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BODY SHAPE DIFFERENCES AMONG FOUR SPECIES OF CORAL-ASSOCIATED DAMSELFISHES FROM THE NORTHERN RED SEA

ABSTRACT:

The great diversity of body shapes among small coral reef fishes suggests differences in life-styles and benthic relationships as well as adaptation to habitats with different physical properties. Damselfishes are among the three most species-rich groups of small coral reef fishes and they exploit numerous habitats ranging from hyperbenthic to cryptobenthic. The latter include many species associated with branching corals to varying degrees. Most eco-morphological studies of damselfishes have focused on the trophic niche and examined the trophic morphology through associated anatomical structures such as the head skeleton. The present study investigates body shape differences with respect to differences in habitat use of four coral-associated damselfishes. *Dascyllus aruanus*, *D. marginatus*, *Chromis viridis* and *C. flavaxilla* represent four of the most abundant coral-associates among damselfishes in the northern Red Sea. Using a combination of traditional and geometric morphometrics, we discovered great shape differences between the two genera, but also within-genus differences along the same difference axis, which can be interpreted as differences in habitat use. The more cryptic species *D. marginatus* has a considerably deeper but less wide body than its larger sister species *D. aruanus*. This body shape pattern and the small maximum size can be explained by the physical constraints provided by the interbranch space of host corals of *D. marginatus*. Similar differences were found in the genus *Chromis*, although these species are generally longer and more compressed. This body shape enables *Chromis* to exploit a wider spatial niche by using more host corals with different architecture than the two species of *Dascyllus*. The high body shape diversity of coral-associated damselfishes mirrors the structural complexity of reef habitats, and small differences in coral architecture lead to a fine-scale tuning of fishes. Apart from interspecific differences, shape examinations revealed a common allometric axis indicating similar ontogenetic shape changes in all species, although to different extents. This shows that certain growth patterns are typical for small reef fishes and may be associated with a change in diet after settlement.

KEY WORDS:
Morphology, habitat associations, adaptation, reef fishes, geometric morphometric, allometry

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INTRODUCTION:

Phenotypic adaptation is an important evolutionary process that increases the fitness of organisms to habitats. Although adaptation is an important field of study in evolutionary biology, examinations of shape variation with respect to microhabitat characteristics are rare. This is mainly due to difficulties in identifying and quantifying exact habitat characteristics, especially in aquatic environments.

Coral reefs represent one of the structurally most complex aquatic ecosystems and harbour a high diversity of microhabitats, which provide shelter to many invertebrates and fishes. Apart from the highly structured reef matrix itself, branching corals of families Pocilloporidae and Acroporidae directly support many associated organisms. Differences in architecture of branching corals causes variation in the spatial niche of associated organisms on a very fine scale (Vytopil and Willis, 2001; Untersteggaber *et al.*, 2014; Wehrberger and Herler, 2014). Variation in branch length and inter-branch spaces affect the habitat selection, size and growth of fishes, and coral architecture has even influenced the evolution of body form of associated fishes (Munday *et al.*, 2001;

Untersteggaber *et al.*, 2014; Wehrberger and Herler, 2014). Much variations of body form thus reflect adaptation to a specifically structured microhabitat. Such differences in form affect the locomotion, growth rate and maximum size of fishes (Wehrberger and Herler, 2014). Although body shape diversification is phylogenetically constrained to various degrees, there are examples of extraordinary high variation even in closely related fish taxa (e.g. East-African cichlids). Moreover, convergent and repeated evolution as a result of adaptation to similar habitats and/or diet has been reported (Kocher *et al.*, 1995; Winemiller *et al.*, 1995; Rüeber *et al.*, 1999&2001; Cooper and Westneat, 2009; Muschick *et al.*, 2012; Frédérich *et al.*, 2013).

