

Trophic ecomorphology of cardinalfish

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ABSTRACT: Trophic diversity in 9 cardinalfish species was investigated by comparing 14 morphological characteristics of their feeding apparatus with dietary data based on stomach content analysis. Analysis of the morphological characteristics separated the 9 species into 3 distinct groups. The first group (*Cheilodipterus macrodon*, *C. artus* and *C. quinquelineatus*) was characterized by elongated heads; the second group (*Archamia fucata*, *Apogon guamensis*, *A. cyanosoma* and *A. fragilis*) by large gapes; and the third group (*Apogon exostigma*, *A. doederleini*) by wider heads and low transmission coefficient in their jaw mechanics. Stomach samples, however, revealed that morphology was of limited utility in predicting dietary groupings. The majority of species examined displayed generalist diets. The results indicate that while morphology may predict feeding potential, or feeding mode, actual resource use in this group may be shaped primarily by other modifying factors such as behaviour and prey availability. In contrast to other reef fish groups, morphology does not appear to play a strong role in influencing diet in the Apogonidae.

KEY WORDS: Coral reef · Diet · Apogonidae · Trophic ecomorphology · Functional morphology

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INTRODUCTION

Cardinalfishes (Apogonidae) are represented in all tropical and warm temperate seas, with over 300 species from 21 genera worldwide, of which 94 species from 18 genera have been recorded in Australia (Randall et al. 1990). Apogonids form a major component of reef fish assemblages, ranking in the top 5 families for both species diversity and numerical abundance (Bellwood & Wainwright 2002, Marnane & Bellwood 2002). Most species are nocturnally active and this is when they are believed to forage for prey such as plankton, benthic invertebrates or other small fishes (Marnane & Bellwood 2002). As such, apogonids are often the dominant component of nocturnal planktivore assemblages on Indo-Pacific reefs, and consequently play an integral role in reef trophodynamics (Marnane 2000, Marnane & Bellwood 2002). Daytime resting sites for apogonids include caves, crevices and amongst the branches of corals, often forming dense multi-specific aggregations that are targeted by diurnal piscivores (Marnane 2000). Despite their importance for coral reef ecosystem function, apogonids remain one of the least studied families of reef fishes.

Considerable advances in our understanding of the mechanical basis of feeding performance in fishes have been made using a functional approach (Wainwright & Bellwood 2002). Such studies have identified predictive relationships between fish form and patterns of prey use (Norton 1991, Winemiller 1991, Wainwright & Richard 1995). Morphological form has been intuitively linked to function for a long time (Bock & Wahlert 1965). In terms of feeding, morphological capabilities can place constraints on the range of prey that can be utilized. Consequently, the vast majority of species will be functionally incapable of successfully feeding on most of the possible prey in their environment (Wainwright & Bellwood 2002). Feeding performance thus places discrete boundaries on potential resources, and defines potential feeding niches.

Feeding abilities can often determine prey usage, and there is often a causal link between functional morphology and prey utilization patterns. In fishes, studies that have used linkages between morphology and feeding have been particularly revealing for understanding patterns of resource use. For example, labrid and cichlid pharyngeal jaws have been found to be strongly correlated with diet (Liem & Sanderson

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1986, Wainwright 1988, Clifton & Motta 1998). Furthermore, functional analyses have revealed similar links between morphology and resource use in other coral reef fishes, including the Scaridae (Bellwood & Choat 1990), Acanthuridae (Purcell & Bellwood 1993), Chaetodontidae (Motta 1985, 1988, Ferry-Graham et al. 2001), and Tetraodontiformes (Turingan & Wainwright 1993, Turingan 1994, Friel & Wainwright 1999).

Three broad methods of prey capture have been identified in fishes: suction feeding, ram feeding and manipulation (Barel 1983, Lauder 1983a, Liem 1991, Norton 1993). Given the different mechanical demands of each method, fish jaw designs are often modified to reflect the style of feeding used by the fish. Specifically, oral jaws of fishes exhibit a trade-off between varying degrees of speed and/or strength, with a continuum ranging from extremes modified for velocity or force. Whilst many fish have intermediate velocity and force, these aspects are normally traded against each other, with manipulating species generally associated with strength, whereas ram and suction methods require speed but little force. A combination of ram and suction feeding is generally thought to be the dominant form of prey capture in coral reef fishes (Wainwright & Bellwood 2002).

