Marine Environmental Research 220 (2026) 108203



Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev



Life in colour: The influence of habitat colouration on the recruitment of coral reef fish

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ARTICLE INFO

Keywords:
Microhabitat
Settlement
Habitat selection
Benthic colouration
Recruitment
Organismal colouration

ABSTRACT

Settlement and early post-settlement survival of fishes are important processes on coral reefs and represent a major demographic bottleneck. While numerous studies have quantified habitat selection of recently-settled fish in terms of benthic composition or physical complexity, few have considered the potential role of habitat colouration. Using image-based analyses to identify key colours and benthic features that create these colours, we explored how recently-settled reef fish select various habitats with respect to their own colouration and habitat colour composition. We conducted visual surveys and took standardized photographs of the settlement locations of four species of damselfishes (f: Pomacentridae) at Lizard Island, Australia; two of which are bright yellow in appearance (*Pomacentrus amboinensis* and *P. moluccensis*) and two that are dark coloured (*P. adelus* and *P. chrysurus*). Each species occupied settlement habitats that had distinct colour profiles when compared to the wider reef environment and the other species examined. When species were grouped according to body colouration (dark vs yellow), there were also significant differences in settlement habitat colouration. These patterns appear to be driven primarily by the presence or absence of live coral, mainly *Acropora* spp., within their settlement location which add a range of unique hues not typical of other substrata. Thus, we provide evidence that habitat colouration, in addition to other physical and environmental attributes, may be important for shaping settlement patterns in coral reef fishes. If so, rapidly changing benthic compositions on coral reefs driven by the loss of live coral may ultimately favour certain coloured species that reside more successfully on drabber habitats which are becoming more common on contemporary reefs.

1. Introduction

Settlement and the first few days post-settlement are critical life stages for coral reef fishes. During this period, settling fishes who are transitioning from pelagic to reef environments are exposed to reef-based predators for the first time (Victor, 1986). Mortality can be extremely high with up to 75% of individuals dying within the first few days (Almany and Webster, 2006; Hoey and McCormick, 2004) which greatly impacts subsequent juvenile and eventually, adult populations (Doherty et al., 2004; Caselle, 1999). Selecting a benthic habitat that reduces predation risk can, therefore, influence the survival and fitness of an individual and ultimately local populations. Indeed, numerous studies have shown that specific physical features of benthic habitats are particularly important for the survival of recently-settled and juvenile reef fishes (Tupper and Boutilier, 1997; Risk, 1997; Fakan et al., 2024). For example, benthic composition (e.g., live coral vs dead coral) and its corresponding structural complexity have both been shown to increase juvenile survivorship (Coker et al., 2009; Feary et al., 2007). Identifying how certain features of benthic habitats influence the settlement and early post-settlement survival of reef fishes, and how these may change due to local and global stressors, is therefore key to understanding the likely future population dynamics of reef fishes.

Habitat selection by reef fishes is a complex process determined by a range of features. Structurally complex habitats provide shelter from predators (Almany, 2004) and support high fish diversity and biomass (Graham and Nash, 2013a). Fishes will actively seek certain habitat features on reefs based on environmental quality (e.g. availability and condition (Coppock et al., 2020);), as well as the abundance and

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https://doi.org/10.1016/j.marenvres.2026.108203
Received 3 November 2025; Received in revised form 12 June 2026; Accepted 13 June 2026
Available online 18 June 2026
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composition of competitors and predators in the area (Booth and Wellington, 1998; Vail and McCormick, 2011). While some studies have shown that juvenile reef fish may be more vulnerable to predation when associated with a bleached vs healthy coral, presumably due to differences in conspicuousness (Coker et al., 2009; Marshall et al., 2019), few studies have investigated the importance of benthic colouration in shaping habitat selection by settling fishes and their subsequent survival during this inherently risky period.

Coral reefs support a wide diversity of organisms which showcase a range of colourations. These colours support a multitude of unique functions and complex behaviours (Justin Marshall, 2000), like distinguishing between con- and heterospecifics (Siebeck, 2004), indicating the fitness of an individual (Maan et al., 2006), identifying species territories (Evans and Norris, 1996; Siebeck, 2004) and delineating species boundaries (Hemingson et al., 2019; Kohda et al., 2015). Other colour patterns can reduce predation through the use of confusing visual stimuli, like eyespots which mimic the real eye making targeting more difficult (Hemingson et al., 2021; Kjernsmo et al., 2013). Colouration can also help individuals blend into the environment which provides a key fitness benefit for both prey and predators (Cott, 1940; Darwin, 1859; Phillips et al., 2017). Interestingly, certain bright and conspicuous colours can actually be advantageous in camouflaging against a colourful and dynamic coral reef habitat (Marshall et al., 2019; Justin Marshall, 2000). Some yellow hues closely resemble the ambient background colour of a coral dominated reef ecosystem (Matz et al., 2006a), while darker coloured species (typified by brown, green, and black hues) tend to more closely resemble darker coloured substrata that lack live coral tissue and are often covered in turf algae and cyanobacteria (da et al., 2020; Whiteley et al., 2009; John et al., 2023; Hodge et al., 1923a). For these reasons, benthic colouration may play a key role in determining habitat selection and survival by recently-settled fishes.

Damselfishes (f: Pomacentridae) are one of the most diverse marine fish families and are commonplace on coral reefs. These fishes typically live in close association with the substratum where they establish home ranges defined by a few square meters (Streit et al., 2021). Their high abundance compared to other taxa (Allen, 1991b; Cooper et al., 2009) and small body size means they are a common prey item for many predators (Frisch et al., 2014; Carr and Hixon, 1995). Since many reside in shallower habitats where translucent water allows for the downwelling of a broad light spectrum, species within this family have evolved both a wide range of colourations and visual capabilities (Siebeck, 2016). Their visual system displays a high level of plasticity with the number of expressed cone opsin genes ranging between three and six (Stieb et al., 2016, 2017, 2023). Most, if not all, damselfish species are capable of perceiving ultraviolet (UV) light through their specialized short-wavelength sensitive cones, with recent research reporting that UV vision is present at settlement in all of the damselfish species examined (Stieb et al., 2017; Tettamanti et al., 2025). Together, this diversity of colourations, tight association to the substratum, small size, and developed colour vision make damselfishes a prime group to understand how environmental colouration dictates settlement habitat selection and post-settlement survival on coral reefs.

Globally, reef ecosystems are undergoing pronounced changes in response to human-induced disturbances (Hughes et al., 2017). The most notable impact from these disturbances is the transition from high coral cover to low coral, algal-dominated states on some reefs (Tebbett et al., 2023). Degraded reefs with low coral cover not only lose their structural complexity (Alvarez-Filip et al., 2009; Morais et al., 2022) but also change in their overall diversity and appearance, resulting in a more homogenous reefscape that supports less colourful fish communities (Hemingson et al., 2022). These findings, together with earlier evidence that degraded algal covered reefs are less favourable to recently settled coral reef associated fish (Lecchini et al., 2013), suggest an important link between settlement success, post-settlement survival, and habitat colouration.

In this study, we investigated how benthic colouration correlates to the early post-settlement habitat preferences of four damselfish species: two of which are yellow in colouration and two that are dark brown. We conducted benthic photo surveys to: (1) characterize the colour profile of the benthic habitat in which recently-settled damselfish occupied on the reef, (2) understand to what extent these colour profiles are related to a species identity and/or its body colouration (yellow or brown), and (3) determine which benthic components are most responsible for shaping differences in the settlement habitat colour profile. We predict that each species will exhibit a distinct habitat colour profile, with species of similar colouration (i.e., yellow vs brown) occupying similarly coloured habitats. We also expect certain benthic features (like live coral or algae) to be mainly responsible for shaping these observed differences. In doing so, we contribute to building a better understanding of how this unique aspect of coral reefs shapes an important ecological process.

