Abstract—The introduced grouper species peacock hind (*Cephalopholis argus*), was the dominant large-body piscivore on the Main Hawaiian Island (MHI) reefs assessed by underwater visual surveys in this study. However, published data on *C. argus* feeding ecology are scarce, and the role of this species in Hawaiian reef ecosystems is presently not well understood. Here we provide the first comprehensive assessment of the diet composition, prey electivity (dietary importance of prey taxa compared to their availability on reefs), and size selectivity (prey sizes in the diet compared to sizes on reefs) of this important predator in the MHI. Diet consisted 97.7% of fishes and was characterized by a wide taxonomic breadth. Surprisingly, feeding was not opportunistic, as indicated by a strongly divergent electivity for different prey fishes. In addition, whereas some families of large-body species were represented in the diet exclusively by recruit-size individuals (e.g., Aulostomidae), several families of smaller-body species were also represented by juveniles or adults (e.g., Chaetodontidae). Both the strength and mechanisms of the effects of *C. argus* predation are therefore likely to differ among prey families. This study provides the basis for a quantitative estimate of prey consumption by *C. argus*, which would further increase understanding of impacts of this species on native fishes in Hawaii.

Diet composition and prey selection of the introduced grouper species peacock hind (*Cephalopholis argus*) in Hawaii

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The grouper species peacock hind (*Cephalopholis argus*) (Serranidae: Epinephelinae), a reef fish predator that is native over most of the Indo-Pacific region, was introduced to the Main Hawaiian Islands (MHI) in 1956 as part of an introduction program of snapper and grouper species intended to enhance nearshore fisheries (Randall, 1987). Today, this non-native predator occupies a dominant position in the guild of large piscivores on many reefs in the MHI (see *Results* section). As impacts of piscivores on prey fishes have been demonstrated in a number of studies (e.g., Webster, 2002; Hixon and Jones, 2005), the abundance of *C. argus* raises the question of how, if at all, it affects native reef fishes in Hawaii. However, the only published study of *C. argus* feeding in the MHI to date was based on a sample of 10 specimens (Hobson, 1974), which is insufficient to elucidate feeding patterns.

Groupers are among the most common predatory reef fishes worldwide (Parrish, 1987). They play an important role in shaping reef communities (Goeden, 1982; Parrish, 1987) and are of large commercial importance in coral reef fisheries (Heemstra and Randall, 1993). However, data on the general feeding ecology of this family remain surprisingly scarce (Beukers-Stewart and Jones, 2004). In addition, although concern about declines of many grouper species worldwide due to overfishing has led to a renewed research focus on this family (Morris et al., 2000), much of the work to date has concentrated on a limited number of species, e.g., the coral trout (*Plectropomus leopardus*) in Australia (e.g., Kingsford, 1992; St. John, 1999), the Nassau grouper (*Epinephelus striatus*) in the Caribbean Sea (e.g., Eggleston et al., 1998), or the dusky grouper (*Epinephelus marginatus*) in the Mediterranean Sea (e.g., Renones et al., 2002).

Most studies of grouper diet have been based on analysis of stomach contents. However, because of the difficulty of obtaining large grouper samples (Beukers-Stewart and Jones, 2004), as well as the high prevalence of empty stomachs due to prey regurgitation during capture and because of the characteristics of grouper feed-

ing ecology (Dierking and Meyer, in press), detailed descriptions of grouper diet remain rare. Notably, only one study of *C. argus* diet (Randall and Brock, 1960), and a few studies of other grouper species (but see Kingsford, 1992; St. John, 1999; Beukers-Stewart and Jones, 2004), have been based on more than 50 full stomachs. Interpretation of feeding patterns is further complicated by the lack of studies comparing dietary composition with prey availability in the wild (but see Beukers-Stewart and Jones, 2004).

We examined the feeding patterns of *C. argus* based on stomach content analysis of the largest sample of this species (*n*=285) available to date. In addition, we assessed the patterns in the context of the composition of the reef fish assemblage in Hawaii, which was determined by underwater visual surveys. The main goal was to describe the diet composition, prey electivity (dietary importance of a taxon compared to its availability on reefs), and size selectivity (prey sizes in the diet compared to sizes on reefs) of *C. argus* in Hawaii. Secondary goals were to assess the mechanisms by which this non-native predator may affect prey fishes and to provide data required for the quantitative estimation of prey consumption by this species.

Material and methods

Study organism and sampling sites

To our knowledge, the establishment of *C. argus* in Hawaii represents the first documented case of the successful invasion of a non-native habitat by a grouper. Today this generally piscivorous species (Parrish, 1987) is found around all of the MHI. It is particularly abundant along the western coastline of the island of Hawaii (Kona coast hereafter, following common terminology in Hawaii), which harbors some of the least disturbed reefs in the MHI and is the source of important economic revenues from diving tourism and the aquarium fish industry (Tissot et al., 2004). Despite its abundance, a fishery for *C. argus* never developed because it turned out to be a carrier of ciguatoxin, the agent of ciguatera fish poisoning (Dierking and Campora, 2009).

Cephalopholis argus specimens from the Kona coast (*n*=179, 11 sites) and from the island of Oahu (*n*=106, 6 sites) (Fig. 1) were obtained by spearfishing with scuba in July 2003. Divers attempted to spear all sighted individuals regardless of size or behavior pattern (e.g., active swimming, resting). Collections took place between 0924 and 1522 hours at a mean depth of 11.6 m. Speared specimens were immediately (i.e., underwater)
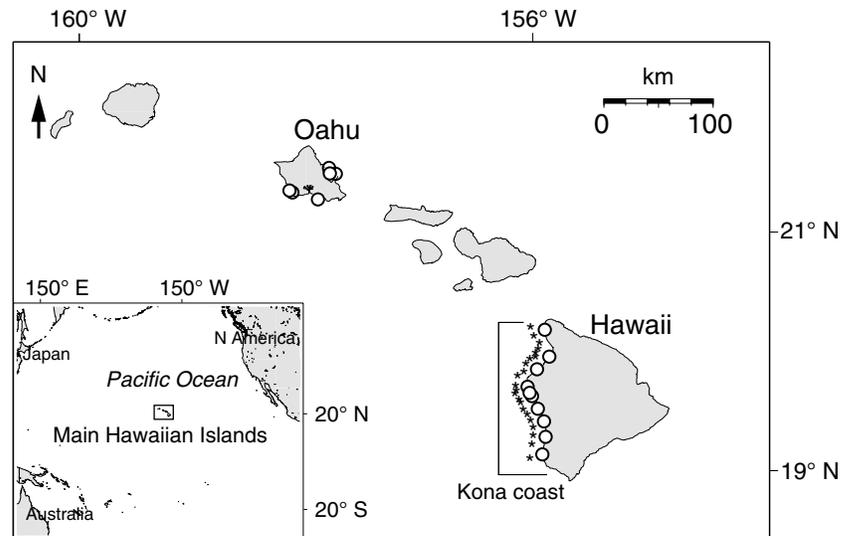

Figure 1

Map of the Main Hawaiian Islands, with peacock hind (*Cephalopholis argus*) collection sites marked by open circles, and underwater visual survey sites along the Kona coast marked by asterisks (Note: asterisks were moved offshore from actual survey locations to avoid overlap with sample site symbols).

