therefore presented for the stomach only. Restriction of analyses to stomach contents also minimizes any biases that may be incurred by varying digestion rates of different food categories. Such biases cannot be completely eliminated; however, the largely constant proportion of unidentifiable material in most fishes suggest that the results are representative of food items consumed for each colour morph. Stomach contents were categorized as: mysid shrimp (*Mysidium* spp.), decapod shrimp (Decapoda), mantis shrimp (Stomatapoda), crabs (including true crabs, Brachyura and porcelain crabs, Anomura), other crustacean parts, fishes and unidentifiable digested matter. Three methods were used to assess the contents of the stomach to give measurements of both bulk and the frequency of each food category (Hyslop, 1980). First, the percentage cover of each food category was estimated. The contents of a 40 mm diameter sampling tray were stirred and the number of 1 mm$^2$ squares on the bottom grid covered by each category was counted, giving an estimate of the total stomach content volume and the volumetric proportion of each food category. Second, individual items of food were counted. Finally, the occurrence of each food item was defined as the number of fishes in the sample containing that item.

### STATISTICAL ANALYSIS

Hamlets were classified into one of four categories according to time collected: 0700–1000, 1000–1300, 1300–1600 and 1600–1900 hours. There was no significant effect of collection time on the number of individual food items in the stomach and the proportion of each prey type for any colour morph (median tests: $P > 0.1$ in all cases). All times were therefore considered together in subsequent analyses.

TABLE I. Frequencies (F) and total length ($L_T$, mean ± S.D.) of each colour morph of *Hypoplectrus* spp. collected from each sampling location

| | Barred hamlet | | Black hamlet | | Yellowtail hamlet | | Butter hamlet | | Indigo hamlet | |
| | F | $L_T$ (mm) | F | $L_T$ (mm) | F | $L_T$ (mm) | F | $L_T$ (mm) | F | $L_T$ (mm) |
|---|---|---|---|---|---|---|---|---|---|---|
| Puerto Rico | 6 | 102·8 ± 12·0 | 3 | 149·0 ± 10·5 | 17 | 105·4 ± 9·5 | 4 | 98·7 ± 11·4 | 0 | |
| U.S.V.I. | 25 | 118·6 ± 12·5 | 28 | 146·3 ± 13·4 | 4 | 127·5 ± 6·2 | 2 | 130·0 ± 5·7 | – | |
| Curaçao | 13 | 108·5 ± 8·9 | 0 | | 25 | 105·4 ± 6·6 | 25 | 107·1 ± 7·6 | – | |
| Belize | 16 | 108·1 ± 6·6 | 16 | 98·4 ± 7·9 | – | | 5 | 99·4 ± 8·3 | 17 | 124·9 ± 13·7 |
| Honduras | 15 | 97·5 ± 6·5 | 4 | 111·8 ± 11·7 | – | | 0 | | 1 | 145·0 |

0, Countries where the morph was present but not collected. These correspond to morphs that were rare in each country.
–, The colour morph was not present in that country.

Twelve individuals had empty stomachs [$n = 2$ black, 5 barred, 3 butter *Hypoplectrus unicolor* (Walbaum), 2 indigo hamlets], and a further 11 individuals contained only unidentifiable digested matter ($n = 3$ black, 3 barred, 2 butter, 3 yellowtail hamlets). These individuals were excluded from analyses of volumetric proportions of food items.

Individual $L_T$ across all morphs ranged from 80 to 167 mm and there were significant differences in $L_T$ between morphs (see Table I). Since fish size may affect diet independently of fish preferences, the volumetric proportion of food categories was adjusted for individual size by expressing each food category as volumetric proportion per mm $L_T$ and compared across morphs. Fishes were also classified into one of four size classes: <99, 100–119, 120–139 and >140 mm and the volumetric proportion of food categories were compared between morphs across size classes. The results did not differ between using individual fish size or size classes. Since categorizing individuals into size classes places fewer assumptions on the relationship between individual size and stomach contents, only the results for the differences in diet between size classes are reported.