Most coral-associated fishes belong to the families Gobiidae (gobies) and Pomacentridae (damselfishes). Pomacentrids are relatively deep-bodied and laterally compressed to different degrees – a body shape pattern also known from gobies associated with corals (Herler, 2007). They are relatively small, species-rich and particularly abundant in coral reefs (Choat and Bellwood, 1991; Munday and Jones, 1998). In general, small fishes can use habitats that are unavailable to larger species (Miller, 1996). Thus, many blennies (Blenniidae) use small holes in the reef as shelter (Lindquist, 1985; Clarke, 1989&1994; Greenfield and Johnson, 1990), and many gobies live among the branches of scleractinian corals (Patton, 1994; Munday *et al.*, 1997; Herler, 2007). Similarly, damselfishes such as several species of *Chromis*, *Dascyllus* and *Plectroglyphidodon* are found in close association with branching corals (Sale, 1971; Robertson and Lassig, 1980). Such specialized and obligate habitat associations are found only in small coral reef fishes, which can be considered to be the most habitat-specialized reef fishes (Herler *et al.*, 2011). Furthermore, there are several examples of mutualistic relationships between damselfishes and corals (Liberman *et al.*, 1995; Goldshmid *et al.*, 2004; Holbrook *et al.*, 2008).

Most fishes show special phenotypic adaptations to their habitat and, in turn, specialized body shapes provide information about the habitat used by a particular species. For example gobiids inhabiting massive corals have a more depressed (dorso-ventrally flattened) body than those inhabiting branching corals (Herler, 2007). Morphological adaptations of damselfishes to different life-styles have been investigated by many researchers, but these studies usually examined trophic morphology, e.g. interspecific differences in food niches and ontogenetic changes in diet, and focussed on the head skeleton (e.g. Frédérich *et al.*, 2008a&b; Cooper and Westneat, 2009). Several of these studies applied geometric morphometrics, revealing that variation in the feeding apparatus is relatively small, and no unique feeding morphologies have evolved in pomacentrids, very likely due to repeated shifts within a small set of niches (Cooper, 2008; Cooper and Westneat, 2009; Frédérich *et al.*, 2008b). In contrast, little is known about body shape adaptation of these highly diverse reef fishes to their habitat. Such information would help explain diversification patterns among fishes that exploit microhabitats differing in physical properties.

The present study examined species-specific morphological adaptations of coral-associated damselfishes with respect to differences in habitat use and maximum fish size. We investigated four species of coral-associated damselfishes, two of each of the two genera *Chromis* and *Dascyllus* from the northern Red Sea, and used traditional and geometric morphometrics to quantify shape differences.

MATERIAL AND METHODS:
Sampling and preservation of specimens:

A total of 98 damselfish specimens were collected for morphological examinations: *C. flavaxilla* (n = 28; of standard length, SL: 18-50 mm), *C. viridis* (n = 22; of SL: 9-37 mm), *D. aruanus* (n = 25; of SL: 15-57 mm) and *D. marginatus* (n = 23; of SL: 10-47 mm). Fishes were collected using SCUBA and by spraying clove oil solution towards the fishes. Clove oil has an anaesthetic effect (Munday and Wilson, 1997) that enables to easily catch the fish by hand or with a hand net. Fishes were then killed in the laboratory by an overdose of clove oil, the viscera was removed with tweezers through a cut in the ventral side of the fish between pelvic and anal fin, and then they were preserved in 10% formalin solution for a few days. Subsequently they were rinsed with water and stored in 70% ethanol.

Traditional and geometric morphometric measurements:

Standard length and head width were measured in the preserved specimens to the closest 0.01mm using a microscope and a digital caliper. Geometric morphometrics – a powerful tool for testing and graphically displaying shape differences (Adams *et al.*, 2004) – was performed on digital images of fishes. Preserved fishes were scanned using an EPSON V30 scanner at 2400 dpi. On the scanner, specimens were submerged left side up in ethanol in a plasticine pool that was fixed on the scanner glass (Herler *et al.,* 2007). Eleven landmarks (LM) were placed on each of the 98 specimens: (1) anterior tip of the snout, (2) centre of orbit, (3) and (4) anterior and posterior insertion of the dorsal fin, (5) and (6) upper and lower insertion of the caudal fin, (7) and (8) posterior and anterior insertion of anal fin, (9) insertion of

the ventral fin, (10) and (11) lower and upper insertion of pelvic fin (Fig. 1). These landmarks were applied according to a well-defined homology of the anatomical points, and to cover the entire body by using tpsUtil 1.44 and tpsDig 2.14 (Rohlf, 2010a&b). Landmark configurations derived from all specimens were superimposed in a Cartesian coordinate system after translation to a common centre (0/0) of their centroid (arithmetic mean of all landmark coordinates