Table 1

Morphometric relationships between total length (TL), standard length (SL, in cm), and wet mass (M, in g) for peacock hind (*Cephalopholis argus*) in Hawaii. r^2 = regression fit.

Relationship	a	b	n	r^2
$M = a\,TL^b$	0.0125	3.122	110	0.98
$M = a\,SL^b$	0.0309	3.013	110	0.97
$SL = a + b\,TL$	−0.244	0.8494	304	0.99

sealed in plastic bags to avoid stomach content loss from regurgitation commonly observed in groupers (Dierking and Meyer, in press). In the laboratory, standard length (SL) and total length (TL) (equal to fork length in *C. argus* due to their rounded caudal fin shape) were recorded to the nearest mm. Wet mass (M) of *C. argus* from the Oahu sites was measured to the nearest 5 g. Based on these measures, morphometric relationships (SL-M, TL-M, SL-TL) (Table 1) were calculated. The SL-M equation was then used to estimate the wet mass of Kona specimens, which could not be measured in the field owing to scale malfunctioning.

Diet composition

To determine the diet composition of *C. argus*, stomachs of all specimens were opened and any prey items were removed. The analysis of contents then followed the procedures described by Hyslop (1980). Specifically, for

the two island samples and the combined overall sample, the vacuity rate (i.e., the proportion of empty stomachs) was determined. Differences in vacuity between islands were assessed with a chi-square test. For full stomachs, the number of prey items was counted, and the SL and TL of fish prey and the carapace length of crustacean prey were determined to the nearest mm, where digestion state allowed reliable measurements. For fishes, SL could be determined more often than TL because skeletons are slow to disintegrate during digestion. In these cases, TL was calculated from SL according to published SL-TL equations for the respective taxon (Froese and Pauly, 2009). The M of all prey items was recorded to the nearest mg. Mean relative stomach content M was then calculated as total M of prey items divided by the total M of *C. argus* specimens.

We identified each prey item to the lowest possible taxonomic level, using Randall's (1996; 2007) key for fish prey, and Hoover's (1998) key for crustacean prey. Cumulative prey curves (Ferry and Cailliet, 1996) derived from plotting the cumulative number of unique prey taxa against the cumulative number of analyzed stomachs allowed us to assess whether sample sizes were large enough to accurately characterize dietary breadth. These curves reach an asymptote if sample size is sufficient. To determine dietary importance of prey, for all identified prey types and families, the numerical importance (%N), frequency of occurrence (%O) (calculated from full stomachs), and gravimetric importance (%M), as well as the index of relative importance (IRI) and the %IRI (proportion of the IRI of a taxon to the sum of IRIs of all taxa) were calculated. The IRI incorporates the individual indices in the formula

$$IRI = (\%N + \%M) \times \%O \qquad (1)$$

and may provide a more accurate description of dietary importance than its components by canceling out their individuals biases, such as the overestimation of the importance of an abundant but small prey item by the %N (Cortes, 1996). Because %N, %M, %O, and %IRI indicated that fishes dominated the diet of *C. argus*, for the comparison of diets between islands and the calculation of electivity, the indices were recalculated for the fish component of the diet alone.

Composition of the reef fish assemblage

Underwater visual surveys with scuba were used to determine reef fish abundances and sizes (in 5-cm bins, i.e., 0–5 cm, 5–10 cm, etc.) at 23 sites (depth range 8.2 m–18.2 m, mean depth 11.9 m). All sites were located in the dominant reef habitat of the Kona coast, reef shelves with moderate to high finger coral (*Porites compressa*) cover. Each survey of a site involved four divers (two pairs), who between them surveyed four 25×4 m (100 m²) belt transects that were permanently installed at each site. Each transect count consisted of one rapid swim to count mobile and midwater species, and a slow return swim closer to the bottom to record fishes in and

around the benthos. Sites were surveyed 4 to 6 times during the year 2003, generally between 0840 and 1600 hours. The detailed sampling regime was described by Tissot et al. (2004). Surveys were conducted under the direction of the West Hawaii Aquarium Project (WHAP, a collaboration of the Hawaii Division of Aquatic Resources (HDAR), the University of Hawaii at Hilo, and Washington State University), and are therefore referred to as "WHAP surveys" here.

WHAP survey counts were used to calculate mean fish densities (individuals/100 m²) and relative numerical importance (%N) of reef fishes in Kona in 2003 (i.e., grand mean of densities for the year 2003 at the 23 sites). In addition, relative importance in terms of biomass (%M) was determined for large (mean body M >50 g) piscivores. For this purpose, the M of individuals was estimated from their TL by using conversion equations for the respective taxa (Froese and Pauly, 2009). Finally, size-frequency distributions of reef fishes in Kona were calculated from the combined WHAP survey counts for 2003.

Abundances of nocturnally active taxa tend to be underestimated by data collected during daytime surveys (Ackerman and Belwood, 2000). For the calculation of electivity (see next section), abundances of the nocturnal apogonids, holocentrids, and priacanthids were therefore estimated by nighttime surveys ("Night WHAP") that took place in 2003 at the same sites surveyed during daytime. The ratios of nighttime to daytime abundances for these families were 90.6, 2.6, and 1.5, respectively.

Prey selection

To determine the taxonomic focus of predation, we used Ivlev's electivity index (Ivlev, 1961):

$$E_i = (r_i - p_i) / (r_i + p_i), \qquad (2)$$

where r_i = numeric importance (%N) of fish family *i* in the diet of *C. argus*; and

p_i = %N of the same family in the reef environment.

E_i can take values between –1 and 1. Positive values indicate "preference" (a taxon overrepresented in the diet in relation to its availability in the environment), and negative values "avoidance" (a taxon underrepresented in the diet in relation to its availability) (Lechowicz, 1982). Because of the scarcity of reef fish abundance data for Oahu for the year 2003, when stomach contents for this study were obtained, we based electivity calculations on diet composition data obtained from the Kona sample, and on reef fish abundance data for the Kona coast from WHAP surveys in 2003.