Non-parametric tests were used where the data did not conform to the assumptions of parametric testing. In addition, dietary differences between morphs were evaluated using Primer (v. 5; Primer-E Ltd, Plymouth, U.K.). Bray–Curtis similarity matrices were constructed to describe similarities between individuals in the proportion and counts of food items (Bray & Curtis, 1957). Multi-dimensional scaling (MDS) using these matrices allowed construction of two-dimensional representations of the similarity in diet between individuals. To test for differences between morphs and between countries, one-way non-parametric analyses of similarity (ANOSIM) were conducted on the matrix values. The significance of the global test statistic ($R$) produced was obtained using a randomization test with 5000 permutations (Clark & Warwick, 1994).
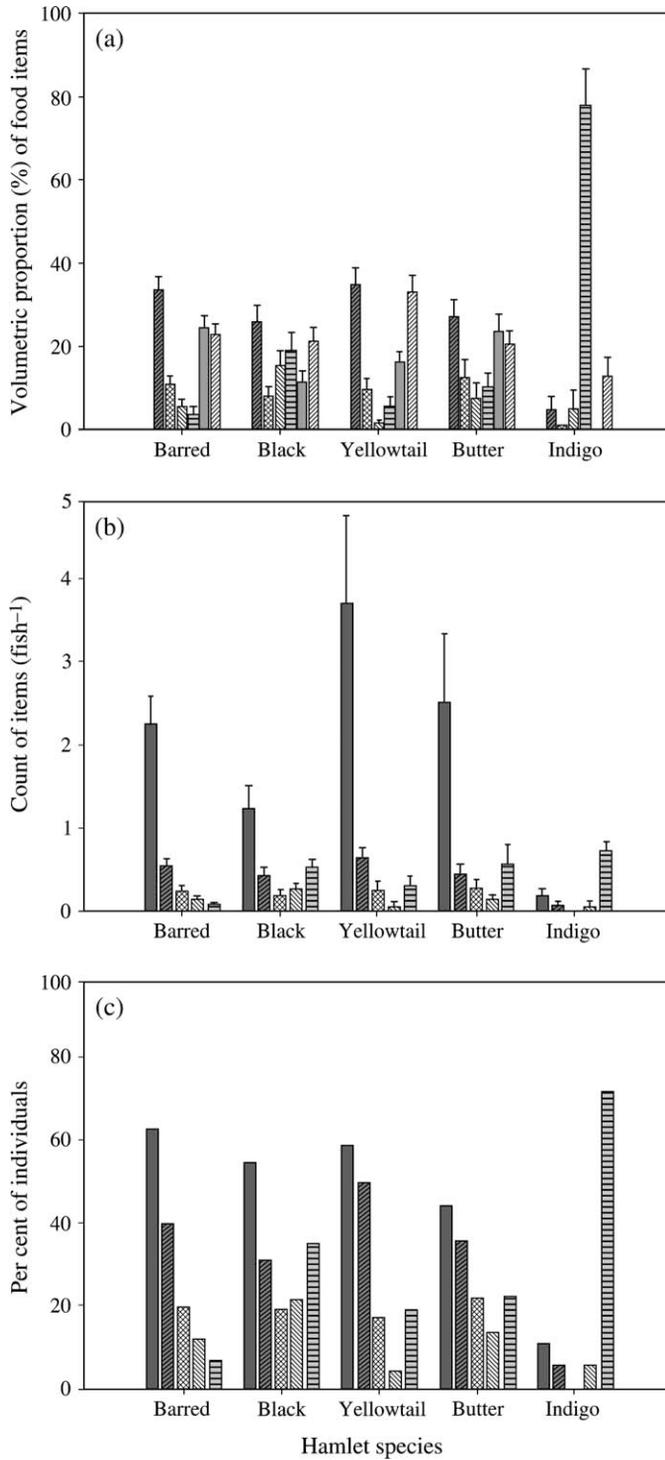
## RESULTS

### DIFFERENCES WITHIN AND BETWEEN COLOUR MORPHS

Within morphs, there were no significant differences between size classes in the volumetric proportion of each food category ingested for all morphs except black hamlets [Jonckheere–Terpstra (J–T) test]. Black hamlets of different sizes differed in the proportion of fishes consumed (J–T test, $n = 46$, $P < 0.01$), and the volume of fishes consumed increased with body size (Spearman $r$, $n = 46$, $P < 0.01$). There was no overall difference between size classes in dietary composition (either volumetric proportions or counts) for any of the hamlet morphs (ANOSIM, $P > 0.05$ in all cases).

Across all countries, the total volume of stomach contents of barred hamlets was significantly smaller than for all other morphs (ANOVA, $F_{4,198}$, $P < 0.001$). Crustaceans represented the largest volumetric proportion of the stomach contents for all morphs (61–74%), except indigo hamlets which ingested mostly fishes (78%). There were significant differences between morphs in the volumetric proportion of shrimp (mysid and other shrimp: median test, d.f. = 4, $P < 0.01$), mantis shrimp (median test, d.f. = 4, $P = 0.01$), total crustaceans (median test, d.f. = 4, $P = 0.001$) and fishes (median test, d.f. = 4, $P < 0.001$) ingested [Fig. 1(a)]. These differences, however, were driven by indigo hamlets. When this morph was removed from analyses, the remaining morphs differed only in the proportion of fishes consumed (median test, d.f. = 3, $P < 0.01$).

