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„Effects of coral shape on the form and habitat preference of coral-associated fishes“

Verfasser

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Abstract

The genus *Gobiodon* represents the most species-rich group of specialized reef fishes that live post-larval in an abiding association with living corals of the genus *Acropora.* The present study, performed in the Gulf of Aqaba, focused on the effect of architecture and size of the two corals *Acropora digitifera* and *A. gemmifera* on the habitat preference and shape of the two gobiids *Gobiodon histrio* and *G. rivulatus*, which inhabit and compete for these corals. Preliminary studies on 132 preserved individuals of seven species of *Gobiodon* aim to examine the total shape variation within this genus in the northern Red Sea and was realized by means of traditional and geometric morphometric techniques. The two techniques were compared to look for qualitative differences in analyses. The same techniques were used at the Red Sea on 30 narcotized but live fishes. Measured and recovered fishes were released back to the reef. To study the influence of coral architecture on fish shape, a total of 59 occupied and unoccupied coral colonies were measured during random swims at the reef flat and reef edge. Measurements include colony size, branch length, branch tip distance and interbranch-distance of adjacent branches of each colony. To measure the interbranch-distance close to branch bases, a new and non-destructive measurement technique employing casts of two-component epoxy resin was developed and performed. Data were analysed with various univariate and multivariate methods. Several discrimination features like the body height at the ventralis-base or the greatest head width were revealed for the interspecific shape variance as well as the presence of a phylogenetic constraint within the genus *Gobiodon*. Geometric morphometrics yielded more detailed results in less time. The pattern of growth of the two species of *Gobiodon* examined in detail show distinctive differences and provide a possible explanation for the superior position of *G. histrio* in competitive hierarchies. The most important factor for the occupation of corals is a branch length exceeding 5 cm. The branch tip distance regulates within occupied corals the fish size. Coral morphologies influence on fish shape is reflected in the interbranch-distance which can be seen as a filter for fish width. Further, half the interbranch-distance seemed to the optimum and desired for the maximal body width extension of associated fish.

Keywords: *Gobiodon*, coral architecture, colony size, morphometrics, interbranch-space

Kurzfassung

Die Gattung *Gobiodon* repräsentiert die artenreichste Gruppe an Rifffischen die post-larval permanent in lebenden Korallen der Gattung *Acropora* leben. Die aktuelle Studie, durchgeführt im Golf von Aqaba, untersuchte die Effekte der Architektur und Größe von den zwei Korallenarten *Acropora digitifera* und *A. gemmifera* auf die Habitatwahl und Körperform von den zwei Korallengrundelarten, *Gobiodon histiro* und *G. rivulatus*, die um dieses Habitat konkurrieren. Einleitende Untersuchungen an 132 konservierten Individuen der sieben im nördlichen Roten Meer vorkommenden Arten von *Gobiodon* hatte zum Ziel, die gesamte Körperformvariation innerhalb der Gattung mittels traditioneller und geometrischer Morphometrie zu ermitteln. Die Ergebnisse wurden miteinander verglichen um mögliche qualitative Unterschiede in den Methoden zu finden. Die selben Methoden wurden im Labor am Roten Meer an betäubten Individuen der zwei Korallengrundelarten angewendet. Vermessene und wieder vollkommen aus der Narkose erwachte Fische wurden zurück ins Riff gebracht. Zur Erhebung des Einflusses der Korallenarchitektur auf die Fischform wurden insgesamt 59 bewohnte und unbewohnte Korallenkolonien am Riffdach und der Riffkante vermessen. Vermessen wurden die Koloniegröße, die Astlänge, der Astendenabstand und der Astzwischenraum zweier benachbarter Korallenäste. Zur Vermessung des Astzwischenraumes nahe der Korallenbasis wurde eine neue und nicht zerstörerische Vermessungsmethode entwickelt und angewendet. Bei dieser Methode wurde ein Epoxidharz mittels Pinzetten dazu verwendet Abdrücke des Astzwischenraumes zu erstellen. Die ausgehärteten Abdrücke wurden anschließend vermessen. Die gewonnenen Daten wurden mit univariater und multivariater Statistik analysiert. Die Körperhöhe an der Ventralis-Ansatzstelle und die maximale Schädelbreite entpuppten sich als zwischenartliche Formunterscheidungsmerkmale. Zudem wurde die Anwesenheit einer phylogenetischen Einschränkung der Wachstumsstruktur innerhalb der Gattung *Gobiodon* festgestellt. Der Methodenvergleich sprach für die geometrische Morphometrie, da sie genauere Ergebnisse in kürzerer Zeit liefert. Die Wachstumsstruktur der zwei *Gobiodon*-Arten wurde im Detail untersucht und weist markante Unterschiede durch höhere Körperform und Körpergröße von *G. histrio* auf, was eine mögliche Erklärung für die höhere Position von *G. histrio* innerhalb der kompetitiven Hierarchie ist. Der wichtigste Besiedlungsfaktor ist eine Astlänge von über 5 cm und innerhalb besiedelter Korallen reguliert der Astendenabstand die Fischgröße. Der Astzwischenraum kann als Filter für die Körperbreite der assoziierten Fische gesehen werden und spiegelt daher den Einfluss der

Korallenmorphologie auf die Fischform wider. Es scheint als ob die Hälfte der Astzwischenraumdistanz das Optimum für die maximale Körperbreite der Korallengrundeln darstellt.

Introduction

Adaptation and habitat specialisation play an important role for the evolution and diversification of organisms. Within coral reefs, the great range of coral growth forms (Wallace 1999; Veron 2000) offer many different ecological niches for occupying organisms. This variability of coral forms provides microhabitats with selective characteristics for organisms. One of those microhabitats is the space between branches of branching corals and it plays a key role for their occupation by other animals. Highly diverse groups of closely related species, such as coral-associated invertebrates (i.e. crabs) and fishes (e.g., gobies and damselfishes) that occupy narrow ecological niches are good models for studying specialisation within such spatially constrained microhabitats.

Corals' complex architecture with its constrained space and wide range of gaps provide retreat areas for organisms against predators (Beukers and Jones 1998; Almany 2004a,b). Fishes and other organisms use the corals as shelter, nursery grounds and also food resource (Lassig 1981). Without these complex areas of retreat in coral reefs, biodiversity would decrease (Doherty and Sale 1986; Roberts and Ormond 1987; Hixon and Beets 1993; Roberts et al. 2002; Hobbs and Munday 2004; Munday 2004). The architecture of coral colonies differs depending on their exposure to wave movement (Bradbury and Young 1981) with according changes in microhabitat characteristics. Microhabitats provided by corals are an important basis for the diversification of occupying species through their structural complexity. Abiotic factors change corals' architecture and influence microhabitat conditions.

Among coral-associated fishes, gobies represent the most species-rich group (Munday and Jones 1998). Most species of the family Gobiidae are small in size and have evolved an extraordinarily high diversity, now representing the most species-rich marine fish family (Nelson 2006). They are very abundant in many ecosystems and occupy a great range of habitats, in particular among coral reefs (Miller 1996; Munday and Jones 1998; Herler 2007).

The genus *Acropora* is the most species-rich genus of reef-building corals and many species are occupied by gobies (Munday et al. 1997; Herler 2007). Small size and compressed body shapes of coral-associated fishes enforced by spatial constraints of corals are expected to be important adaptive traits that enhance the fitness of occupants. All small-scaled habitats cause body-form related adaptations and this often leads to an advantage, to occupy an ecological niche and use the resources the habitat provides in an appropriate way, only through this specific adaptation (Miller 1996). Body shape of occupying fish species is assumed to differ with respect

to their most preferred host corals: narrow interbranch-distances lead to more compress species with deeper bodies (Herler et al. 2007) and growth rates and survival of *Gobiodon* spp. is also related to interbranch-space (Munday 2001; Munday et al. 2001). In addition, the decrease of body size often provides access to new, spatially constrained, environments and new trophic levels in the food chain, even in a saturated ecosystem (Miller 1979; Munday and Jones 1998).

Corals of the species *Acropora digitifera* and *A. gemmifera* are both occupied by *Gobiodon histrio* and *G. rivulatus* and this overlap in habitat-demand leads to interspecific competition (Dirnwöber and Herler 2007). Achieving an advantage in fitness by reaching a higher rank in the competitive hierarchy by growing larger (Munday 2001) is limited through the interbranch-distance of corals and its possibility as hide-out. During turf wars body length is important but the lateral appearance plays a mayor role (Collyer et al. 2005) and adult specimens of *G. histrios* got about 44 % body height of its total body length in contrast to *G. rivulatus* with only about 38 % (Herler and Hilgers 2005). Comparisons of body width and total body length of different sized specimens of these two species suggest that the differences in shape are a consequence of allometric growth.

After proceeding studies on preserved specimens, which focused on the shape variation among seven species of *Gobiodon*, two species (*G. histrio and G. rivulatus*), were chosen for examination of fish shape and its relation to host coral shape. Two morphometric approaches (traditional and geometric morphometrics (Mitteroecker and Gunz 2009)) were applied on preserved and live fishes and compared with each other. In this study, only corals of the genus *Acropora* were investigated because of their great range of spatial niches their architecture provides. In addition to various direct linear measurements of corals, a new technique was implemented to measure the corals interbranch-distance indirectly, by employing a two-component epoxy resin to create casts of the interbranch-space. The focus of the present study lies on the relation between body shape variation in these two *Gobiodon* species and their host corals' architecture.

Material & Methods

1. Body shape variation within the genus *Gobiodon*

Proceeding shape studies focused on seven species of *Gobiodon* (described in detail by Herler and Hilgers (2005)) from the northern Red Sea. A total of 132 preserved specimens (*G. citrinus*: n = 13, *G. histrio*: n = 26, *G. reticulatus*: n = 25, *G. rivulatus*: n = 18, *G.* sp.1: n = 20, *G.* sp.2: n = 13 and *G.* sp.3: n = 17; dataset A) were examined. The size ranges for all species are indicated in Figure 1.

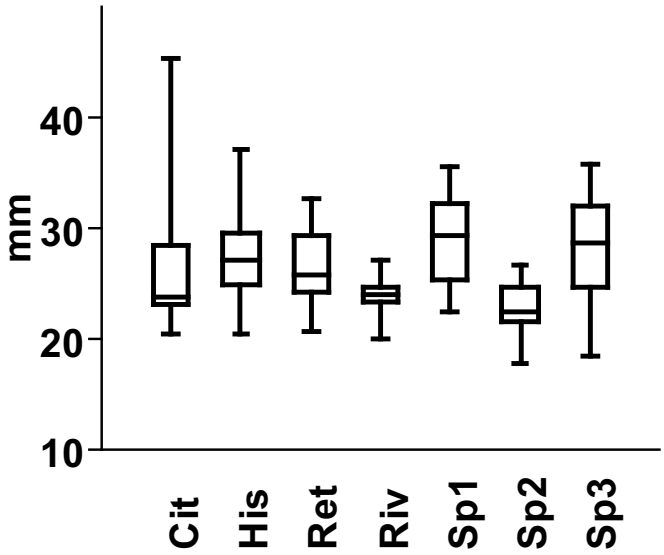

Fig. 1: Size ranges of preserved specimens of seven species of *Gobiodon* (n = 132) used for traditional and geometric morphometric investigations. The box plots show median, first and third quartiles, and range of standard lengths of *Gobiodon citrinus* (Cit, n = 13), *G. histrio* (His, n = 26), *G. reticulatus* (Ret, n = 25), *G. rivulatus* (Riv, n = 18), *G.* sp.1 (Sp1, n = 20), *G.* sp.2 (Sp2, n = 13) and *G.* sp.3 (Sp3, n = 17).

Two methodological approaches – traditional morphometrics (TM) and geometric morphometrics (GM) – were used and compared with each other to reveal whether the two general techniques yield differences in quality of shape discrimination (Maderbacher et al. 2008) across species of *Gobiodon*.

1.1 Traditional morphometrics

Sixteen standard linear measurements were taken from 132 specimens with a digital caliper to the closest 0.01 mm (figure 2a, table 1).