Prey-size selection

To assess the size focus of *C. argus* predation, length-frequency distributions of important fish families in the diet of *C. argus* were compared with length-frequency

Table 2

Diet composition of peacock hind (*Cephalopholis argus*) in Hawaii, based on Kona and Oahu samples combined (n_{total}=285, $n_{full\ stomachs}$=159), by number (N), occurrence (i.e., number of stomachs in which a taxon occurred) (O), and mass (M, in g). Dietary importance is indicated by percent by number (%N), percent by occurrence (%O) (calculated on the basis of full stomachs), percent by mass (%M), and percent index of relative importance (%IRI, based on the index of relative importance IRI = (%N + %M) ×%O). %O and %IRI for fishes and crustaceans are nonadded values (i.e., they correspond to these two food types, not the sum of their components). Unidentified fish and crustacean prey were excluded from family-level calculations of % indices.

Prey taxon	N	O	M	%N	%O	%M	%IRI
Fish	185	144	1346.0	84.5	90.6	95.5	97.7
Acanthuridae	14	13	137.8	12.3	8.2	11.9	17.3
Acanthurus nigrofuscus	3	3	11.2				
Acanthurus nigroris	2	2	89.8				
Zebrasoma flavescens	2	2	18.7				
unidentified Acanthuridae	7	6	18.2				
Apogonidae	3	3	15.3	2.6	1.9	1.3	0.7
unidentified Apogonidae	3	3	15.3				
Aulostomidae	6	6	29.4	5.3	3.8	2.5	4.3
Aulostomus chinensis	6	6	29.4				
Balistidae	3	3	63.5	2.6	1.9	5.5	1.3
Xanthichthys auromarginatus	1	1	53.5				
unidentified Balistidae	2	2	10.0				
Chaetodontidae	6	6	78.6	5.3	3.8	6.8	4.0
Chaetodon multicinctus	1	1	16.9				
Forcipiger flavissimus	3	3	21.8				
Hemitaurichthys polylepis	1	1	24.8				
unidentified Chaetodontidae	1	1	15.1				
Cirrhitidae	4	4	37.7	3.5	2.5	3.3	1.5
Amblycirrhitus bimacula	1	1	4.6				
unidentified Cirrhitidae	3	3	33.1				
Holocentridae	16	16	52.6	14.0	10.1	4.6	16.3
Sargocentron punctatissimum	1	1	4.0				
unidentified Holocentrinae	15	15	48.6				
Kuhliidae	1	1	17.5	0.9	0.6	1.5	0.1
Kuhlia spp.	1	1	17.5				

distributions of the same taxa in the reef environment in Kona, by using 2-sample Kolmogorov-Smirnov tests. The family Priacanthidae was excluded from the analysis despite its dietary importance because low counts in underwater surveys did not allow for meaningful comparison. Minitab 14 software (Minitab Inc., State College, PA) was used for all statistical analyses, and results were considered significant at $P<0.05$.

Results

Morphometrics of *C. argus*

Cephalopholis argus SL ranged from 13.2 to 44.0 cm (mean: 26.9 cm), and M from 69 g to 2847 g (mean: 721 g). Morphometric relationships (M-TL, M-SL, SL-TL), which have not been reported for this species from large sample sizes, are summarized in Table 1.

Diet composition

The stomach vacuity rate for the overall sample of 285 analyzed stomachs was 44.2%, and the mean relative stomach content M was 0.74% of *C. argus* body M (empty stomachs included in the calculation). Overall, 219 prey items were recovered from 159 full stomachs. Reef fishes were the principal diet component (97.7% by %IRI). Crustaceans were the only other higher taxonomic group in the diet, but were of minor importance (2.3% by %IRI) (Table 2). Dietary breadth was wide; a total of 24 prey species (20 fish species) in 20 different prey families (16 fish families) were found in the diet. At the same time, the three most important families in the diet made up almost 60%, and the eight most important fish families close to 90% of the total diet (by %IRI). In declining order of importance, these families were the Scaridae, Acanthuridae, Holocentridae (exclusively of the subfamily Holocentrinae, the squirrelfishes), Monacanthidae,