The same pattern is evident in multivariate analysis of dietary similarities. Indigo hamlets differed significantly from all other morphs in the volumetric proportion of prey items (ANOSIM $R$, $n = 202$, $P < 0.001$, *post hoc* pair-wise

comparisons including indigo: $P < 0.05$ in all cases). These differences may be partially explained by differences in fish size across morphs. Across all countries, black and indigo hamlets were significantly larger than other morphs (Table I, ANOVA, $F_{4,217}$, $P < 0.001$, Tukey HSD: $P < 0.05$). Size alone, however, did not account for the dietary differences between morphs. Considering each size class separately, indigo hamlets within the size classes 100–119 and 120–139 mm showed significant differences from all other morphs in these size classes in the volumetric proportions of prey items consumed (ANOSIM $R$, 100–119 mm: $n = 101$, $P < 0.001$; 120–139 mm: $n = 32$; $P < 0.001$; post hoc pair-wise comparisons including indigo: $P < 0.05$ in all cases). Within each size class, the remaining morphs did not differ in the proportions of prey items consumed (ANOSIM post hoc pair-wise comparisons: $P > 0.05$ in all cases).

The most frequently consumed items across all morphs were mysid shrimp (0–40 per individual). Colour morphs differed significantly in the number of mysid shrimp (median test, d.f. = 4, $P = 0.01$), decapod shrimp (median test, d.f. = 4, $P < 0.05$) and fishes (median test, d.f. = 4, $P < 0.001$) ingested [Fig. 1(b)].

The differences between morphs were also reflected in the number of individuals having ingested each food category [Fig. 1(c)]. Mysid shrimp were most commonly seen in barred hamlets (60% of individuals) but were frequently seen in individuals of all morphs (45–60%), except indigo (11%). By comparison, crabs were less frequently seen but did not vary in frequency between morphs (17–22% of individuals). Mantis shrimp (total length, from the carapace to the telson, 10–47 mm) were observed in a single yellowtail hamlet, a single indigo hamlet and 12–21% of the remaining colour morphs. Only three of 17 indigo hamlets contained crustaceans while 13 individuals contained fishes. In nine of these 13 cases, the fishes consumed was identifiable as either *C. cyanea* or sunshinefish *Chromis insolata* (Cuvier). Aside from indigo hamlets, fishes were most commonly seen in black, butter and yellowtail hamlets (33, 21 and 19% of individuals respectively) and were identifiable as settlement stage Gobiidae, Blenniidae, Pomacentridae or Acanthuridae. In addition, a single butter hamlet contained a batfish *Ogcocephalus* spp. and a single yellowtail hamlet ingested a filefish *Monocanthus* spp.

## DIFFERENCES WITHIN AND BETWEEN COUNTRIES

In all countries except Curaçao, the morphs occurring in a given country differed significantly from each other in the volumetric proportion of fishes consumed (Table II). In the U.S. Virgin Islands and Belize, colour morphs also differed in the total volumetric proportion of crustaceans consumed (Table II).

There were no significant differences between countries in the volumetric proportions of various prey items of barred and butter hamlets (median tests:

FIG. 1. Diet of barred *Hypoplectrus puella*, black *Hypoplectrus nigricans*, yellowtail *Hypoplectrus chlorurus*, butter *Hypoplectrus unicolor* and indigo *Hypoplectrus indigo* hamlets: (a) volumetric proportion of each food category per fish, (b) number of countable items per fish and (c) proportion of individuals containing each food category. Stomach contents were categorized as: mysid shrimp (*Mysidium* spp.) (■), decapod shrimp (▨), mantis shrimp (⊠), crabs (◩), fishes (▤) other crustacean parts (□) and unidentifiable digested matter (▩). Values are means + S.E.

TABLE II. Differences between colour morphs in the volumetric proportion of crusta-
ceans and fishes ingested (median tests) within each country sampled

| Country | Crustaceans | | Fishes | |
|---|---|---|---|---|
| | d.f. | $P$ | d.f. | $P$ |
| Puerto Rico | 3 | <0·5 | 3 | <0·001 |
| U.S. Virgin Islands | 3 | <0·1 | 3 | <0·05 |
| Curaçao | 2 | <0·5 | 2 | <0·5 |
| Belize | 3 | <0·001 | 3 | <0·001 |
| Honduras | 2 | <0·5 | 2 | <0·1 |

