

# Coral reef flounders, *Bothus lunatus*, choose substrates on which they can achieve camouflage with their limited body pattern repertoire

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Camouflage is a common tactic to avoid detection or recognition by predators and prey. Flounders have adaptive camouflage but a limited body pattern repertoire. We tested whether peacock flounders actively select or avoid certain substrates to more effectively use their limited camouflaging ability. We acquired and analyzed ten 30-min videos of individual flounders on a coral reef in Bonaire, Dutch Caribbean. Using Manly's beta resource selection indices, we were able to confirm that peacock flounders at this location preferred to settle on neutral-coloured substrates, such as sand and dead coral. Moreover, they avoided live coral, cyanobacteria, and sponges, which are often brightly coloured (e.g. yellow, orange, and purple). Quantitative analyses of photographs of settled flounders indicate that they use uniform and mottled camouflage patterns, and that the small-to-moderate spatial scale of their physiologically controlled light and dark skin components limits their camouflage capabilities to substrates with similar colour and spatial frequencies. These fishes changed their body pattern very fast. We did not observe disruptive body patterns, which are generally characterized by large-scale skin components and higher contrast. The results suggest that flounders are using visual information to actively choose substrates on which they can achieve general background resemblance. © 2014 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **114**, 629–638.

**ADDITIONAL KEYWORDS:** background matching – behaviour – body patterning – colour – crypsis – granularity analysis – habitat choice – preference – selection.

## INTRODUCTION

Visual camouflage is a powerful utility shaping predator–prey interactions in the biological world (Stevens & Merilaita, 2009, 2011). Essentially, cryptic animal patterns have evolved to retard either detection or recognition by visual predators. Background

matching helps avoid detection by visual predators by generally resembling background features of pattern, contrast, brightness, colour, and physical surface texture. Disruptive coloration is assumed to impede recognition of the prey species by creating false edges and boundaries in the prey species' body pattern, thus hindering recognition of its true outline and shape; such patterns often have large-scale and high-contrast markings, and also provide some degree of background resemblance to retard detection. Animal pattern types have not been universally characterized or compared; however, in cephalopods, which change

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quickly in highly diverse environments, three general pattern types are acknowledged: uniform, mottled, and disruptive (Hanlon *et al.*, 2009). Uniform patterns (i.e. little to no contrast) are cryptic on uniform backgrounds and mottled patterns (small-scale light and dark components of moderate contrast) retard detection when on similarly mottled backgrounds. Disruptive patterns tend to be shown when resemblance to the background is not possible and, despite being detectable, these patterns are considered to disrupt the ability of the predator to recognize the prey.

Most animals have a fixed or very slowly changing cryptic body pattern, which requires them to go to the right visual background at the right time, and assume the correct posture to interfere with their detection or recognition by predators. Among aquatic animals, some species of flatfishes (e.g. flounders, soles) and other bottom dwellers prefer to settle on sands or painted tank areas with background coloration and patterning similar to their own (Sumner, 1911, 1935; Mast, 1914; Hower, 1930; Fairchild & Howell, 2004; Ryer *et al.*, 2008). Freshwater guppies and least killifish also prefer certain backgrounds (Kjernsmo & Merilaita, 2012; Rodgers *et al.*, 2013). Among terrestrial animals, moths show a preference for backgrounds with colours similar to their own (Kettlewell & Conn, 1977; Steward, 1977; Endler, 1984) and they position their bodies to maximize crypsis (Webster *et al.*, 2009; Kang *et al.*, 2012).

Some animals have evolved the capability to change their body pattern quickly in response to different visual backgrounds, thus enabling them more flexibility to move within different habitats throughout the day and night when remaining camouflaged (Cott, 1940; Edmunds, 1974; Ruxton, Sherratt & Speed, 2004). Taxa with a wide repertoire of pattern change may not always have to choose their substrate. For example, cephalopods (i.e. marine molluscs that include octopus, cuttlefish, and squid) do not show strong preferences (Hanlon, Forsythe & Joneschild, 1999; Allen *et al.*, 2010), presumably because they have a faster and more diverse coloration system than other animals, although they may have habitat preference for certain other activities such as intraspecific signalling (Zylinski *et al.*, 2011).

Although many fishes are able to change their camouflage quickly, this has seldom been investigated in any detail, especially under natural field conditions (Sumner, 1911; Mast, 1914; Townsend, 1929; Cott, 1940; Saidel, 1988; Ramachandran *et al.*, 1996; Healey, 1999; Humann & DeLoach, 2002; Allen *et al.*, 2003; Kelman, Tiptus & Osorio, 2006; Marshall & Johnsen, 2011). In addition to the skill to change appearance for camouflage, bottom-dwelling marine fishes such as flounders and other flatfish may choose

different benthic substrate types that enable them to better camouflage or bury themselves for an additional defence tactic against visual predators (Stoner & Ottmar, 2003; Stoner & Titgen, 2003; Ryer, Stoner & Titgen, 2004).

In the present study, we consider the case of the common bottom-dwelling peacock flounder, *Bothus lunatus*, found in sand/coral reef environments throughout the Caribbean Sea. This species can quickly change its appearance (e.g. in 1–3 s) from conspicuous to cryptic to both avoid predators and better position itself to prey on fish, shrimps, and octopus (Humann & DeLoach, 2007). On pure sand substrates, it can also choose to bury itself completely or partially as an additional camouflage tactic (Fig. 1A, B, C). Neither the camouflage pattern repertoires and their relative effectiveness, nor the most preferred/avoided areas to settle down, have been investigated in detailed field studies of tropical marine flounders. We tested the hypothesis that flounders preferentially choose to settle on certain substrates enhancing crypsis. The habitats that we chose are the diverse tropical coral reefs of Bonaire.