2. Methods

2.1. Study species and location

Recently-settled damselfish surveys occurred in November 2023 at three shallow reef sites on the leeward (western) aspect of Lizard Island (14.6645°S, 145.4651°E), Australia. We focused on the habitat selection by recently-settled individuals of four common site-attached damselfish species (family: Pomacentridae, Fig. 1). *Pomacentrus adelus* (Fig. 1A) is brown in colour and typically resides in areas with a high cover of rubble, dead coral, and pavement (rocks or exposed reef structure covered by the epilithic algal matrix) (Pratchett et al., 2016). The other dark coloured species, *P. chrysurus* (Fig. 1B), is typically found inhabiting algal covered rubble areas (Fakan et al., 2024; Öhman et al., 1998). The first yellow coloured species, *P. amboinensis* (Fig. 1C) is a habitat generalist that associates with a wide variety of substrata including live and dead coral (Öhman et al., 1998). *P. moluccensis* (Fig. 1D) is bright yellow in colour and is an obligate coral dweller associating mainly with fine branching corals (Allen, 1991a; Coker et al., 2014). These four species were selected as they showed generally high abundance at the study site and different habitat preferences (Fakan et al., 2024; Pratchett et al., 2016). Moreover, two are bright yellow and the other two are dark brown in colouration. If matching body colouration to the substratum is important for determining habitat selection, we would expect to see that potentially mirrored across species with similar colouration.

2.2. Benthic and fish surveys

At each site, a 20 m transect was laid along the reef substratum starting 1m in the sand from the reef edge running towards the reef flat. Divers then swam along the transect searching for all recently-settled individuals of each damselfish species that occurred within 0.5 m on either side of the transect tape. Recently-settled individuals (approximately 2-3 days spent on the reef) were identified based on their much smaller body size compared to other juvenile fishes, their colouration, and behaviour (McCormick and Leane, 1997). Four passes were made along the transect with each pass dedicated to identifying one of the four focal species. When a recently-settled individual of the study species was identified, a 0.5 m^2 PVC quadrat was placed on the substratum such that the focal fish was in the centre of the quadrat. The reef substrate within the quadrat was then photographed directly from above using an Olympus TG6 in manual mode that was mounted to the quadrat frame using two 0.5 m long PVC pipes. This setup ensured that the camera, and corresponding images, were taken equidistant from the benthos. Two Ikelite DS51 strobes attached to the camera were used to create standardized light conditions between all images. Although the depth of the transects did not exceed 4 m and was on average 1-2 m deep (meaning there was negligible filtering of light due to depth) (Marshall, 2017), these strobes ensured that all quadrat pictures were comparable

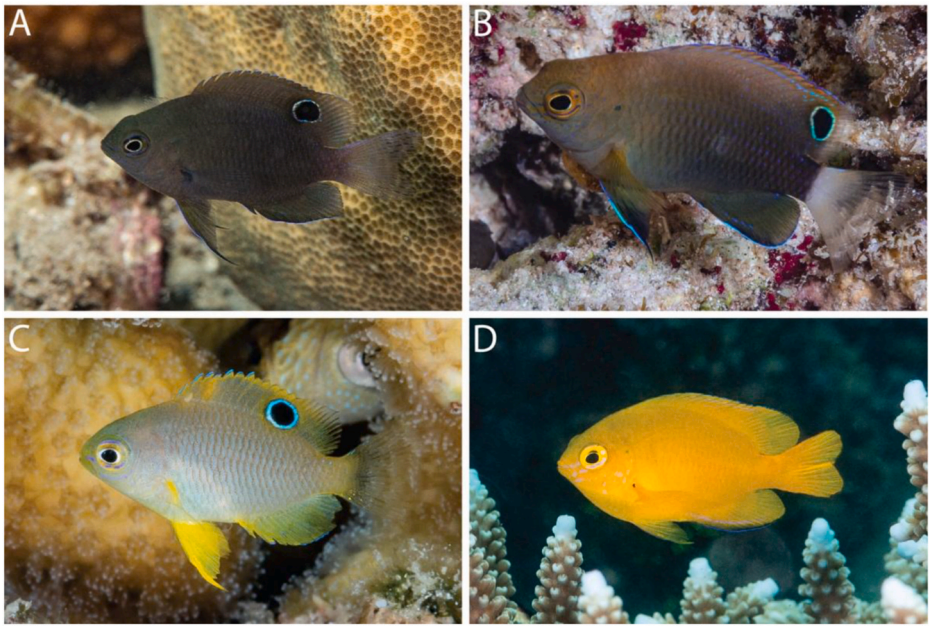


Fig. 1. The four focal study species. (A) *Pomacentru adelus,* (B) *P. chrysurus,* (C) *P. amboinensis* and (D) *P. moluccensis.* Please note the individual in panel D is of a slightly older age than the individuals shown in panels A-C. All photos credit: François Libert

amongst transects. This was important as variation in cloud cover, time of day, or difference in water clarity could affect the colour accuracy of the images (Bergman and Beehler, 2008). To further ensure images were representative, an X-Rite ColorChecker Passport was attached to the side of the quadrat and was present in every photo. UV light was not captured in these images due to the specialized equipment required and previous research suggesting that UV vision in damselfishes is primarily used for intraspecific communication (Siebeck, 2004; Stieb et al., 2017; Tettamanti et al., 2025). That said, we cannot discount the potential use of UV for other functions, including habitat election. All images were captured in raw format to ensure the greatest amount of colour data recorded and to combat any internal colour corrections done in other file formats (like JPEG). Prior to image analysis, colour standards in a subset of images were analysed using colorChecker function in the *patternize* package in R (Team, 2014; Van Belleghem et al., 2018) to ensure photos were colour accurate.

Control pictures were taken to capture the average colours that typified the benthos at each study site. These pictures provided a baseline of the typical reef colouration to which the colour quadrat photos occupied by the four damselfish species could be compared against. Control pictures were taken every metre along every transect with each subsequent image taken from the opposite side of the transect (i.e., one image was taken on the left, followed by an image on the right, and so on). By taking photos every metre, the entire length of the transect was covered across multiple reef locations to provide representation of most benthic features.

In total, we conducted 12 transects across the three survey locations (n = 4 transects at each site). A total of 640 recently-settled fish were recorded (*P. adelus* = 259, *P. chrysurus* = 35, *P. amboinensis* = 109, *P. moluccensis* = 237) and 21 control pictures per transect were taken (total control picture n = 231). Due to image corruption, data for the control group from the last transect was not available, resulting in a total of 871 total images for the study. As the juvenile fish within each image often hid when the quadrat was placed, this prevented any direct comparisons between the fish's colouration and the benthic colouration.

2.3. Image processing and statistical analyses

Adobe Photoshop (CC2019) was used to crop each quadrat image, ensuring that only the area of reef depicted inside the quadrat remained. These images were then exported from Photoshop as.*png* files which minimizes data loss. The colouration of every photo quadrat was then analysed with the *colordistance* package in R (Weller et al., 2019). In short, *colordistance* measures colouration by calculating the total amount of pixels that fall within a set of specified regions of the red-green-blue (RGB) colourspace. This colourspace was chosen specifically because of its symmetric 3D shape (a cube) which allows for objective, equal-area colour categories to be created (e.g. blues, reds, browns, etc) in which a pixel could be classified. *Colordistance* was therefore a suitable choice for characterizing the colouration of the benthos (Hemingson et al., 2024).

We divided each axis of the RGB colourspace into 3 sections (the default recommendation by *colordistance*) which resulted in a total of 27 possible colour categories for each pixel to be classified within (3 sections per axis ^3 axes = 27). Thus, after analysis, every quadrat image had the amount of colour within each of these 27 categories recorded, generating a multivariate dataset. The chi-squared dissimilarity measure was used to calculate pairwise dissimilarity values between all images as this has been previously shown to work well for this type of colour data (Hemingson et al., 2022, 2024). A non-metric multidimensional scaling (nMDS) analysis was then applied to the dissimilarity matrix to visualize the multivariate colourspace of all quadrats analysed. Convex hulls, i.e. the smallest possible polygon in a two-dimensional space that encompasses all points within a specified group, were drawn onto the nMDS to visualize apparent differences among damselfish species in their quadrat colourspace. Two separate permutational multivariate analysis of variance (PERMANOVA) were performed on the colourspace ordination: one in which species identity was used as the predictor, and another in which body colouration (brown or yellow) was the predictor.

