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Colour change in a filefish (*Monacanthus chinensis*) faced with the challenge of changing backgrounds

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Abstract The marine macroalga *Caulerpa taxifolia* is increasing its distribution worldwide, both within its natural range, where it can replace seagrass following a disturbance, and in areas where it is invasive. *C. taxifolia* presents a bright green background colouration for inhabitants, while seagrass habitats are typically much deeper green in coloration. The fan-bellied leatherjacket, *Monacanthus chinensis* inhabits both seagrass *Zostera muelleri* and *C. taxifolia* habitats in Moreton Bay, Australia and is camouflaged in these contrasting habitats by brown and bright green colour morphs, respectively. Aquarium experiments measuring colour change of brown and green morphs with respect to contrasting habitats (i.e., brown morphs in *C. taxofolia* and green morphs in seagrass) revealed that over 21 days, brown morphs significantly altered their skin colouration towards the colouration of green morphs, but green morphs did not alter their colouration. In a habitat preference experiment, brown morphs, which match the colouration of the seagrass, significantly preferred seagrass to *C. taxifolia*, whilst green morphs showed no preference. We conclude that variations in *C. taxifolia* coverage present a substantial challenge to this species at short time scales (weeks). This challenge may be overcome by colouration changes at longer timescales assuming fish can survive predation during the adjustment period.

Keywords *Caulerpa taxifolia* · Seagrass · Habitat change · Colouration · Habitat selection

Introduction

The capacity for some animals to match their external colouration to that of their background habitat, camouflage, is important for the survival of both individuals and populations (Houston et al. 2007; Johansen et al. 2010; Riou and Christides 2010; Tsurui et al. 2010). Camouflage may either be necessary for avoiding predators (Stachowicz and Hay 1999; Stuart-Fox et al. 2006) or ambushing prey (Abbott 2010; Brechbuehl et al. 2010). Changes in colouration patterns to match colour changes in the environment are well established at an evolutionary scale, which is exemplified by the classic work on industrial melanism in the moth *Biston betularia* (Kettlewell 1955). Other organisms can change their colour in response to changes in their background. A well-established example of this occurs in the flatfishes, which can change colour to camouflage against the substrates on which they rest, albeit over several days (Ryer et al. 2008). Other animals are faced with the problem of changes in habitat colour either as a function of seasonal

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changes (e.g., arctic fox; Carro 2009), ontogenetic changes in habitat (e.g., pythons; Wilson et al. 2007) or anthropogenic changes to the environment. Anthropogenic driven change in habitat colour has occurred in coastal marine systems that have been subject to invasion or habitat expansion by a bright green, fast growing marine macroalga, Caulerpa taxifolia.

Caulerpa taxifolia is distributed tropically and subtropically across the globe, with Moreton Bay in subtropical eastern Australia being the southern limit of its native range (Phillips and Price 2002; Burfeind 2009). It is bright green and spreads via fragments at a larger scale and grows at a local scale by horizontal stolon growth. It has been suggested that C. taxifolia has actively displaced seagrasses through competition; however, most of the locations where C. taxifolia has spread had been degraded by anthropogenic disturbances (e.g., dredging, overfishing, poor water quality from runoff). Such disturbances contribute to decreased seagrass resilience and/or seagrass extirpation, thus enabling C. taxifolia to colonise (Boudouresque et al. 1995; Thomas 2003). While both seagrasses and C. taxifolia offer similar habitat complexity, the alga does not contain the same abundant food resources as seagrass (Street 2007; McKinnon et al. 2009). Seagrasses also filter suspended sediments and nutrients from coastal waters, stabilize sediments and dampen wave action (Short and Wyllie-Echeverria 1996), driving a positive feedback that assists in maintaining water quality and habitat stability at a local scale. Such differences between C. taxifolia and seagrass can drive changes in fish community structure within an area following the colonisation of the alga. For example, in Moreton Bay, fish abundance is similar between the C. taxifolia and seagrass habitats, however populations of seagrass-dependent taxa, such as some pipefishes and seahorses, are significantly lower in C. taxifolia than seagrass (York et al. 2006; Burfeind 2009).