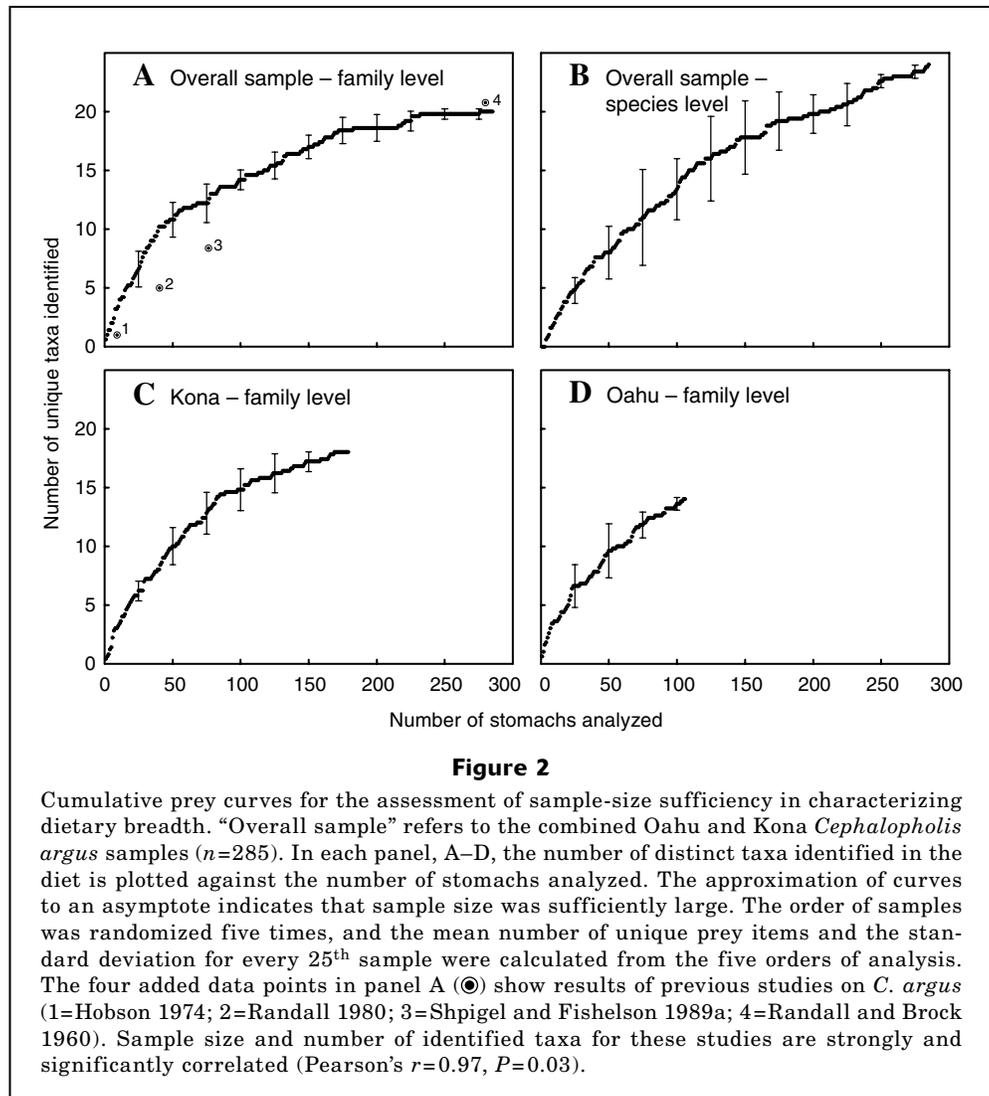| Prey taxon	N	O	M	%N	%O	%M	%IRI
Table 2 (continued)							
Labridae	2	2	29.5	1.8	1.3	2.6	0.5
Pseudocheilinus tetrataenia	1	1	1.7				
Stethojulis balteata	1	1	27.8				
Monacanthidae	15	13	52.5	13.2	8.2	4.5	12.6
Pervagor aspricaudus	2	2	19.5				
unidentified Monacanthidae	13	11	33.0				
Mullidae	3	3	40.3	2.6	1.9	3.5	1.0
Unidentified Mullidae	3	3	40.3				
Pomacanthidae	1	1	19.8	0.9	0.6	1.7	0.1
Centropyge potteri	1	1	19.8				
Pomacentridae	3	3	35.4	2.6	1.9	3.1	0.9
Stegastes marginatus	2	2	29.1				
unidentified Pomacentridae	1	1	6.3				
Priacanthidae	10	8	125.1	8.8	5.0	10.8	8.6
Heteropriacanthus cruentatus	9	7	122.2				
unidentified Priacanthidae	1	1	2.9				
Scaridae	12	12	319.0	10.5	7.5	27.6	25.1
Calotomus carolinus	1	1	72.0				
Scarus psittacus	4	4	107.1				
unidentified Scaridae	7	7	139.9				
Synodontidae	1	1	41.6	0.9	0.6	3.6	0.2
Saurida gracilis	1	1	41.6				
Unidentified fishes	85	70	250.4				
Crustaceans	34	29	78.6	15.5	18.2	5.5	2.3
Grapsidae	1	1	9.0	0.9	0.6	0.8	0.1
Plagusia depressa	1	1	9.0				
Hippolytidae	10	10	38.1	8.8	6.3	3.3	6.6
Saron marmoratus	10	10	38.1				
Portunidae	2	2	12.0	1.8	1.3	1.0	0.3
Charybdis hawaiensis	1	1	10.6				
Charybdis paucidentata	1	1	1.4				
Rhynchocinetidae	1	1	0.3	0.9	0.6	0.0	0.0
unidentified Rhynchocinetidae	1	1	0.3				
Unidentified crustaceans	20	18	19.2				
Subtotal (unidentified fishes and crustaceans excluded)	114	109	1154.9	100.0	108.8	100.0	100.0
Total (all prey items)	219	197	1424.5				

Priacanthidae, Chaetodontidae, Aulostomidae, and Cirrhitidae (Table 2).

Oahu and Kona *C. argus* populations did not differ significantly in either stomach vacuity rate (50.0% vs. 40.7%; chi-square test, n=285, P=0.13) or relative stomach fullness (0.73% vs. 0.76% of own body M; t-test, n=285: P=0.84). Both island populations also revealed the importance of fish prey in their diet (96.7% vs. 98.1% by *%IRI*) and showed a similar overall dietary breadth (14 versus 18 families). In addition, the Scaridae, Acanthuridae, and Priacanthidae were concurrently among the five most important prey families by *%IRI* for both islands (Table 3). Still, diet composition differed in several respects. Most importantly, the dominant prey

family by *%IRI* in the diet of *C. argus* from Kona (Holocentridae) was not found in the diet of *C. argus* from Oahu, and vice versa, the dominant family in the diet of Oahu *C. argus* (Monacanthidae) was rare in the diet of *C. argus* from Kona. The only other family for which *%IRI* values differed by >5% was the Chaetodontidae, which was more important in the Kona than the Oahu diet. Balistidae and Mullidae were slightly more important in the Kona diet, and Pomacentridae, Cirrhitidae, and Synodontidae in the Oahu diet. For all remaining families, absolute *%IRI* values differed by <1% (Table 3).

Cumulative prey curves for family-level analyses based on the overall (i.e., Oahu and Kona samples combined) and on the Kona sample showed strong asymp-

Figure 2

Cumulative prey curves for the assessment of sample-size sufficiency in characterizing dietary breadth. "Overall sample" refers to the combined Oahu and Kona *Cephalopholis argus* samples (n=285). In each panel, A–D, the number of distinct taxa identified in the diet is plotted against the number of stomachs analyzed. The approximation of curves to an asymptote indicates that sample size was sufficiently large. The order of samples was randomized five times, and the mean number of unique prey items and the standard deviation for every 25th sample were calculated from the five orders of analysis. The four added data points in panel A (⊚) show results of previous studies on *C. argus* (1=Hobson 1974; 2=Randall 1980; 3=Shpigel and Fishelson 1989a; 4=Randall and Brock 1960). Sample size and number of identified taxa for these studies are strongly and significantly correlated (Pearson's r=0.97, P=0.03).

totic behavior (Fig. 2, left panels), which indicates that sample size was sufficiently large to describe dietary breadth. In contrast, curves for the species-level analysis based on the overall sample and for the family-level analysis based on the Oahu sample (Fig. 2, right panels) showed only a slight approximation to an asymptote, and dietary breadth may therefore be incompletely described at these levels.

Composition of the reef fish assemblage

Figure 3 summarizes the mean densities of the 32 different families of reef fishes observed on Kona reefs during the 2003 WHAP surveys. The families Acanthuridae and Pomacentridae, with densities of 69.2 and 61.8 individuals/100 m², together accounted for almost 75% of the total fish assemblage in terms of %N. Seven other families contributed at more than 1% by %N, the most important ones being the Labridae (9.0%) and Chaetodontidae (4.6%). The importance of nocturnally active

families may be higher than shown in Figure 3, which is based on daytime WHAP surveys alone. In particular, recalculated numerical importance for the nocturnal families Apogonidae, Holocentridae, and Priacanthidae (based on nighttime surveys showing a 90.6, 2.6, and 1.5 times higher abundance than during daytime; see *Material and methods* section) would be 7.5%, 6.8%, and <0.1%, respectively. The guild of large-body piscivores contributed 0.7% to total fish abundance. Within this guild, *C. argus* (density=0.70 individuals/100 m²) was the dominant taxon, contributing 56% by %N (Fig. 3) and 84% by %M—the larger value for the latter being due to a higher mean body M for *C. argus* compared to the other predators in the analysis.