## MATERIAL AND METHODS

### STUDY SITE

We conducted this field study in the island of Bonaire, Dutch Caribbean (12°12'06.60"N, 68°15'42.88"W), during the months of October to December 2010. Bonaire coral reefs are protected down to a contour depth of 60 m by the Bonaire National Marine Park (BNMP).

Based on local recommendations (D. Scarr, pers. comm.), we selected the North side of Yellow Submarine Reef (12°09'36.5"N, 68°16'55.0"W) as a dive location where the probability of sighting cryptic peacock flounders was expected to be high. Through preliminary research dives, it was concluded that depths ranging between 7 m and 10 m (above and below the reef crest) would be the principal area for research as a result of multiple sightings of peacock flounders and the diversity of substrates (e.g. sand flats, rubble, and reefs) (Fig. 1D).

### PEACOCK FLOUNDER BACKGROUND HABITAT SELECTION BEHAVIOUR

Using an underwater Sony Handycam HDR-SR7 video camera with Ocean Images housing, we filmed the behaviour of 10 peacock flounders for 30 min each. In the very few occasions in which a peacock flounder settled for 2 min (average = 3.7 times 30 min<sup>-1</sup> video), a member of the buddy team would gently provoke the flounder to swim by moving a 50-cm PVC measuring stick within 10 cm of its field



**Figure 1.** Flounder colour and pattern change in a sand/coral habitat. A, *Bothus lunatus* swimming in a conspicuous coloration pattern. B, *B. lunatus* settled in a cryptic mottle pattern. C, *B. lunatus* buried in the sand, with only the eyes protruding (top left). D, typical habitat at the study site in Bonaire, Dutch Caribbean. Note the mix of live coral, dead coral, rubble, and sand.

of vision (Eterovick, Oliveira & Tattersall, 2010), avoiding causing anomalies in their behaviour (e.g. erecting the dorsal fin, display of dark blotches, etc.).

We analyzed these videos using VEGAS MOVIE STUDIO HD, version 9.0 and MOTION PICTURE BROWSER (Sony). Photographs of standard Sony colour charts were taken at 7 m and 10 m, corresponding to the depth range at which flounders were filmed and photographed. These colour charts were used as references to roughly determine the colours of substrates analyzed in the video recordings, mostly taken at those depths, placing them into broadly defined colour categories as perceived by human observers. In cases where colour could not be determined by viewing depth colour charts on a computer screen, knowledge of Caribbean reef species and their known coloration was used in the analysis.

The video analysis allowed us to determine the substrate availability at the study site and the selection/avoidance of peacock flounders for different substrates. To determine the substrate availability at the study site, we recorded the time peacock flounders

spent swimming directly over the different substrate types and colours. The proportion of the total time spent by the 10 flounders swimming over the different substrate types and colours was used as a proxy for substrate availability.

To understand whether the peacock flounders actively choose or avoid settling on specific substrates, we first applied two Spearman's rank correlation tests to the video data. These tests were run between the benthic composition (or swimming backgrounds) and settling backgrounds used by flounders, at the level of substrate types and colours. When settlement was not significantly correlated with substrate availability, we calculated the Manly beta resource selection index (RSI) for each flounder and habitat type (Manly, McDonald & Thomas, 1993; McLoughlin *et al.*, 2004). The Manly beta RSI can be used to summarize an animal's behaviour relative to the availability of a habitat type. Values can range from 0 to 1, with values of all available habitat types for an individual animal adding up to 1. Zero values indicate that substrates are avoided (i.e. not settled



upon but available). By contrast, values > 0 indicate a preference for certain substrates; that is, peacock flounders settle on certain substrates more frequently than would normally be expected from the substrate availability. The RSI is described as:

$$RSI = \frac{w_i}{\sum_{i=1}^H w_i} \quad \text{where} \quad w_i = \frac{\text{proportion used}_i}{\text{proportion available}_i}$$

where the selection ratio  $w_i$  is the proportion of habitat  $H$  used (settlement data) versus the proportion available (swimming data).

To determine whether there are significant differences between the RSI values, we conducted Friedman tests, followed by post-hoc Wilcoxon tests (Bonferroni-Holm corrected) to determine which pairs of RSI values are significantly different.

#### PEACOCK FLOUNDER VISUAL CAMOUFLAGE CAPABILITIES

We photographed settled peacock flounders on different substrates using a Canon S-90 digital camera. We obtained 230 photographs of 12 flounders settled on various substrate types, including sand, rubble, dead coral, and artificial debris (such as concrete). Each settled flounder that was encountered was photographed in North, South, East, and West directions, from a distance of 2.5 m and at a 45° angle, the angle at which many predators often hover in search of prey in the water column. The team also captured a wide-angle image of the area where the flounder was settled.

To characterize peacock flounder camouflage patterns, we used MATLAB granularity software originally developed for cuttlefish (Barbosa *et al.*, 2008). The granularity software has also been used to characterize bird egg patterns (Spottiswoode & Stevens, 2010; Stoddard & Stevens, 2010). Granularity analysis bins the pattern markings into seven spatial frequency bands, which range in size from large (Band 1) to very small (Band 7) and quantifies the contrast at each spatial scale. The fish are cut out of each image and set to a standard size, and these processed images are filtered through a series of octave-wide (doubling in size) band-pass filters. The resulting granularity spectrum curve can be used for body pattern classification. For example, curves for cuttlefish disruptive body patterns have contrast (energy) peaks in bands 1 and 2, highlighting the prominent large pattern markings relative to animal body size. Similarly, curves for mottle patterns have contrast peaks in bands 3 and 4, indicating pattern markings of medium size, and curves for uniform patterns are relatively flat with low contrast across all seven bands because pattern markings are mostly absent (Barbosa *et al.*, 2008).