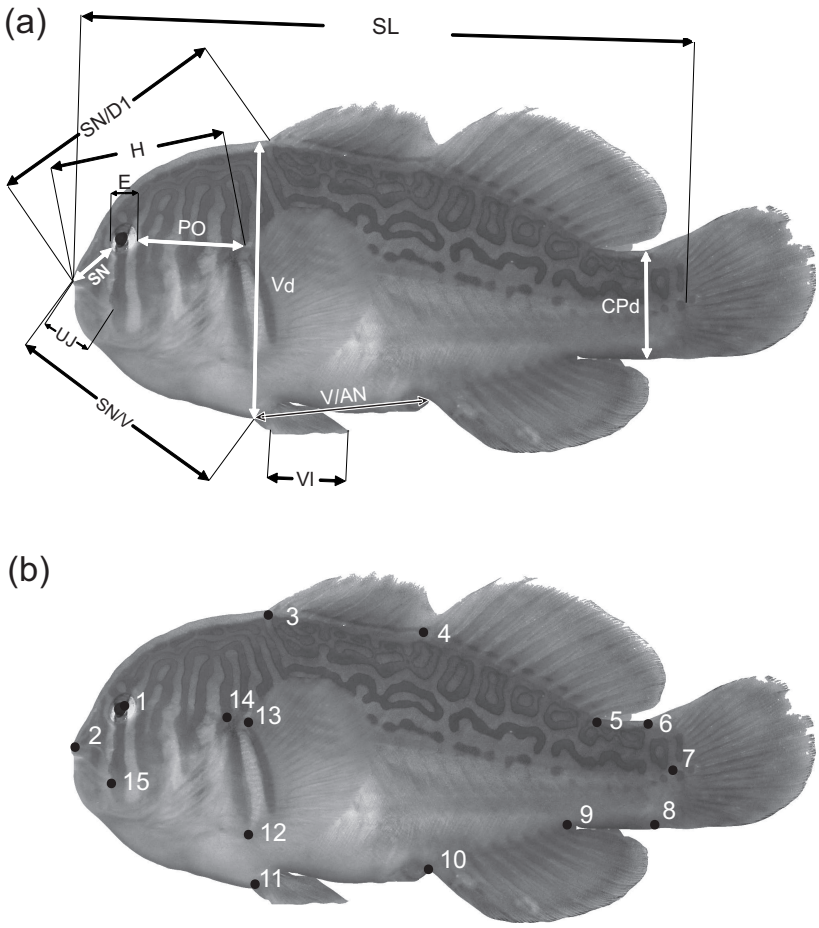

Fig. 2: Morphometric techniques applied to species of *Gobiodon* from the northern Red Sea: (a) Schematic representation of lateral measurements (traditional morphometrics). Head and body width measurements in the transversal plane are not indicated. (b) Positions of 15 landmarks for geometric morphometric analyses. Abbreviations respectively explanation for measurements and landmark positions are given in table 1.

Table 1: 16 standardized distances for traditional morphometrics and description of 15 landmarks for geometric morphometrics.

Nr.	Abbreviation	Description
1	SL	Snout tip to caudal fin base
2	CPd	Smallest heights of the caudal-peduncle
3	gBw	Greatest body width
4	Aw	Anal width
5	Hw	Head width
6	gHw	Greatest head width
7	H	Head length
8	SN/E	Snout to eye distance
9	UJ	Upper jaw length
10	SN/D1	Snout to first dorsal fin origin
11	SN/V	Snout to ventral fin origin
12	PO	Postorbital-distance
13	E	Horizontal eye diameter
14	Vl	Ventralis lenght
15	Vd	Body height at ventral fin origin
16	V/AN	Distance ventral fin to anus

LM	Description
1	Center of orbit
2	Anterior tip of the snout
3	Anterior insertion of first dorsal fin
4	Anterior insertion of second dorsal fin
5	Posterior insertion of second dorsal fin
6	Dorsal insertion of caudal fin
7	Midpoint of the origin of the caudal fin
8	Ventral insertion of caudal fin
9	Posterior insertion of the anal fin
10	Anterior insertion of the anal fin
11	Insertion of the ventral fin
12	Ventral insertion of pectoral fin
13	Dorsal insertion of pectoral fin
14	Dorsal insertion of operculum
15	Snout tip

All specimens were preserved in alcohol. The thick epidermal mucus layer, typical for species of *Gobiodon*, was scraped off with a scalpel to reveal the anatomical points (landmarks) required for measurements. Measurements were converted to proportions through expressing them as percentage of standard length (table 2). Proportions were analysed through a principal component analysis (PCA) and plotted with the program PAST 2.03 .

1.2 Geometric morphometrics

The same 132 specimens as used for traditional measurements were scanned on an EPSON Perfection 4990 flatbed scanner using a 3200 dpi resolution, according to the protocol of Herler et al. (2007). The jpg-images were compiled to a tps-file and randomized with the program tpsUtil 1.44 (Rohlf 2009b). The program tpsDig 2.14 (Rohlf 2009a) was used to put landmarks (Bookstein 1997) on the images in the tps-file. A set of 15 standardized landmarks (LM) was used for shape discrimination (figure 2b, table 1).

Table 2: 15 body proportions in percentage standard length of seven preserved species of *Gobiodon* (n = 132). Values show ranges and, in parentheses, mean and standard deviation. Abbreviations are listed in figure 1 and table 1.

	G. cit. (n = 13)	*G.his.* (n = 26)	*G. ret.* (n = 25)	*G.riv.* (n = 18)	*G.* sp.1 (n = 20)	*G.* sp.2 (n = 13)	*G.* sp.3 (n = 17)
SL	20.4 – 45.3 mm	20.5 – 37.1 mm	20.8 – 32.7 mm	19.9 – 27.2 mm	22.4 – 35.5 mm	17.8 – 26.7 mm	18.4 – 35.9 mm
%SL							
CPd	12.6 - 16.7 (14.0; 1.3)	13.6 - 16.2 (15.1; 0.7)	12.0 - 16.0 (13.6; 0.9)	13.5 - 17.8 (15.3; 1.1)	13.0 - 17.7 (15.1; 0.9)	12.1 - 14.6 (13.5; 0.8)	12.9 - 15.3 (14.3; 0.7)
gBw	14.2 - 20.5 (15.8; 1.9)	9.4 - 16.0 (12.6; 1.6)	6.7 - 20.1 (12.9; 3.1)	11.5 - 17.9 (14.1; 1.9)	9.1 - 16.3 (12.6; 1.7)	10.7 - 15.4 (13.6; 1.5)	9.9 - 16.1 (12.4; 1.6)
Aw	8.7 - 14.5 (11.4; 1.4)	8.8 - 11.5 (10.1; 0.8)	8.2 - 14.3 (10.9; 1.5)	8.2 - 16.5 (10.8; 2.0)	8.8 - 14.1 (11.1; 1.6)	8.1 - 10.5 (9.3; 0.7)	8.0 - 17.5 (11.1; 2.8)
Hw	11.3 - 14.9 (13.0; 0.9)	10.7 - 14.2 (12.4; 0.9)	11.5 - 16.4 (14.2; 1.1)	10.2 - 15.9 (13.5; 1.4)	11.3 - 15.1 (13.1; 1.0)	11.3 - 14.1 (12.6; 0.8)	11.6 - 15.0 (13.6; 1.0)
gHw	17.0 - 20.6 (18.5; 1.1)	15.0 - 19.2 (16.7; 1.0)	15.5 - 21.2 (19.1; 1.4)	16.3 - 20.0 (18.3; 0.9)	16.3 - 21.1 (18.4; 1.3)	16.1 - 19.6 (17.8; 0.9)	17.3 - 20.6 (18.5; 0.7)
H	27.6 - 31.3 (29.3; 1.1)	26.3 - 31.2 (29.0; 1.1)	12.5 - 31.9 (28.3; 3.5)	26.1 - 31.5 (28.7; 1.8)	26.7 - 30.8 (28.2; 1.2)	26.7 - 31.2 (28.5; 1.2)	26.8 - 32.2 (29.5; 1.4)
SN/E	7.1 - 10.3 (8.2; 1.0)	6.7 - 8.8 (7.8; 0.5)	6.9 - 8.9 (7.8; 0.5)	6.2 - 8.7 (7.4; 0.7)	6.9 - 9.5 (8.0; 0.6)	6.4 - 9.6 (7.6; 1.0)	6.9 - 10.1 (8.2; 0.8)
UJ	9.5 - 11.1 (10.5; 0.5)	10.6 - 12.9 (11.7; 0.6)	10.7 - 14.1 (12.3; 0.7)	9.9 - 12.3 (11.1; 0.6)	9.7 - 12.9 (11.3; 0.7)	11.8 - 14.4 (12.9; 0.7)	11.8 - 14.1 (13.1; 0.7)
SN/D1	30.6 - 34.5 (32.5; 1.1)	32.9 - 39.6 (35.4; 1.6)	30.3 - 35.4 (32.8; 1.6)	32.0 - 35.7 (33.8; 0.8)	31.0 - 36.3 (34.0; 1.5)	31.9 - 48.4 (35.4; 4.3)	33.8 - 37.9 (35.4; 1.1)
SN/V	35.8 - 42.3 (37.7; 2.0)	36.6 - 40.5 (38.3; 1.1)	35.6 - 41.5 (38.0; 1.4)	35.3 - 40.2 (37.6; 1.2)	34.8 - 41.4 (38.4; 1.7)	37.3 - 40.7 (39.0; 1.0)	37.6 - 43.5 (40.1; 2.0)
PO	12.9 - 16.1 (14.3; 0.9)	16.0 - 18.2 (16.8; 0.6)	12.0 - 17.3 (15.0; 1.3)	13.0 - 19.4 (15.9; 1.7)	13.7 - 17.4 (15.8; 1.1)	14.6 - 18.7 (16.5; 1.3)	15.0 - 17.5 (16.4; 0.8)
E	7.5 - 10.7 (9.3; 1.0)	5.4 - 7.4 (6.3; 0.6)	6.8 - 9.5 (7.9; 0.8)	6.1 - 8.8 (7.1; 0.7)	5.9 - 8.5 (6.9; 0.6)	5.5 - 7.5 (6.5; 0.6)	5.5 - 7.7 (6.7; 0.7)
Vl	15.6 - 20.1 (18.0; 1.7)	14.3 - 18.1 (15.8; 1.0)	12.8 - 18.5 (16.0; 1.4)	11.6 - 16.9 (14.7; 1.4)	10.8 - 18.8 (15.0; 2.3)	14.3 - 18.7 (15.9; 1.3)	15.2 - 20.3 (17.6; 1.5)
Vd	33.6 - 40.2 (36.0; 2.0)	38.1 - 47.1 (42.3; 2.3)	32.9 - 40.5 (36.7; 2.1)	32.7 - 37.4 (35.1; 1.1)	32.7 - 41.6 (35.8; 2.1)	33.3 - 39.7 (36.3; 1.7)	35.6 - 42.5 (38.6; 2.0)
V/AN	19.5 - 29.1 (24.9; 3.2)	18.7 - 25.4 (21.6; 1.7)	16.8 - 21.2 (19.1; 1.1)	16.7 - 23.5 (19.3; 1.8)	13.8 - 22.6 (18.7; 2.2)	20.4 - 31.1 (25.9; 2.9)	18.4 - 29.0 (24.0; 3.3)

Further, all non-shape variation (location, orientation (or rotation) and scale) was removed: usually a generalized Procrustes analysis (Dryden and Mardia 1998 Rohlf 1999) is employed. In the present study a Procrustes superimposition was performed: each landmark configuration receives a geometric center (the centroid) through calculating the arithmetic mean of all landmark coordinates. The geometric size of landmark configurations (centroid size; CS) is calculated by the square root of the sum of squared distances (SSD) between each landmark and the centroid, and is used to rescale all configurations to a common size (CS = 1). A translation to a common center is performed by shifting all configurations to the centroid coordinates 0/0. Finally, the configurations are rotated against each other (using a least-squares procedure), until an optimal fit is obtained (Dryden and Mardia 1998; Rohlf 1999). These newly established Procrustes shape coordinates are required for the study of true shape differences in these landmark configurations.