Prey selection

All of the 10 most abundant species on Kona reefs were found in the stomachs of *C. argus*. However, although some fishes that were rare in the reef environment

Table 3

Composition of the fish portion of the diet of peacock hind (*Cephalopholis argus*) from Hawaii Island (*n*=179) and Oahu (*n*=106), based on fish prey identified to at least the family level. Crustaceans were excluded from the analysis because of their relatively minor dietary importance for *C. argus* from both islands (%*IRI* =1.9% and 3.3%, respectively). Dietary importance is indicated by percent by number (%*N*), percent by occurrence (%*O*) (calculated on the basis of full stomachs), percent by mass (%*M*), and percent index of relative importance (%*IRI*).

Family	Island							
	Hawaii				Oahu			
	%*N*	%*O*	%*M*	%*IRI*	%*N*	%*O*	%*M*	%*IRI*
Acanthuridae	16.9	9.4	13.0	20.9	8.6	5.7	11.9	7.1
Apogonidae	3.1	1.9	1.2	0.6	2.9	1.9	1.7	0.5
Aulostomidae	6.2	3.8	3.1	2.6	5.7	3.8	2.0	1.8
Balistidae	4.6	2.8	9.1	2.9	—	—	—	—
Chaetodontidae	7.7	4.7	10.1	6.2	2.9	1.9	2.1	0.6
Cirrhitidae	3.1	1.9	0.9	0.6	5.7	3.8	7.9	3.2
Holocentridae	24.6	15.1	7.5	35.8	—	—	—	—
Kuhliidae	1.5	0.9	2.5	0.3	—	—	—	—
Labridae	1.5	0.9	0.2	0.1	2.9	1.9	7.0	1.1
Monacanthidae	6.2	2.8	1.6	1.6	31.4	18.9	10.3	48.6
Mullidae	4.6	2.8	5.8	2.2	—	—	—	—
Pomacanthidae	—	—	—	—	2.9	1.9	5.0	0.9
Pomacentridae	1.5	0.9	0.9	0.2	5.7	3.8	7.3	3.0
Priacanthidae	9.2	5.7	9.2	7.7	11.4	3.8	15.2	6.2
Scaridae	9.2	5.7	34.8	18.4	17.1	11.3	19.1	25.3
Synodontidae	—	—	—	—	2.9	1.9	10.5	1.6

("the wild") in Kona were important components of *C. argus* diet (e.g., Priacanthidae: %$N_{reef\ environment}$ <0.1%, %N_{diet}=9.2%), others such as the Pomacentridae, although highly abundant on Kona reefs (%*N*=31.5%), had low dietary importance (%*N*=1.5%) (Fig. 3, Table 2). Consequently, the electivity values of prey families ranged widely, from values of E_i near 1 (strong preference) to −0.91 (strong avoidance). This pattern was consistent both for diurnally and nocturnally active taxa (Fig. 4). Specifically, of the nocturnal taxa, priacanthids and holocentrids were highly preferred, whereas apogonids were avoided. Diurnally active families can be divided into three broad categories based on their electivity (Fig. 4) and their abundance on reefs (Fig. 3): 1) negative electivity, large wild abundance (Pomacentridae, Labridae, Acanthuridae); 2) moderate positive electivity, moderate to large wild abundance (e.g., Chaetodontidae, Mullidae, Scaridae); and 3) large positive electivity, low wild abundance (Aulostomidae, Monacanthidae).

Prey-size selection

The mean TL of reef fishes in the diet of *C. argus* was 7.2 cm, and was thus significantly smaller than the mean TL of reef fishes in the wild of 9.1 cm (Kolmogorov-Smirnov test, *D*=0.11, *P*=0.034) (Fig. 5). Mean size in the diet was consistently lower than mean size in the wild for all analyzed prey families. However, specific patterns differed strongly. On one end of the spectrum, for generally small-body families, such as the Acanthuridae and Chaetodontidae, differences between consumed and wild sizes were near significant ($D_{Acanthuridae}$=0.32, *P*=0.057) or significant ($D_{Chaetodontidae}$=0.55, *P*=0.026), but small in absolute terms, with size classes occurring in the diet overlapping strongly with those observed in the wild. The Scaridae (*D*=0.42, *P*=0.021) represented an intermediate case, with predation focused on the smaller size classes present in the wild, but clear overlap between size-frequency distributions in the diet and in the wild. Finally, for the generally large-body families Monacanthidae (*D*=0.47), Aulostomidae (*D*=0.82), and Holocentridae (*D*=0.99), size differences between the diet and the wild were large and highly significant (*P*<0.01), and sizes as small as in the diet were rarely observed in the wild (Fig. 5).

Discussion

The comparison of reef fish densities in this study showed that *C. argus* constituted more than half of the guild of large piscivores in Kona by numerical abundance, and more than 80% of this guild by biomass. Because consumption partly depends on the biomass of a predator (Cortes, 1996), it therefore appears safe to say that *C. argus* has become the dominant large-body predatory

reef fish in this area. Densities of *Cephalopholis argus* observed in Kona (0.70 ind./100 m^2) were lower than those in the Red Sea at shallow depths (1.32 ind./100 m^2), but much higher than in the Red Sea at depths >10 m, where other species of the genus *Cephalopholis* outcompete *C. argus* (Shpigel and Fishelson, 1989b). In addition, the density of *C. argus* was higher than that of the ecologically important grouper *Plectropomus leopardus* in Australia (0.53 ind/100 m^2) (St. John, 1999). In this context, knowledge of the feeding patterns of *C. argus* in Hawaii is particularly relevant because it provides the basis for the assessment of effects of *C. argus* on native species.

Diet composition was characterized by the large dietary importance of fishes (97.7% by *%IRI*), wide dietary breadth (4 crustacean and 16 fish families present in the diet), and a nearly exclusive focus on benthic reef-associated fishes. These patterns are typical for groupers, which are usually ambush predators that hunt close to the reef and prey on a wide range of different fishes, as well as crustaceans and, in some cases, cephalopods (Parrish, 1987). In *C. argus*, a strong focus on fish prey was also previously observed in locations outside the MHI (e.g., 77.5% by *%N* in the Society Islands [Randall and Brock, 1960]; 95.7% by *%M* in Madagascar [Harmelin-Vivien and Bouchon, 1976]; 92% by *%N* in the South Pacific [Randall, 1980]; 95% by *%N* in the Red Sea [Shpigel and Fishelson, 1989a]). Although *C. argus* is a non-native species in Hawaii, its feeding ecology thus appears to reflect the feeding ecology of the species in native habitats.