Due to C. taxifolia's capacity to rapidly colonise new areas, inhabiting species must withstand a rapid change in functional habitat forming species and the associated changes in habitat characteristics (e.g., changed background coloration). C. taxifolia expansion can result in areas of interspersed seagrass-C. taxifolia, as opposed to homogeneous stands of each habitat type (Burfeind and Udy 2009). Some faunal species, especially those that rely on crypsis, may be able to cope with this sudden habitat change by modifying their colouration to match. For example, some wrasses (Symphodus spp.) change their colour to green when exposed to C. taxifolia under laboratory conditions over a time scale of weeks to months (Arigoni 2002). However, there exists a trade-off between maximizing crypsis in a single microhabitat (e.g., a single patch of seagrass) versus a compromise where coloration is suitable for crypsis in a range of microhabitats (e.g., mosaic of seagrass and C. taxifolia; Merilaita et al. 1999).

Filefishes (Monacanthidae) are a globally-distributed group of bony fishes that are particularly abundant and diverse in the Australasian region (Pollard 1984). The fan-bellied leatherjacket Monacanthus chinensis is common throughout eastern Australia, where it can be found in both seagrass and adjacent C. taxifolia habitats as juveniles and sub-adults (Burfeind 2009; Burfeind and Udy 2009). A demersal omnivore, its diet is dominated (60 % of estimated gut volume) by seagrass and epiphytic algae whilst also consuming small gastropods, polychaetes and crustaceans (Bell et al. 1978). Within Moreton Bay, two colour morphs of M. chinensis occur in subtidal mixed seagrass and C. taxifolia habitat; a brown colour morph with a dark brown skin and heavy dark brown to black stripes, that appears suited to camouflage well against the darker patches of seagrass Zostera muelleri; and a bright green morph that appears to camouflage well against C. taxifolia (Fig. 1).

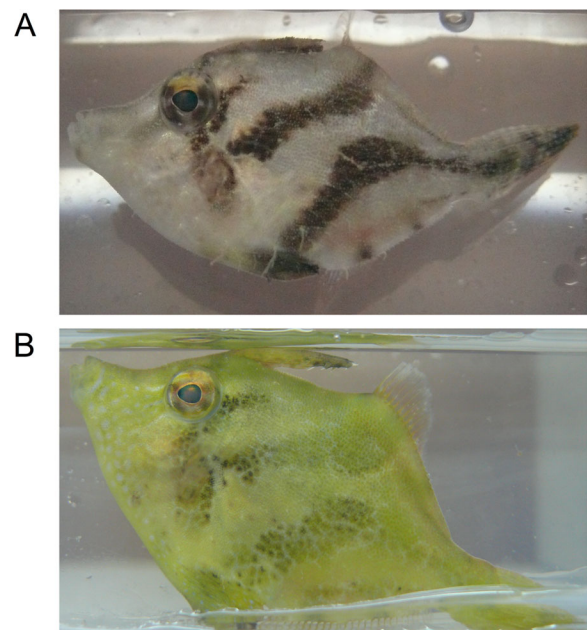**Fig. 1** Brown (**a**) and green (**b**) colour morphs of the filefish *Monacanthus chinensis* from Moreton Bay, Australia. The two individuals presented obtained RGB scores of 139.2:132.5:119.8 and 124.5:125.2:103.4 for the brown and green morph, respectively

Observations of seagrass inhabiting fishes within Moreton Bay (via beam trawl) suggested a greater abundance of green colour morphs where *C. taxifolia* was more abundant (Burfeind 2009). To examine the ability of *M. chinensis* to change colour in response to range expansion of *C. taxifolia*, we conducted an aquarium experiment to test whether both green and brown morphs were able to change colour when placed in a contrasting environment. A second experiment to compare the habitat preferences of the two morphs was also conducted. We expected morphs to change colour towards the opposite morph's colour when placed within a habitat in which they were not matched. In addition, we expected that fish would prefer the habitat in which they were most camouflaged and that this trend would not be as strong at night when colouration is less conspicuous.