We discarded photographs from our analysis when fishes showed signs of responding to the presence of a diver (e.g. raised dorsal fin or dark central blotch) rather than camouflaging against the substrate, as well as when fish were partially covered by sand. In the final analysis, we used images of five individuals on multiple backgrounds (i.e. one individual presented both mottle and uniform patterns, one individual was photographed showing uniform pattern only, and three individuals showed mottle pattern only). We also used granularity analysis to compare the patterns of typical uniform and mottle flounder to regions in their surroundings to address the hypothesis that the flounders actively resembled the general characteristics of spatial scale, contrast, and brightness of light patches of comparable area in their immediate vicinity.

## RESULTS

#### STUDY SITE BENTHIC COMPOSITION

The study site included the transition from sand to live coral (Figs 1D, 2A); beyond 10 m, the reef crest drops off sharply as is typical of many Caribbean reefs. The substrate composition of the study site was diverse in terms of different substrate types and colour availability (Fig. 2A, B).

The overall composition of the study site, which was estimated using the swimming data from the 10 flounders, was characterized by eight substrate types (i.e. sand, small rubble, large rubble, dead coral, cyanobacteria, live coral, artificial debris, and sponges) (Fig. 2A) and nine colours (i.e. white/grey, grey/variegated, yellow, red, red/brown, orange, purple, pink, and green) (Fig. 2B). The most abundant substrates were small rubble (48%), sand (32%), large rubble (11%) and dead coral (4%); and white/grey (88%), and grey/variegated (7%) colours.

#### PEACOCK FLOUNDER HABITAT SELECTION

During the research dives, we observed peacock flounders foraging, mating, and cruising the seabed. However, the 10 filmed peacock flounders performed only cruising and foraging behaviour. These individuals settled an average of  $21 \pm 7$  times  $30 \text{ min}^{-1}$ . Flounders never settled on live coral, sponges or cyanobacteria, nor did they settle on six of the nine substrate colours identified by the observers and available at the study site. They settled predominantly on sand (74%) and white/grey substrates (90%) to the general exclusion of many other substrate types and colours. The selection of substrate types and colours was independent of substrate availability (Spearman's correlation  $r^2 = 0.68$ , d.f. = 8,  $P = 0.075$  and  $r^2 = 0.56$ , d.f. = 9,  $P = 0.119$ , respectively).

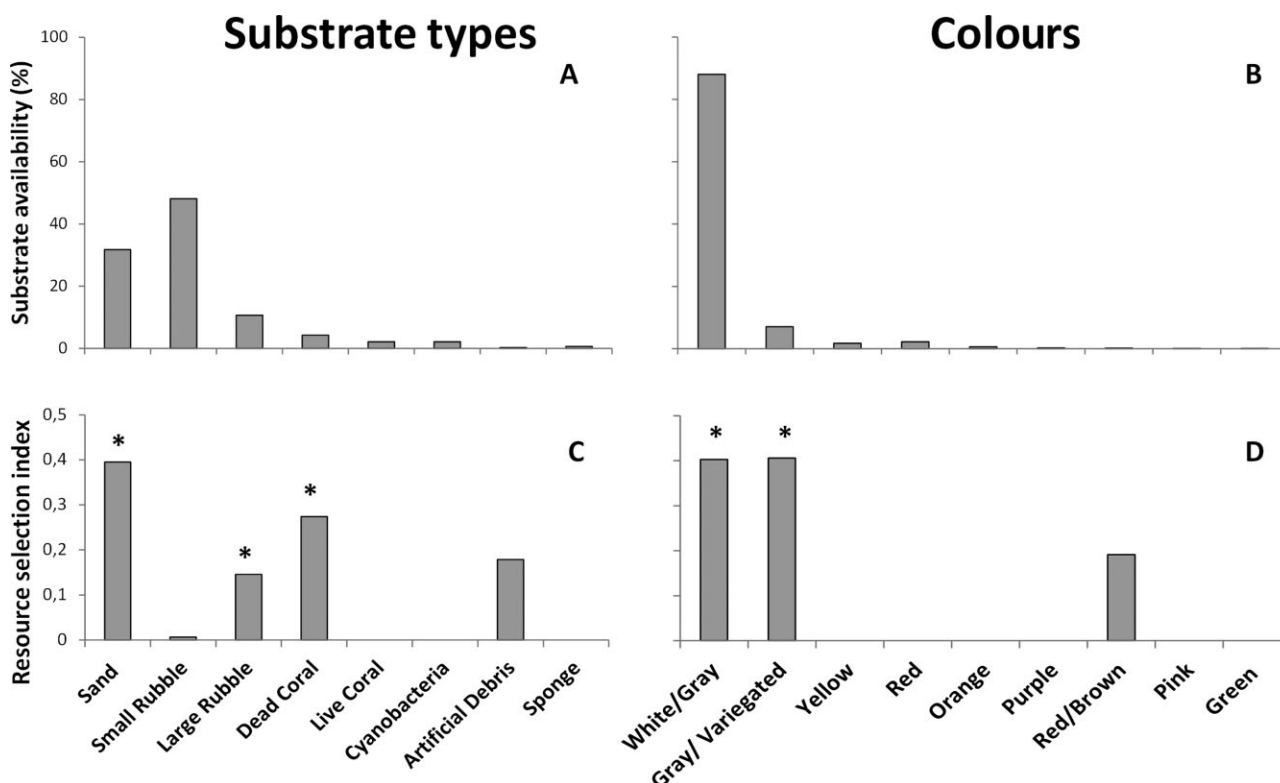
The RSI results suggest that the lack of correlation between the substrate types used for settling and substrate type availability was the result of: (1) an unexpected proportion of settlements on sand, large rubble, dead coral, and artificial debris and (2) a lower proportion of settlements on small rubble, cyanobacteria, live coral, and sponges (Fig. 2C). A nonparametric Friedman test showed significant differences between RSI for substrate types ( $\chi^2 = 45.6$ , d.f. = 7,  $P < 0.001$ ). Post-hoc Wilcoxon tests showed that sand, large rubble and dead coral were preferred for settlement significantly more than cyanobacteria, live coral, sponges, or small rubble ( $P < 0.05$ , Bonferroni-Holm correction).