of each coordinate axis), scaled to unit centroid size (square root of the summed squared distances of each landmark to the centroid) = 1 by dividing the landmark coordinates of each configuration through its centroid size, and rotated through a least-squares procedure to minimize the deviation between corresponding landmarks. This procedure (Procrustes superimposition) yields Procrustes coordinates of landmarks.
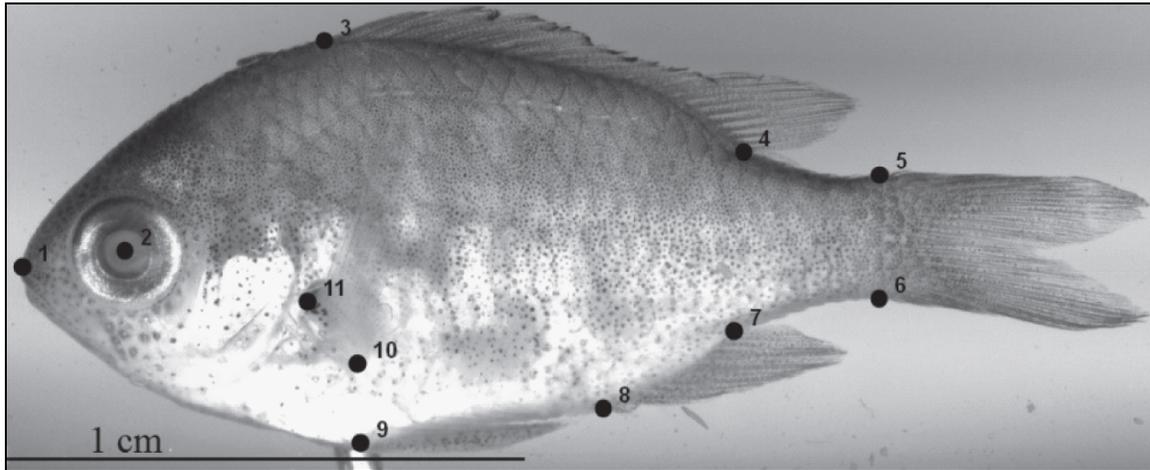

Fig. 1. Set of eleven landmarks used to quantify shape differences in 4 species of coral-associated damselfishes.

Statistical analysis:

A one-way ANCOVA was performed between head width and standard length in preserved damselfish species to compare the growth pattern between the four species of damselfish using the program PAST, version 2.15 (Hammer *et al.*, 2001). Regressions between PCs, head width and centroid size were calculated in Microsoft Excel for Windows and in SPSS version 17.

Principal components analysis (PCA; of the partial warps of Procrustes coordinates) was used to investigate shape differences between species; deformation grids were used to visualize shape variation (Bookstein, 1991). PC-scores and deformation grids were calculated in tpsRelwarp version 1.49 Rohlf (2010c). Expansions or contractions of the grid help to visually locate where certain body parts have deformed. To test statistical differences between the mean shape of all species, a MANOVA was performed on the first six PCs (each contributing more than 1% to the total variance) using the program PAST, version 2.15 (Hammer *et al.*, 2001).

RESULTS:

One-way ANCOVA of head width (HW) and fish standard length was calculated for all four damselfish species (Fig. 2) to test different growth patterns. The adjusted means differed significantly (p < 0.001) between all species and the homogeneity of slopes were significantly different between most pairs of species. The exceptions were between *D.*

marginatus and *C. flavaxilla* (p = 0.75), between *D. marginatus* and *C. viridis* (p = 0.27), and between the two *Chromis* species (p = 0.08). Therefore, the increase of head width is greatest in *D. aruanus*, whereas its congener *D. marginatus* shows a similar growth patterns with the two species of *Chromis*. The greatest body length was measured in *D. aruanus.* Linear regression analysis showed a positive correlation between standard length (SL) and centroid size (CS) of all specimens of damselfish species (r^2 = 0.99, p < 0.001). This demonstrates a high equivalence between these two size measures.
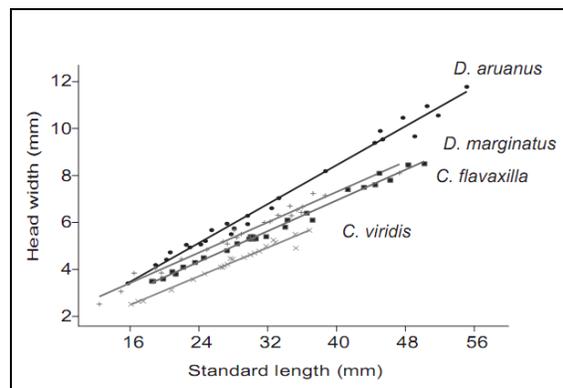