2. Morphology of selected species (*Gobiodon histrio* and *G. rivulatus*)

Examinations of live fishes were made in April and May 2010 in the Gulf of Aqaba, close to the Napoleon Reef in the region of Dahab, Sinai, Egypt (28°28’ N, 34°30’ E). Fish were caught by taking random swims using SCUBA at two different reef zones (reef flat and reef edge). Fishes were narcotized with clove oil (Munday and Wilson 1997), captured, recovered and stored in numbered plastic boxes. In the laboratory, fish were stored in aquaria (L x W x H = 0.8 x 0.5 x 0.4 m) and supplied with fresh sea-water from a flow-through system. Pairs were kept in the same container but separated from other pairs by small perforated plastic boxes.

Thirty specimens of the two *Gobiodon* species (21 *G. histrio* and 9 *G. rivulatus*; dataset C; plate 1) were collected from randomly selected coral colonies of *A. digitifera* and *A. gemmifera* (plate 2) and used for traditional and geometric morphometrics. Digital images were acquired in the laboratory using a flatbed scanner. Fishes were narcotized with clove oil, following the protocol of Munday and Wilson (1997) and scanned on an EPSON Perfection V30 flatbed scanner using a 3200 dpi resolution, following the protocol of the Herler et al. (2007) Standard length and body depth were measured on the lateral scans, whereas 3 linear measurements (head width (Hw), greatest head width (gHw) and greatest body width (gBw)) were directly measured on the narcotised fishes with a digital caliper to the closest 0.01 mm. After scanning and taking measurements, fishes were recovered in aerated sea-water and released back to the reef.

3. Coral morphology: colony size, architecture and interbranch-distance

Altogether, 59 colonies of two coral species (*Acropora digitifera* (D); n = 31; plate 2) and *A. gemmifera* (G); n = 28); plate 2), inhabited by 30 individuals of two species of *Gobiodon* (*G. histrio* and *G. rivulatus*; plate 1) from the reef flat (RF) and the reef edge (RE) were examined. RF – D: ten colonies occupied with six individuals of *G. histrio* and six of *G. rivulatus*, nine unoccupied colonies; G: seven colonies occupied with ten individuals of *G. histrio* and one of *G. rivulatus*, ten unoccupied colonies. RE – D: seven colonies occupied with five individuals of *G. histrio* and two of *G. rivulatus*, five unoccupied colonies; G: eleven unoccupied colonies were examined. Maximum colony diameter was measured to the closest cm by using a reference ruler. As proxies for coral branch architecture, two dimensions of coral branches were measured. Branch length (BL) of two adjacent branches was measured from the branch tip (represented by the axial corallite) to the base (the deepest point between two main branches) by using the depth gauge of a plastic caliper. In addition, for the same two branches, branch-tip distance (BTD) was measured as the distance from the center of the axial corallite of one branch to that of the adjacent branch. Both were measured to the closest mm from ten branch pairs per colony (figure 3).

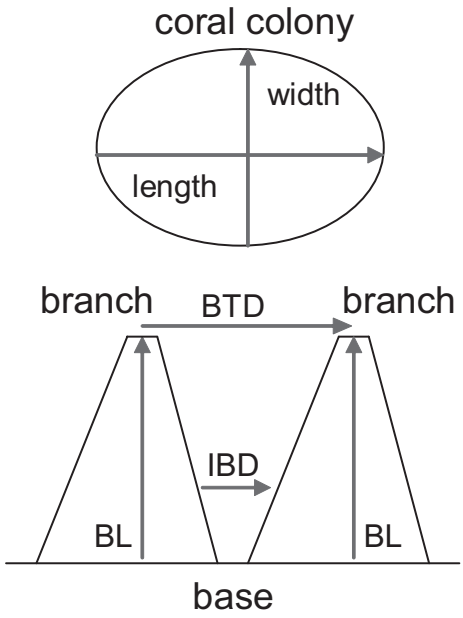

Fig. 3: Schematic illustration of measured distances of coral colonies (length and width = maximum colony length respectively width was measured to the closest cm by using a reference ruler; BL = branch length of two adjacent branches from the branch tip (represented by the axial corallite) to the base (the

deepest point between two main branches); BTD = branch-tip distance is the distance from the center of the axial corallite of one branch to that of the adjacent branch; IBD = interbranch-distance in 3.5 and 7 mmabove the base of two adjacent branches)

Most species of the genus *Gobiodon* live in the innermost space of corals (Herler 2007). To measure the interbranch-distance (IBD) close to branch bases, a new and non-destructive measurement technique was developed and performed on the two coral species *A. digitifera* and *A. gemmifera* (figure 3). Custom-made forceps (anatomic forceps DP11 with a grooved jaw-profile) of two different lengths (145 and 300 mm) were grinded over most of their length prior to their use in the field to facilitate insertion between even narrowly spaced coral branches. A two component epoxy resin (Reef Construct ™, Aqua Medic GmbH) was mixed with plastic gloves at the study site immediately before diving. This epoxy was then used to create casts of coral branch bases. A cylindrical piece of epoxy (approximately 3 cm long and 0.5 cm wide) was inserted into the coral by using the forceps and pressed against the base of two adjacent branches. Every piece of epoxy, before usage, was size-adjusted by hand to assure that it will fill the corals IBD to a minimum height of 1.5 cm. The casts were carefully removed from the interbranch-spaces and stored in small, subdivided and numbered plastic boxes to secure their shape and order. The casts hardened within 2 hours and were then measured in the laboratory with a digital caliper. Cast width was measured at two fixed heights (3.5 mm and 7 mm from the base) with a digital caliper to the closest 0.01 mm. These heights were chosen based on the mean of the half anterior body height of juvenile and adult *Gobiodon* species, considered as the height of maximum fish body width (Herler, unpublished data) and tested for correlation with each other. The grooved jaw-profile on the cast was useful for re-establishing a similar holding position (approximately perpendicular to the measuring axis of the IBD) as when the cast was taken in the field. Tiny imprints of radial corallites of the two coral branches in the cast also helped in finding the correct measuring position.

4. Statistical analysis

4.1 Body shape variation within the genus *Gobiodon*

A PCA of proportional (in % SL) traditional morphometric (TM) distances was performed to test for the most important distances and further the first six principal component scores (limit of explained variance: > 3%)(Mitteroecker and Gunz 2009) were adducted for a multigroup discriminant analysis (test for the equality of the means) respectively a one-way multivariate analysis of variance (MANOVA)(Tabachnick and Fidell 2001; Mitteroecker and Gunz 2009).

Furthermore, a PCA was carried out on Procrustes shape coordinates (GM) with the program tpsrelw 1.49 (Rohlf 2010) and visualized through a scatter-plot with the program PAST 2.03. In the next step, the tps-file was processed with the program CoordGen6h (Sheets 2009) to visualize the Procrustes superimposition coordinates (Rohlf 1999). The coordinates were saved in a file that was processed with PCAGen6p (Sheets 2007) to visualize PC scatter-plots and thin-plate-spline deformation grids and vectors for each PC (Bookstein 1989). Additionally, a MANOVA (Tabachnick and Fidell 2001) was performed on the first eight principal component scores of the PCA (limit of explained variance > 3%)(Mitteroecker and Gunz 2009) with the program PAST 2.03 .

4.2 Shape studies of live and preserved fish of selected species

After a PCA on traditional width values (gBw, gHw and hw) and geometric morphometric data (dataset B) of *G. histrio* (n = 47) and *G. rivulatus* (n = 27), the first PC-scores of both morphometric approaches were taken for a two-way analysis of variance (ANOVA)(Miller 1986). This test shall reveal differences between PC1 of live and preserved specimens and searches for possible conservation artefacts.

Moreover, a MANOVA (Tabachnick and Fidell 2001) on the first three PC-scores of traditional width measurements and on the first six PC-scores of Procrustes coordinates were performed (limit of explained variance > 3% in both) with the program PAST 2.03 (Hammer et al. 2001) to see if there are morphological differences between two species of *Gobiodon* in two different conditions (live and preserved)

Selected TM distances (SL and body depth at the ventral fin origin (Vd) and SL and greatest head width (gHw)) of live and preserved specimens of *G. histrio* (n = 47) and *G. rivulatus* (n = 27) were used for a one-way analysis of covariance (ANCOVA)(Tabachnick and Fidell 2001) to test allometric differences between these two species.

4.3 Coral morphology and relation between host coral and fish shape

A Wilcoxon-Mann-Whitney-Test was performed between occupied and unoccupied colonies for their colony size, BL, BTD, IBD at 3.5 mm and 7 mm height with the program PAST 2.03 (Hammer et al. 2001) to find potential significant differences in the shape of occupied and unoccupied colonies. It is a non-parametric statistical hypothesis test for assessing whether two independent samples of observations have equally large values (Wilcoxon 1945; Mann and Whitney 1947). To compare coral measurement data of occupied and unoccupied colonies a PCA of colonies occupied by *G. histrio* and *G. rivulatus* specimens was done with the program PAST 2.03 (Hammer et al. 2001).

To find the coral parameters which are most important for goby occupation through a multivariate analysis, a logistic regression was performed on BL, BTD, IBD (at 3.5 and 7 mm height) and mean colony diameter (arithmetic mean of maximum colony length and width) of occupied and unoccupied colonies of *A. digitifera* and *A. gemmifera* from two different reef zones (reef flat and reef edge) with the program SPSS 17.0 (Nie et al. 1970) to describe the relationship between independent variables (e.g. coral measurements) and binary response variables, expressed as a probability, that has only two values, such as coral occupation (occupied or unoccupied: 0 or 1).

To find relationships between the shape of fishes and that of host corals two separate two-block partial least squares (2B-PLS) analysis (Sampson et al. 1989; Streissguth et al. 1993) was performed on logarithmic as well as on normalised (z-transformed) measurements of corals (BL, BTD and IBD (at 3.5 and 7 mm height) and mean colony diameter) and fishes (traditionally measured distances of gBw, gHw, Hw, SL and Vd) with the program PAST 2.03 (Hammer et al. 2001). The 2B-PLS is an ordination method like PCA but with the objective to maximize covariance between two different sets of variables, in this case fish and coral morphometric data. The algorithm of the 2B-PLS of the program PAST 2.03 follows Rohlf & Corti (2000).

Results

1. Body shape variation of seven species of *Gobiodon*

1.1 Traditional morphometrics

Examination of 132 preserved *Gobiodon* specimens showed species-specific shapes. In a PCA of body proportions (in % SL), PC 1, 2 and 3 accounted for about 60 % of all shape variation (figure 4). According to the loadings of variables onto the first three PCs (figure 4), mainly 3 distances (gBw, Vd and V/AN) were important for species separation. Plotting PC 1 against PC 2, specimens cluster according to species although several species overlap to varying extent (figure 4). Regressions of the three head and body width measurements (gBw, gHw and Hw; in % SL) against each other were all highly significant (table 3) in three datasets (1: n = 132 (*G. citrinus* (n = 13), *G. histrio* (n = 26), *G. reticulatus* (n = 25), *G. rivulatus* (n = 18), *G.* sp.1 (n = 20), *G.* sp.2 (n = 13) and *G.* sp.3 (n = 17)); 2: n = 44 (*G. histrio* (n = 26) and *G. rivulatus* (n = 18)), and 3: n = 30 (*G. histrio* (n = 21) and *G. rivulatus* (n = 9)).