Similarly, the RSI results show that the lack of correlation between the substrate colours used for settling and substrate colour availability was a result of frequent settlements on white/grey, grey/variegated, and red/brown substrates versus no settlements on yellow, red, orange, purple, pink, and green (Fig. 2D). A Friedman test showed significant differences between RSI for substrate colours ( $\chi^2 = 60.5$ , d.f. = 8,

$P < 0.001$ ). Post-hoc Wilcoxon tests showed that white/grey and grey/variegated substrates were preferred for settlement significantly more than yellow, red, orange, purple, pink, and green substrates ( $P < 0.05$ , Bonferroni-Holm correction).

#### PEACOCK FLOUNDER CAMOUFLAGE CAPABILITIES

Flounder body patterns can be quantified and differentiated based on the size scale and contrast of the pattern components. The uniform patterns (example shown in Fig. 3A) had flat granularity spectrum curves with low contrast at all seven spatial scales (Fig. 3C). The granularity curves for the mottle patterns (example shown in Fig. 3B) demonstrated some variability of curve shape and overall pattern contrast, yet all four peacock flounders peaked in bands 2 through 6 (Fig. 3C), characteristic of mottle patterns, which have moderately sized light and dark patches throughout the body. Disruptive body patterns, which would have curves that peak in bands 1 and 2, were not observed in these habitats.



**Figure 2.** Proxy for substrate type (A) and colour (B) availability, based on swimming data. Average Manly beta resource selection indices for settlement on different substrate types (C) and colours (D) by peacock flounders. Larger positive values indicate stronger preferences for those settlement backgrounds. Zero values indicate the substrate is available but not settled upon. An asterisk (\*) in (C) and (D) indicates that there is a significant preference for peacock flounder settlement on that substrate type or colour relative to at least three of the less preferred substrates (post-hoc Wilcoxon tests).

Granularity analysis was used to compare example peacock flounders to similar-sized regions in their surroundings. On areas dominated by sandy regions, peacock flounders performed two tactics: they either buried themselves fully or partially in the sand and deployed a light uniform pattern, or they sat motionless on the sand deploying a light uniform pattern (Fig. 4A). The mean intensity and granularity spectrum of the flounder was compared to: (1) three nearby regions of sand; (2) one region of large rubble; and (3) one region of dead coral (Fig. 4B). The granularity spectrum and mean intensity of the flounder closely resembled the same statistics for the three sandy regions but not the darker large rubble and dead coral (Figs. 4C, D).

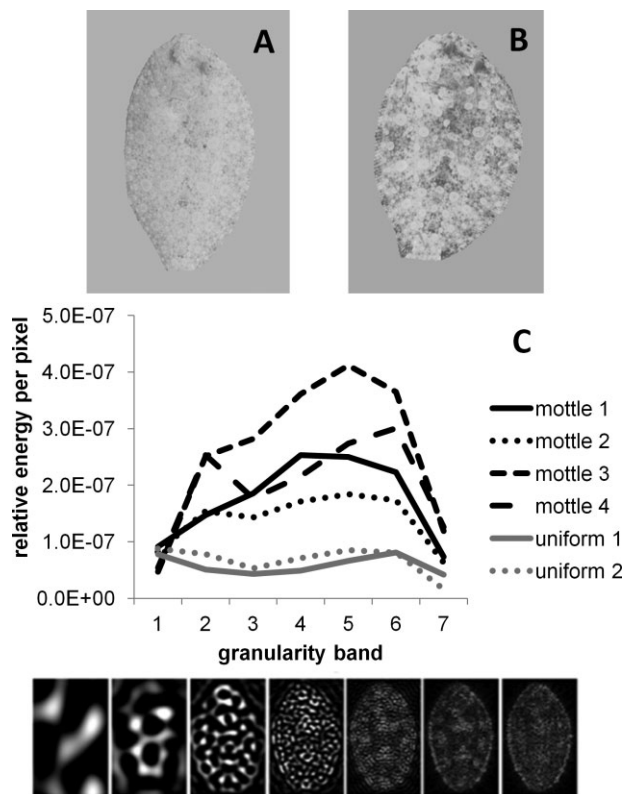
On heterogeneous backgrounds, such as dead coral or coral rubble, flounders produced mottled body patterns that enabled general resemblance to portions of the background that were mottled in appearance as well. Figure 5A shows two flounders settled on dead

coral promontories. Both are showing mottled patterns that create effective crypsis when viewed by humans looking at digital images. Granularity analysis of the flounder compared to seven dead coral and two live coral regions showed a general resemblance between the flounder body patterns and the dead coral regions (Fig. 5A, B). Although the granularity curves for the seven dead coral regions peaked in different bands (Fig. 5C), the average dead coral pattern curve shape and contrast (i.e. energy) was similar to the shape and contrast of the granularity curves for the two fish (Fig. 5D). The two live corals, not preferred for settlement by flounder, showed a granularity curve mismatch with the fish (Fig. 5D).