Regardless of feeding mode, all teleost fishes use a common feeding apparatus of muscles, bones and soft connective tissues. Fishes involve a large number of moving elements in feeding, with more than 20 major skeletal components set in motion by approximately 40 muscles in all modes of prey capture. However, only a small number of these elements need be scrutinised to embody the major features of the feeding mechanics. Carefully chosen morphological traits have been used as indicators of feeding ability, where these traits have been shown to be significant in gaining some understanding of performance capabilities (Wainwright & Bellwood 2002). Lever systems have been linked to feeding performance and trophic diversity and potential resource usage in several groups of fishes (Wainwright & Richard 1995, Wainwright 1996). Fish mouth size (gape), degree of jaw protrusion and protrusion angle have also been identified as good predictors of resource use in fishes (Motta 1985, 1988, Wainwright 1988, Wainwright et al. 2000). Ultimately, understanding the functional significance of morphology is a crucial step in identifying morphological constraints on the function of the feeding structures, performance patterns and resource use in fishes. Such a conceptual link between morphology and ecology, therefore, provides a tool for predicting processes within a fish's life, such as how they feed, move and reproduce (Fulton et al. 2001, Wainwright et al. 2002).

Dietary segregation has previously been documented for several species within the Apogonidae

(Vivien 1975, Chave 1978, Marnane & Bellwood 2002). Apogonids appear to be broadly carnivorous, and although many apogonids display a degree of generalist behaviour (Hiatt & Strasburg 1960, Hobson & Chess 1978), many species appear to have specific prey item preferences. On the Great Barrier Reef, apogonids have very fine habitat distribution and can be tentatively segregated into piscivores, midwater planktivores, and benthic prey feeders (Marnane & Bellwood 2002). Whilst there is some indication of dietary diversification in apogonids, the extent to which this has a morphological or function basis is yet to be established. The aim of the present study therefore is to determine to what extent dietary diversification within apogonids is reflected in the morphology of functionally significant features. Measurements of key morphological attributes of the head and jaw regions will be used as indicators to examine differences in critical functional traits among species, and will be compared directly with dietary characteristics to evaluate the links between diet and jaw morphology in this abundant reef fish group.

MATERIALS AND METHODS

The 9 study species were selected to encompass the full range of trophic and ecological modes, and the maximum range of body sizes of species recorded from the Great Barrier Reef (Marnane & Bellwood 2002). Of the 9 species, 3 were from the genus *Cheilodipterus* (*C. quinquelineatus*, *C. artus* and *C. macrodon*), with *C. macrodon* being the largest species in the family (maximum total length of at least 22 cm; Randall et al. 1990). Of the remaining species, one was in the genus *Archamia* (*A. fucata*) and 5 from the genus *Apogon* (*A. guamensis*, *A. doederleini*, *A. fragilis*, *A. exostigma*, *A. cyanosoma*). Of these, *A. fragilis* is one of the smallest species found on the Great Barrier Reef (maximum total length of 5 cm). Specimens were collected during October and November 2003 at Lizard Island, a mid shelf reef in the northern section of the Great Barrier Reef (14° 40' S, 145° 28' E). A mixture of 5 parts ethanol to 1 part clove oil (see Munday & Wilson 1997) was sprayed in the vicinity of fish to anaesthetize them, enabling their collection. Immediately after collection, fish were euthanized in ice water. Fresh specimens were identified to species using the taxonomic texts of Randall et al. (1990) and Allen et al. (2003) and then individually labelled. All individuals were fixed in 10% seawater buffered formalin for approximately 3 wk before being transferred to 70% ethanol for storage.

Trophic morphological characteristics. Differences in the morphological structures associated with feed-

ing among the species were investigated by examining 14 morphological characteristics of 20 individuals of each species (Table 1). External measurements were recorded in the field prior to fixation. Internal measurements were recorded after the fish were cleared and stained. The clear and stain protocol (modified after Gosztanyi 1984) used pre-soak detergent to remove the majority of lipids before finishing the clearing process in a 1.5% potassium hydroxide solution. Specimens were stained using Alizarin red to highlight osteological elements. Measurements were recorded to the nearest 0.01 mm using vernier callipers and a microscope equipped with a graduated eyepiece. Dimensions of lower jaw and tooth length were recorded using a dissecting microscope with a graduated eyepiece. Opening and closing lever ratios were calculated by dividing the respective in-lever by the out-lever (Fig. 1). No other transformations were used. Morphological measurements were standardized by the cubed-root of fish mass to minimise the influence of size differences among individuals. An analysis of residuals showed no deviation from expected patterns, indicating that using residuals to standardize varying fish size had the same results as using mass ratios. For ease of comparisons with past literature, morphological measurements were therefore standardized to the cube-root of body mass (i.e. value/cube-root mass). The means of each raw variable were calculated across