The habitat composition within each quadrat was quantified to identify key benthic features that may be responsible for driving any observable differences in the colourspace. Twenty stratified random points (the size of one pixel) were placed on each photo quadrat using PhotoQuad (Supplementary Fig. 2) (Trygonis et al., 2012). The substrate immediately under each of the 20 points was then identified and classified into one of nine different benthic categories: sand, rubble, macroalgae, pavement (rock covered by the epilithic algal matrix), fine branching coral (e.g., branching *Acropora, Seriatopora,* and *Pocillopora*),

coarse branching coral (e.g., staghorn *Acropora*), mounding coral, soft coral and 'other'. This provided measurements used to characterize the benthic composition inherent to each quadrat. The habitat features were then fitted onto the nMDS quadrat colourspace using the envfit function implemented through the vegan package (Oksanen et al., 2013) to determine if there were any significant correlations between benthic composition data and the quadrat colourspace.

Finally, to visualize the visible light colours across the RGB colourspace of each benthic category, 30 random pictures for each benthic category were selected using a random number generator in the PhotoQuad data base. The category "other" was excluded from these analyses because most pictures in this category consisted of dark areas on the quadrats or poorly visible objects. Pictures were cropped in Adobe Photoshop (CC2019) to showcase only the specific feature of a category (e.g. a cropped picture of rubble, fine branching coral without any background). The colour content of each benthic category obtained from the pictures were also visualized using the R *colordistance* package in a similar manner as before (Supplementary Fig. 1).

All data analyses were performed in R v.4.4.3 (Team, 2014). Specific packages used for colour analyses were *patternize* (Van Belleghem et al., 2018) and *colordistance* (Weller et al., 2019), *dplyr* was used for data manipulation (Wickham, 2015), *vegan* (Oksanen et al., 2013) for model fitting and testing, and *ggplot2* for data visualization (Wickham, 2016).

3. Results

3.1. Visualizing habitat colouration on coral reefs

The non-metric multidimensional scaling (nMDS) analysis indicated substantial variation in the colouration of specific habitat features both across and within benthic categories, with high ordination accuracy (Fig. 2). The grey, full convex hull encompasses eight different benthic categories: fine branching coral, coarse branching coral, mounding coral, soft coral, pavement, macroalgae, sand and rubble. Coloured polygons denote the convex hulls for fine branching corals, mounding corals, macroalgae and sand, allowing for visual comparison of group-level clustering. The degree of overlap among groups equates to shared or transitional colouration, whereas distinct separation between clusters indicates more pronounced differences in appearance. Categories representing degraded reef habitats (macroalgae, rubble) tended to cluster towards the lower left of the ordination space while those that represent healthy coral reefs (fine and coarse branching corals, mounding corals) appeared towards the upper right. Importantly, this separation suggests that benthic composition colouration differs consistently between habitat types and is detectable using our approach. The observed benthic category groupings were statistically supported by PERMANOVA, which revealed significant differences in multivariate composition among groups ($F = 21.675$, $R^2 = 0.40$, $p < 0.001$). Post-hoc pairwise comparisons indicated significant differences in composition between all benthic categories (adjusted $p < 0.05$), except between

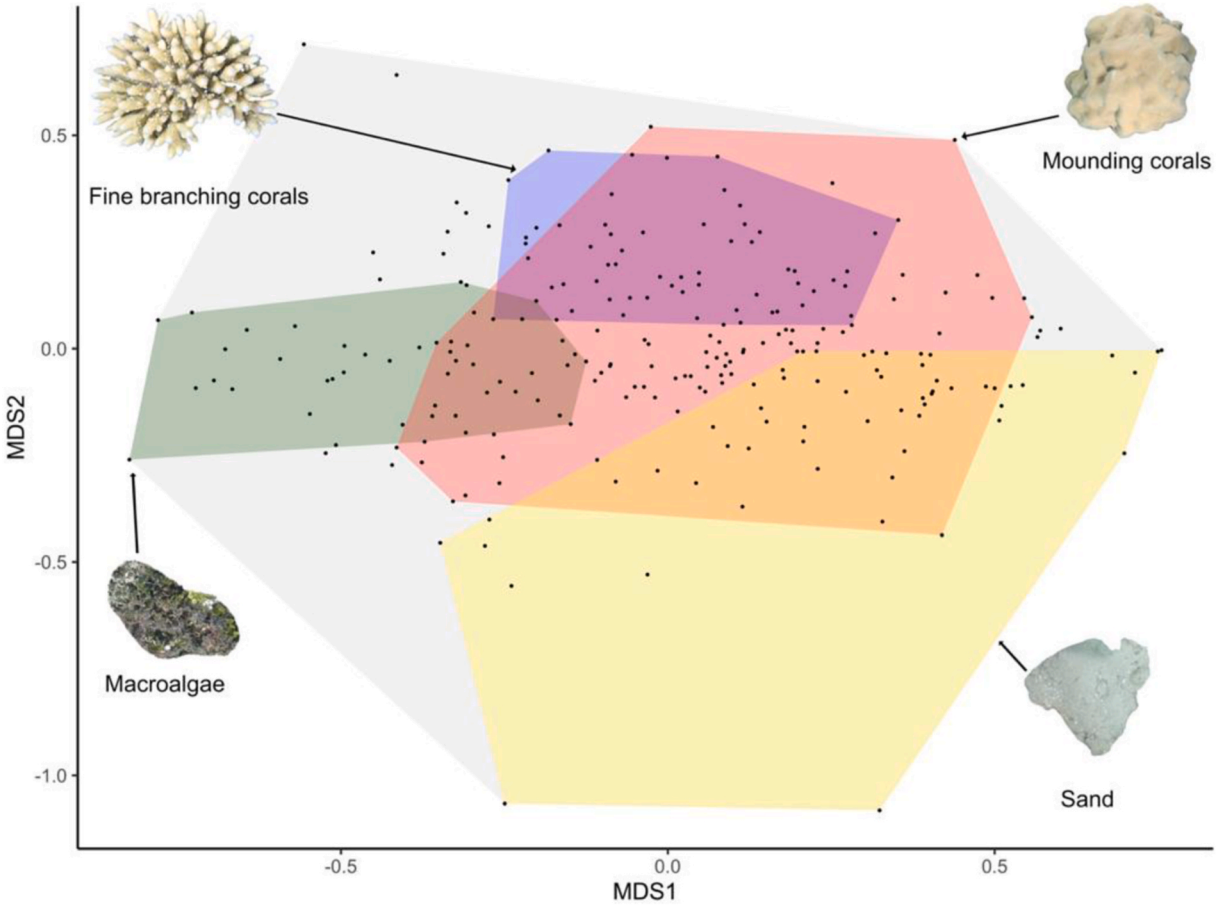


Fig. 2. Benthic community colouration at the three study sites. The non-metric multidimensional scaling (nMDS) ordination exhibits the heterogeneity of benthic colouration contributed by different substrate types. From each category, 30 randomly selected replicates (total = 240) were plotted. The grey polygon denotes the full area created by all categories, while macroalgae (green), fine branching coral (blue), mounding coral (red) and sand (yellow) have been highlighted to show the different spectrums represented in the ordination. Stress = 0.126. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

coarse branching and mounding coral, and between pavement and rubble, where no statistically significant differences were detected (Supplementary Table 1).

3.2. Colourspace occupied by the four damselfish species

There were significant differences between the quadrats colour composition occupied by the four damselfish species (PERMANOVA $R^2 = 0.14$, $p < 0.001$). Pairwise comparisons showed that the colour composition of the habitats of all four species significantly differed from one another, but only *P. moluccensis* showed significant differences from the control group (Supplementary Table 2). Damselfish habitat colourations occupied a wide range of different colour compositions (Fig. 3.1, stress = 0.129). The convex hulls of each species occupied distinct areas within the control group space and differed in sizes. Habitat vectors overlaying the ordination represent the contribution of specific benthic categories such as rubble, pavement, sand, fine and coarse branching coral, and mounding coral to the overall colourspace variation in the ordination space. These variables can be categorized into two distinguished habitat groups. The first group (with positive values on MDS2) includes habitat features typically dominant in degraded habitats (i.e. rubble, pavement, algae), which are usually less colourful and share similarly drab colour signature. The second group (with negative values on MDS2) contains coarse branching corals, fine branching corals and mounding corals, which are often associated with a greater diversity of colours.