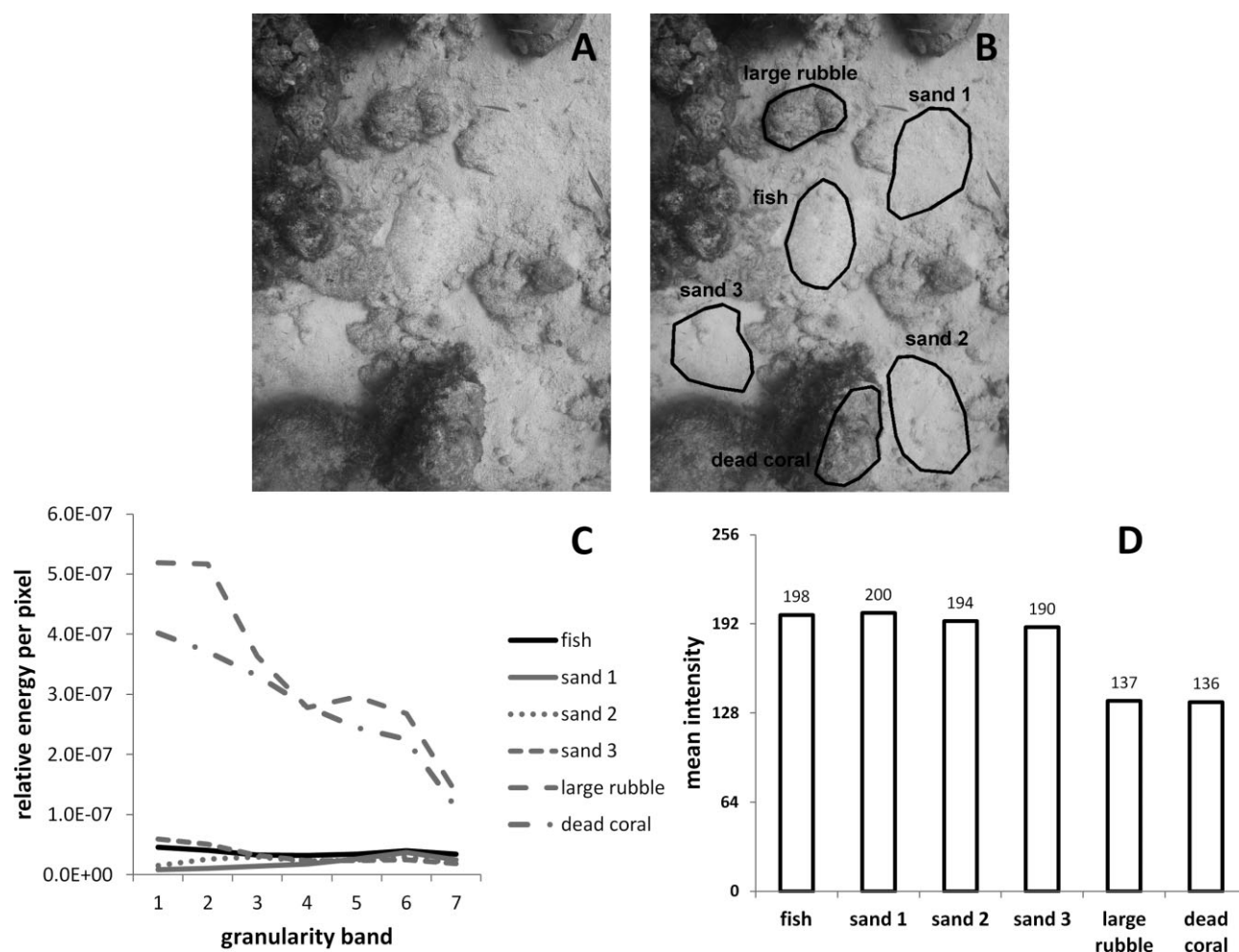
## DISCUSSION

This field study provides data showing that the tropical marine flounder *B. lunatus* has changeable camouflage capabilities, although its body pattern repertoire may be limited and thus it chooses specific substrates on which to settle to maximize crypsis. This apparent capability imparts obvious utility in terms of natural selection because it enables this species to forage in and around coral reef ecosystems at the same time as using background matching to deceive visual predators and prey. Most coral reefs are surrounded by (and interspersed with) sand, as well as relatively homogeneous low-contrast hard substrates such as coral rubble and small-scale dark patches from sponges. Thus, the limited pattern repertoire of uniform and mottle camouflage patterns coupled with tailored behavioural choices for settlement enables flounders to move in and around an expanded set of complex visual ecohabitats but without developing a more versatile set of camouflage patterns that would be required to achieve crypsis amidst the numerous colours and structures of Caribbean hard corals.

The Bonaire study site known as Yellow Submarine was chosen for its large diversity of habitats and abundance of peacock flounders. Indeed, we sighted a minimum of four flounders during each research dive allowing for filming them in a wide diversity of habitats; however, relatively few sightings lasted the required 30 min. We note that, despite the diverse habitats (e.g. sandy patches, reef crest, multiple colours, etc.), this site was dominated by sand and small rubble with white/grey and grey variegated colorations (Fig. 1). Habitats with these characteristics have been described as commonly used by peacock flounders throughout the Caribbean Sea (Randall, 1967; Humann & DeLoach, 2002, 2007). Therefore, the observed behaviour of flounders in the present study (i.e. frequent settlements over certain substrates) was determined by the intrinsic



**Figure 3.** Examples of cryptic flounder uniform (A) and mottle (B) patterns. The background for each image is the mean intensity of the flounder. C, granularity curves for two uniform and four mottle patterns show characteristic curves for each pattern type (note: relative energy is a measure of contrast; see text). The first mottle and uniform patterns were shown by the same flounder during one dive.



**Figure 4.** Granularity spectrum analysis of a peacock flounder in a light uniform pattern and surrounding substrate areas. A, image showing a flounder settled on sand. B, image with the flounder, three sandy areas, large rubble, and two dead coral regions used in the analysis outlined in black. C, granularity curves for the flounder in black, and the sand and dead coral in grey. D, mean intensities for the flounder, the three sand regions, and the two dead coral regions. Mean intensity values for each region are shown above the bars.

characteristics of the study site as well as the active selection/avoidance of certain substrates.