Table 1. Morphological characteristics used to compare feeding morphology among 9 apogonid species

Abbreviation	Characteristic/definition
M ^a	Mass: blotted wet weight to nearest 0.1 g
HW ^a	Head width: at posterior margin of orbit
VG ^a	Vertical gape: mouth fully opened, internal measure from tip of premaxilla to dentary
GW ^a	Gape width: mouth opened, internal distance between angle of mouth
SNOUT ^a	Snout length: anterior margin of orbit to tip of premaxilla with mouth closed
PDU ^a	Protrusion distance upper jaw: maximum distance of premaxilla extension from anterior margin of orbit to tip of premaxilla with mouth fully extended
PDL ^a	Protrusion distance lower jaw: orbit to tip of lower jaw with mouth extended
HL	Head length: tip of premaxilla to posterior margin of operculum
LJL	Lower jaw length: anterior end of the dentary to the posterior end of articulation
PA ^a	Protrusion angle: angle that mouth protrudes when open
TOOTH	Length of longest tooth
PDU-S	Protrusion distance upper jaw minus snout length
CIL	Closing in lever ratio (see Fig. 1)
OIL	Opening in lever ratio (see Fig. 1)
^a Measurement recorded prior to specimens being fixed	

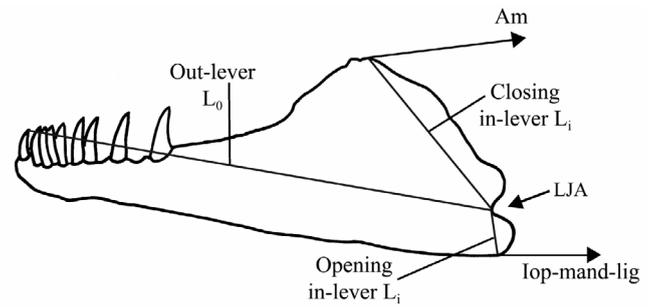


Fig. 1. Lower jaw of an Apogonidae fish showing the measurements taken to calculate closing (closing in-lever/out-lever) (L_i/L_o) and opening lever ratios (opening in-lever/out-lever). The force applied to the jaws by the abductor mandibulae (Am) to close the jaw and interopercular-mandibular ligament (lop-mand-lig) opens the jaw by rotation about the lower jaw articulation (LJA) (modified after Wainwright & Bellwood 2002)

all individuals in each species after standardization by body size.

Stomach content analysis. Published analyses of stomach contents for 6 of the 9 study species (Marnane & Bellwood 2002) were combined with additional data collected using the same protocol for the remaining 3 species (see Table 2). As apogonids are predominately nocturnal carnivores, all specimens were collected from dawn to early morning (05:20 until 07:30 h) to maximise the chance of stomachs being full after a night of foraging (Marnane & Bellwood 2002). Specimens were immediately placed in an ice water slurry to euthanize them before being fixed in 10% buffered seawater formalin.

Stomach analyses were performed using the methods of Marnane & Bellwood (2002). The complete stomach was removed, opened lengthways, and the entire contents spread on a petri dish for examination. Prey items were identified and placed in taxonomic categories. The mean weight of each prey item for each species was calculated by weighing a random sample of intact specimens. Mean weights were then used to multiply by the number of occurrences in the stomach analysis of each individual apogonid to provide an estimate of the mass of material in each dietary category. The percentage mass of each prey item found within the stomach of each species was then calculated.

Statistical analysis. The composition of species groups, based on head and jaw morphology, was explored by reducing the dimensionality of the data with a principal component analysis (PCA) based on the covariance matrix. A Ward's cluster analysis was performed on squared euclidean distances derived from the data matrix to identify any groupings among species within the morphological data set. The morphological structures responsible for grouping species were expressed in the vector plot, enabling structures responsible for segregation of species to be identified. PCA and Ward's cluster analysis were also performed on stomach content data to identify natural groupings of species based on diet. A canonical correlation analysis between the 2 data sets could not be undertaken due to the limited number of species given the high number of variables.