Half of all fish families that inhabit reefs in Kona (32 families in 2003) were present in the diet of *C. argus*—a finding that demonstrates that groupers may prey on a large proportion of the fish taxa present in their habitat. The dietary breadth (fishes and crustaceans combined) observed in our study was much wider than those previously reported for *C. argus* in Hawaii (1 family observed in 10 samples [Hobson, 1974]), in the South Pacific (5 families in 39 samples [Randall, 1980], and in the Red Sea (8 families in 78 samples [Shpigel and Fishelson, 1989a]). In contrast, the dietary breadth equaled the breadth reported for the Society Islands (21 families in 280 samples [Randall and Brock, 1960]). Considering the small samples sizes of most previous studies, and the association of dietary breadth with sample size (see *Results* section on cumulative prey curves), differences were likely related to sample size and not to divergent feeding ecology. This interpretation is supported by the strong correlation of the number of identified taxa and sample sizes of previous studies (see added data points in Figure 2).

The similar vacuity rate, stomach fullness, importance of fish prey, and dietary breadth observed in the Kona and Oahu samples indicated that feeding ecology
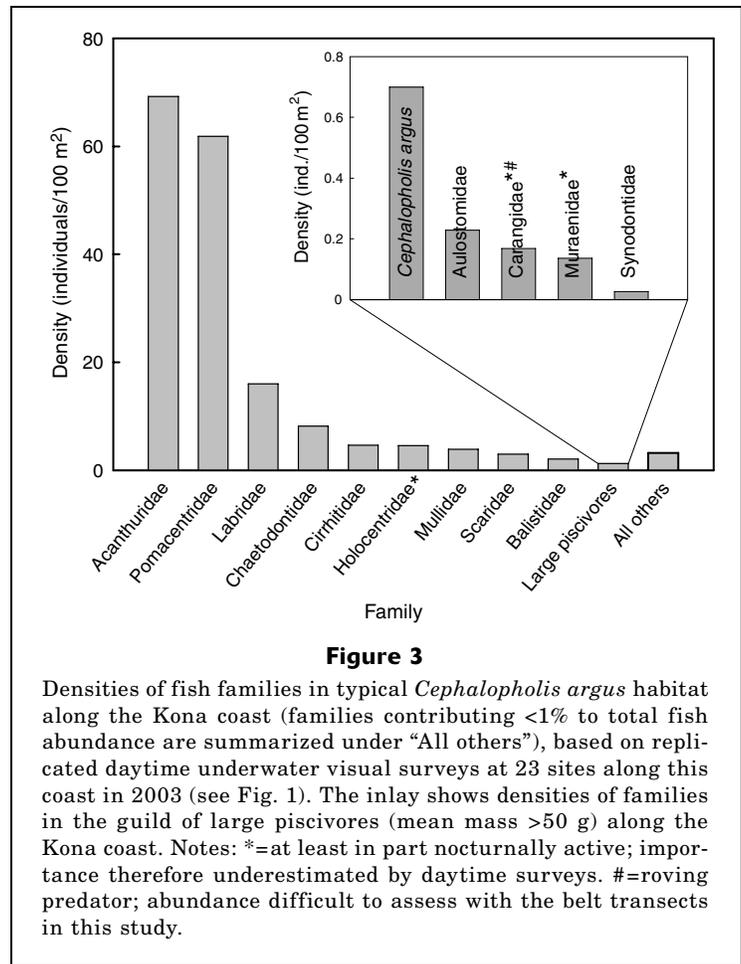

Figure 3

Densities of fish families in typical *Cephalopholis argus* habitat along the Kona coast (families contributing <1% to total fish abundance are summarized under "All others"), based on replicated daytime underwater visual surveys at 23 sites along this coast in 2003 (see Fig. 1). The inlay shows densities of families in the guild of large piscivores (mean mass >50 g) along the Kona coast. Notes: *=at least in part nocturnally active; importance therefore underestimated by daytime surveys. #=roving predator; abundance difficult to assess with the belt transects in this study.

was consistent between those islands. The small differences in dietary importance observed for some families could be related to chance variation, in particular if occurrence of a family in the diet is infrequent. Although the lack of a reef fish survey program comparable to the WHAP program for Kona does not allow a direct comparison between Oahu and Kona reef fish assemblages, divergent dietary importance could also reflect variations in fish assemblages, for example, variations due to differences in reef habitat or fishing pressure. In particular, Williams et al. (2008) demonstrated that the abundance of fishery target species in the MHI is negatively correlated with local human population density, which is noteworthy in this context because population density on Oahu is more than 30-fold higher than on Hawaii Island. In contrast, the large differences observed for small individuals of the Holocentridae and Monacanthidae are probably related to local recruitment pulses, which is further discussed in the section on size selection below.

Prey selection

The wide range of electivity values for prey fishes in the diet of *C. argus* in this study indicates that feeding was

not opportunistic. This finding is surprising because groupers are often considered generalist, opportunistic predators on account of their wide dietary breadth (Parrish, 1987). However, the only other study in which the relative importance of prey fishes in the wild was compared with that in grouper diet (Beukers-Stewart and Jones, 2004) showed a strong preference for clupeids and the avoidance of pomacentrids in the grouper species *Cephalopholis boenak* and *C. cyanostigma* in Australia, and it was concluded that this selective feeding behavior contrasted with the perception of opportunistic predation. The agreement between Beukers-Stewart and Jones's and our findings shows that grouper predation may diverge from opportunistic predation more commonly than previously thought.

The concurrent avoidance of pomacentrids by *C. argus* in Hawaii and Australia indicates a low vulnerability of this family to grouper predation. An explanation may lie in the close reef association and resulting proximity to refuges of many pomacentrids (Beukers-Stewart and Jones, 2004). Incidentally, such a connection between refuges and low vulnerability to predation may help to explain the recent observation by Jones et al. (2004) that coral-associated fishes (including pomacentrids) decline with loss of coral cover during bleaching epi-

Figure 4

Ivlev's electivity index E_i for prey fishes present in the diet of *Cephalopholis argus* in Kona (Kuhliidae excluded because of a lack of observations in reef fish surveys). Positive values of E_i indicate higher relative importance ("preference") in the diet than in the environment, and negative values of E_i indicate lower relative importance ("avoidance") in the diet than in the environment. Abundances of nocturnally active species (*), underestimated by daytime surveys, were adjusted on the basis of abundances observed in nighttime surveys (see *Methods* section).

sodes. At the same time, the few pomacentrids in the diet of *C. argus* in Hawaii belonged to the reef-associated genus *Stegastes*, whereas *Chromis* spp., which are abundant in mid-water, were completely absent. Such low vulnerability of mid-water pomacentrids may be related to the close reef association of *C. argus*, which rarely ventures into the open water column (Hobson, 1974). Low clupeid abundance on Kona reefs in 2003 presumably explains the absence of this family in the diet of *C. argus*.