Materials and methods

Colour change experimental aquaria

Caulerpa taxifolia and *Zostera muelleri* habitats were recreated as experimental aquaria at Moreton Bay Research Station (MBRS) on North Stradbroke Island, Queensland, Australia (27°51′S, 153°41′E). Glass aquaria (dimensions: 60×30×30 cm) were filled with 4 cm of washed fine beach sand collected from Adam's Beach, Dunwich, and placed into the MBRS recirculation and filtration system. The system is approximately 20,000 L in total volume and is filtered mechanically and biologically in a centralised sump, which includes a customised protein skimmer. Water for the recirculation system is sourced from Moreton Bay itself and water quality metrics (temperature, salinity, DO etc.) are checked daily and rectified where needed (including by regular water changes). Each aquarium contains a single intake and outtake tube, which circulates water back into the main filtration sump. Aquaria were filled with seawater to a depth of approximately 25 cm and allowed to filter over night to clear any residual detritus. *C. taxifolia* and *Z. muelleri* were collected by hand from the sub-tidal region of One Mile Harbor, Dunwich and then replanted at field densities in 28 aquaria of single vegetation habitats (14 per habitat). Light was provided to the aquaria by growth-promoting fluorescent tubes (Sylvania Growlux T8 tubes, 36 w, 6500 K) over a 12–12 h light–dark diurnal cycle.

Colour change monitoring

The fanbellied leatherjacket *Monacanthus chinensis* is a reef and weed-inhabiting monacanthid (filefish) found throughout the west Pacific. Adults attain a length of 38 cm and are targeted by fisheries in some countries (Allen 2009). Juvenile *M. chinensis* (both green and brown colour morphs, 40–70 mm standard length) were collected using a seine net in One Mile Harbor, North Stradbroke Island, grouped according to coloration and transported to aerated holding tanks at MBRS within 5 min. To serve as controls for colour change, seven brown morphs were placed in separate *Z. muelleri* aquaria and seven green morphs were placed in *C. taxifolia* aquaria. Seven brown morphs were placed in the remaining *C. taxifolia* aquaria and seven green morphs in *Z. muelleri* (i.e., the opposite habitat to which the fish are apparently camouflaged). Throughout the trials, fish were fed daily with thawed brine shrimp and were able to feed on any available epiphytes. Colour change was monitored by photographing (Panasonic FZ50 digital camera, using the automatic shoot feature) the left hand side of each fish every 7 days for 21 days, starting at day one (thus, a total of four observations per fish). To ensure consistent photography, fish were transferred to a 'V-shaped' cross-section tank for image capture. The tank was placed in a dark box illuminated by a generic T5 fluorescent light bulb (4 w, 6500 K) to ensure consistent illumination among image captures. This method gives an excellent relative measure of fish colouration between individuals and measurement periods, where all factors influencing potential variations in the resultant photographs have been controlled. Note that absolute colour quantification in this sense is difficult, especially as fishes must remain in water (which itself has certain colour and light refracting properties) for our photographs.

Image analysis and statistical analysis

Only background skin colour was measured due to observations made between potential associations with stripe colour and stress (BG pers. obs.), as well as avoiding the potential confounding effects of stripe colouration versus background colouration. Ten 10× 10 pixel sized samples were taken randomly from each fish, with each 10×10 sample equal to approximately 1 mm^2 on the fish itself. The image analysis program Image J (version 1.44) was then used to measure the

average RGB (red, green, blue) scale values for the 100 pixels in each sample. The RGB scale (or RGB colour model) is an additive colour model that uses a scale of 0 to 255 for each of the red, green, and blue colour channels, which combine to create a total of approximately 16.5 million individual colour combinations. A figure of 255 for each of the red, green, and blue channels results in a 100 % white coloration, whereas values of zero for each channel results in 100 % black colouration. As RGB scale is a multivariate response with colour channels not necessarily independent of each other, a multivariate statistics approach was preferred for the analysis. Changes in colour between photographic samples were determined statistically by two factor (time (fixed factor, four levels) x treatment (fixed factor, four levels)) permutational multivariate analysis of variance (PERMANOVA; Anderson et al. 2008) using Euclidian (square root) similarity, with associated pair-wise tests in Primer v 6.1.13. These analyses tested our colour change hypotheses and determined the presence of overall colour change, changes from week to week, and changes from the first to fourth measurements (start and end points).