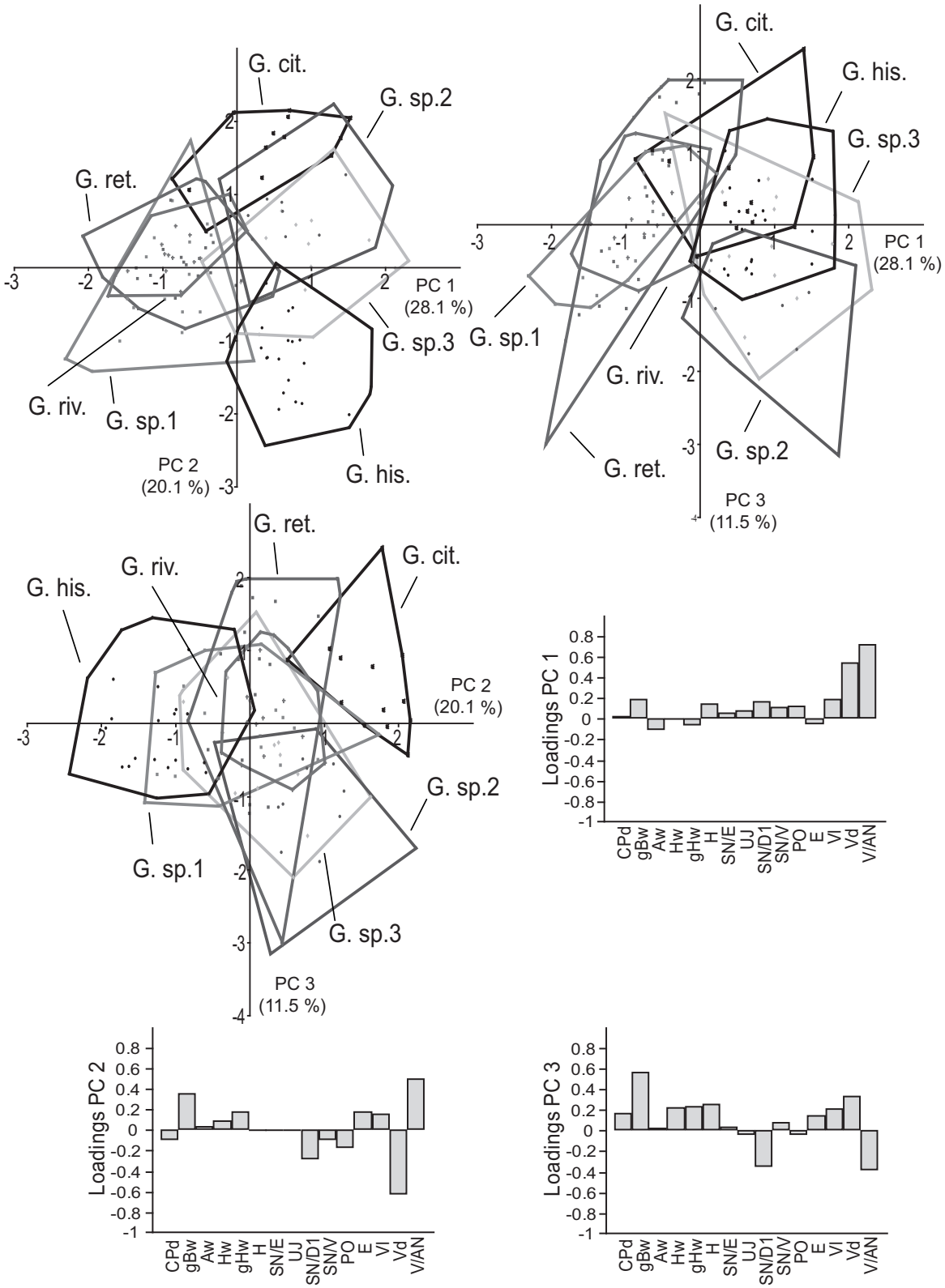

Fig. 4: Scatter-plots and loadings (principal components 1 to 3) of a PCA on traditional morphometric measurements (15 body proportions) of seven species of *Gobiodon* (n = 132; *G. citrinus* (n = 13), *G. histrio* (n = 26), *G. reticulatus* (n = 25), *G. rivulatus* (n = 18), *G.* sp.1 (n = 20), *G.* sp.2 (n = 13) and *G.* sp.3 (n = 17)).

Table 3: List of F-Test results (R^2-values; *** = p-value < 0.001) of regressions of three selected traditional morphometric variables (gHw, gBw and Hw; in %SL) against each other, and of logarithmic centroid size (log CS) against logarithmic SL from three different datasets: A: n = 132 preserved specimens (*G. citrinus* (n = 13), *G. histrio* (n = 26), *G. reticulatus* (n = 25), *G. rivulatus* (n = 18), *G.* sp.1 (n = 20), *G.* sp.2 (n = 13) and *G.* sp.3 (n = 17)); B: n = 44 preserved specimens (*G. histrio* (n = 26) and *G. rivulatus* (n = 18)), and C: n = 30 live specimens (*G. histrio* (n = 21) and *G. rivulatus* (n = 9)).

dataset		gHw : gBw	gHw : Hw	gBw : Hw	log CS : log SL
A	R^2	0.31 ***	0.81 ***	0.34 ***	0.83 ***
B	R^2	0.43 ***	0.77 ***	0.40 ***	0.82 ***
C	R^2	0.61 ***	0.73 ***	0.82 ***	0.99 ***

A MANOVA (Hotelling's pairwise comparisons, Bonferroni corrected; table 4) on PC-scores of traditional measurements and on Procrustes shape coordinates showed significant differences between most pairs of species, except for the pairs *G. reticulatus*/*G.* sp.1, *G. rivulatus*/*G.* sp.1 and *G.* sp.2/*G.* sp.3.

Table 4: P-values of MANOVA (Hotelling's pairwise comparisons, Bonferroni corrected) of TM-data (above diagonal) and GM-data (below diagonal). In case of TM, the scores of the first eight, in case of GM, the scores of the first six principal components were used (chosen limit: explained variance of PC > 3%) of seven species of *Gobiodon* (n = 132; *G. histrio* (n = 26), *G. reticulatus* (n = 25), *G. rivulatus* (n = 18), *G.* sp.1 (n = 20), *G.* sp.2 (n = 13), *G.* sp.3 (n = 17) and *G. citrinus* (n = 13)). n.s. = not significant.

	His	Ret	Riv	Sp.1	Sp.2	Sp.3	Cit
His		< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Ret	< 0.001		< 0.05	n.s.	< 0.001	< 0.001	< 0.001
Riv	< 0.001	< 0.001		n.s.	< 0.001	< 0.001	< 0.001
Sp.1	< 0.001	< 0.01	n.s.		< 0.001	< 0.001	< 0.01
Sp.2	< 0.001	< 0.001	< 0.01	< 0.001		n.s.	< 0.01
Sp.3	< 0.001	< 0.001	< 0.001	< 0.001	n.s.		< 0.001
Cit	< 0.001	< 0.01	< 0.001	< 0.001	< 0.001	< 0.001	

1.2 Geometric morphometrics

A PCA of Procrustes shape coordinates of preserved specimens of seven species of *Gobiodon* showed species-specific clusters but with variable overlap in several clusters (figure 5).

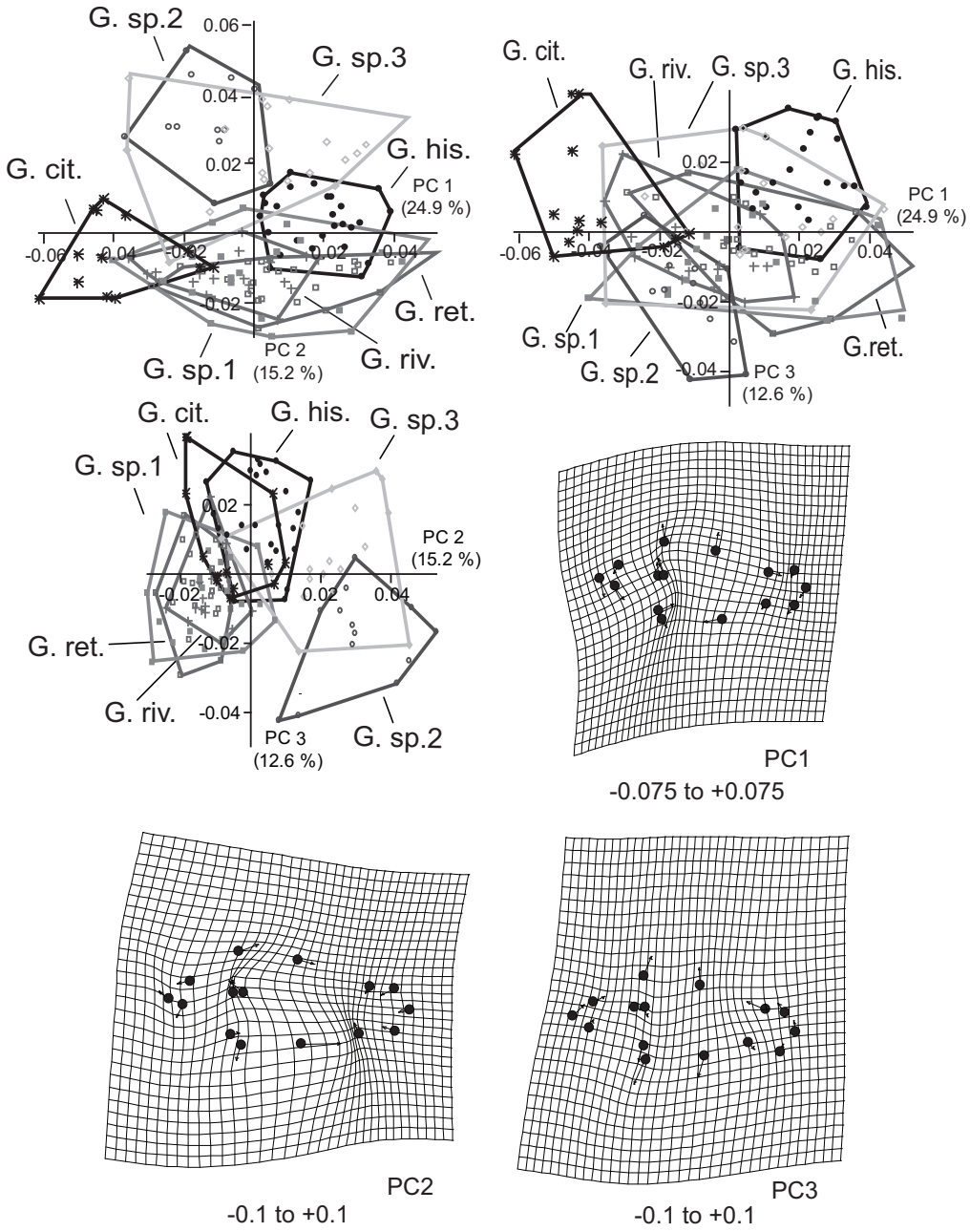

Fig. 5: Scatter-plots and deformation grids of the first three principal components of Procrustes shape coordinates (15 landmarks) of seven species of *Gobiodon* (n = 132; *G. citrinus* (n = 13), *G. histrio* (n = 26), *G. reticulatus* (n = 25), *G. rivulatus* (n = 18), *G.* sp.1 (n = 20), *G.* sp.2 (n = 13) and *G.* sp.3 (n = 17)). Deformation grids visualize shape deformations between two reference shapes along the corresponding principal component axis. Axis ranges between these reference shapes are indicated below each grid.

As the deformation grid implies, specimens at the negative end of PC 1 (e.g. *Gobiodon citrinus*) have depressed bodies. Moreover, the mouth is positioned more dorsally. At the positive end of PC 1, deep-bodied forms like *G. histrio* and some specimens of *G. reticulatus*, *G.* sp.1 and *G.* sp.3 are clustering (figure 5). Intermediate forms along PC 1 are represented by *G. reticulatus*,

G. rivulatus and *G.* sp.1. These, on the other hand, are forming the cluster at the negative end of the PC 2, which indicates a compression in the pectoral region. The opposite end of PC 2, indicating an extension of the abdominal region and a shear between the upper pectoral base and the dorsal fin origin, is dominated by the cluster of *G.* sp.2 and the majority of *G.* sp.3 individuals (figure 5). The deformation grid of PC 3 shows a dorso-ventral body extension, particularly obvious in the abdominal region. *G.* sp.2 clusters at its negative end and individuals of *G. citrinus* and *G. histrio* cluster at the positive end of PC 3. When plotted against PC 2, species separation is low with the exception of *G.* sp.2 and G. sp.3, which are distant from the others although they overlap with each other to some extent.

Log CS was significantly positively correlated with log SL in dataset A (table 3). Moreover, regressions of PC 1 of Procrustes shape coordinates against log CS and log SL showed significant correlations in all datasets (table 5). MANOVA results (Hotelling's pairwise comparisons, Bonferroni corrected) revealed significant differences between most pairs of species, except those of *G.* sp.1/*G. rivulatus* and *G.* sp.2/*G.* sp.3 (table 4). Regressions of PC 1 and 3 of Procrustes shape coordinates against size (log CS and SL) and two transversal body measurements (Hw and gHw; in % SL) showed positive correlations among the dataset (A) of all seven *Gobiodon* species (table 5).