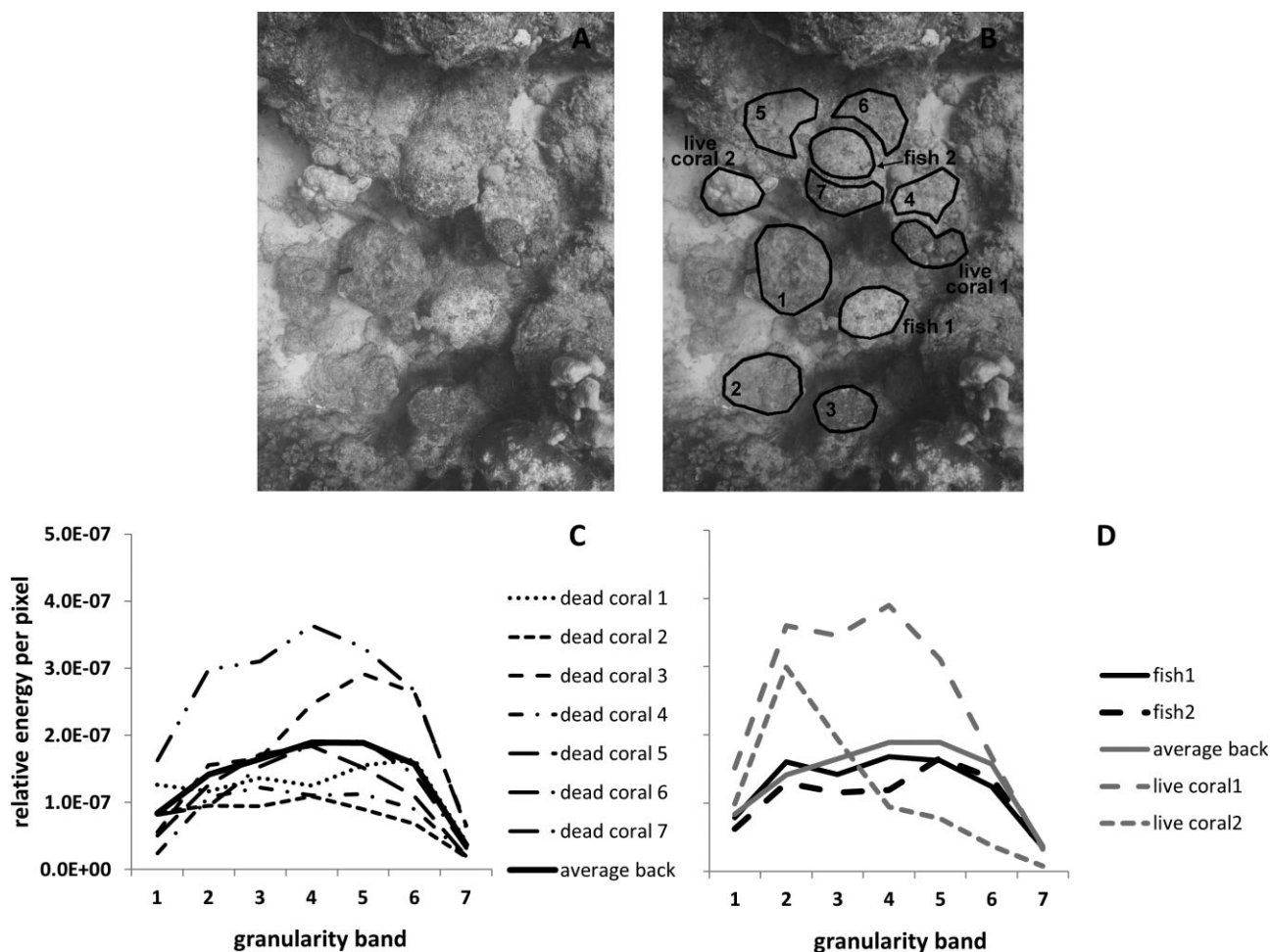
The active selection by peacock flounders to settle not only mostly on sand, but also on large rubble and dead coral (Fig. 2C), may have functions other than crypsis. The latter types of substrates may facilitate good positioning for finding mates and provide a vantage point for potential prey capture (Konstantinou & Shen, 1994). We also observed flounder using the thin crevices among these substrates, most likely for predation on small prey as well as predator avoidance.

Although peacock flounders preferred sand, large rubble, and dead coral, they avoided small rubble, cyanobacteria, live coral, and sponges. Our data do not provide an explanation for why peacock flounders avoided such substrates. However, presumably

peacock flounders are unable to achieve crypsis on such backgrounds as a result of the large colour varieties of corals and sponges. Some of these organisms have defence mechanisms (e.g. spicules in sponges, nematocysts in corals, etc.) that may also deter fishes from settling on them. In a laboratory experiment carried out with Pacific flatfishes, Ryer *et al.* (2008) showed that individuals with a mismatch to their substrate were more vulnerable to predation. Furthermore, peacock flounders showed a preference for light-coloured substrates, such as that of white/grey sand, versus brightly coloured substrates (e.g. yellow coral, orange sponges).