The terms "preference" and "avoidance" as related to electivity indices do not necessarily solely reflect active choice (e.g., one that is based on nutritional value) but also depend on the vulnerability of prey to capture (Scharf et al., 1998). In the present study, this differentiation was useful in interpreting electivity patterns. In particular, vulnerability provided a straightforward explanation for the contrast between a strong preference for the nocturnal priacanthids and holocentrids and a strong avoidance of the equally nocturnal apogonids: whereas the two preferred taxa hide under ledges or in caves during daytime, which are commonly frequented by *C. argus* (Randall, 2007), the apogonids hide in small reef crevices inaccessible to a large-body predator. Similarly, the complete lack of cryptic families (e.g., Blenniidae, Gobidae, Scorpaenidae) and the rareness of planktonic taxa in the diet of *C. argus* may be due to their low vulnerability, if one considers the low visibility of and proximity to cover for cryptic taxa and the usually loose reef association for planktonic taxa.

The patterns observed for nocturnal taxa, as well as the low importance of crustaceans and large importance of diurnally active fishes in *C. argus* diet, indicate that feeding of this predator in Hawaii was diurnal or crepuscular. This finding confirms that of Hobson (1974) that *C. argus* is a diurnal feeder in Hawaii and is consistent with limited nocturnal movement of *C. argus* in Hawaii (A. Meyer, personal commun.[1]). In contrast, *C. argus* in Madagascar feeds during day and night (Harmelin-Vivien and Bouchon, 1976). The rhythm of feeding activity of *C. argus* thus appears to be variable among regions.

Regarding diurnally active prey taxa, differential vulnerability may offer an explanation for divergent electivity among the abundant families Pomacentridae, Labridae, and Acanthuridae, and among moderately abundant families such as the Chaetodontidae and Scaridae. However, it cannot reasonably account for the strong preference for the rare aulostomids, holocentrids, and monacanthids. This latter pattern appears to be an artifact of recruitment pulses and is further discussed in the context of size selection below.
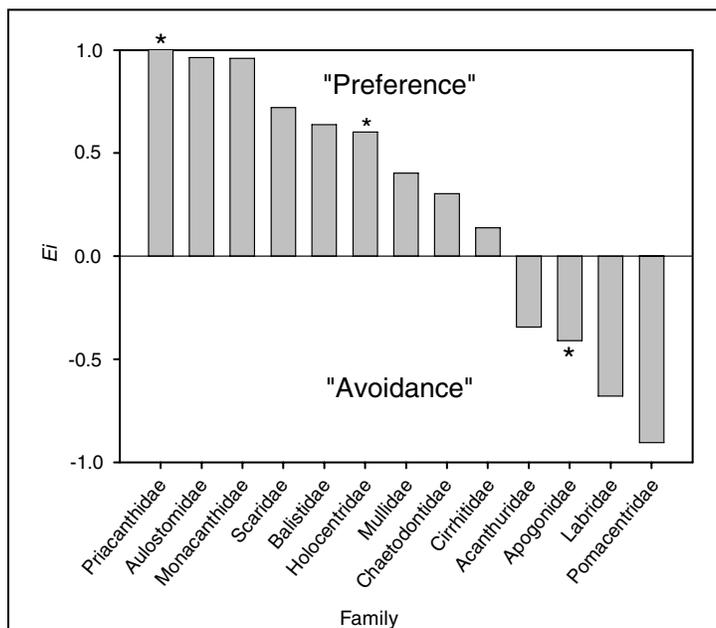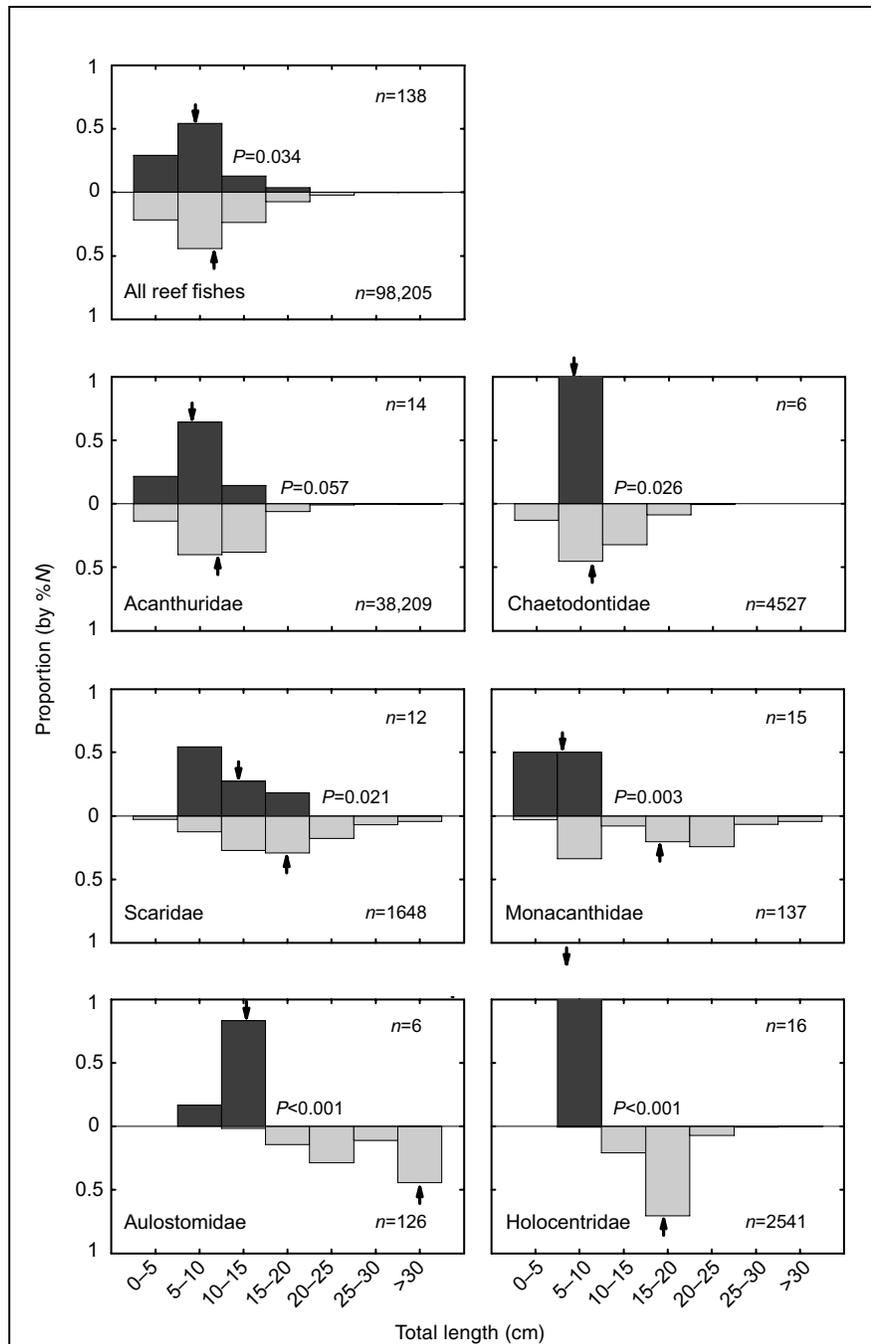
Figure 5