Table 5: F-Test results (R^2-values; * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, not significant = n.s.) of regressions of the first two respectively three principal components of Procrustes shape coordinates against five different values (log Cs, log SL, gHw, gBw and Hw) from three different datasets: A: n = 132, (*G. citrinus* (n = 13), *G. histrio* (n = 26), *G. reticulatus* (n = 25), *G. rivulatus* (n = 18), *G.* sp.1 (n = 20), *G.* sp.2 (n = 13) and *G.* sp.3 (n = 17)); B: n = 44 (preserved *G. histrio* (n = 26) and *G. rivulatus* (n = 18)); and C: n = 30 (live *G. histrio* (n = 21) and *G. rivulatus* (n = 9)). + = positive and - = negative correlation.

	Log_CS	Log_SL	gHw(%SL)	gBw(%SL)	Hw(%SL)
dataset A					
PC 1	+0.06 **	+0.09 ***	+0.05 **	+0.02 n.s.	+0.09 ***
PC 2	-0.00 n.s.	-0.00 n.s.	-0.01 n.s.	+0.00 n.s.	-0.01 n.s.
PC 3	+0.21 ***	+0.16 ***	+0.10 ***	+0.08 **	+0.15 ***
dataset B					
PC 1	+0.37 ***	+0.35 ***	+0.17 **	+0.10 *	+0.15 *
PC 2	+0.17 **	-0.18 **	-0.10 *	-0.02 n.s.	-0.16 **
dataset C					
PC 1	+0.59 ***	+0.57 ***	+0.38 ***	+0.43 ***	+0.49 ***
PC 2	+0.09 n.s.	-0.11 n.s.	-0.06 n.s.	-0.01 n.s.	-0.02 n.s.

2. Morphology of selected species (*Gobiodon histrio* and *G. rivulatus*)

Body shapes of *G. histrio* and *G. rivulatus* differed significantly (table 6). Traditional morphometric values revealed that *Gobiodon histrio* is more deep-bodied (about 30% higher Vd) at similar body width-values (only 7% higher gHw), and is thus much more compressed than *G. rivulatus*. Log CS was significantly positively correlated with log SL in dataset B and C (table 3).

Regressions of PC 1- and PC 2-scores of Procrustes shape coordinates of preserved specimens of *G. histrio* (n = 26) and *G. rivulatus* (n = 18) on size and body width measurements were all significant, except of PC 2 against gBw (table 5). In live specimens of *G. histrio* (n = 21) and *G. rivulatus* (n = 9) only regressions of PC 1 against size and width measurements were highly significant, whereas PC 2 and 3 showed no correlations (table 5).

Principal component analysis of body width measurements did not reveal a distinct separation between the two species, but there is a clear shift of preserved specimens along PC 1 in both species. In contrast, PC 2 collects only intraspecific variation (figure 5). In GM, PC 1 also separates live from preserved specimens, whereas both PC 1 and 2 contribute to a distinct species separation.

A two-way ANOVA for *G. histrio* and *G. rivulatus* in two conditions (live and preserved) on the scores of PC 1 of head and body width measurements (see also figure 6a) showed significant differences across each of the two factors (sum of squares for species: 156.6, $p < 0.001$; sum of squares for condition: 130.4, $p < 0.001$) but no significant interaction between them (sum of squares: 3.3, $p = 0.073$).

Similarly, two-way ANOVA of these two species in the two different conditions performed on the scores of PC 1 of Procrustes shape coordinates (see also figure 6b) yielded significant differences across each of the two factors (species: sum of squares: 0.011, $p < 0.001$; condition: sum of squares: 0.017, $p < 0.001$) but, in contrast to TM-data, the interaction was also significant between them (sum of squares: 0.0007, $p < 0.05$).

Two MANOVAs were carried out to test significant differences between live and preserved *G. histrio* and *G. rivulatus* (n = 74; Hotelling's pairwise comparisons, Bonferroni corrected; table 6). While MANOVA on PC-scores of Procrustes coordinates revealed significant differences between all groups, MANOVA on PC-scores of traditional width measurements showed significant differences between most groups, except for the pairs of preserved/live *G. rivulatus* and preserved *G. histrio*/live *G. rivulatus*.

Table 6: P-values of MANOVA (Hotelling's pairwise comparisons, Bonferroni corrected) of TM-data (above diagonal) and GM-data (below diagonal). In case of TM, the scores of the first three, in case of GM, the scores of the first seven principal components were used (chosen limit: explained variance of PC > 3%) of *Gobiodon histrio* (His) *and G. rivulatus* (Riv) (n = 74, His_live (n = 21), Riv_live (n = 9), His_preserved (n = 26) and Riv_preserved (n = 18)) were analysed. n.s. = not significant.

	His_live	Riv_live	His_preserved	Riv_preserved
His_live		< 0.001	< 0.001	< 0.001
Riv_live	< 0.001		n.s.	n.s.
His_preserved	< 0.001	< 0.001		< 0.001
Riv_preserved	< 0.001	< 0.001	< 0.001	

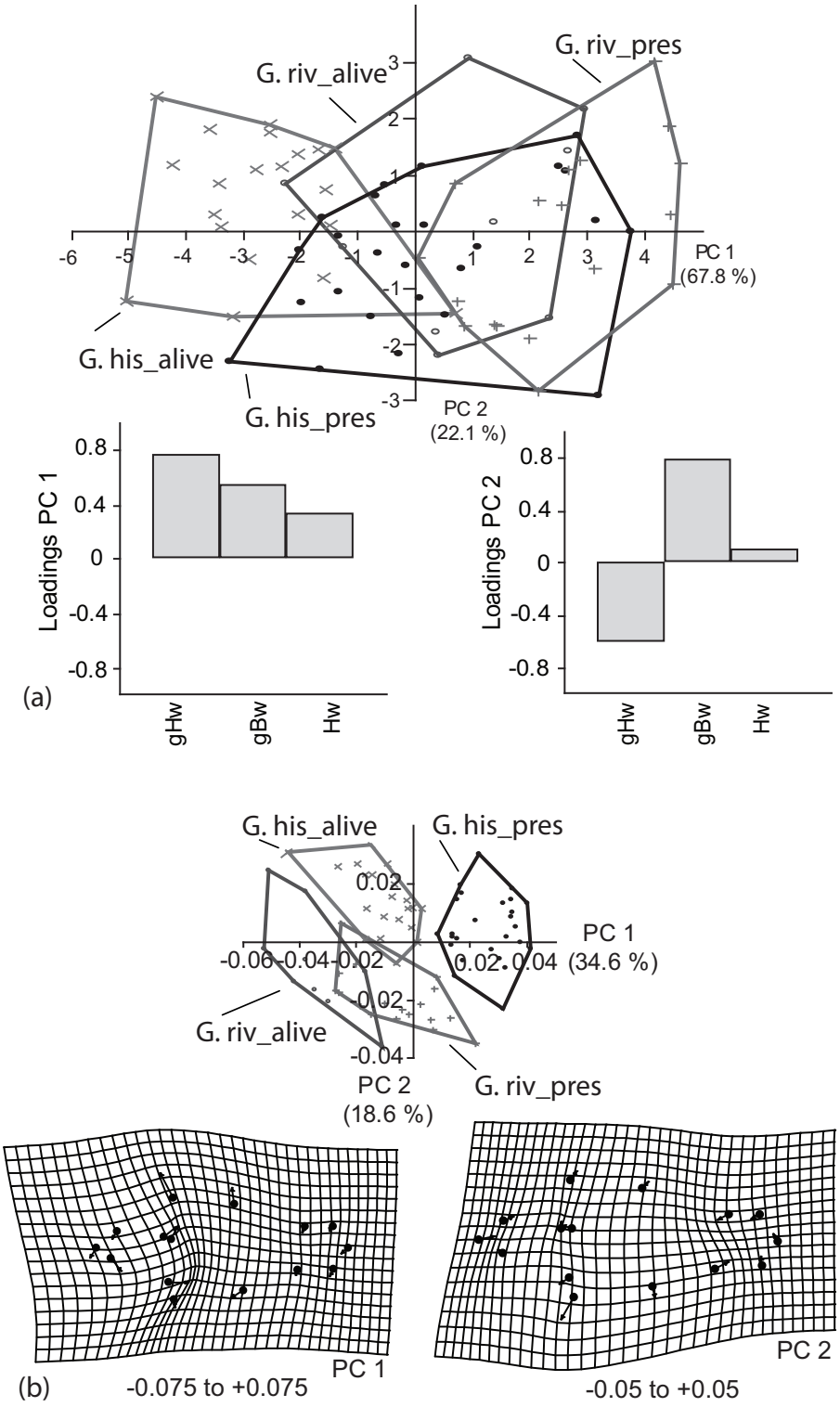

Fig. 6: Scatter-plot and loadings respectively deformation grids of the first two principal components of (a) three traditional head and body width measurements (abbreviations are listed in table 1) and (b) Procrustes coordinates of 15 landmarks of *G. histrio* (n = 47) and *G. rivulatus* (n = 27). Deformation grids visualize shape deformations between two reference shapes along the corresponding principal component axis. Axis ranges between these reference shapes are indicated below each grid.

To reveal differences in allometric growth of body depth and width between the two species, a one-way ANCOVA was performed for body depth (Vd) and greatest head width (gHw) across standard length (SL) on preserved specimens of *G. histrio* and *G. rivulatus* (figure 7). It revealed high between-group-effects and significant F-test results for both measurements but with higher significance for Vd (sum of squares: 0.161, $p < 0.001$) than for gHw (sum of squares: 0.006; $p < 0.05$). Vd showed a significantly higher mean in *G. histrio* (n = 26, mean Vd = 1.17 cm ± 0.24 S.D.) than in *G. rivulatus* (n = 18, 0.84 cm ± 0.07; one way ANCOVA: $p < 0.001$). In contrast, mean gHw was not significantly different between *G. histrio* (n = 26, 0.46 cm ± 0.06) and *G. rivulatus* (n = 18, 0.43 cm ± 0.03; one way ANCOVA: $p = 0.054$), although SL was significantly higher ($p < 0.001$) in *G. histrio*. One-way ANCOVA also tested for the equality of regression slopes, which was significantly different only for Vd ($p < 0.01$) but not for gHw ($p = 0.76$) against SL.

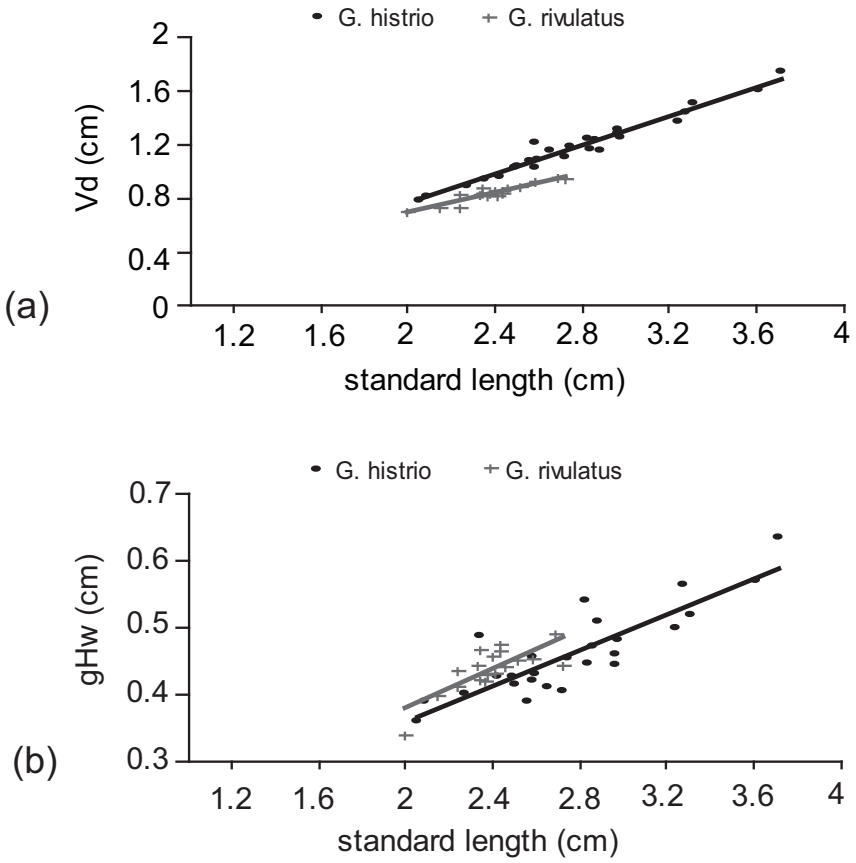

Fig. 7: Regressions of (a) body depth at ventral fin origin (Vd) and (b) greatest head width (gHw) against standard length (SL) in preserved *G. histrio* (n = 26) and *G. rivulatus* (n = 18) specimens.