Flounder skin coloration has not been studied in detail, although our high-resolution photographs of *Bothus* from this location and elsewhere in the Caribbean suggest that they do not have chromatophores





**Figure 5.** Granularity spectrum analysis of two peacock flounders in mottle patterns and surrounding substrate areas. A, image showing two flounders settled on dead coral promontories. B, image with the two flounder, seven dead coral regions (numbers inside regions), and two live corals used in the analysis outlined in black. C, granularity curves for the seven dead coral regions, with the average curve in the centre in solid black. D, granularity curves for the two flounders in black, the average curve for the seven dead coral regions in solid grey, and the two live corals in dashed grey.

or iridophores that can produce yellow, orange or red. Thus, they may not be able to colour-match those corals and sponges that have such colours. Known predators of *B. lunatus* are various teleost fishes (such as snappers, Family Lutjanidae) many of which are known to have colour vision, so some degree of colour resemblance is expected to be part of their cryptic coloration (Stuart-Fox & Moussalli, 2009; Marshall & Johnsen, 2011). Moreover, camouflaging against those substrates may require the deployment of a disruptive body pattern, which we did not observe during our field study. However, high-contrast patterns that could be described as disruptive patterns have been observed during laboratory experiments with other tropical congeneric flounders, *Bothus ocellatus* and *Bothus podas*, suggesting that *B. lunatus* may also have the ability to produce a

disruptive pattern for camouflage (Sumner, 1911; Ramachandran *et al.*, 1996).

The capability to selectively choose certain substrates relies upon the flounder's visual perception, although this has been studied rarely. Studies of other flatfish species indicate that their visual capabilities are good (Matsuda *et al.*, 2008) and it is known from laboratory studies in several species that vision guides body patterning according to the visual information in their immediate surrounds (Sumner, 1911; Mast, 1914; Saidel, 1988; Ramachandran *et al.*, 1996; Kelman *et al.*, 2006). Our study provides field data that at least one species, *B. lunatus*, is visually choosing the substrate on which to settle.

Peacock flounders in the present study preferred to settle on substrates with colours, contrasts, and pattern scales that allowed them to achieve crypsis



with two body patterns: uniform and mottle. Our granularity image analyses suggest that their pattern repertoire achieves general background resemblance with respect to size, scale, and contrast of small surrounding light and dark areas of sand and rocks. It remains to be clarified whether peacock flounders use colour to choose where they settle or which body pattern they deploy; their visual pigments have not been characterized, yet other flounder species have photoreceptors that would allow colour vision (Hárosi, 1996). Early studies on coloured background selection by individual gulf and ocellated flounder (Mast, 1914) indicated that blue- and green-adapted flounder preferentially turn toward blue and green backgrounds, respectively, whereas red- and yellow-adapted flounder did not show similar preferences, indicating that colour may be involved in background selection.

More expansive field research with a larger sample size would help refine the findings that we report in the present study. Complementary laboratory experiments under controlled lighting and substrate conditions (including both natural and artificial backgrounds) would also help determine how visual perception of *B. lunatus* controls body patterning for crypsis (Ramachandran *et al.*, 1996; Kelman *et al.*, 2006). Additional focused research aims to uncover additional attributes of the adaptive behaviours that are linked to static or changeable camouflage patterns found throughout the animal kingdom.

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#### REFERENCES

- Allen G, Steene R, Humann P, DeLoach N. 2003. *Reef fish identification – Tropical Pacific*. Jacksonville, FL: New World Publications.
- Allen JJ, Mäthger LM, Barbosa A, Buresch KC, Sogin E, Schwartz J, Chubb C, Hanlon RT. 2010. Cuttlefish dynamic camouflage: responses to substrate choice and inte-

- gration of multiple visual cues. *Proceedings of the Royal Society of London Series B, Biological Sciences* **277**: 1031–1039.
- Barbosa A, Mäthger LM, Buresch KC, Kelly J, Chubb C, Chiao C-C, Hanlon RT. 2008. Cuttlefish camouflage: the effects of substrate contrast and size in evoking uniform, mottle or disruptive body patterns. *Vision Research* **48**: 1242–1253.
- Cott HB. 1940. *Adaptive coloration in animals*. London: Methuen.
- Edmunds M. 1974. *Defence in animals. A survey of anti-predator defences*. New York, NY: Longman Group, Ltd..
- Endler JA. 1984. Progressive background matching in moths, and a quantitative measure of crypsis. *Biological Journal of the Linnean Society* **22**: 187–231.
- Eterovick PC, Oliveira FFR, Tattersall GJ. 2010. Threatened tadpoles of *Bokermannohyla alvarengai* (Anura: Hylidae) choose backgrounds that enhance crypsis potential. *Biological Journal of the Linnean Society* **101**: 437–446.
- Fairchild EA, Howell WH. 2004. Factors affecting the post-release survival of cultured juvenile *Pseudopleuronectes americanus*. *Journal of Fish Biology* **65**: 69–87.
- Hanlon RT, Chiao C, Mäthger L, Barbosa A, Buresch KC, Chubb C. 2009. Cephalopod dynamic camouflage: bridging the continuum between background matching and disruptive coloration. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **364**: 429–437.
- Hanlon RT, Forsythe JW, Joneschild DE. 1999. Crypsis, conspicuousness, mimicry and polyphenism as antipredator defences of foraging octopuses on Indo-Pacific coral reefs, with a method of quantifying crypsis from video tapes. *Biological Journal of the Linnean Society* **66**: 1–22.
- Hárosi FI. 1996. Visual pigment types and quantum-catch ratios: implications from three marine teleosts. *Biological Bulletin* **190**: 203–212.
- Healey EG. 1999. The skin pattern of young plaice and its rapid modification in response to graded changes in background tint and pattern. *Journal of Fish Biology* **55**: 937–971.
- Hewer HR. 1930. Studies in colour-changes in fish. – Part V. The colour patterns in certain flat fish and their relation to the environment. *Journal of the Linnean Society of Zoology* **37**: 493–513.
- Humann P, DeLoach N. 2002. *Reef creature identification: Florida, Caribbean, Bahamas*. Jacksonville, FL: New World Publications.
- Humann P, DeLoach N. 2007. *Reef fish behavior: Florida, Caribbean, Bahamas*. Jacksonville, FL: New World Publications.
- Kang CK, Moon JY, Lee SI, Jablonski PG. 2012. Camouflage through an active choice of a resting spot and body orientation in moths. *Journal of Evolutionary Biology* **25**: 1695–1702.
- Kelman EJ, Tiptus P, Osorio D. 2006. Juvenile plaice (*Pleuronectes platessa*) produce camouflage by flexibly combining two separate patterns. *Journal of Experimental Biology* **209**: 3288–3292.