RESULTS

Morphological measurements

The first 2 axes of the PCA explained over 82% of the variation in the data, with the first axis responsible for approximately 57% and the second axis responsible for 26% (Fig. 2a). PC1 was driven by differences in lower jaw protrusion, gape, head length and body mass, whereas PC2 was predominately influenced by head width, lower jaw length and opening lever ratio. The Ward's cluster analysis identified 3 clusters of species, grouping *Cheilodipterus macrodon*, *C. artus* and *C. quinquelineatus* as one functional group, *Archamia fucata*, *Apogon fragilis*, *A. guamensis* and *A. cyanosoma* as a second group and *A. exostigma* and *A. doederleini* as the third group (Fig. 2a). PC2 was most influential in separating the third group from the other 2 groups. Vector plots indicated that this group was characterised by wider heads and had a larger opening lever ratio (Fig. 2b). The remaining groups are separated primarily along PC1. The second group was defined by greater flexibility of the lower jaws in association with larger gapes (Fig. 2b). The first functional group differed from the other groups as these 3 *Cheilodipterus* species possessed longer heads, snouts, teeth and lower jaws, and they displayed greater protrusion of the upper jaw (Fig. 2b).

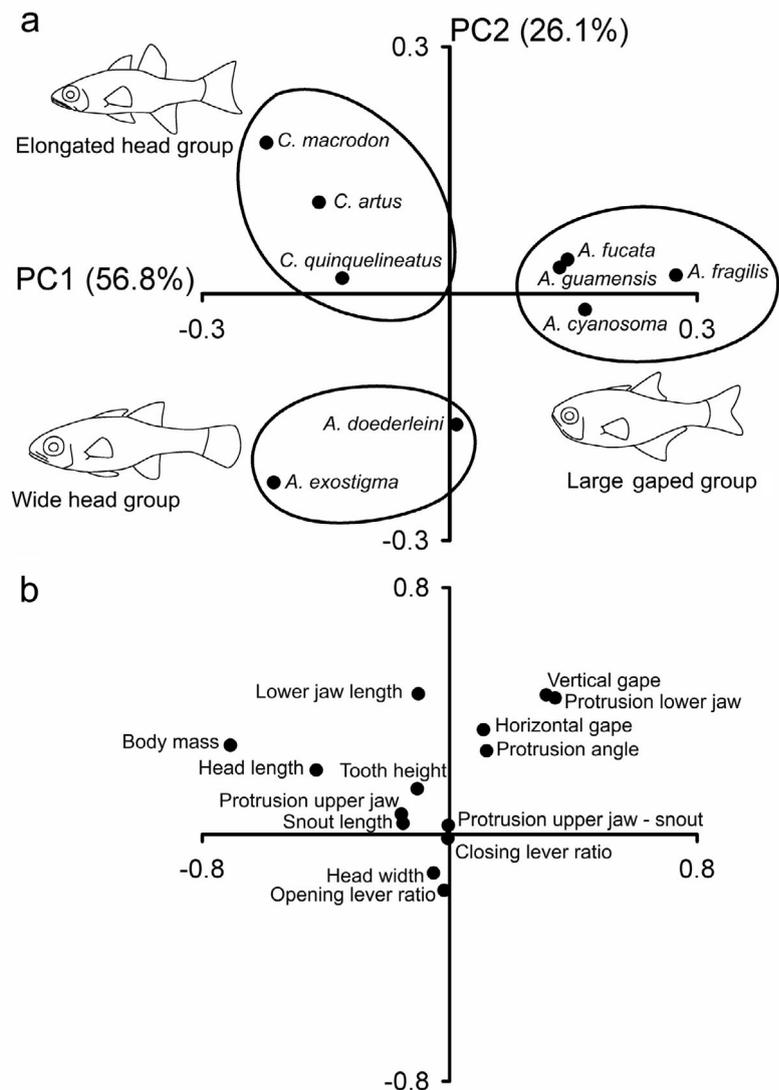


Fig 2. Principal component analysis of mouth morphology among the 9 study species. (a) Ordination plot displaying morphological groupings of species. Encircled species indicate functional groups identified in a Ward's cluster analysis. (b) Vector plot of morphometric characteristics responsible for species loadings. See Table 2 for full species names

Stomach content analysis

Approximately 78% of the variation in the stomach content data was explained on the first 2 axes of the principal component analysis. PC1 was responsible for almost 54% of variation while PC2 explained approximately 23% (Fig. 3). In contrast to the morphological data, the ordination plot of stomach content data indicated that species were separated into just 2 dietary groups (Fig. 3a). Ward's cluster analysis provided independent support for 2 species groups (Fig. 3a). This was due almost entirely to *Cheilodipterus macrodon* and *C. artus* being distinguished from the remaining species by their predominately piscivorous diets