Each species colourspace was nested within the broader colourspace of the benthos but showed species-specific variation. *P. adelus* occupied the largest colourspace on the ordination, however, the highest density of points was located to the left of the origin, coinciding with habitats that have a greater coverage of sand and soft coral (Fig. 3.2a). The *P. amboinensis* quadrats were relatively evenly spread within their convex hull and did not show a clear correlation with a specific benthic group (Fig. 3.2b). *P. chrysurus* occupied a relatively limited colourspace characterised by a greater coverage of sand, rubble and soft coral (Fig. 3.2c). In contrast, *P. moluccensis* had a moderately-sized convex hull that aligned most strongly with the presence of mounding coral, pavement and algae (Fig. 3.2d).

Of the nine habitat features assessed in our study, fine branching coral was the only category that showed significant correlation to the nMDS quadrat colourspace ($p < 0.05$). This suggests that fine branching corals are the most prominent driver of differences in colour between quadrats where the four damselfish species settle (Supplementary Table 3).

3.3. Body colouration as a predictor

Body colouration was also found to be a significant predictor of early post-settlement habitat colouration (PERMANOVA $R^2 = 0.13$, $p < 0.001$). Pairwise comparisons of the colour groups (brown and yellow) showed the two groups occupied distinct and significantly different areas within the multivariate habitat colourspace ($R^2 = 0.13$, $p < 0.001$) (Fig. 4). The brown species clustered lower in the nMDS space showing the strongest correlation to sand, soft coral, and 'other' substrate groups. In contrast, yellow species clustered in the upper right of the nMDS space with a strong correlation to pavement, algae, and mounding corals. Pairwise comparisons of the three groups (brown, yellow, and control), showed the colour profile of habitats occupied by brown species was not significantly different from the control quadrats ($R^2 = 0.00$, $p > 0.05$), whereas the habitat colouration of yellow species differed significantly from the control ($R^2 = 0.08$, $p < 0.05$). Therefore, it appears that the brown coloured species occupy habitats that are 'typical' of the average reef appearance with no apparent selection, while yellow species are targeting habitats with a distinct and unique colour profile relative to what is available in the wider reef area.

4. Discussion

This study explored how habitat colouration shapes the settlement patterns of four common coral reef damselfish species. We show that newly-settled damselfishes occupy distinct, species-specific habitat colourspaces across the reefscape. Furthermore, we show that body colouration, in place of species identity, also predicts significant differences in habitat colouration. Thus, while species show distinct, colour-based patterns of association within habitats, these patterns are also predicted by body colouration at a broader scale. Habitat colourspace was most strongly shaped by the presence of branching corals, suggesting a prominent link between this specific group and the visual environment encountered by settling fishes. By providing a highly diverse and colourful substrate, branching corals not only shape the 3D environment of coral reefs (Pratchett et al., 2015; Graham and Nash, 2013b) but also influence the appearance of the environment available to resident fishes.

4.1. Species specific colour preference – does colour matter?

Our study showed that habitat colour association differs among species as well as between taxa with the similar general body colourations (brown vs yellow). Species identity was a more parsimonious predictor of habitat colouration (based on AIC values). Thus, at a broader scale, it appears that habitat colouration for coral reef-dwelling damselfishes is correlated to their body colouration. Despite the vast diversity of colourful benthic organisms on coral reefs (Cox et al., 2021; Matz et al., 2006b) fishes do rely to some extent on camouflage (Justin Marshall, 2000; Tyrie et al., 2015). While we did not directly compare individual damselfish colouration to the occupied habitat's colouration herein, we did see species of similar appearance grouping accordingly in the habitat colourspace, akin to findings from other marine reef fish taxa (Fark et al., 2022). The exact mechanism underpinning this relationship remains uncertain (e.g. camouflage, signalling, etc), however, we do establish a statistically robust correlation that links species appearances to environmental colouration priming future lines of research. The more parsimonious differences detected at the species level could suggest a certain degree of niche partitioning between taxa that closely resemble one another (Hemingson et al., 2019; Whitney et al., 2018) which agrees with patterns of character displacement in traits amongst closely related, co-occurring taxa (Pfennig et al., 2009).

Interestingly, the colouration of the habitat occupied by brown species did not differ significantly from the average reef colouration (i.e. the control quadrats), while for the yellow species, it did. It is therefore possible that bright and colourful species may be more reliant on the equally colourful backdrop unique to coral reefs, allowing them to better communicate and function within their environment (Jennifer et al., 2017; Huertas et al., 2025). Indeed, this relationship may be partially responsible for why coral reefs evolved such colourful taxa, and why non-reef dwelling species tend to be less colourful in appearance (Hodge et al., 1923b). The brown coloured species tended to reside on habitats that were "average" in colour. One hypothesis could be that the dark and more cryptic species match a greater spread of non-coral substrates. However, *P. chrysurus;* despite being one of the darker coloured species, settled primarily on habitats whose colourspace was mainly characterized by lighter hues associated with sand. *P. chrysurus* had the smallest colourspace amongst the studied damselfishes, corresponding to associations with fewer benthic taxa than the three other damselfish species. From above, *P. chrysurus* exhibits a brown colouration on its back that closely resembles similar colouration to the brown algae found on reef flats. This may be an effective camouflage against aerial predators as their swimming may mimic the movement of brown algae. However, this hypothesis needs to be tested. The occupation of reef flats and small colourspace by *P. chrysurus* may be the result of having extra double cones with long-wavelength sensitivity (LWS) in their eyes which allows them to have a more sensitive colour vision then other members of the family Pomacentridae (Cortesi et al., 2020). Longer wavelength