3. Coral colony size and architecture, and relation to fish shape

Mean colony size (figure 8a) of all occupied colonies was larger (mean 2023 cm² ± 1271.5 S.D.) than those of unoccupied colonies (1907.3 cm² ± 1433.9). Mean branch length (figure 8b) of all occupied colonies was greater (5.97 cm ± 1.06) than in unoccupied colonies (4.76 cm ± 1.28), whereas mean branch tip distance (BTD) of occupied colonies (1.91 cm ± 0.56) was slightly smaller than in unoccupied (2.04 cm ± 0.57) colonies (figure 8c). Interbranch-distance (IBD) measurements at 3.5 and 7 mm height were significantly correlated with each other in both occupied colonies ($R^2 = 0.7914$, $p < 0.001$) and unoccupied colonies ($R^2 = 0.8161$, $p < 0.001$). Therefore, only the values at 7 mm height (representing the assumed constraint for adult fishes) were used for test statistics. Mean IBD at 7 mm height (figure 8d) of all occupied colonies (0.78 cm ± 0.06) was greater than in unoccupied colonies (0.74 cm ± 0.12).

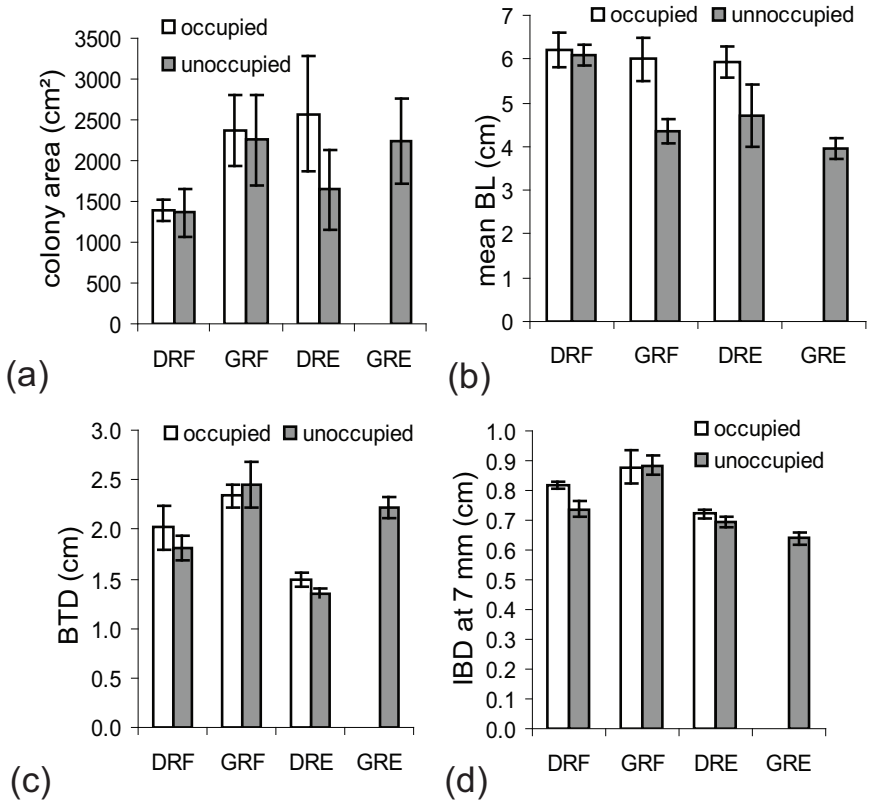

Fig. 8: Two different occupied (n = 24) and unoccupied (n = 35) coral species (*Acropora digitifera* (D) and *A. gemmifera* (G)) were measured at two different reef zones – reef flat (RF) and reef edge (RE). Measurements include total colony area (a), branch length (BL) (b), branch tip distance (BTD) (c) and interbranch-distance (IBD) at 7 mm height (d). Values are means and standard errors.

Wilcoxon-Mann-Whitney-Tests showed significant differences between occupied (n = 21) and unoccupied (n = 33) colonies for colony size ($p < 0.05$), BL ($p < 0.001$) and IBD (at 7 mm height; $p < 0.05$), but nor for BTD.

A PCA of BL, BTD, and IBD (at 3.5 and 7 mm height) of all colonies showed a good separation of *A. digitifera* from *A. gemmifera* along PC 2, whereas occupied and unoccupied colonies were (with one exception) separated along PC 1 (figure 9). Decisive for PC 1 was BL, whereas BTD was most important for the separation along PC 2.

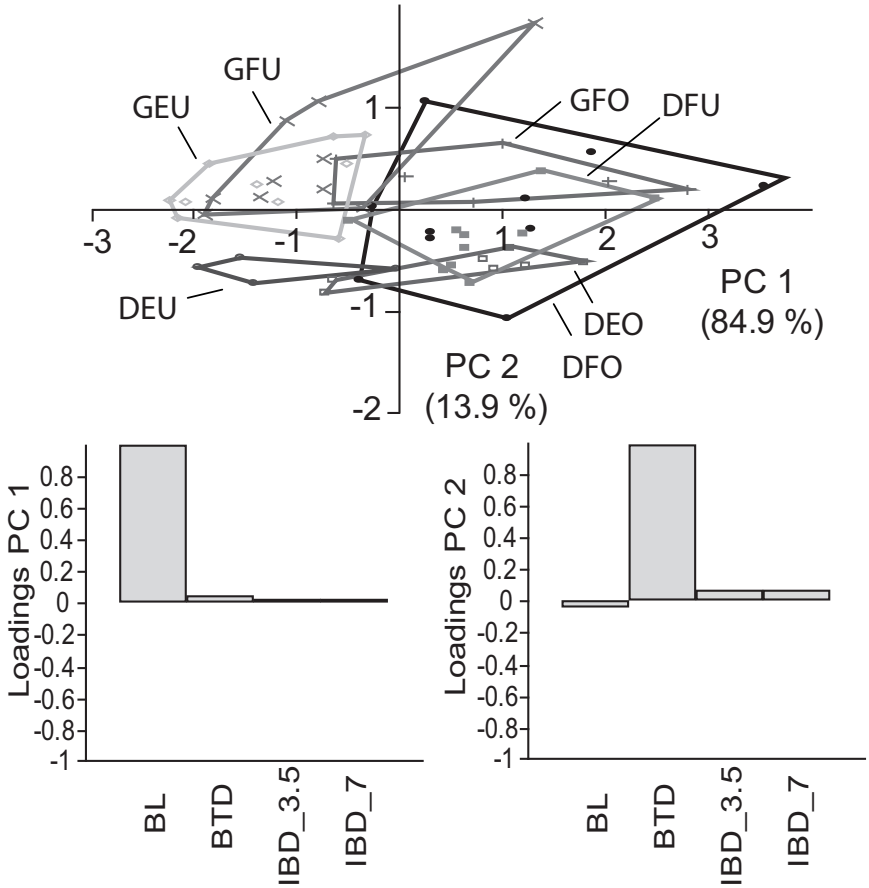

Fig. 9: Scatter-plot and loadings of principal component 1 and 2 of a PCA of BL, BTD and IBD at 3.5 mm at 7 mm height for *A. digitifera* (D) and *A. gemmifera* (G) from the reef flat (F) respectively reef edge (E) of occupied (O) and unoccupied (U) colonies.

When fish morphometrics are compared to measures from corals, mean gHw of *Gobiodon histrio* specimens is 52% of the mean IBD of their host corals and there was a significant correlation between these variables ($p < 0.05$; figure 10).

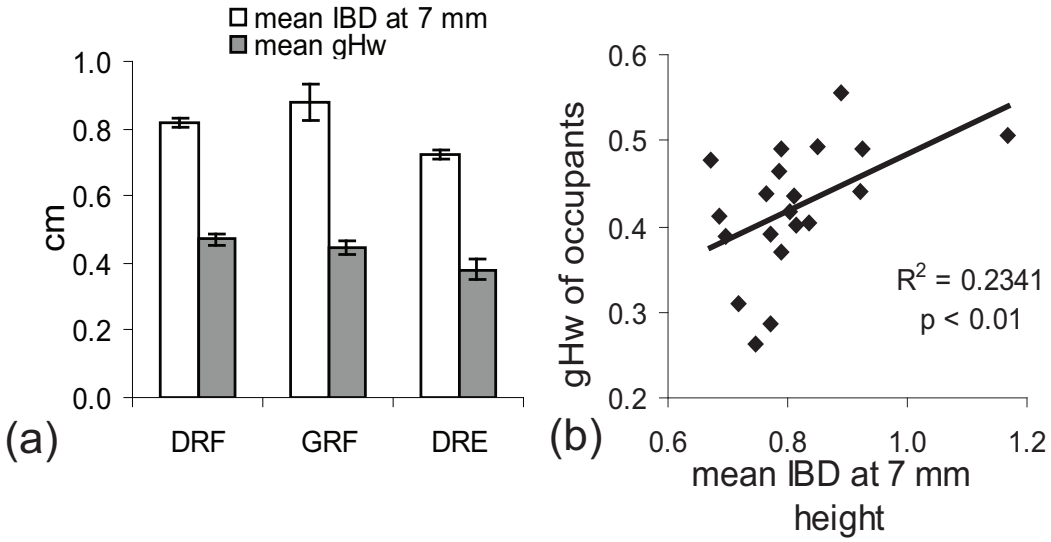

Fig. 10: Measurements of fishes and corals from occupied colonies (*Acropora digitifera* (D) and *A. gemmifera* (G) from two reef zones (reef flat (RF) and reef edge (RE)). Interbranch-distance (IBD) and greatest head width (gHw) of associated *G. histrio* specimens are plotted against (a) and correlated with (b) each other. Values (in a) are means and standard errors.

Logistic regression of BL, BTD and IBD (at 3.5 mm height and 7 mm height) and mean colony diameter values of occupied versus unoccupied corals revealed that BL was the only variable with a significant ($p < 0.01$) effect on the occupation of gobies.

Two-block partial least squares analyses (Rohlf and Corti 2000) of both logarithmic (explained covariance: axis 1: 97%; axis 2: 2.6%) and normalised (axis 1: 95.9%; axis 2: 3.4%) coral and fish measurements showed significant correlations ($p < 0.01$) only between BTD and SL respectively Vd.