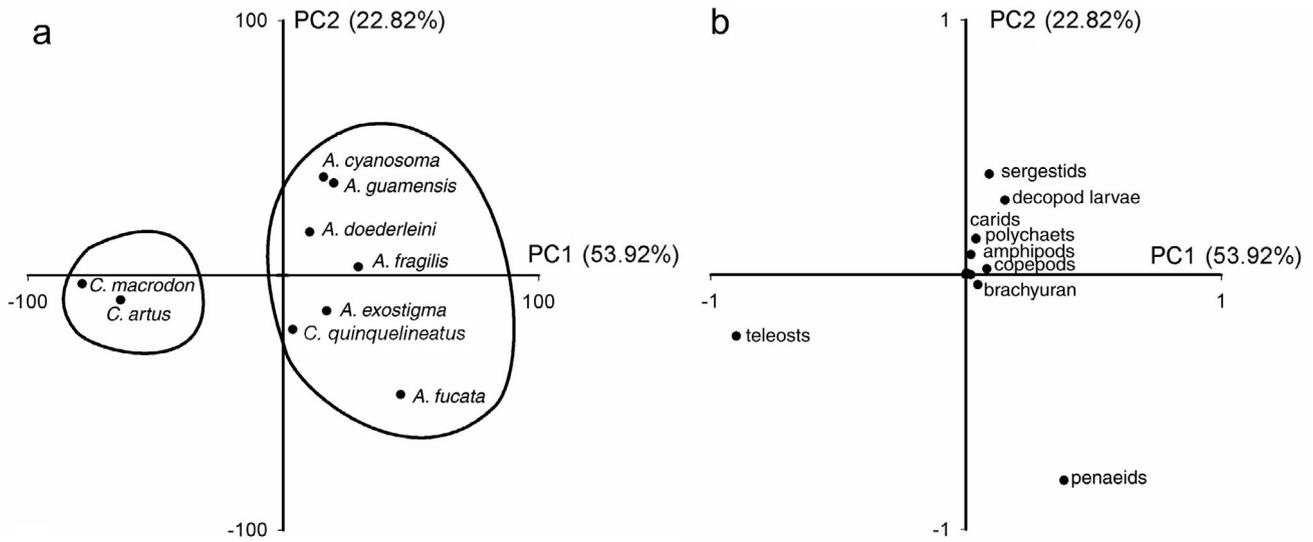


Fig. 3. Principal component analysis of prey items found in stomach contents of 9 apogonid species. (a) Ordination plot displaying dietary groupings of species. Encircled species indicate dietary groups identified in a Ward's cluster analysis. (b) Vector plot of prey items responsible for species loadings. See Table 2 for full species names

(Fig. 3b). In the remaining species, finer groupings were hard to distinguish, with most species having generalised diets that are characterised by crustaceans of both benthic and planktonic origin (Table 2). Although many of the study species appeared to consume a range of prey, some species displayed a tendency towards specific dietary components. *Archamia fucata* stomachs contained a high proportion of penaeid prawns (Fig. 3, Table 2), while *Apogon doederleini* and *A. exostigma* consumed the largest

amounts of benthic prey, particularly brachyurans (Table 2). *Cheilodipterus quinquelineatus* was notable in that it was found to be a generalist even though 30% of its diet consisted of fish. Interestingly, the morphology of *C. quinquelineatus* was similar to that of *C. macrodon* and *C. artus*, which were mainly piscivorous species (Fig. 3, Table 3). With regards to *A. guamensis* and *A. cyanosoma*, although both species were located in a similar morphospace, the predominant prey item for *A. guamensis* was decapod larvae,

Table 2. Diet in 9 apogonid species expressed as the mean percentage mass of prey items found in the stomach contents. x: pre-dominant prey items habitat; -: not recorded in diet or not a significant habitat

Species	n	Amphipoda	Brachyurans	Decapod larvae	Caridae	Chaetognatha	Copepoda	Isopoda	Mollusca	Mysidacea	Ostracoda	Penaeidae	Polychaeta	Sergestidae	Stomatopoda	Tanaidacea	Teleostei
<i>Apogon cyanosoma</i> ^a	32	5.1	-	-	22.5	0.5	-	0.2	-	0.1	0.3	7.8	4.0	53.7	0.5	0.3	5.0
<i>Apogon doederleini</i> ^a	47	11.6	14.6	4.3	2.9	-	-	0.7	0.2	0.5	1.1	17.1	4.7	26.7	2.0	0.4	13.1
<i>Apogon exostigma</i> ^a	35	0.2	25.5	-	6.7	-	-	0.1	-	-	-	42.2	3.0	5.9	2.1	0.3	13.9
<i>Apogon guamensis</i> ^a	35	2.4	3.1	56.6	2.8	0.2	0.1	0.7	-	-	-	5.3	19.4	2.3	3.2	-	3.9
<i>Cheilodipterus artus</i> ^a	45	-	0.4	-	-	-	-	-	-	-	-	11.4	-	-	-	-	88.2
<i>Cheilodipterus quinquelineatus</i> ^a	40	-	11.2	-	3.2	-	-	0.2	-	0.3	-	46.7	1.7	6.7	0.2	0.1	29.7
<i>Cheilodipterus macrodon</i>	30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100
<i>Apogon fragilis</i>	30	8.0	-	20.8	-	2.7	39.8	-	-	-	0.5	30.5	-	2.7	-	-	-
<i>Archamia fucata</i>	30	0.1	-	9.0	-	-	-	-	-	-	-	87.0	0.1	-	3.0	-	-
Pelagic	-	-	-	x	-	x	-	-	-	-	x	-	-	-	-	-	x
Epibenthic	-	x	x	-	x	-	x	x	-	x	x	x	-	x	-	-	x
Benthic	-	x	x	-	x	-	x	x	x	-	x	x	x	x	x	x	-