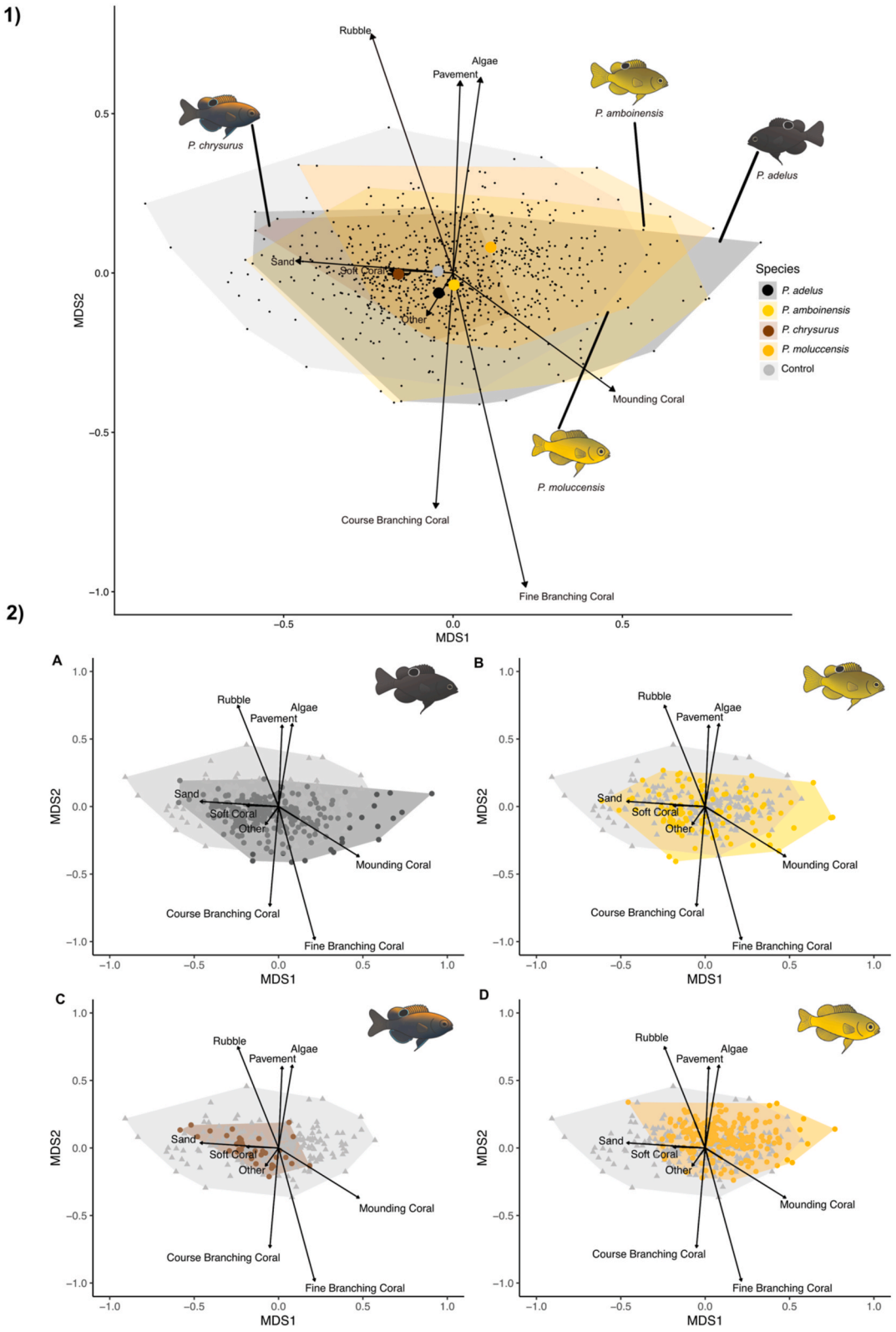


Fig. 3. The non-metric multidimensional scaling (nMDS) ordination displaying the habitat colour space occupied by four damselfish species at early post-settlement; **1** shows the colourspace habitat occupied by all fours study species occupied in the same ordination space in comparison with the control group, **2** displays species-specific colourspace habitat in comparison with the control group for (A) *P. adelus*, (B) *P. amboinensis*, (C) *P. chrysurus* and (D) *P. moluccensis*. Habitat vectors represent habitat types correlated to the settlement colourspace. All recruits of the four focal species (n = 640) and their selected habitat are plotted. Coloured convex hulls represent the full range of habitat colours associated with each species. The grey, shaded convex hull shows the control habitat colouration found along the reef gradient. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

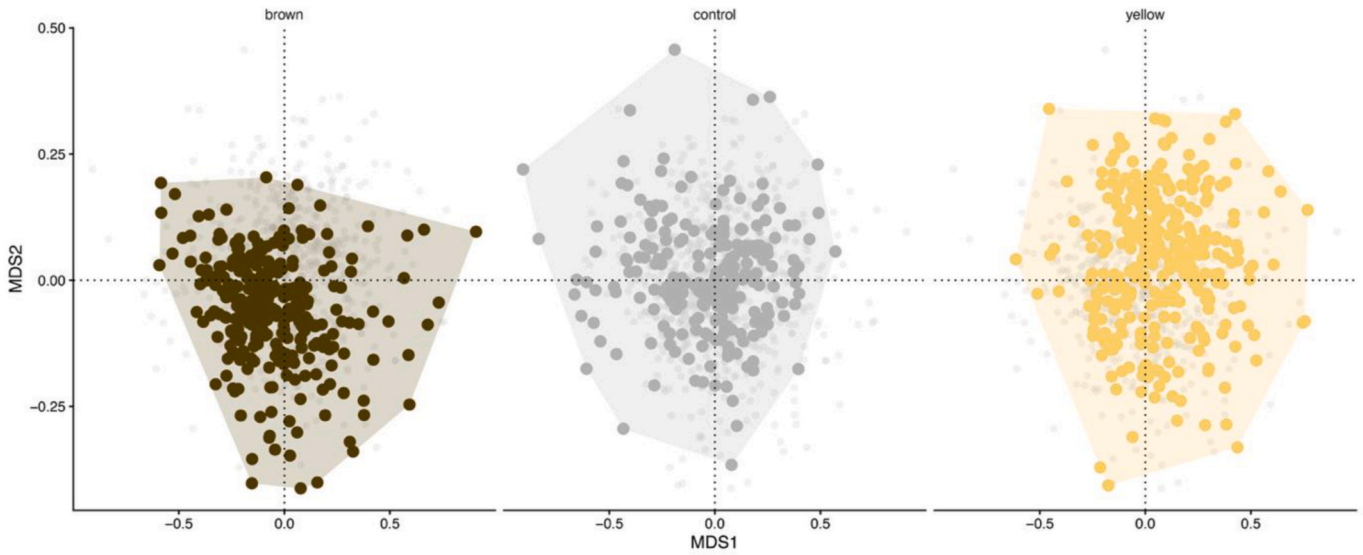


Fig. 4. The same multivariate habitat colourspace as shown previously, but now grouped by colour. Left: brown species, *P. adelus* and *P. chrysurus*. Middle: the control quadrats. Right: the yellow species, *P. amboinensis* and *P. moluccensis*. In each panel, the smaller grey points denote the quadrats from the other two groups. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

sensitivities are a trait of many herbivorous species (as their main dietary component reflect longer wavelength spectra, like green and red) which may allow this species to more effectively determine high vs. low quality algal foods (Marshall et al., 2003; Stieb et al., 2017, 2023).

Three out of four damselfishes occupied similar colourspace compared to the control quadrats. However, the colourspace of occupied habitat by *P. moluccensis* differs the greatest from the typical reef colourspace. *P. moluccensis* is a known coral obligate dwelling species and predominantly settles on live coral (Sale et al., 1984). Previous research has shown cues from live coral can have a positive effect on the settlement of some damselfish species (McCormick et al., 2010), but the visual cues provided by the colours of live coral compared to degraded or dead corals may also play an important role in the final step of specific habitat selection. As our findings suggested, the colourspace of recently-settled *P. moluccensis* is influenced most likely by the presence of certain coral groups. These differences in colourspace preferences may demonstrate a more complex use of colour vision in this species. Vision may not be just important for mating, foraging and predator avoidance (Siebeck, 2004), but also critical for finding the most suitable habitat available which ultimately increases recruitment success and long-term survival on reefs. A recent study on damselfishes has shown highly specific species responses to habitat changes (Fakan et al., 2025). Thus, the importance of habitat colouration may be species-specific as well. Further research on colour vision and how it relates to habitat selection will yield detailed insights as to how this environmental feature shapes the ecology and behaviour of various reef-dwelling organisms.

4.2. Habitat colouration – what drives colours on modern coral reefs?

Here we show that four species of recently-settled damselfishes have distinct habitat colour profiles that were a subset of the broader colourspace of the study sites. Specifically, our data suggest that fine branching coral growth forms exhibit the greatest influence on the colours that characterize specific habitats occupied by recently-settled damselfishes (Supplementary Table 3). Fine branching corals (e.g., *Acropora*) possess unique colours that are not present in other reef associated organisms and benthic space occupiers. These bright colours of corals (see Supplementary Fig. 1) are the results of the combination of green, red, and cyan fluorescent proteins (FPs) and nonfluorescent blue/purple chromoproteins (ChrP) (Dove et al., 2001; Kelmanson et al., 2003; Salih et al., 2000; Smith et al., 2013). Thus, habitat colour may represent a previously unrecognized environmental factor influencing coral reef fish settlement and post-settlement behaviour and survival. However, it remains unclear whether colouration is directly driving settlement by providing a visual cue for new recruits or the colours of corals are indicators-for and correlate-with overall habitat quality (Leiper et al., 2009).

From an environmental perspective, fine branching corals are typically more sensitive to heat stress than mounding or massive corals (Hueerkamp et al., 2001; Morais et al., 2024; Hughes et al., 2018). Thus, it is reasonable to assume that contemporary changes occurring to coral reefs may result in a decrease in total colour diversity. As coral reefs go through compositional changes on a global scale (i.e., decreases in coral cover and increases in algal cover (Tebbett et al., 2023)), the appearance of reef ecosystems may transition towards drabber colours that typify degraded reef habitats. The significant effect of fine branching corals mainly representing *Acropora* spp. on habitat colouration and the previously shown relationship between branching corals and the broader colouration of the resident fish community (Hemingson et al., 2022) may therefore have important ramifications for the settlement success and survival amongst certain reef fish species. Declines in the cover of these corals may favour the settlement of a lower diversity of fishes on coral reefs (Lecchini et al., 2013) which negatively affects fish community assemblages (Pratchett et al., 2016; Jones et al., 2004; Wilson et al., 2008). Further, colour loss may lead to increases in predation risk as fish colourations may no longer provide adequate camouflage against bleached coral backdrops making them more visible to predators (Victor, 1986; Coker et al., 2009). These unique, visual-based insights may inform future research that works towards understanding how visual characteristics of coral reefs modify fish assemblages. Further study is required to determine whether the colour of benthic habitat has a direct effect on coral reef fish settlement preferences, or if other habitat features that are colinear with colour are the primary factors influencing the habitat associations of recently-settled reef fish.