Discussion

1. Body shape variation within the genus *Gobiodon*

Significant size and shape differences were found among seven species of coral-associated gobies of the genus *Gobiodon* from the Red Sea. Mainly three traditionally measured distances were decisive for the separation of the species. *Gobiodon histrio* and *G.* sp.3 represent the largest species among the seven species examined, although *G. citrinus* can grow significantly larger (Herler and Hilgers 2005). However, such large specimens of the latter species were not included in this study since they do not dwell the limited interbranch area of corals but prefer other microhabitats (Herler 2007). *Gobiodon histrio* and *G.* sp.3 are highly specialized, breeding-pair establishing and strongly coral-colony-bound species, with the most compress body forms, in contrast to *G. citrinus,* which is the most depress form. Further, *G. citrinus* prefers large and open colonies and moves between corals, sitting on top of their branches frequently, and showing no strong linkage to a single colony or their interbranch-space like other species of *Gobiodon* do. As revealed by a multivariate geometric morphometric shape analysis, the dorso-lateral expansion of the body and the pectoral fin base compression are the most important discrimination features between the seven species. This indicates adaptations to a life between branches of different coral species. The great dorso-lateral body appearance is considered to be important during turf wars (Munday et al. 2001) and this body extension appears to be limited through branch length, which is essential to provide shelter. The pectoral fin base compression suggests an adaptation in the locomotion-system to keep moving fast between branches or nearby colonies (Webb 1984). These adaptations are often at the expense of other abilities like swimming fast in the open water column. Both discrimination features show the selective pressure on the seven species of *Gobiodon* that were carried out by corals. *Gobiodon citrinus* has a rather cylindrical form and appears more like a true swimmer which moves more frequently between colonies (Herler 2007), and, particularly contrasting *G. histrio*, represents a more extreme body form within these seven species. *Gobiodon rivulatus*, *G. reticulatus* and *G.* sp.2 evolved intermediate body shapes compared to the other species. Their great shape overlap can, on the one hand, be explained with the great range of host corals these species occupy and their therefore relatively unspecialised body shapes. On the other hand, these species are close relatives (Herler et al. 2009) which also suggests the presence of a phylogenetic constraint that species of the genus *Gobiodon* underlie while adapting to corals of the genus

Acropora during their evolutionary history (Hedrick and Temeles 1989; Herler et al. 2010). Among these seven species of *Gobiodon* they represent generalists. In contrast, *G.* sp.2 and G. sp.3 occupy only one coral species each (Dirnwöber and Herler 2007). *Gobiodon* sp.1 and *G.* sp.3 are similar in their size ranges but, as revealed by GM-analysis (PC 2), the anal fin base appears more compressed in *G.* sp.3 than in G. sp1. A phylogenetic constraint could explain the different number of fin spines which influence the anal fin base length. However, also a homology problem with landmark number nine at the posterior insertion of the anal fin could explain this deviation (Herler et al. 2010).

The comparison of two morphological approaches (traditional and geometric morphometrics) on the same 132 individuals of seven species of *Gobiodon* showed that TM is the less precise technique. In multivariate geometric morphometrics, species clusters are smaller and more defined but rotated by 90 degrees compared to TM's. This swap of axes does not alter the relative position of species against each other. It just shows that the set of TM-distances is probably not big enough and that perhaps some important distances are missing, such as those describing the mouth position, which was important for defining the PC 1 of GM-data. After the consideration of all pros and contras, TM is more time-consuming and yields less defined results compared to an analysis of landmark data. Further, geometric morphometric tools like deformation grids visualize body shape changes and the way body proportions change from one to the other end of the corresponding axis, which makes interpretations much easier. The opportunity to extrapolate such differences to outside the true data even allows the visualization of very subtle differences.

2. Morphology of selected species (*Gobiodon histrio* and *G. rivulatus*)

Body width measurements of *G. histrio* and *G. rivulatus* imply that the greatest head width is more important for the separation of species than body width. It is also important for the determination of conservation artefacts underlined by PCA. The greatest head width of *G. rivulatus* specimens is increasing faster but not significantly during growth compared to *G. histrio*, and it is the opposite with body depth. Highly correlated SL respectively CS with PC 1 of Procrustes shape coordinates underlines the importance of allometry in this relation.

In contrast, body width is related to and limited by physical habitat constraints, i.e. interbranch-space. To gain a competitive advantage through a large lateral body display, it is

therefore necessary to have a relatively narrow head in combination with a deep body to grow as large as possible in the restricted interbranch-space.

Geometric morphometric results, whether of preserved or live specimens, are significantly different when compared to traditional width measurements. Further, all preserved specimens show a slight displacement of the ventral insertion of the pelvic fin from anterior to posterior. This local deformation also bends the head towards the abdomen. A contraction of the abdomen suggests that soft body parts shrink more than muscles do, when preserved in alcohol. Additionally, traditional morphometric results suggest significant difference between live and preserved specimens only in *G. histrio* but not in *G. rivulatus*. The difference results from larger head and body width measurements in preserved specimens. This is very likely caused by different biases of measurements of hardened and incompressible preserved fishes versus soft and compressible live fishes. However, a distinct difference is visible in both morphometric methods between live and preserved fish, which suggests that live and dead specimens must not be pooled for comparative datasets.

3. Coral morphology and its influence on fish shape

Occupied colonies at the reef edge were significantly larger in size than unoccupied ones – this is in accordance with a previous study in the same region (Schiemer et al. 2009). The preference of large-sized colonies over small-sized corals seems reasonable because a larger shelter and breeding ground, combined with a greater food resource, are ideal conditions for occupation.

Occupied colonies also had significantly longer branches. This is expected to offer effective shelter from predators and that gobies prefer long-branched colonies over short-branched to reduce predation risk. Revealed here, the most important feature for separating occupied and unoccupied colonies was branch length. Logistic regression analysis showed that BL was the only relevant factor for occupation by gobies. This indicates that providing shelter from predators through long branches is more important than variation in IBD, BTD or mean colony diameter. Branch length differences in occupied and unoccupied colonies of *Acropora gemmifera* from the reef flat, in *A. digitifera* from the reef edge and in unoccupied *A. gemmifera* from the reef edge indicate that colonies with BL < 5 cm are generally unoccupied. Colonies with characteristics like these are obviously rarely inhabited because they either do not provide efficient shelter for associated fishes against predators so that settling fish will be soon removed, or fish in general avoid these unsuitable habitats during habitat selection. As a consequence, the

small sized and short-branched *Acropora gemmifera* colonies at the reef edge were not occupied by gobies at all. Therefore, physical stress on coral architecture through wave movement, and corresponding shaping of colonies, appears to be a relevant factor for occupation. In addition, fishes may in general avoid zones with high hydrodynamic stress (Munday et al. 1997) although *Acropora digitifera* colonies in the same zone, representing preferably shaped colonies, were frequently occupied by gobies. Interestingly, several *Acropora digitifera* on the reef flat, which seem to be inhabitable from their morphometric characters, were unoccupied. Previous studies report occupation rates of approximately 80 % among certain species of *Acropora* (Patton 1994; Munday and Jones 1998; Dirnwöber 2005; Dirnwöber and Herler 2007) concluding an inverse relationship between coral abundance and occupation rates of *Gobiodon* spp. for each reef zone. Schiemer (2007) found the highest fish densities at the reef flat with *G. histrio* occupying and further the highest occupation rate for goby breeding pairs with 41.1 % in *A. digitifera*. The most likely explanation for the emptiness of basically suitable corals is that such colonies were unoccupied just at the time of investigation and were actually waiting for occupation.

Another important coral characteristic is branch tip distance (BTD), which differs between coral species. The two-block partial least squares analyses of occupied colonies and corresponding fish morphometics revealed a connection between BTD and length respectively body depth of fishes This suggests that BTD governs fish size in a way that colonies with a higher BTD offer a better habitat for larger fishes, which require more space between branches. In this relation, it seems reasonable that coral species like *A. gemmifera* with their greater BTD than *A. digitifera* are inhabited by larger species and specimens. Furthermore, BTD separates *A. digitifera* from *A. gemmifera* except for occupied colonies of *A. digitifera* from the reef flat (DFO), which are, at least partly, more similar to occupied colonies of *A. gemmifera* from the reef flat (GFO). These two groups of corals offer both good conditions for occupation through their similar architecture. It seems that fish therefore also decide on the colony structure and not on the coral species alone whether they settle/stay or not. There was a high range of BTD of the long-branched colonies of *A. digitifera* at the reef flat, which provide habitat for a greater size spectrum of gobies.

In this relation described a linkage between predation and competition. In our study this would mean that gobies choose long-branched colonies with a BTD matching their body size/body depth to reduce predation risk. A small body width, in combination with a higher body depth to maintain body volume seems to be favoured. The latter also increases the lateral appearance, which is expected to enhance the rank within the competitive hierarchy among coral-dwelling gobies.

The examination of interbranch-distances (IBD) at 7 mm height above branch base showed that 0.7 cm is the minimum for occupation by gobies. Colonies with IBD below this limit are usually not occupied by adult fishes. The IBD can be recognized as a "filter" for fish size (and shape) through its restriction of the greatest body width, or, as is the case in the genus *Gobiodon*, greatest head width. Greatest head width of *Gobiodon histrio* is increasing slower and this species develops a higher head and body at the same body length when compared to *G. rivulatus*. The morphological difference of having a narrow head and body coupled with a high back gives *G. histrio* an interspecific advantage during turf wars, since it is assumed that the (larger) lateral body area displayed during turf wars is more important for territorial fish than total body length (Munday et al. 2001; Collyer et al. 2005). Therefore, the larger *G. histrio* is more successful than *G. rivulatus* (or other species) when competing for the same corals. A higher body depth does not only result in competitive interactions but it may also represent a functional constraint. A body which is decreasing in width needs to become higher to retain its volume, which may be crucial for a constant body mass allocation of abdominal organs.

Coral morphology plays a major role in habitat complexity (Almany 2004a,b) and according community structure of reef associated organisms (Chabanet et al. 1996; Vytopil and Willis 2001). Vytopil and Willis (2001) described that tightly branched coral species show a greater abundance and species richness of epifauna compared to open-branched species, suggesting that protection afforded by complex habitats is important in structuring coral communities. They also showed that interbranch-space significantly affected the size of *Tetralia* crabs which are associated with different coral species. This suggests that coral-associated invertebrates as well as fishes select host corals according to interbranch-space and change hosts as they grow larger. In this connection, Wall and Herler (2008) showed the frequent habitat change of *G. histrio* individuals and this suggests that they migrate to find their ideal breeding coral.

The development of such body shape differences – as revealed between *G. histrio* and *G. rivulatus* – despite the occupation of the same set of coral species reveal that rather genetic determination than phenotypic plasticity is responsible for their different growth patterns. Several studies indicate that body shape in fishes is correlated with diet, foraging behaviour (Trapani 2003) and eco-morphology, meaning, species separation along morphological axes appears to be related to microhabitat utilization (Motta et al. 1995). Further, an optimal swimming performance within decreasing space among coral branches with increasing body size is only possible through allometric body growth, leading to a compress shape with a higher lateral display. Such adaptations prove the strong ecological selection for fish body shape with

respect to coral geometry and display the close morphological match and abiding relationship of the two partners, coral and fish.

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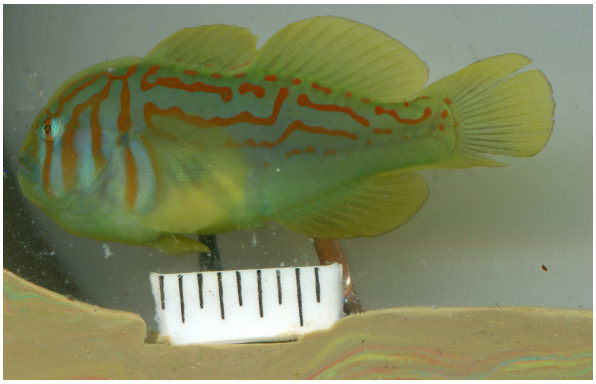
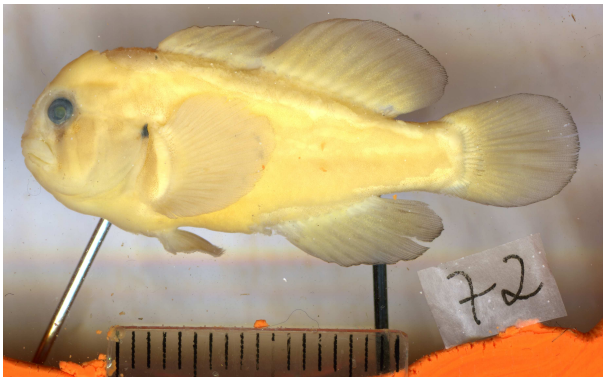
Appendix

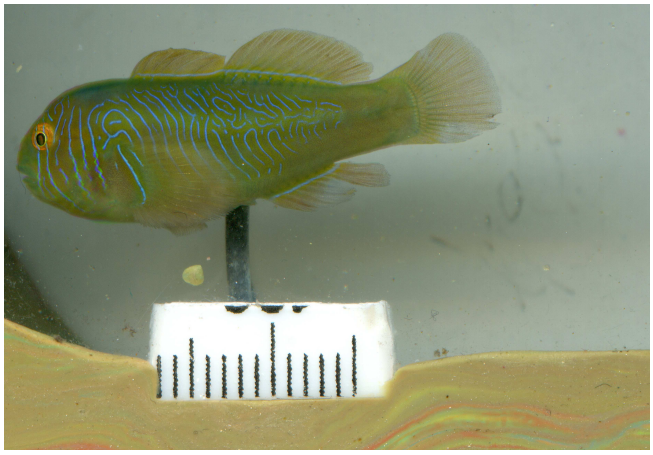
Plate 1: Pictures of live but narcotized and preserved specimens of *Gobiodon histrio* and *G. rivulatus*. Live specimens were captured from measured coral colonies at the Napoleon Reef next to Dahab. Preserved specimens were captured during random swims at fringing reefs next to Dahab, Egypt. Reference bars have 1 mm steps. (Photographs made by the author)