^aData obtained from Marnane & Bellwood (2002)

Table 3. The 14 morphological characteristics used to express feeding morphology for 9 species of apogonids. Note that all measurements are mean values (n = 20) (in cm, except mass in g). Explanations of abbreviations for characteristics are in Table 1; see Table 2 for full species names. SL: average standard length (cm)

Species	LJL	TOOTH	HL	HW	VG	GW	SNOUT	PDU	PDU-S	PDL	CIL	OIL	PA	M	SL
<i>C. quinquelineatus</i>	1.71	0.08	2.76	1.19	1.88	1.87	0.84	1.06	0.23	2.01	0.31	0.07	0.67	12.13	8
<i>A. fucata</i>	1.21	0.02	1.82	0.86	1.64	1.35	0.58	0.73	0.15	1.85	0.31	0.07	0.74	5.56	5.8
<i>A. guamensis</i>	1.20	0.01	1.84	0.92	1.67	1.49	0.47	0.59	0.12	1.62	0.30	0.07	0.66	5.05	5
<i>A. doederleini</i>	1.01	0.02	1.86	0.90	1.28	1.26	0.51	0.62	0.12	1.36	0.31	0.13	0.68	4.26	5.2
<i>A. fragilis</i>	0.80	0.01	1.22	0.59	1.03	0.96	0.39	0.52	0.13	1.29	0.34	0.07	0.76	1.59	3.5
<i>C. artus</i>	1.93	0.17	3.12	1.31	2.06	2.01	0.95	1.17	0.21	2.33	0.32	0.06	0.70	14.98	9
<i>C. macrodon</i>	2.53	0.23	4.06	1.70	2.74	2.65	1.16	1.45	0.29	3.03	0.31	0.07	0.72	31.66	10.4
<i>A. cyanosoma</i>	0.93	0.01	1.46	0.75	1.19	1.09	0.41	0.50	0.09	1.25	0.30	0.09	0.67	2.20	4.4
<i>A. exostigma</i>	1.50	0.02	2.83	1.39	1.63	1.62	0.91	1.12	0.21	1.97	0.33	0.12	0.59	14.35	7.4

whereas *A. cyanosoma*'s diet was composed mainly of sergestids (Table 2). Potential explanations for this anomaly include the fact that the 2 food items, although taxonomically different, are similar sized crustaceans and are therefore effectively equivalent types of prey. Furthermore the absence (or low scores) of penaeids and fish in both species may have influenced their position in the PCA.

DISCUSSION

Analyses of key morphological features of the feeding apparatus identified 3 distinct functional groups within the 9 apogonid species examined. In contrast, only 2 dietary groups were identified from stomach content analysis, these being either piscivores or generalists that predominately feed on a range of benthic and planktonic crustaceans. While morphology may be used to predict diet (Wainwright & Bellwood 2002), for apogonids at least, morphology is not strongly linked to diet. Morphology may shape the way that the fish feeds but not the taxa consumed. This concept has been proposed previously for both chaetodontid and cichlid fishes (Barel 1983, Motta 1988). Indeed, resource use in apogonids appears to be influenced more by foraging locations and habitat utilisation than by morphology. Marnane & Bellwood (2002) recorded the distribution of apogonids at night when foraging. Combined with stomach content analysis, this provided some insight into foraging behaviour. Specifically, it appeared that apogonids may be separated into benthic or midwater foragers. In the present study, however, it was difficult to segregate species into clear sub-groups of planktonic and benthic feeders based on stomach contents, as the diets of many species overlapped, with species consuming prey from both sources.