Fig. 2. One-way ANCOVA for head width against standard length in four preserved coral-associated damselfish species

A principal component analysis of Procrustes shape coordinates of 98 preserved specimens of all four species revealed 72.9 %

of explained variance of PC 1 and 9.7% of PC2. PC 1 is most suitable to differentiate species and genera (Fig. 3). The genus *Chromis*, located on the positive end of PC 1, is much more elongated, where as *Dascyllus* specimens are deep-bodied and relatively short. In addition, *Chromis* has a longer caudal peduncle and head. *Chromis viridis* represents the one extreme of an elongated body shape, while *D. marginatus* represents the most extreme deep-bodied species. The other two species are intermediate, although there is considerable distance between the shapes of the two less extreme species.
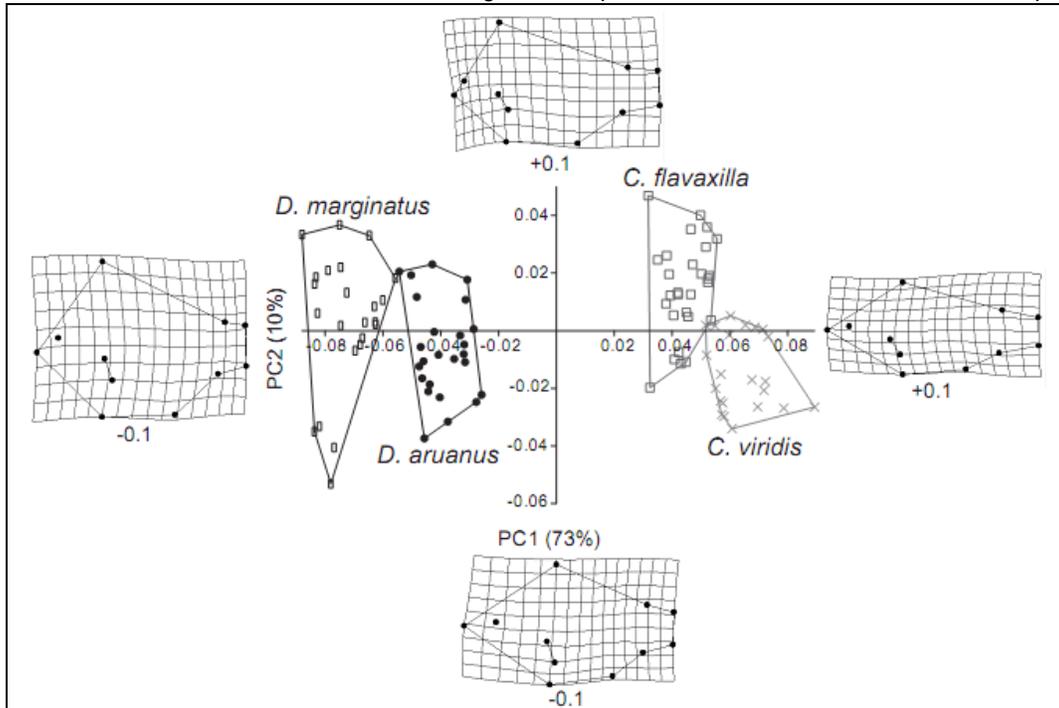

Fig. 3. Plot of PC 1 against PC 2 (explained variance of each indicated) of Procrustes shape coordinates of juvenile and adult specimens (n = 98) of *C. flavaxilla, C. viridis, D. aruanus* and *D. marginatus* based on 11 landmarks. Deformation grids depict shape changes along PC 1 and PC 2, and the axis range of the deformation shown is below each grid.

Linear regressions between CS and the first two PCs across all species were performed, this yielded no significant correlation between CS and PC 1 (r = 0.1, p = 0.15) but a highly significant positive correlation between CS and PC 2 (r = 0.74, p < 0.001). This demonstrates that PC2 mainly shows a common ontogenetic allometry, in which smaller fishes of all taxa differ from larger ones mainly by a relatively larger head, a more posterior orbital centre (indicating larger eyes) and a shorter abdomen.