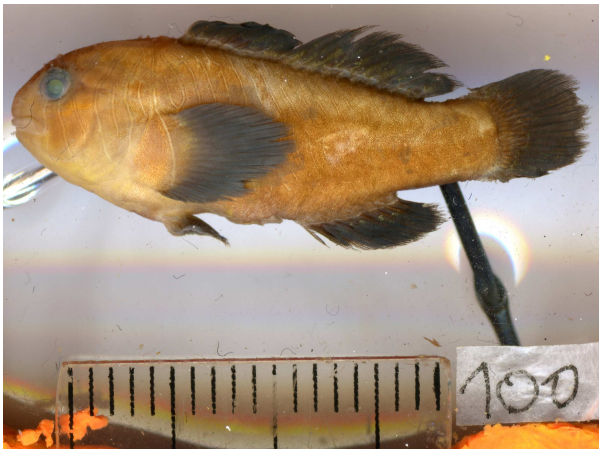
Gobiodon histrio (alive)



Gobiodon histrio (preserved)

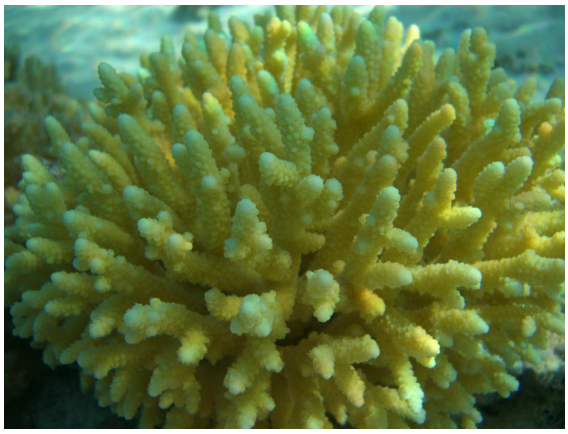


Gobiodon rivulatus (alive)

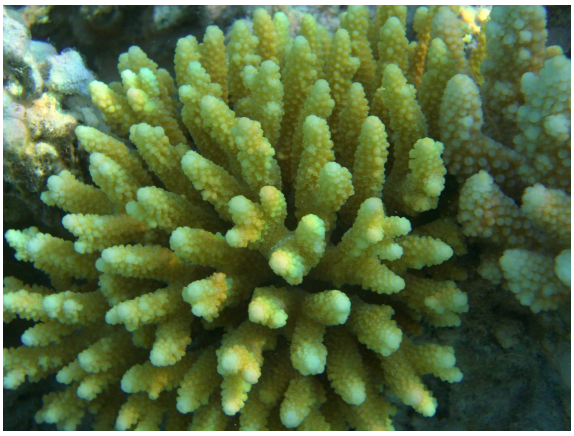


Gobiodon rivulatus (preserved)

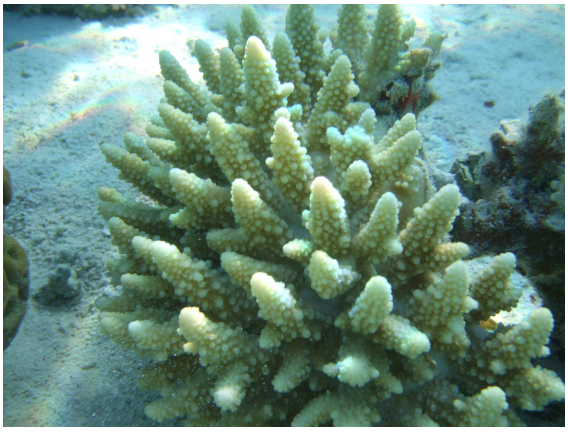
Plate 2: Pictures of *Acropora digitifera* and *A. gemmifera* found at fringing reefs around Dahab, Egypt. Each photo was made *in situ* (by the author).



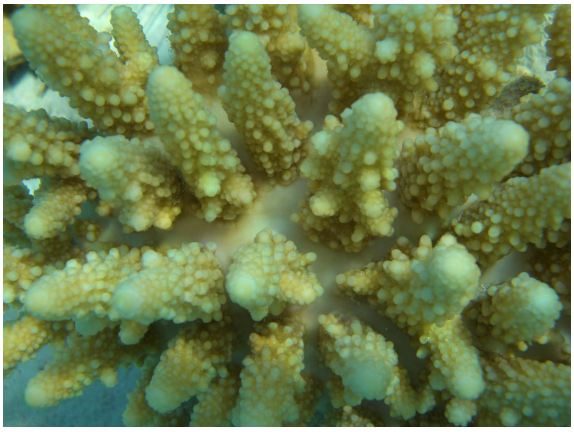
Acropora digitifera



Acropora digitifera



Acropora gemmifera



Acropora gemmifera

Zusammenfassung

Das Ziel meiner Arbeit war es zu evaluieren, ob die Architektur zweier Steinkorallenarten (*Acropora digitifera* und *A. gemmifera*) Auswirkungen auf die Morphologie zweier sie besiedelnde Korallengrundelarten (*Gobiodon histrio* und *G. rivulatus*) hat. Zu diesem Zweck wurde traditionelle und geometrische Morphometrie (Fig. 2; Tabelle 1 und 2) an lebenden aber betäubten Fischen angewandt sowie mehrere Parameter der jeweiligen Wirtskorallen (Fig. 8) aufgenommen. Diese kleinen (< 5 cm Totallänge) im Roten Meer vorkommenden Fische der Gattung *Gobiodon* sind sehr stark mit ihren Wirtskorallen der Gattung *Acropora* assoziiert und sind im Astzwischenraum zu finden. Um einen Überblick über die morphologischen Unterschiede dieser sieben im Roten Meer vorkommenden *Gobiodon* Arten zu erhalten, wurden zusätzlich konservierte Fische mit denselben morphometrischen Techniken bearbeitet (Fig. 1, 4 und 5). Die Daten dieser Studie wurden zwischen Anfang April und Mitte Mai 2010 im nördlichen Roten Meer in Dahab (28° 28` N, 34° 30` E), Ägypten aufgenommen. Der Untersuchungsstandort war das Napoleonriff nahe Dahab und dort wurden zwei Korallenarten (*Acropora digitifera* und *A. gemmifera*) vom Riffdach und der Riffkante hinsichtlich ihrer Besiedlung durch *Gobiodon histrio* und *G. rivulatus* beprobt. Es wurden sowohl besiedelte als auch unbesiedelte Korallen vermessen um einen möglichen Zusammenhang zwischen der Korallenarchitektur und Besiedelung zu finden. Besonderes Augenmerk lag auf den Astzwischenräumen, welche mit einer neuen Technik vermessen wurden. Ein schnell aushärtender Zweikomponenten-Epoxidharzkleber (Reef Construct ™, Aqua Medic GmbH) wurde mithilfe von Pinzetten an die Basis der Korallenäste gedrückt, um Abdrücke des Astzwischenraumes zu erhalten. Diese wurden anschließend im Labor vermessen. Messdaten konservierter und lebender Fische wurden anschließend miteinander verglichen und weisen auf ein Konservierungsartefakt hin. Es scheint so, dass Fische nach ihrer Alkoholkonservierung eine Kompression im abdominalen Bereich erleiden (Fig. 6). Alkoholkonservierung beeinflusst offenbar die Deformation weicherer Teile (Organe) des Abdomens stärker als jene von z.B. Muskeln. Zusätzlich wurden die Ergebnisse der verwendeten Techniken mit verschiedenen mathematischen Verfahren und Programmen analysiert und verglichen (Tabelle 3 bis 6). Der Vergleich der morphometrischen Verfahren zeigt, dass die geometrische der traditionellen Morphometrie generell vorzuziehen ist, da sie genauere Ergebnisse in kürzerer Zeit liefert.

Bei meinen Untersuchungen und Analysen bin ich auf 3 Parameter in der Korallenmorphologie gestoßen, die wesentlichen Einfluss auf Besiedelung und Körperform der Fische haben. Der

erste wichtige Parameter ist die Astlänge. Kolonien beider *Acropora*-Arten wurden von Meergrundeln nicht besiedelt, wenn sie eine Astlänge von weniger als 5 cm aufweisen. Offensichtlich bieten Korallen mit dieser Eigenschaft Korallengrundeln keinen ausreichenden Schutz gegen Fressfeinde. Die Meergrundeln werden daher entweder stets aus diesen Kolonien gefressen oder sie vermeiden solche Korallen generell. Der zweite wichtige Parameter ist der Astzwischenraum. Die zwei *Gobiodon*-Arten streben in ihrem Wachstum offensichtlich eine maximale Schädelbreite, die der Hälfte des Astzwischenraumes entspricht, an (Fig. 10a). Der dritte Parameter zeigt eine positive Korrelation der BTD mit der Körpergröße.

Weiters weisen die zwei Fischarten unterschiedliche Wachstumsmuster auf (Fig 7). Die Schädelbreite von *G. rivulatus* erhöht sich schneller mit zunehmender Körperlänge als bei *G. histrio* (Fig. 7b). Dessen Schädelbreite wächst im Verhältnis zum Längenwachstum weniger stark, aber dafür wird *G. histrio* hochrückiger. In weiterer Folge kann *G. histrio* eine größere Körperlänge erreichen, da er später das durch den Astzwischenraum vorgegebene Kopfbreiten-Maximum erreicht. Dies verschafft ihm vermutlich einen Vorteil in Revierkämpfen (Fig. 7a) und versetzt ihn in einer auf Konkurrenz basierenden zwischenartlichen Rangordnung in eine hohe Position.

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Principal subjects / occupational skills covered	Marine ecological special internship (Calvi, Corsika, France)
Dates	03 July 2009 - 31 July 2009

Principal subjects / occupational skills covered	Reaseach and preservation of sea turtles (Calis, Turkey)
Dates	03 November 2007 - 17 November 2007
Principal subjects / occupational skills covered	Coral reef study trip (Dahab, Egypt)
Dates	02 July 2007 - 14 July 2007
Principal subjects / occupational skills covered	Introduction into the flora and fauna of marine habitats (Rovinj, Croatia)
Dates	05 May 2007 - 19 May 2007
Principal subjects / occupational skills covered	North sea study trip (Sylt & Helgoland, Germany)
Dates	01 July 2006 - 05 August 2006
Principal subjects / occupational skills covered	Research and preservation of sea turtles (Calis, Turkey)

Personal skills and competences

Mother tongue(s) **German**

Other language(s)

Self-assessment	**Understanding**				**Speaking**				**W r i t i n g**	
European level (*)	Listening		Reading		Spoken interaction		Spoken production			
English	C2	Proficient user	C2	Proficient user	C1	Proficient user	C1	Proficient user	C1	Proficient user
French	A2	Basic User	A2	Basic User	A1	Basic User	A1	Basic User	A1	Basic User

(*) Common European Framework of Reference (CEF) level

Social skills and competences	- Soccer coach for kids between 6 and 16 years
Computer skills and competences	- Good command of Microsoft Office™ tools (Word, Excel and PowerPoint) - Good command of ARG GIS - Good knowledge of graphic design applications (Adobe Illustrator).
Other skills and competences	- Advanced Open Water Diver (AOWD)(PADI)
Driving licence(s)	A, B

Additional information

Relevant courses (completed):

UE Meeresbiologische Laborarbeiten 1+ 2, VO Meeresverschmutzung: Meeresnutzung, VO Biologie rezenter Riffe, VO+SE Einführung in die Meereskunde, VO Biologie des marinen Plankton, VO Grundlagen der aquatischen Ökotoxikologie, VO Marine Symbiosen, UE Marine Lebensräume im Gesteinsdünnschliff (Mikrofaziesanalyse),VO Fossile aquatische Ökosysteme - Känozoische Scleractinia, Steinkorallen bestimmen