Piscivorous apogonids displayed the clearest evidence of possible modification of mouth and jaw morphologies in association with their diet. *Cheilodipterus macrodon* and *C. artus* feed almost exclusively on fish prey. This co-

incided with their head and jaws being characterised by greater snout length, longer lower jaws, and larger tooth size. Such head and jaw morphological traits in these species have been associated previously with piscivorous feeding in a range of taxa (Liem 1991, Wainwright & Bellwood 2002). Large teeth are typically associated with the capture of large and elusive prey, such as other fishes, where they usually serve as a friction device preventing prey from escaping (Wainwright & Bellwood 2002). In these 2 piscivorous species differences in jaw morphology appear to be good indicators of diet.

Within the generalist dietary groups, *Archamia fucata*, *Apogon fragilis*, *Apogon guamensis* and *Apogon cyanosoma* possessed greater lower jaw protrusion and larger gaping mouths. Such traits may be advantageous for midwater feeding, where a large gape enables the fish to swim through the water column with mouth wide open to engulf planktonic organisms (essentially a form of ram feeding). Accordingly, free swimming and planktonic prey items were conspicuous in the diet of these species. Furthermore, Marnane & Bellwood (2002) found that *A. guamensis* foraged high in the water column at night.

In contrast, the wide mouthed species *Apogon exostigma* and *A. doederleini* have higher jaw opening lever ratios, indicating that their jaws probably open at a slower rate. Previous studies have found that slower, stronger jaws are generally associated with species that consume benthic prey (Turingan & Wainwright 1993, Turingan 1994, Ferry-Graham et al. 2002). In comparison to the other 7 species, this may suggest that *A. exostigma* and *A. doederleini* have a preference for less mobile prey. This again agrees with the results of Marnane & Bellwood (2002), who found that both of these species are associated with the benthos when foraging at night. The stomach contents also revealed that both species possessed high amounts of benthic prey within their diets.

A possible explanation for discrepancies in linking morphology to a distinct resource use in the majority of species is that the apparent morphological diversification may be important in dictating a preferable re-

source or feeding mode, but most species are still capable of feeding on a range of prey items mediated through variation in other mechanisms such as foraging behaviour. Liem (1980) suggested that in cichlid fishes many specialist feeders were also capable of consuming a wide range of prey items, which he referred to as being 'Jacks of all trades', or, as in the case of many species, 'Jacks of some trades'. A similar situation has recently been described in wrasses (Bellwood et al. 2006), for which there is a weak relationship between morphology and diet, despite morphological variation among species. In the present study, *Cheilodipterus quinquelineatus* may represent a further example of the 'Jack of all trades' model. *C. quinquelineatus* was functionally grouped with *C. macrodon* and *C. artus*, which were predominately piscivorous, but *C. quinquelineatus* displayed a generalist diet. However, 30% of the diet of *C. quinquelineatus* did consist of fish prey, indicating that although it may have a preference or ability to include fish in its diet, as its morphology implies, other factors such as foraging activities and prey availability probably play an important role in dictating prey utilisation patterns.

Previous work in the Indian Ocean (Madagascar) has suggested that apogonid diets are influenced by several factors acting in concert, including prey selectivity and relative availability of prey during the day and night (Vivien 1975). Apogonids are predominately nocturnal feeders; however, Vivien (1975) suggested that whilst many species feed from the water column during the night, they may also feed opportunistically during the day on benthic prey available within or around their diurnal resting sites. This may involve consuming different food sources. This concept was also alluded to by Chave (1978), who identified differences in foraging areas in 6 apogonid species from Hawaii. However, in contrast to these observations, diurnal feeding has only been recorded on the Great Barrier Reef in one species, *Apogon cyanosoma* (Marnane & Bellwood 2002). Whilst morphological differences may dictate the range of dietary items that can be exploited, predators are subject to prey availability. Past examples of morphology being linked to diet have focused almost exclusively on diurnal feeding fishes (Lauder 1983b, Clifton & Motta 1998, Wainwright et al. 2000, Wainwright & Bellwood 2002). This is the first study to investigate a number of representatives from a group of nocturnal predators. For diurnal feeders, the morphology of the feeding apparatus may be of critical importance when procuring prey, given the ability of the prey to visually detect and evade predators. For nocturnal predators, however, morphological adaptations might be secondary to sensory capabilities. In darkness the ability to detect prey may be of primary importance. The limited variation in morphology seen

in apogonids may thus be reflecting the limited role of morphology in shaping patterns of prey procurement. Ultimately, it is likely that sensory ability, behaviour and morphology all play complementary roles in determining feeding patterns within apogonids.