5. Conclusions

We demonstrated that recently-settled damselfish show species-specific preferences for reef habitats that display different visible light colour profiles. We also highlight that when grouped according to their body colouration, damselfishes still occupy distinct and significantly different coloured habitats. Different types of substrates contain specific

colours that may influence habitat selection during the settlement and post-settlement life stages. By identifying key habitats that shape the colouration of coral reefs, we can emphasize the importance of these habitat types and their role in recruitment success (Lecchini et al., 2013). Our findings suggest that as coral reefs experience rapid habitat shifts (Reverter et al., 2022), cues that fish may use to identify suitable habitat might change and locating optimal habitat as determined by colour may become more difficult. This may affect the survival rate amongst new recruits, and ultimately shape broadscale population dynamics. Future work exploring habitat colour preferences among other species and other light spectra, namely UV light, will therefore assist in understanding how colouration shapes key processes on coral reefs.

Data accessibility

Pending acceptance, data will be made publicly available in a data repository.

Ethics and permits

All research was carried out under approval of James Cook University animal ethics committee and according to the University's animal ethics guidelines (permit: A2683) and conducted in accordance with GBRMPA (permit: G23/49203.1).

Funding statement

Funding was provided by the Lizard Island Reef Research Foundation (Gough Fellowship awarded to EPF).

CRediT authorship contribution statement

Norbert Rapolthy: Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Eric P. Fakan:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Supervision, Visualization, Writing – review & editing. **Alexia Dubuc:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Supervision, Visualization, Writing – review & editing. **Andrew S. Hoey:** Funding acquisition, Investigation, Resources, Supervision, Validation, Writing – review & editing. **Christopher R. Hemingson:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Supervision, Validation, Visualization, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank the staff at Lizard Island Field Station (the facility of the Australian Museum) for their logistical support.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2026.108203.

Data availability

Data will be made available on request.

References

Allen, Gerald R., 1991a. Damselfishes of the World.
Allen, Gerald R., 1991b. Damselfishes of the world. Aquarium Systems. Mentor, Ohio.
Almany, G., 2004. Different effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. Oecologia 141 (1), 105–113. https://doi.org/10.1007/s00442-004-1617-0.
Almany, G.R., Webster, M.S., 2006. The predation gauntlet: early post-settlement mortality in reef fishes. Coral Reefs 25 (1), 19–22. https://doi.org/10.1007/s00338-005-0044-y.
Alvarez-Filip, Lorenzo, Dulvy, Nicholas K., Gill, Jennifer A., Cote, Isabelle M., Watkinson Andrew, R., 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. Proc. R. Soc. B. 276, 3019–3025. https://doi.org/10.1098/rspb.2009.0339.
Bergman, Thore J., Beehler, Jacinta C., 2008. A simple method for measuring colour in wild animals: validation and use on chest patch colour in geladas (*Theropithecus gelada*). Biol. J. Linn. Soc. 94 (2), 231–240. https://doi.org/10.1111/j.1095-8312.2008.00981.x.
Booth, D.J., Wellington, G., 1998. Settlement preferences in coral-reef fishes: effects on patterns of adult and juvenile distributions, individual fitness and population structure. Aust. J. Ecol. 23 (3), 274–279. https://doi.org/10.1098/rsbl.2011.0380.
Carr, M.H., Hixon, M.A., 1995. Predation effects on early post-settlement survivorship of coral-reef fishes. Mar. Ecol. Prog. Ser. 124, 31–42. https://doi.org/10.3354/meps124031.
Caselle, J.E., 1999. Early post-settlement mortality in a coral reef fish and its effect on local population size. Ecol. Monogr. 69 (2), 177–194. https://doi.org/10.1890/0012-9615(1999)069[0177:EPSMIA]2.0.C);2.
Coker, D.J., Pratchett, M.S., Munday, P.L., 2009. Coral bleaching and habitat degradation increase susceptibility to predation for coral-dwelling fishes. Behav. Ecol. 20 (6), 1204–1210. https://doi.org/10.1093/beheco/arp113.
Coker, D.J., Wilson, S.K., Pratchett, M.S., 2014. Importance of live coral habitat for reef fishes. Rev. Fish Biol. Fish. 24, 89–126. https://doi.org/10.1007/s11160-013-9319-5.
Cooper, W. James, Smith, Lydia L., Westneat, Mark W., 2009. Exploring the radiation of a diverse reef fish family: phylogenetics of the damselfishes (Pomacentridae), with new classifications based on molecular analyses of all genera. Mol. Phylogenet. Evol. 52 (1), 1–16. https://doi.org/10.1016/j.ympev.2008.12.010.
Coppock, A.G., González-Murcia, S.O., Srinivasan, M., Gardiner, N.M., Jones, G.P., 2020. Different responses of coral and rubble-dwelling coral reef damselfishes (Family: pomacentridae) to chemosensory cues from coral reef microhabitats. Mar. Biol. 167 (6), 74. https://doi.org/10.1007/s00227-020-03687-w.
Cortesi, Fabio, Mitchell, Laurie J., Tettamanti, Valerio, Fogg, Lily G., de Busserolles, Fanny, Cheney, Karen L., Justin Marshall, N., 2020. Visual system diversity in coral reef fishes. Semin. Cell Dev. Biol. 106, 31–42. https://doi.org/10.1016/j.semcdb.2020.06.007. ISSN 1084-9521.
Cott, H.B., 1940. Adaptive Coloration in Animals.
Cox, K.D., Woods, M.B., Reimchen, T.E., 2021. Regional heterogeneity in coral species richness and hue reveals novel global predictors of reef fish intra-family diversity. Sci. Rep. 11, 18275. https://doi.org/10.1038/s41598-021-97862-8.
da, Silva, Carmen, R.B., et al., 2020. Intertidal gobies acclimate rate of luminance change for background matching with shifts in seasonal temperature. J. Anim. Ecol. 89 (7), 1735–1746. https://doi.org/10.1111/1365-2656.13226.
Darwin, C., 1859. On the Origin of Species: Facsimile of the First Edition.
Doherty, P.J., Dufour, V., Galzin, R., Hixon, M.A., Meekan, M.G., Planes, S., 2004. High mortality during settlement is a population bottleneck for a tropical surgeonfish. Ecology 85 (9), 2422–2428. https://doi.org/10.1890/04-0366.
Dove, S.G., Hoegh-Guldberg, O., Shoba, Ranganathan, 2001. Major colour patterns of reef-building corals are due to a family of GFP-like proteins. Coral Reefs 19 (3), 197–204. https://doi.org/10.1007/PL00006956.
Evans, M.R., Norris, K., 1996. The importance of carotenoids in signaling during aggressive interactions between male firemouth cichlids (Cichlasoma meeki). Behav. Ecol. 7 (1), 1–6. https://doi.org/10.1093/beheco/7.1.1.
Fakan, E.P., McCormick, M.I., Jones, G.P., Hoey, A.S., 2024. Habitat and morphological characteristics affect juvenile mortality in five coral reef damselfishes. Coral Reefs 43 (1), 171–183. https://doi.org/10.1007/s00338-023-02462-9.
Fakan, Eric P., Dubuc, Alexia, Hemingson, Christopher R., McCormick, Mark I., Hoey, Andrew S., 2025. Habitat degradation has species-specific effects on the stress response of coral reef fishes. J. Exp. Mar. Biol. Ecol. 582, 152070. https://doi.org/10.1016/j.jembe.2024.152070. ISSN 0022-0981.
Fark, S.N., Gerber, S., Alonzo, S.H., Kindsvater, H.K., Meier, J.I., Seehausen, O., 2022. Multispecies colour polymorphisms associated with contrasting microhabitats in two Mediterranean wrasse radiations. J. Evol. Biol. 35, 633–647. https://doi.org/10.1111/jeb.13999.
Feary, D.A., Almany, G.R., McCormick, M.I., Jones, G.P., 2007. Habitat choice, recruitment and the response of coral reef fishes to coral degradation. Oecologia 153 (3), 727–737. https://doi.org/10.1007/s00442-007-0773-4.
Frisch, A.J., Ireland, M., Baker, R., 2014. Trophic ecology of large predatory reef fishes: energy pathways, trophic level, and implications for fisheries in a changing climate. Mar. Biol. 161, 61–73. https://doi.org/10.1007/s00227-013-2315-4.
Graham, N.A., Nash, K.L., 2013a. The importance of structural complexity in coral reef ecosystems. Coral Reefs 32 (2), 315–326. https://doi.org/10.1007/s00338-012-0984-y.
Graham, N.A.J., Nash, K.L., 2013b. The importance of structural complexity in coral reef ecosystems. Coral Reefs 32, 315–326. https://doi.org/10.1007/s00338-012-0984-y.