- Kettlewell HBD, Conn DLT. 1977.** Further background choice experiments on cryptic Lepidoptera. *Journal of Zoology* **181**: 371–376.
- Kjernsmo K, Merilaita S. 2012.** Background choice as an anti-predator strategy: the roles of background matching and visual complexity in the habitat choice of the least killifish. *Proceedings of the Royal Society of London Series B, Biological Sciences* **279**: 4192–4198.
- Konstantinou H, Shen DC. 1994.** The social and reproductive behavior of the eyed flounder, *Bothus ocellatus*, with notes on the spawning of *Bothus lunatus* and *Bothus ellipticus*. *Environmental Biology of Fishes* **44/4**: 311–324.
- Manly BFJ, McDonald LL, Thomas DL. 1993.** *Resource selection by animals: statistical design and analysis for field studies*. London: Chapman & Hall.
- Marshall J, Johnsen S. 2011.** Camouflage in marine fish. In: Stevens M, Merilaita S, eds. *Animal camouflage: mechanisms and functions*. Cambridge: Cambridge University Press, 186–211.
- Mast SO. 1914.** Changes in shade, color, and pattern in fishes and their bearing on the problems of adaptation and behavior, with especial reference to the flounders *Paralichthys* and *Ancylopsetta*. *Bulletin of the Bureau of Fisheries* **34**: 173–238.
- Matsuda K, Torisawa S, Hiraishi T, Yamamoto K. 2008.** Comparison of visual acuity and visual axis of three flatfish species with different ecotypes. *Fisheries Science* **74**: 562–572.
- McLoughlin PD, Walton LR, Cluff HD, Paquet C, Ramsay MA. 2004.** Hierarchical habitat selection by tundra wolves. *Journal of Mammalogy* **85**: 576–580.
- Ramachandran VS, Tyler CW, Gregory RL, Rogers-Ramachandran D, Duensing S, Pillsbury C, Ramachandran C. 1996.** Rapid adaptive camouflage in tropical flounders. *Nature* **379**: 815–818.
- Randall JE. 1967.** Food habits of reef fishes of West Indies. *Studies in Tropical Oceanography* **5**: 665–847.
- Rodgers GM, Gladman NW, Corless HF, Morrell LJ. 2013.** Costs of colour change in fish: food intake and behavioural decisions. *Journal of Experimental Biology* **216**: 2760–2767.
- Ruxton GD, Sherratt TN, Speed MP. 2004.** *Avoiding attack: the evolutionary ecology of crypsis, warning signals, and mimicry*. Oxford: Oxford University Press.
- Ryer CH, Lemke JL, Boersma K, Levas S. 2008.** Adaptive coloration, behavior and predation vulnerability in three juvenile north Pacific flatfishes. *Journal of Experimental Marine Biology and Ecology* **359**: 62–66.
- Ryer CH, Stoner AW, Titgen RH. 2004.** Behavioral mechanisms underlying the refuge value of benthic habitat structure for two flatfishes with differing anti-predator strategies. *Marine Ecology-Progress Series* **268**: 231–243.
- Saidel WM. 1988.** How to be unseen: an essay in obscurity. In: Atema J, Fay R, Popper AN, Tavolga W, eds. *Sensory biology of aquatic animals*. New York, NY: Springer, 487–513.
- Spottiswoode CN, Stevens M. 2010.** Visual modeling shows that avian host parents use multiple visual cues in rejecting parasitic eggs. *Proceedings of the National Academy of Sciences* **107**: 8672–8676.
- Stevens M, Merilaita S. 2009.** Animal camouflage: current issues and new perspectives. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **364**: 423–427.
- Stevens M, Merilaita S, eds. 2011.** *Animal camouflage: mechanisms and function*. Cambridge: Cambridge University Press.
- Steward RC. 1977.** Industrial and non-industrial melanism in peppered moth, *Biston betularia* (L). *Ecological Entomology* **2**: 231–243.
- Stoddard MC, Stevens M. 2010.** Pattern mimicry of host eggs by the common cuckoo, as seen through a bird's eye. *Proceedings of the Royal Society of London Series B, Biological Sciences* **277**: 1387–1393.
- Stoner AW, Ottmar ML. 2003.** Relationships between size-specific sediment preferences and burial capabilities in juveniles of two Alaska flatfishes. *Journal of Experimental Marine Biology and Ecology* **282**: 85–101.
- Stoner AW, Titgen RH. 2003.** Biological structures and bottom type influence habitat choices made by Alaska flatfishes. *Journal of Experimental Marine Biology and Ecology* **292**: 43–59.
- Stuart-Fox D, Moussalli A. 2009.** Camouflage, communication and thermoregulation: lessons from colour changing organisms. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **364**: 463–470.
- Sumner FB. 1911.** The adjustment of flatfishes to various backgrounds: a study of adaptive colour change. *Journal of Experimental Zoology* **2**: 409–504.
- Sumner FB. 1935.** Evidence for protective value of changeable coloration in fishes. *American Naturalist* **69**: 245–266.
- Townsend CH. 1929.** Records of changes in color among fishes. *Zoologica* **9**: 321–378.
- Webster RJ, Callahan A, Godin JGJ, Sherratt TN. 2009.** Behaviourally mediated crypsis in two nocturnal moths with contrasting appearance. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **364**: 503–510.
- Zylinski S, Osorio D, Hanlon RT, Marshall NJ. 2011.** To be seen or to hide: visual characteristics of body patterns for camouflage and communication in the Australian Giant Cuttlefish *Sepia apama*. *American Naturalist* **177**: 681–690.