Levels of ecological diversity often reflect the level of functional diversity in a group of fishes. For example, labrids are diverse in terms of both morphology and diet (Wainwright et al. 2004); this is in marked contrast to the pomacentrids, which show little of the ecological diversity found in labrids. Pomacentrids exploit only a small range of feeding types and lack the specialised feeding repertoires seen in labrids, with relatively restricted ecological diversity being associated with what appears to be low morphological variation (Emery 1973, Wainwright & Bellwood 2002). Similarly, apogonids showed limited trophic diversity in comparison to other reef fish families such as the Labridae and Chaetodontidae (Motta 1985, 1988, 1989, Wainwright et al. 2004). This limited ecological and morphological variation is reflected in the simple segregation of feeding types in apogonids, and from a morphological perspective is clearly shown by comparing closing lever ratios of apogonids with those of labrids.

To emphasise the low degree of variation in jaw morphology amongst the 9 species of apogonids, lower jaw function (i.e. relative strength against speed) was summarized by plotting closing lever ratios and comparing results with labrids, a group known for their morphological diversity (Fig. 4). There is a range of variation in

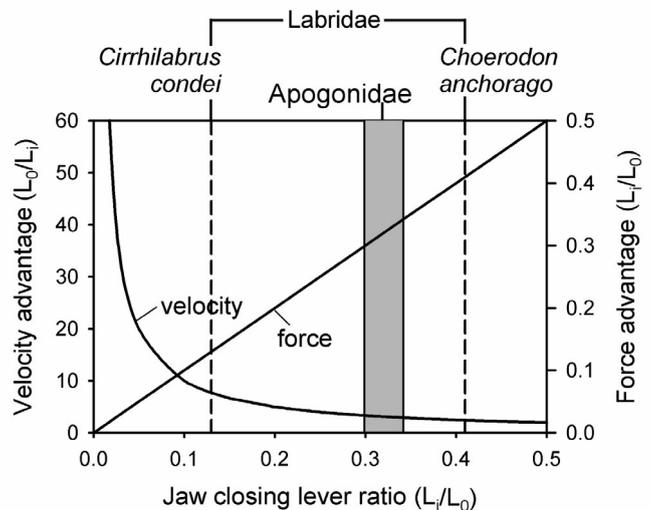


Fig. 4. Closing in-lever ratio scores of 9 apogonid species compared to the range of values displayed by labrids (modified after Wainwright & Bellwood 2002). The trade-off between force and velocity in the lower jaw is highlighted. *Cirrhilabrus condei* has a low closing in-lever ratio, indicating a jaw modified for speed rather than strength; *Choerodon anchorago* possess a high ratio, reflecting a potential for strength at the expense of speed. Note all 9 apogonids are within the range highlighted on the graph. L_i : opening or closing in-lever; L_o : out-lever

the lower jaw morphology of the 126 labrid species found on the Great Barrier Reef (Fig. 4). The 2 labrid extremes are represented by different styles of jaw morphology: *Cirrhilabrus condei* has a low closing lever ratio, indicating that it has a jaw able to close fast, possibly to catch elusive prey; *Choerodon anchorago* has a high closing lever ratio score, indicating a jaw that is likely to be slower in closing, but trades speed for strength. In contrast, closing lever ratios for the 9 apogonids showed little variation, falling within an extremely narrow range of 0.30 to 0.34 (Fig. 4). Apogonids show much lower variation in comparison to labrids (despite there being approximately 94 apogonid species on the Great Barrier Reef), with values indicating that the apogonid feeding mechanism is of a much more generalised construction and function. Overall, although apogonids show some degree of specialisation (e.g. *Cheilodipterus macrodon*), when compared with some other reef fish families, they appear to be of a more uniform, generalized design. It is possible that this generalized design may be a consequence of functional constraints related to mouthbrooding. Even though there is evidence of sexual dimorphism (Barnett & Bellwood 2005), mouthbrooding may constrain potential for diversification in feeding structures.

In conclusion, morphological differences divided the 9 apogonid species examined in the present study into 3 distinct functional groups. However, the majority of apogonids appear to be predominately generalist feeders, indicating that while species may feed in distinctly different ways they are capable of eating a wide range of prey items, with extensive overlap among species. These results are unusual in that prey use is not strongly related to jaw morphology in the traditional sense. This is a clear example of a family in which jaw morphology is not overly important. While morphology may predict the potential range of dietary items, (potential niche), and the way in which they feed (feeding mode), actual resource use appears to be strongly influenced by other factors, including feeding location and behaviour.

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