DISCUSSION:

Damselfishes are among the most species-rich groups of coral reef fishes and may live in close association with corals (Allen, 1991). The present study on the four most abundant coral-associated damselfish species from the northern Red Sea found not only considerable shape differences between them even within the two genera *Chromis* and *Dascyllus*, as observed also by Frédérich and Sheets (2010). They declared interspecific shape and size variation within *Dascyllus* by using *Chromis* as outgroup. In the genus level, *Chromis* has a more compressed and elongated head and body than *Dascyllus*. The major axis of shape difference revealed a transition from the very deep-bodied *D. marginatus* to the most elongated *C. viridis* across the two other species, *D. aruanus* and *C. flavaxilla*. Nevertheless, there was a significant distance between the shapes of the two genera. The genus-specific shapes indicate a phylogenetic constraint, although *Chromis* and *Dascyllus* are very closely related to each other and the current delineation of the two genera requires revision (Cooper *et al.*, 2008).

The intra-generic differences along the same and main axis of shape difference indicate a convergent evolution during which similar body parts are affected by physical constraints of coral colonies. *Dascyllus marginatus* remains smaller and grows more deep-bodied and narrower than its congener *D. aruanus*. Such an extremely compressed (laterally flattened) body is necessary to maneuver within the narrow interbranch space of digitate and corymbose *Acropora* corals. Corals provide physical constraints for inhabiting organisms (Vytopil and Willis, 2001; Untersteggaber *et al.*, 2014; Wehrberger and Herler, 2014) and specific host coral architecture is expected to shape associated fishes through strong ecological selection.

Dascyllus marginatus preferentially inhabits *A. valida* and *A. samoensis* in the northern Red Sea (Negm, 2013). These corals are also frequently occupied by coral gobies of the genus *Gobiodon* (Dirnwöber and Herler, 2007), whose body shapes also vary depending on the corals they occupy (Untersteggaber *et al.*, 2014; Wehrberger and Herler, 2014). This represents an interesting case of convergent body shape evolution among coral reef fishes. The high diversity of body shapes among reef fishes thus mirrors the structural complexity of reef habitats, with small but crucial differences in coral architecture leading to a fine-scale tuning of the fishes.

In addition to shape differences, body size plays a major role. Size is a variable that helps explain the diversity in damselfishes through exploitation of different niches (Frédérich *et al.,* 2008b). In the present sample, *D. aruanus* was the largest species (SL up to 6 cm), the other 3 species measuring less than 5 cm SL. In fact, *Dascyllus aruanus* and *C. viridis* can grow up to about 10 cm TL, whereas *D. marginatus* and *C. flavaxilla* do not exceed 6 or 7 cm TL (Froese and Pauly, 2013). Frédérich *et al.* (2008b) mentioned that size differences among damselfishes could be related to differences in diet (type or size of the selected plankton). Although the more compressed body facilitates movement among coral branches, maximum fish size may be strongly limited depending on coral size and architecture (Wehrberger and Herler, 2014). The two larger representatives of both genera – *C. viridis* and *D. aruanus* – also show similar patterns of shape difference when compared to their smaller sister species. The larger species have a more elongate and depressed (dorso-ventrally flattened) body. This may reflect a less cryptic adult behavior in the larger species, especially when fully grown up. Large adult *D. aruanus* and *C. viridis* were not found among the interstices of the corals occupied by juveniles and small adults because they change habitat when they grow.

The juveniles of both species commonly use *A. valida* and *A. eurystoma*, and, in the case of *D. aruanus*, also narrow-branched *Pocillopora* species (Negm, 2013), whereas small adults of *C. viridis* occupy *A. samoensis*. By contrast, very large *D. aruanus* were observed between coral colonies and in large and wide-branched indetermined-growing colonies of *A. variolosa* rather than within colonies of small digitate and corymbose *Acropora* species. Relating to body shape, especially *D. aruanus* exhibited a strong increase in head width with growth: larger specimens are clearly too wide to fit into narrow-branched corals. The other two species, *D. marginatus* and *C. flavaxilla*, also forage in the water column (Liberman *et al.*,

1995; Froese and Pauly, 2013). However, as observed in the present study, they are more cryptic and spend most of the time among host coral branches (Personal observations). They also do not show such obvious shift in habitat when they grow: both juveniles and adults of *D. marginatus* prefer *A. valida*, and those of *C. flavaxilla* prefer *A. variolosa* (Negm, 2013). This different habitat is also in concordance with the shape difference and expected swimming performance. The open-branched *A. variolosa* provides more space for true swimmers as the corymbose colonies of *A. valida* do. Smaller and more compressed (laterally flattened) bodies facilitate the movement within narrow coral branches, while elongated bodies perform better when swimming and feeding in the water column (Webb, 1984).