Habitat selection trials

Habitat selection trials were performed subsequently to the colour change trials, using newly captured fish. Aquaria (60×30×30 cm) for habitat selection trials were set up as per colour change directions; however, each aquarium was planted half with *C. taxifolia* and half with *Z. muelleri*. To eliminate any directional bias in habitat selections, orientation of *Z. muelleri* and *C. taxifolia* habitats were selected haphazardly as not to maintain a consistent orientation. All fish were allowed 1 h to acclimatize before the start of each trial and a new fish was selected for each trial. In total, 24 replicates were conducted per colour morph. Trials were

conducted at both day and night to determining potential diurnal, light-related effects. We observed whether fish inhabited *C. taxifolia* or *Z. muelleri* every 30 min between 12:00–16:00 h for daytime trials and 19:00–23:00 h for nocturnal trials. Any observations of fish behind or underneath the filter drainpipe or with the lowest portion of their bodies above the level of the tallest *C. taxifolia* or *Z. muelleri* blades were excluded from the analysis as this was not considered to be positive habitat selection.

As *M. chinensis* is a bottom-associated and relatively sedentary species, issues with respect to fish movement patterns were not applicable. Data were converted to a proportion of the total number of observations in each habitat for each replicate. To ensure independence in the habitat pairings, 12 of our 24 replicates were considered with *Z. muelleri* as the focal habitat species, with the other 12 considered with *C. taxifolia* as the focal species. Therefore Student's T tests (conducted in R v3.1.2; R Core Team 2014) assessing habitat preference for each colour morph during day and night (separately) were run on $n=12$ replicates. T tests were conducted with the null hypothesis equalling 50 % of time spent in each habitat. The total length of each fish was measured at the conclusion of the experiment. A Student's *T* test comparing standard lengths between treatments was used to ensure that habitat selection trends were not attributable to size related variables.

Results

Colour change

The overall two factor PERMANOVA suggested significant main effects of sampling period and treatment, but no interaction between the two factors (See Table 1). Green morph controls (green in *C. taxifolia*) did not

Table 1 Permutational multivariate analysis of variance (PERMANOVA) table of results for two factor PERMANOVA (time (in weeks, fixed) X treatment (fixed)) for colour change in the filefish *Monacanthus chinensis*

Source	df	SS	MS	Pseudo-F	P	Unique perms
Week	3	24.622	8.2074	5.1848	0.002	996
Treatment	3	58.677	19.559	12.356	0.001	999
Week×Treatment	9	25.125	2.7917	1.7636	0.64	999
Residuals	96	1.5383	1.583			
Total	111					

change overall colouration during the experiment (Fig. 2a, Table 2; PERMANOVA, $P>0.1$). Brown morph controls (browns in *Z. muelleri*) did, however, show a trend for colour change from measurements one to four with significantly different colourations between measurements one and two and one and three (Fig. 2b, Table 2; PERMANOVA, $P=0.05$). These observations are reflected in Fig. 2b by the brown morphs in *Z. muelleri* trend lines changing significantly between measurements one and two, and then remaining constant over the remaining samplings.

Brown morphs in *C. taxifolia* exhibited a significant colour change overall (Fig. 2c; Table 2, weeks 1 to 4, PERMANOVA, $P=0.004$), whereas green morphs within *Z. muelleri* did not exhibit any colour change over the duration of the experiment (Fig. 2d, Table 2; PERMANOVA, $P>0.07$), which was consistent with the no change result found for green fish controls in *C. taxifolia*. Fourth measurements of brown morphs in seagrass were differently coloured to fourth measurement green morphs in seagrass (PERMANOVA, $t=2.75$, $P=0.02$), indicating that seagrass treatments resulted in different colourations for differently coloured fish. The opposite was true for measurement four green morphs in *C. taxifolia* versus measurement four brown fish in *C. taxifolia*, which were not differently coloured after experimentation (PERMANOVA, $t=0.67$, $P=0.55$), indicating that brown morphs had changed colouration towards that of the green morphs. These observations are shown in Fig. 2, where brown morphs in *C. taxifolia* begin differently to green morphs in *C. taxifolia*, but both become a similar colour. This colour, in turn, is not statistically different from the starting colour of green morphs in *C. taxifolia*. Finally, fourth measurements of brown morphs in *C. taxifolia* vs first measurements of green morphs in *C. taxifolia* (to determine if fish changed colour from their colour-counterparts over the duration of the experiment) were not statistically different (PERMANOVA, $t=0.66$, $P=0.5$) and nor were final measurement green morphs in seagrass and first measurement brown morphs in seagrass (PERMANOVA, $t=0.42$, $P=0.75$).