Hemingson, C.R., Cowman, P.F., Hodge, J.R., Bellwood, D.R., 2019. Colour pattern divergence in reef fish species is rapid and driven by both range overlap and symmetry. Ecol. Lett. 22 (1), 190–199. https://doi.org/10.1111/ele.13180.
Hemingson, C.R., Mihalitsis, M., Bellwood, D.R., 2022. Are fish communities on coral reefs becoming less colourful? Glob. Change Biol. 28, 3321–3332. https://doi.org/10.1111/gcb.16095.
Hemingson, Christopher R., Cowman, Peter F., Bellwood, David R., 2024. Analysing biological colour patterns from digital images: an introduction to the current toolbox. Ecol. Evol. 14 (3), e11045. https://doi.org/10.1002/ece3.11045.
Hemingson, Christopher R., Siqueira, Alexandre C., Cowman, Peter F., Bellwood, David R., 2021. Drivers of eyespot evolution in coral reef fishes. Evolution 75 (4), 903–914.
Öhman, Marcus C., et al., 1998. Settlement strategies and distribution patterns of coral-reef fishes. J. Exp. Mar. Biol. Ecol. 225 (2), 219–238. https://doi.org/10.1016/S0022-0981(97)00224-4.
Hodge, J.R., Santini, F., Wainwright, P.C., 1923a. Colour dimorphism in labrid fishes as an adaptation to life on coral reefs. Proc. Biol. Sci. 287, 20200167. https://doi.org/10.1098/rspb.2020.0167, 1 March 2020.
Hodge, J.R., Santini, F., Wainwright, P.C., 1923b. Colour dimorphism in labrid fishes as an adaptation to life on coral reefs. Proc. Biol. Sci. 287, 20200167. https://doi.org/10.1098/rspb.2020.0167, 1 March 2020.
Hoey, A.S., McCormick, M.I., 2004. Selective predation for low body condition at the larval-juvenile transition of a coral reef fish. Oecologia 139 (1), 23–29. https://doi.org/10.1007/s00442-004-1489-3.
Hueerkamp, Christiane, et al., 2001. Bleaching and recovery of five eastern Pacific corals in an El Niño-related temperature experiment. Bull. Mar. Sci. 69 (1), 215–236.
Huertas, V., Hemingson, C.R., 2025. The morphology and colouration of rabbitfishes. In: Hoey, A.S., Taylor, B.M. (Eds.), Biology of Rabbitfishes. CRC Press, Boca Raton, pp. 22–45.
Hughes, T., Kerry, J., Álvarez-Noriega, M., et al., 2017. Global warming and recurrent mass bleaching of corals. Nature 543, 373–377. https://doi.org/10.1038/nature21707.
Hughes, T.P., Kerry, J.T., Baird, A.H., Connolly, S.R., Dietzel, A., Eakin, C.M., Heron, S. F., Hoey, A.S., Hoogenboom, M.O., Liu, G., McWilliam, M.J., 2018. Global warming transforms coral reef assemblages. Nature 556 (7702), 492–496. https://doi.org/10.1038/s41586-018-0041-2.
Jennifer, Kelley J., Taylor, Ian, Hart, Nathan S., Partridge, Julian C., 2017. Aquatic prey use countershading camouflage to match the visual background. Behav. Ecol. 28 (5), 1314–1322. https://doi.org/10.1093/beheco/arx093. September-October.
John, Leonie, Santon, Matteo, Michiels, Nico K., 2023. Scorpionfish rapidly change colour in response to their background. Front. Zool. 20 (1), 10. https://doi.org/10.1186/s12983-023-00488-x.
Jones, Geoffrey P., et al., 2004. Coral decline threatens fish biodiversity in marine reserves. Proc. Natl. Acad. Sci. 101 (21), 8251–8253. https://doi.org/10.1073/pnas.0401277101.
Justin Marshall, N., 2000. Communication and camouflage with the same 'bright'colours in reef fishes. Phil. Trans. Roy. Soc. Lond. B Biol. Sci. 355 (1401), 1243–1248. https://doi.org/10.1098/rstb.2000.0676.
Kelmanson, Ilya V., Matz, Mikhail V., 2003. Molecular basis and evolutionary origins of color diversity in great star coral Montastraea cavernosa (Scleractinia: faviida). Mol. Biol. Evol. 20 (7), 1125–1133. https://doi.org/10.1093/molbev/msg130.
Kjernsmo, Karin, Merilaita, Sami, 2013. Eyespots divert attacks by fish. Proc. Biol. Sci. 280, 1766. https://doi.org/10.1098/rspb.2013.1458.
Kohda, M., Jordan, L.A., Hotta, T., Kosaka, N., Karino, K., Tanaka, H., et al., 2015. Facial recognition in a group-living cichlid fish. PLoS One 10 (11), e0142552, 101371/journal.pone.0142552.
Lecchini, David, et al., 2013. Fish larvae prefer coral over algal water cues: implications of coral reef degradation. Mar. Ecol. Prog. Ser. 475, 303–307. https://doi.org/10.3354/meps10094.
Leiper, Ian A., et al., 2009. Coral health monitoring: linking coral colour and remote sensing techniques. Can. J. Rem. Sens. 35 (3), 276–286. https://doi.org/10.5589/m09-016.
Maan, M.E., Van Der Spoel, M., Jimenez, P.Q., Van Alphen, J.J., Seehausen, O., 2006. Fitness correlates of male coloration in a Lake Victoria cichlid fish. Behav. Ecol. 17 (5), 691–699. https://doi.org/10.1093/beheco/ark020.
Marshall, Justin, 2017. Vision and lack of vision in the ocean. Curr. Biol. 27 (11), R494–R502.
Marshall, N.J., et al., 2003. Visual biology of Hawaiian coral reef fishes. III. Environmental light and an integrated approach to the ecology of reef fish vision. Ichthyology & Herpetology 3, 467–480. https://doi.org/10.1643/01-056, 2003.
Marshall, N.J., Cortesi, F., de Busserolles, F., Siebeck, U.E., Cheney, K.L., 2019. Colours and colour vision in reef fishes: past, present and future research directions. J. Fish. Biol. 95 (1), 5–38, 10.1111.jfb.13849.
Matz, M.V., Marshall, N.J., Vorobyev, M., 2006a. Are corals colorful? Photochem. Photobiol. 82, 345–350, 10.1562.2005-08-18-RA-653.
Matz, M.V., Marshall, N.J., Vorobyev, M., 2006b. Are corals colorful? Photochem. Photobiol. 82, 345–350. https://doi.org/10.1562/2005-08-18-RA-653.
McCormick, M.I., Moore, J.A.Y., Munday, P.L., 2010. Influence of habitat degradation on fish replenishment. Coral Reefs 29, 537–546. https://doi.org/10.1007/s00338-010-0620-7.
McCormick, Mark I., Leane, J. Makey, 1997. Post-settlement transition in coral reef fishes: overlooked complexity in niche shifts. Mar. Ecol. Prog. Ser. 153, 247–257. https://doi.org/10.3354/meps.
Morais, J., Morais, R., Tebbett, S.B., Bellwood, D.R., 2022. On the fate of dead coral colonies. Funct. Ecol. 36, 3148–3160. https://doi.org/10.1111/1365-2435.14182.
Morais, Juliano, et al., 2024. Hot spots of bleaching in massive Porites coral colonies. Mar. Environ. Res. 193, 106276. https://doi.org/10.1016/j.marenvres.2023.106276.
Oksanen, J., et al., 2013. Community Ecology Package. R Package Version 2.0-2. CRAN, Vienna, Austria [Google Scholar].
Pfennig, KarinS., Pfennig, DavidW., 2009. Character displacement: ecological and reproductive responses to a common evolutionary problem. Q. Rev. Biol. 84 (3), 253–276. https://doi.org/10.1086/605079.