Comparison of the size distribution of prey fishes in the diet of *Cephalopholis argus* (dark gray bars), and of the same prey taxa observed during underwater visual surveys (WHAP surveys) on reefs in Kona (light gray bars), for all fishes combined, and for six of the most important families in the diet of *C. argus* (by %N). Sample sizes (*n*) in the upper half of each panel refer to the number of samples of each taxon found in *C. argus* stomachs, and in the lower panel to the total number of individuals of the taxon observed in WHAP surveys in 2003. Mean total lengths for distributions are indicated by arrows. *P*-values are outcomes of Kolmogorov-Smirnov comparisons of the two size distributions in each panel, and significant values indicate that distributions were different.

Size selection

The patterns of prey-size selection by *C. argus* in Hawaii are of particular interest in the context of questions regarding the high mortality of coral reef fish recruits (here defined as postsettlement individuals less than several months of age). During recruitment pulses, large numbers of fish that have completed their planktonic phase settle on reefs (Walsh, 1987). Mortality of these recruits in the first 100 days after arrival can exceed 99% (Werner and Gilliam, 1984; Doherty et al., 2004). Although predation is thought to be an important cause of this mortality (Beets, 1997; Webster, 2002), few studies have conclusively shown the implication of specific predators (Connell, 1998; Beukers-Stewart and Jones, 2004). In this study, the majority of aulostomids, holocentrids, and monacanthids consumed by *C. argus* were recruits, as indicated by comparison of sizes in the diet (TL as small as 9.3, 5.2, 3.8 cm, respectively) with published size ranges for different life history stages of these families (Leis and Carson-Ewart, 2000; Randall, 2007). This finding indicates that the large-body predator *C. argus* contributes to early mortality of reef fishes.

Interestingly, the smallest consumed sizes of the prey families above were rarely or never observed in WHAP underwater visual surveys. This inability to account for recruits may in part be due to low detectability of these small and potentially cryptic individuals. However, the surveys were designed to account for fishes closely associated with the bottom, new recruits, and fishes hiding in cracks (Tissot et al., 2004). It therefore appears more likely that high mortality of recruits between their arrival on the reef and the occurrence of the surveys (4–6 surveys per site in 2003, i.e., every 2–3 months) explains this pattern. Considering the spatial and temporal heterogeneity of recruitment (Dufour et al., 1996), predation on recruits may also account for the divergent dietary importance of small holocentrids and monacanthids between islands in this study.

In contrast to the focus on recruits for the families above, for several families of smaller-body individuals (e.g., Acanthuridae, Chatodontidae), differences between mean size in the diet and in the wild were small. In these cases, comparison with published size ranges (Leis and Carson-Ewart, 2000; Randall, 2007; Claisse et al., 2009) showed that consumed individuals represented in large parts juveniles and small adults, and not recruits. This result indicates that ecological effects of *C. argus* predation differ between prey families. In particular, although predation-induced mortality in several families of larger-body individuals would be limited to recruits (adults finding escape from predation through their large size), in several families of smaller-body individuals, it can also affect juveniles and adults. From a predator perspective, *C. argus* nutrition was then based on 1) accessible sizes of reef fishes such as Acanthuridae, Chaetodontidae, or Scaridae, present year-round on the reef, and 2) recruitment pulses providing access to small individuals of different families, including the

Aulostomidae and Monacanthidae, of which adults escape predation because of their large size.

Methodological considerations

Despite the large sample size of the present study compared to that of many previous grouper feeding studies, cumulative prey curves indicated that sample size was too small to fully characterize dietary breadth at the species level, and dietary breadth of Oahu *C. argus* at the family level. This stresses the importance of assessing sample size sufficiency in grouper studies with analytical tools such as cumulative prey curves (Ferry and Cailliet, 1996). The strong correlation of the number of identified taxa with the sample size of *C. argus* studies in the literature impressively confirms the importance of this issue. Secondly, several authors have pointed out that daytime visual surveys may not accurately reflect the importance of nocturnal taxa (e.g., Ackerman and Belwood, 2000). The 90-fold higher abundance of apogonids observed in nighttime surveys compared to that observed in daytime surveys at the same sites in this study underscores this potential limitation of daytime surveys. Finally, in this study, feeding on recruit-sized individuals of some prey fishes of which adults were only rarely observed on Kona reefs was able to explain the high preference for these species. This demonstrates that inclusion of ecological information to interpret electivity values is as important as the choice of a suitable index of electivity (Lechowicz, 1982).

Conclusions

The dominant position of *C. argus* in the guild of large piscivores in Kona shows that this species has become an important component of MHI reef ecosystems since its introduction and raises the question of how this species affects native fishes. The differences in the strength and mechanism of effects of predation among prey families in this study indicate that *C. argus* has the potential to affect the composition of reef fish assemblages. However, structuring effects of predation on fish assemblages are also important in systems without introduced predators (Hixon, 1991). In addition, native predators in the MHI have sharply declined owing to overfishing over the past century—a decline that is reflected in low predator densities in the MHI compared to the remote northwestern Hawaiian Islands (protected from fishing) (Friedlander and DeMartini, 2002). This raises the question of whether *C. argus* is only fulfilling the ecological role previously played by native predators. The results presented here do not suffice to answer these questions. However, by identifying the prey taxa and sizes constituting *C. argus* diet, they open the way partly (the missing part being data on *C. argus* daily ration) for a quantitative estimate of consumption by this species (Bromley, 1994), which could further advance our understanding of its effects on native fishes in Hawaii.

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