Habitat selection

Overall, brown morphs significantly preferred *Z. muelleri* during both day (Student's *T* test; $t=3.67$, $P<0.01$; Fig. 3) and night trials (Student's *T* test; $t=2.13$, $P=0.04$), but green morphs did not show any
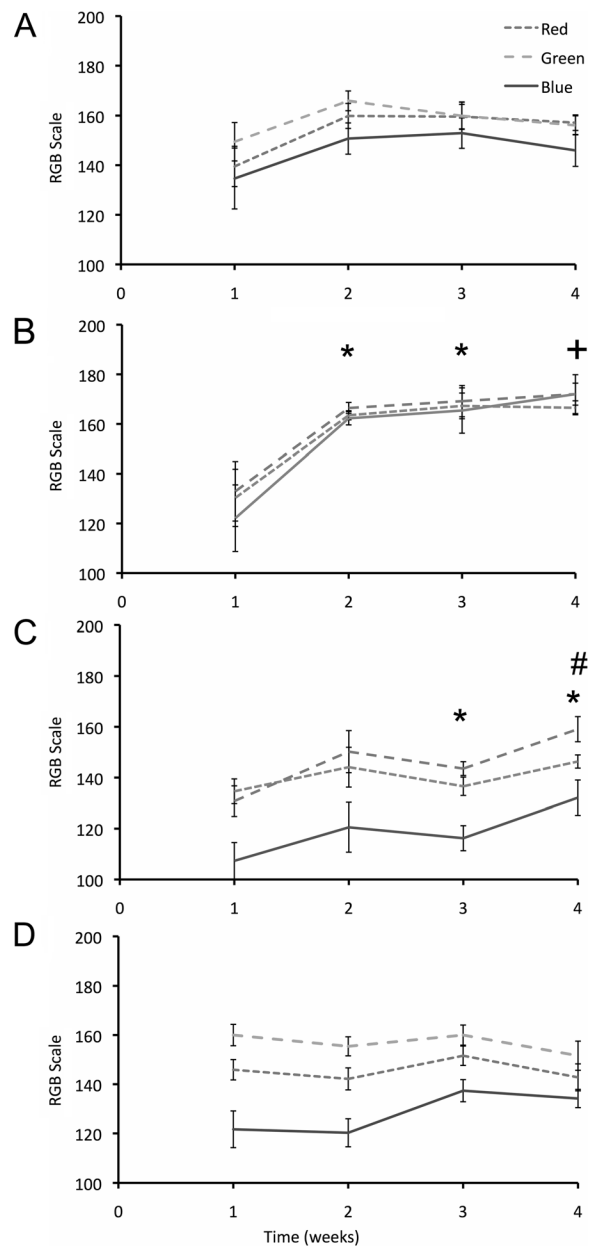

Fig. 2 RGB scale coloration for the filefish *Monacanthus chinensis* (**a**) green colour morphs colour change within *Caulerpa taxifolia*, (**b**) brown colour morphs within *Zostera muelleri* single habitat aquaria, (**c**) brown colour morphs within *Caulerpa taxifolia* single habitat aquaria (**d**) and for green colour morphs within *Zostera muelleri* aquaria over the four weekly measurements. * indicates significant differences ($P<0.05$) between that week's colouration and the first weeks colouration (as determined by pairwise PERMANOVA tests) and # indicates a significant difference between that weeks colouration and the previous week. + in the green colour morphs within *Zostera muelleri* experiment indicates a non-significant trend in overall colour change from weeks one to four ($P=0.05$). See Table 1 for P-values and pairwise comparisons