Phillips, Genevieve AC., How, Martin J., Lange, Julia E., Marshall, N Justin, Cheney, Karen L., 2017. Disruptive colouration in reef fish: does matching the background reduce predation risk? J. Exp. Biol. 220 (11), 1962–1974. https://doi.org/10.1242/jeb.151480.
Pratchett, Morgan S., et al., 2016. Habitat-use and specialisation among coral reef damselfishes. Biology of Damselfishes. CRC Press, pp. 84–121.
Pratchett, Morgan S., Anderson, Kristen D., Hoogenboom, Mia O., Widman, Elizabeth, Baird, Andrew H., Pandolfi, John M., Edmunds, Peter J., Lough, Janice M., 2015. Spatial, temporal and taxonomic variation in coral growth—implications for the structure and function of coral reef ecosystems. Oceanogr. Mar. Biol. Annu. Rev. 53, 215–295.
Reverter, M., Helber, S.B., Rohde, S., de Goeij, J.M., Schupp, P.J., 2022. Coral reef benthic community changes in the Anthropocene: biogeographic heterogeneity, overlooked configurations, and methodology. Glob. Change Biol. 28, 1956–1971. https://doi.org/10.1111/gcb.16034.
Risk, A., 1997. Effect of habitat on the settlement and post-settlement success of the ocean surgeonfish *Acanthurus bahianus*. Mar. Ecol. Prog. Ser. 161, 51–59. https://doi.org/10.3354/meps161051.
Sale, Peter F., Douglas, William A., Doherty, Peter J., 1984. Choice of microhabitats by coral reef fishes at settlement. Coral Reefs 3 (2), 91–99. https://doi.org/10.1007/BF00263759.
Salih, Anya, et al., 2000. Fluorescent pigments in corals are photoprotective. Nature 408 (6814), 850–853. https://doi.org/10.1038/35048564.
Siebeck, U.E., 2004. Communication in coral reef fish: the role of ultraviolet colour patterns in damselfish territorial behaviour. Anim. Behav. 68 (2), 273–282. https://doi.org/10.1016/j.anbehav.2003.11.010.
Siebeck, Ulrike E., 2016. Vision and colour diversity in damselfishes. In: Biology of Damselfishes. CRC Press, pp. 267–294.
Smith, Edward G., et al., 2013. Screening by coral green fluorescent protein (GFP)-like chromoproteins supports a role in photoprotection of zooxanthellae. Coral Reefs 32 (2), 463–474. https://doi.org/10.1007/s00338-012-0994-9.
Stieb, S.M., Cortesi, F., Jardim de Queiroz, L., Carleton, K.L., Seehausen, O., Marshall, N. J., 2023. Long-wavelength-sensitive (*lws*) opsin gene expression, foraging and visual communication in coral reef fishes. Mol. Ecol. 32, 1656–1672. https://doi.org/10.1111/mec.16831.
Stieb, S.M., Cortesi, F., Sueess, L., Carleton, K.L., Salzburger, W., Marshall, N.J., 2017. Why UV vision and red vision are important for damselfish (Pomacentridae): structural and expression variation in opsin genes. Mol. Ecol. 26, 1323–1342. https://doi.org/10.1111/mec.13968.
Stieb, Sara M., Carleton, Karen L., Cortesi, Fabio, Justin Marshall, N., Salzburger, Walter, 2016. Depth-dependent plasticity in opsin gene expression varies between damselfish (Pomacentridae) species. Mol. Ecol. 25 (15), 3645–3661. https://doi.org/10.1111/mec.13712.
Streit, R.P., Hemingson, C.R., Cumming, G.S., et al., 2021. How flexible are habitat specialists? short-term space use in obligate coral-dwelling damselfishes. Rev. Fish Biol. Fish. 31, 381–398. https://doi.org/10.1007/s11160-021-09646-y.
Team, R., 2014. Care [Internet] R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing. https://www.r-project.org/ [Google Scholar] 3075 (2020).
Tebbett, S.B., Connolly, S.R., Bellwood, D.R., 2023. Benthic composition changes on coral reefs at global scales. Nat. Ecol. Evol. 7, 71–81. https://doi.org/10.1038/s41559-022-01937-2.
Tettamanti, V., Marshall, N.J., Cheney, K.L., Cortesi, F., 2025. Damsels in disguise: development of ultraviolet sensitivity and colour patterns in damselfishes (Pomacentridae). Mol. Ecol. 34, e17680. https://doi.org/10.1111/mec.17680.
Trygonis, Vasilis, Sini, Maria, 2012. photoQuad: a dedicated seabed image processing software, and a comparative error analysis of four photoquadrat methods. J. Exp. Mar. Biol. Ecol. 424, 99–108. https://doi.org/10.1016/j.jembe.2012.04.018.
Tupper, M., Boutilier, R.G., 1997. Effects of habitat on settlement, growth, predation risk and survival of a temperate reef fish. Mar. Ecol. Prog. Ser. 151, 225–236. https://doi.org/10.3354/meps1512255.
Tyrie, Elizabeth K., Hanlon, Roger T., Siemann, Liese A., Uyarra, Maria C., 2015. Coral reef flounders, *Bothus lunatus*, choose substrates on which they can achieve camouflage with their limited body pattern repertoire. Biol. J. Linn. Soc. 114 (3), 629–638. https://doi.org/10.1111/bij.12442.
Vail, A.L., McCormick, M.I., 2011. Metamorphosing reef fishes avoid predator scent when choosing a home. Biol. Lett. 7 (6), 921–924, 10/1098/rsbl.2011.0380.
Van Belleghem, Steven M., et al., 2018. Patternize: an R package for quantifying colour pattern variation. Methods Ecol. Evol. 9 (2), 390–398. https://doi.org/10.1111/2041-210X.12853.
Victor, B.C., 1986. Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. Ecol. Monogr. 56 (2), 145–160. https://doi.org/10.2307/1942506.
Weller, Hannah I., Westneat, Mark W., 2019. Quantitative color profiling of digital images with earth mover's distance using the R package colordistance. PeerJ 7, e6398. https://doi.org/10.7717/peerj.6398.

Whiteley, Andrew R., et al., 2009. Background matching and color-change plasticity in colonizing freshwater sculpin populations following rapid deglaciation. Evolution 63 (6), 1519–1529. https://doi.org/10.1111/j.1558-5646.2009.00627.x.

Whitney, J.L., Bowen, B.W., Karl, S.A., 2018. Flickers of speciation: sympatric colour morphs of the arc-eye hawkfish, Paracirrhites arcatus, reveal key elements of divergence with gene flow. Mol. Ecol. 27, 1479–1493. https://doi.org/10.1111/mec.14527.

Wickham, Hadley, 2015. Dplyr: a grammar of data manipulation. R package version 04. 3, p156.

Wickham, Hadley, 2016. Data analysis. ggplot2: Elegant Graphics for Data Analysis. Springer international publishing, Cham, pp. 189–201. https://doi.org/10.1007/978-3-319-24277-4_9.

Wilson, Shaun K., et al., 2008. Exploitation and habitat degradation as agents of change within coral reef fish communities. Glob. Change Biol. 14 (12), 2796–2809. https://doi.org/10.1111/j.1365-2486.2008.01696.x.