$P < 0·05$ in all cases). By comparison, black hamlets contained significantly different volumetric proportions of fishes between countries (median test, d.f. = 3, $P = 0·005$). Moreover, across counts of all food categories, there were significant differences in diet of black hamlets between countries (ANOSIM $R$, $n = 202$, $P < 0·001$) and *post hoc* pair-wise comparisons of countries showed that the diet of black hamlets from Belize was significantly different from the U.S.V.I. (ANOSIM $R$, $n = 202$, $P < 0·005$). These differences may in part be related to fish size. Black hamlets from Puerto Rico and the U.S.V.I. were significantly larger than those from Belize and Honduras (Table I, ANOVA, $F_{3,47}$, $P < 0·001$). There were also significant differences between countries in the volumetric proportions of fishes consumed by yellowtail hamlets (median test: d.f. = 2, $P < 0·05$). Yellowtail hamlets from Puerto Rico and the U.S.V.I. combined were significantly larger than those from Curaçao (Table I, ANOVA, $F_{2,42}$, $P < 0·001$). A single yellowtail from Puerto Rico and the U.S. Virgin Islands, however, ingested a settlement stage gobioid while eight of 25 yellowtail hamlets from Curaçao each ingested between one and four fishes.

## DISCUSSION

Hamlet diet across all countries was characterized by large overlap between most colour morphs in both the volumetric proportion and numbers of prey items consumed. Some differences between morphs, however, were apparent. Indigo hamlets were the only morph to consume fishes almost exclusively (blue chromis and sunshinefish). Broad dietary overlap between morphs is consistent with previous analyses of hamlet diet (Randall, 1967; Fischer, 1980). Moreover, these results confirm the previously noted difference between indigo hamlets and other morphs in both diet and foraging behaviour (Fischer, 1980). Indigo hamlets appear to feed almost exclusively on a single fish genus (*Chromis* spp.) and can be seen preying on these fishes in the water column (pers. obs.). Indigo hamlets are also typically larger than other hamlet morphs (Fischer, 1980). Successful capture of fish prey may be generally related to size; however, smaller indigo hamlets, of sizes similar to other colour morphs, were also observed to contain mostly *Chromis* spp. Size alone can therefore not explain the specific preference of indigo hamlet for fish prey.

Aggressive mimicry of non-predatory reef fishes has been suggested as a mechanism promoting speciation in hamlets (Thresher, 1978). It is possible that the

dietary preference for blue chromis and sunshinefish, alongside apparently close colour matching by indigo hamlets to schools of non-threatening *Chromis* species, has evolved by aggressive mimicry. Invoking mimicry, however, requires direct tests of the co-evolution and behavioural dependence of both model and mimic because the colour similarity between indigo hamlets and their prey could have arisen as a by-product of alternative evolutionary processes, including parallel adaptation to a specific habitat type (Eagle & Jones, 2004; Moland & Jones, 2004). In any case, indigo hamlets display significant ecological differences from other morphs. An increased understanding of the ecological and genetic mechanisms creating these differences may also shed light on the genetic processes involved in population divergence of the other hamlet colour morphs.

Within-morph geographic variation in diet may have arisen because of geographic variation in food availability. Black hamlets from Belize, which have a diet consisting largely of small mysids, were also significantly smaller than those from the U.S.V.I., which preyed on larger crustaceans and fishes. It is unlikely that this size difference results from sampling biases; hamlets were sampled haphazardly within each country and the size differences are also consistent with ecological surveys conducted in both places (unpubl. data). Within-morph geographical variation in diet also adds to an increasing body of evidence suggesting that individual morphs vary more in ecology, morphology and colour between locations than previously recognized (Aguilar-Perera, 2004; unpubl. data). While the dietary results from this study show geographic variation most clearly in black hamlets, it is perhaps likely that differences in ecology or genetics occur within other morphs for which spatial variation in colour have been noted (Thresher, 1978; Fischer, 1980; Domeier, 1994). Whether arising from variable food availability, individual size or other ecological processes, this variation is indicative of differing local ecological processes. Again, understanding this ecological variation may increase the understanding of population divergence among hamlets.

Finally, from a speciation perspective, hamlets display both colour variation and some concurrent dietary differences. The variable extent of dietary differences, combined with the sympatric occurrence of ecologically indistinguishable colour morphs, suggests that divergent ecological selection alone cannot explain population divergence in hamlets. In this respect, divergence among hamlets appears similar to speciation among cichlids in which closely related species display differing but overlapping diet. In these species, dietary niche partitioning contributes to species coexistence but sexual selection acting on male colour appears to be the most plausible mechanism for initial population divergence (*e.g.* mbuna cichlids; Genner & Turner, 2005). Linking further studies of ecology and behaviour with local population genetics will lead to a more comprehensive understanding of the interactions between ecological and sexual selection in creating and maintaining diverse colour morphs, such as those seen in hamlets.

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