Table 2 P and *t* values for pair-wise comparisons (from PERMANOVA) from all relevant comparisons for colour change in the filefish *Monacanthus chinensis* in green algae (*Caulerpa taxifolia*) and seagrass (*Zostera muelleri*) aquarium experiments over 4 weeks

Comparison	Greens in *C. taxifolia* (Fig. 2a)		Browns in *C. taxifolia* (Fig. 2c)		Browns in *Z. muelleri* (Fig. 2b)		Greens in *Z. muelleri* (Fig. 2d)	
	t	P	*t*	P	*t*	P	*t*	P
Week 1 v 2	1.54	0.15	1.9	0.07	**2.7**	**0.04**	0.42	0.81
Week 1 v 3	1.61	0.1	**2.1**	**0.04**	**2.13**	**0.04**	0.19	0.2
Week 1 v 4	8.6×10^{-9}	1.0	**3.39**	**0.004**	**2.3**	**0.05**	0.22	0.22
Week 2 v 3	0.5	0.69	0.57	0.66	0.11	0.99	0.07	0.07
Week 3 v 4	1.61	0.14	**2.14**	**0.04**	0.28	0.85	0.031	0.3

Significant (P<0.05) figures are given in bold

habitat preferences (Student's *T* test; day, $t=0.8$, $P=0.4$; night $t=1.23$, $P=0.23$; Fig. 3). There was no significant difference in standard lengths between green and brown colour morph (Student's *T* test, $t=0.03$, $P=0.9$).

Discussion

Habitat type was found to influence the colour of *Monacanthus chinensis,* with brown morphs changing colour to match the starting colourations of green morphs when placed into single habitat *Caulerpa taxifolia* environments. Green morphs, on the other hand, did not change colour significantly, in either *C. taxifolia* or seagrass *Zostera muelleri* habitats (Fig. 2, Table 2). These results indicate that there is a greater propensity for brown morphs to alter their colouration to match the colouration of a non-matching habitat than green morphs over the time scale examined. As such, changing from a darker colouration

to a lighter colouration occurs more quickly, potentially due to differing rates in the acquisition or loss of pigments (Stepien 1987; Arigoni 2002). Despite the capacity for brown morphs to exhibit colour change, green morphs placed in seagrass did not reach similar colourations to the brown morphs. As crypsis was background and morph-specific, this could potentially be caused by a trade-off between crypsis in a single microhabitat versus being partially suited to two visually different microhabitats (Merilaita et al. 1999; Hernandez-Gallegos and Dominguez-Vega 2012; Magellan and Swartz 2013). Depending on the nature of the trade-off, the optimal coloration could be either a compromise between the requirements of the differing microhabitats or entirely adapted to only one of them. So, an adaptive compromise may be found where being partially adapted to both habitats is beneficial (Arigoni 2002; Magellan and Swartz 2013), hence the lack of strong change or trends in green morphs.