Body size also plays a major role in space competition, larger species being better competitors (Munday *et al.,* 2001). Although maximum size and growth rate of fishes are restricted by host coral structure (Munday, 2001; Wehrberger and Herler, 2014), a larger size is favorable in terms of competitive success, reproductive output and protection from small predators that could access the corals. This requires shape adaptations that enable large body sizes among corals. This phenomenon has also been observed among coral-associated gobies of the genus *Gobiodon* spp.: a size-based competitive hierarchy (Munday *et al.*, 2001) drives strong ecological selection for a large body size and thus extremely compressed body shapes that enable maximum body size within coral interbranch space (Untersteggaber *et al.*, 2014; Wehrberger and Herler, 2014).

A deeper body can be seen as a compensation of the less wide body: it helps retain a similar body volume, which may be crucial for vital organs as it was assumed in coral gobies (Wehrberger and Herler, 2014). In addition, a deeper body yields a greater lateral display size, enhancing the appearing size and facilitating territorial defense (Collyer *et al.*, 2005). Unlike *Dascyllus*, *Chromis* appears to be more mobile between colonies because it inhabits different corals with different branching patterns and interbranch distance. This genus generally has a very compressed body that enables it to live in various spatially restricted habitats. The very different general body shape despite similar habitat demands of *Dascyllus* and *Chromis* makes it doubtful that both genera have evolved the coral-dwelling life-style simultaneously or primarily. Evolutionary hypotheses are difficult to prove, but a shape study of more genera – including species that do not dwell corals but have other well-known habitat demands – would shed light on the specific adaptations required to successfully exploit the spatially restricted interbranch space of reef-building corals. In turn, specific

phenotypic adaptations would also indicate the degree of specialisation of fishes and help estimate their vulnerability to changes in coral communities, reef structure and to habitat loss.

Apart from size and shape differences between genera and species, there was a common pattern of ontogenetic shape change in all species, although at different levels and extend of allometry. Small juveniles have larger heads and eyes than adults but, although these differences were found in all species, the magnitude was not the same and did not depend solely on the fish size range within the samples. As mentioned, the greatest size range was sampled in *D. aruanus* but the greatest morphological range was found in *D. marginatus*; in contrast, the range of size and shape in the two *Chromis* species was more similar. Differences in the length of ontogenetic trajectories were also observed in the head skeleton of *D. aruanus* and *Pomacentrus pavo* (Frédérich *et al.,* 2008a). This was explained by allometric heterochrony, and different diet or feeding behaviour could play a role.

The great shape differences between juvenile and adult *D. marginatus* may be partly explained by the inclusion of four very small specimens. Although they were not much smaller than the smallest *D. aruanus* sampled, the significant distance between these and larger *D. marginatus* specimens indicates a rapid morphological change in an early settlement stage, as has also been observed in other damselfishes (Frédérich *et al.*, 2008a). Independent of this size-based shape difference, the ontogenetic shape difference was also greater within adults of *D. marginatus* than of *D. aruanus*. As the ontogenetic development mainly involved head shape and mouth position, this indicates an extended morphological development in the former, perhaps associated with a greater change in diet after settlement. Dietary shifts may differ in species that behave cryptically after settlement when compared with species that continue feeding on plankton in the water column. The four species are mainly plankton feeders (Frédérich *et al.*, 2013; Froese and Pauly, 2013), although *D. aruanus* also feeds on benthic prey when smaller (Frédérich *et al.*, 2010). *Dascyllus marginatus* also feeds in the water column (Liberman *et al.*, 1995), however, in the present study; even larger specimens of *D. marginatus* were rarely seen outside of the coral. This more cryptic life-style suggests a substrate-related component

of the diet and differences in the diet and/or feeding modes of adult fishes are the main drivers for ontogenetic head shape divergence between early settlers and adults (Frédérich *et al.*, 2008a; Frédérich and Vandewalle, 2011).