Fig. 3 Percent time spent by each colour morph of *Monacanthus chinensis* within habitats of the green alga *Caulerpa taxifolia* and the seagrass *Zostera muelleri* during habitat choice experiments during day and night observations
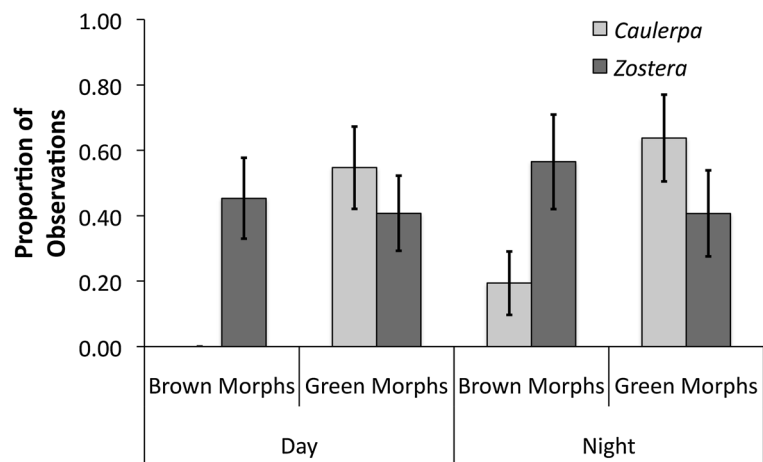
Brown morphs significantly preferred seagrass over *C. taxifolia* during both day and night trials, indicating that this morph positively selects for environments in which they are best camouflaged. Conversely, green morphs showed no significant preference for either habitat. Green morphs are likely associated with *C. taxifolia* areas; however, *C. taxifolia* does not contain the same food resources as seagrasses (Burfeind 2009). As *M. chinensis* is a mixed epiphytic algae and microinvertebrate feeder (Bell et al. 1978), *C. taxifolia* provides significantly lower food resources through epiphytical algae coverage (Burfeind 2009) and lower abundance of benthic invertebrates (Street 2007; McKinnon et al. 2009). As a result, it is likely that green morphs must move beyond the limits of the *C. taxifolia* beds, into seagrasses to encounter food resources (Heck and Valentine 2006), suggesting the use of both *Z. muelleri* and *C. taxifolia* habitats.

As the coverage of *C. taxifolia* expands and replaces seagrass, *M. chinensis* lose a habitat that is rich in food resources and protective characteristics (Street 2007). It is likely, however, that the time scale of increases in *C. taxifolia* coverage would be relatively similar to the time period required for colour adjustment to be made by brown *M. chinensis* (weeks to a month or two; Thibaut et al. 2004; Burfeind and Udy 2009). As such, the potential for adaptive coloration in *M. chinensis* gives this species an advantage in a variable environment over other species that do not have this ability. Despite the capacity for colour changes being identified in brown morphs, the secondary effects of habitat loss or change (e.g., decreased or altered food availability, changes in habitat chemical cues or complete habitat loss) are likely to be felt more strongly by this species in the long term.

Although our study did not evaluate any potential ontogenetic variation in the capacity for colour change, the size range of *M. chinensis* evaluated in this study are the highest risk group with respect to *C. taxifolia* expansion or seagrass loss, as larger adults of this species are not usually found within seagrass habitats (Tibbetts 1991; Allen 2009). Events such as large floods that bring a thick layer of silt to shallow seagrass environments in Moreton Bay (Maxwell et al. 2014) and increased regularity and intensity of human disturbance events, such as dredging, are significant risk factors for seagrass communities (Tibbetts et al. 1998). The likely reliance of juvenile *M. chinensis* on seagrass habitats for food and protection has been well documented (Bell et al. 1978; Burfeind et al. 2009). Thus, any reductions in seagrass habitats will directly impact upon the capacity for juvenile *M. chinensis* to avoid predation and readily access appropriate sources of food. In the event of seagrass loss, *C. taxifolia* would likely replace the bed due to its greater ability to settle rapidly after disturbance (Byers et al. 2010). Brown morphs appear able to withstand increased *C. taxifolia* coverage, as demonstrated by their capacity to change colour rapidly over the first week of exposure. Conversely, if a habitat-altering event, such as those described above, caused the loss of *C. taxifolia*, green morphs are likely to be disadvantaged by their lesser ability to change colouration from the brighter green to a darker colouration. Given the rapid onset of such events (floods, dredging), this capacity may be important in the long-term.

M. chinensis has shown a capacity to adapt to the colour of a new habitat and to positively select for environments in which they are most camouflaged. This makes these fish less vulnerable than other species to *C. taxifolia* expansion. An individual is unlikely to develop a coloration that would fulfil the crypsis requirements of both environments, hence, brown and green morphs become specialised to a specific microhabitat. This appears to be particularly the case for brown morphs, which show a strong association with the habitat in which they are camouflaged, but compensate for this by showing greater capacity for colour change. Furthermore, the primary reason behind the selection of this species for this study is that they appeared to exhibit a capacity to change colour due to the presence of green and brown morphs in the field. Their capacity to elicit even minor changes in colouration likely surpasses the capacity of the majority of other fishes to accommodate such change in habitat colour.

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