In *Chromis*, *C. flavaxilla* had a higher ontogenetic shape difference than *C. viridis*, which is mainly explained by the larger body size range of the former and the absence of large adult *C. viridis* in the sample. The lower maximum size of *C. flavaxilla*, seen as an adaption to a more cryptic life-style, explains why relatively small specimens already have an adult shape when compared with *C. viridis*. This includes the same change of head size and shift of mouth position as in *Dascyllus*, probably also related to differences in the diet or feeding mode. Although more detailed examinations of the head skeleton and feeding behaviour of these species are necessary to derive trustworthy conclusions about diet-based allometric differences, the pattern of ontogenetic shape changes makes further investigations highly promising.

In conclusion, our morphological study demonstrated that fishes with compressed and elongated bodies have greater opportunities to inhabit corals with narrow branches and can remain within corals throughout their live-span more easily. Fishes with robust bodies and wider heads, in contrast, must specialize on certain coral structures (wider-branching coral species) that better match their body shape and size, or must shift their host during growth. The degree of habitat specialisation will also be a determinant for fish survival when reef deterioration through coral bleaching and ocean acidification continues, when host corals begin to disappear from reefs, and when average colony size becomes smaller (McClanahan *et al.*, 2008), reducing the opportunity for larger fish species and specimens to find suitable shelter.

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اختلافات شكل الجسم بين أربعة أنواع من أسماك العذراء المصاحبة للشعاب المرجانية في شمال البحر الأحمر

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التنوع الكبير في أشكال الجسم بين أسماك الشعاب المرجانية الصغيرة قد يشير إلى وجود اختلافات في أنماط الحياة وعلاقاتها بالقاع بالإضافة إلى قابلية التكيف للبيئات ببعض الخصائص الفيزيائية للسمك. تعتبر أسماك العذراء واحدة من ثلاثة أكثر أنواع أسماك الشعاب الصغيرة وفرة كما أنها منتشرة في بيئات كثيرة وبنطاق كبير من المرتبطة بالقاع وغير المرتبطة بالقاع. الأخيرة تتضمن الأنواع المصاحبة للشعاب المرجانية المتفرعة بدرجات مختلفة. معظم الدراسات الخاصة بالشكل الظاهري مع البيئة المحيط لأسماك العذراء تركزت حول البيئة الغذائية ودرست التكيف المرتبط بالتركيب التشريحي مثل تركيب الهيكل العظمي للرأس. الدراسة الحالية درست اختلافات شكل الجسم وارتباطها باختلافات البيئة التي تعيش فيها لأربعة أنواع من أسماك العذراء (ديسلس أورانس, ديسلس مرجيناتس, كرومس فيردس, كرومس فلاڤاكسيلا). هذه الأنواع من أسماك العذراء وفره وتعايش بالشعاب المرجانية في شمال البحر الأحمر. وباستخدام كلا من القياسات الظاهرية التقليدية والحديثة, توصلنا إلى وجود اختلافات كبيرة لأجناس السمكية والذي قد يرجع سببه إلى اختلاف البيئة التي يعيشوا فيها. النوع ديسلس مرجيناتس تميز بجسم أكثر سمكا ولكن أقل عرضا من النوع ديسلس أورانس. هذا النمط من شكل الجسم والحد الأقصى للحجم الصغير يمكن تفسيره بوجود القيود الفيزيائية الموجودة خلال الفراغات البينية لأفرع الشعاب المرجانية المضيفة. كذلك وجدت اختلافات مشابهه في جنس كرومس وهذا النوع عامة يكون أطول وأكثر انضغاطا. وشكل الجسم هذا يتيح لجنس كرومس التمدد في نطاق أرحب عن طريق استغلال شعاب مرجانية مضيفة أكثر بأشكال بنائه أكثر من النوعين الآخرين للجنس ديسلس. التنوع الهائل لأشكال الجسم لأسماك العذراء المصاحبة للشعاب المرجانية يعكس تعقد ألتركيبي لبيئة الشعاب المرجانية, كما أن الاختلافات الصغيرة في بناء شكل الشعاب المرجانية يؤدي إلى تناغم ودقة أشكال الأسماك المصاحبة. جزء من الاختلافات البينية في دراسة الأنماط الشكلية كشفت عن تفاوت محوري متكرر وذلك دليل على تشابه في أنماط النمو في جميع الأنواع على الرغم من اختلاف نطاقها. وذلك يوضح ان أنماط النمو متماثلة لأسماك الشعاب المرجانية الصغيرة وربما تكون مرتبطة باختلاف نظم التغذية بعد التوطين فى البيئات التي تعيش بها.

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