

Devil in the Details: High-Resolution Dietary Analysis Contradicts a Basic Assumption of Reef-Fish Diversity Models

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Reef-fish diversity models, unlike general diversity-gradient hypotheses, assume food specialization by reef fishes is too low to influence community structure. This assumption may be an artifact of low taxonomic resolution in studies of fish diets. I performed detailed dietary analyses on adults of eight small, cryptic, diurnal fish species from the spur-and-groove habitat outside Kaneohe Bay, Oahu, Hawaii to test whether dietary specialization may facilitate high species richness in reef fish communities. Mean dietary overlap (0.179) among these fishes is similar to overlap in communities thought to be structured by fine-scale food specialization. Dietary studies with high taxonomic resolution indicate a significant decrease in food overlap among fishes as latitude decreases. These results, along with the generally recognized increase in prey diversity toward the tropics, are consistent with diversity-gradient hypotheses and suggest that food specialization allows the local coexistence of many fish species on coral reefs. Local relative abundances of reef fishes may be influenced by prey availability. The densities of five of six fish species were related to densities of important prey. Food choice and availability may influence richness and relative abundances, respectively, in reef fishes, and reef-fish communities may be structured in the same manner as other tropical communities.

A small set of conceptual models, summarized by Jones (1991), forms the framework for more than three decades of research into the determinants of coral-reef-fish community structure. The high species richness of fishes on coral reefs is part of a general increase in diversity toward the tropics that has been recognized for over a century. Empirical evidence, generated primarily from terrestrial studies (Sale, 1977), led to the development of several hypotheses about the cause of this diversity gradient (Pianka, 1966). All of these diversity-gradient models suggest that greater resource specialization by residents or greater resource availability in the habitat leads to higher species richness in tropical regions.

Reef-fish-diversity models represent a significant departure from diversity-gradient models by assuming that community structure is not influenced by food specialization. Smith and Tyler (1972, 1973) and Sale (1974) explicitly state that dietary overlap among coral reef fishes is too high to explain high diversity. Goldman and Talbot (1976), Bohnsack and Talbot (1980), and Doherty (1981), in arguing that reef fish populations are held below carrying capacity, imply that food specialization is not capable of influencing community structure.

This assumption has never been critically examined, even though specialization on food resources is thought to allow the coexistence of species in many other systems. In a review of resource use, Schoener (1974) found that food

was the most important resource in 40 of the 80 systems examined and noted that similar species living in the same habitat usually eat different foods. Ross' (1986) review of resource use in fishes suggests that trophic separation is the most important factor allowing species to coexist, especially in marine systems.

The reef-fish-diversity models cite the dietary studies of Hiatt and Strasburg (1960) and Randall (1967) as evidence of high food overlap among coral reef fishes. Later studies by Hobson (1974) and Harmelin-Vivien (1979) provided more supporting evidence. These studies, although remarkable in scope, were not designed to test whether dietary specialization influences reef-fish diversity. A potential problem with using them to draw conclusions about dietary overlap is that prey were grouped into broad taxonomic or pseudo-taxonomic categories (Jones et al., 1991). The degree to which resource states are separated can have a major influence on overlap values (Colwell and Futuyama, 1971). This effect is demonstrated by studies that identified prey to species and presented data in a fashion that can be used in an overlap index (Table 1). Overlap estimates depend greatly on whether prey are identified to species (high resolution) or to levels (class or order) typically seen in dietary studies of reef fishes (low resolution). Dietary overlap appears significantly higher when taxonomic resolution is low. Of special interest is Kohn's (1959, 1968) work on predatory snails, which has been cited as an example of fine-scale resource

TABLE 1. A COMPARISON OF DIETARY OVERLAP WHEN TAXONOMIC RESOLUTION IS HIGH VS. LOW. Values in the "high" column represent mean overlap calculated from data presented in species-level dietary analyses, whereas the "low" values were calculated from the same data grouped into more-inclusive taxa typically used in dietary analyses of reef fishes. A paired two-tailed t-test results indicate overlap values differ significantly ($P = 0.00004$).

Study	Mean overlap w/ resolution:	
	High	Low
Arculeo et al., 1993	0.417	0.956
Hacunda, 1981	0.519	0.737
Jenni, 1969	0.397	0.544
Kohn, 1959	0.067	0.575
Kohn, 1968 (Chagos Islands)	0.103	1.000
Kohn, 1968 (Maldives)	0.115	1.000
Maitland, 1965	0.692	0.979
Martell and McClellan, 1994	0.265	0.633
Newton, 1967	0.091	0.956
Paine, 1963	0.313	0.575
Prochazka, 1998	0.106	0.523
Ueckert and Hansen, 1971	0.422	0.988
Mean	0.292	0.790

specialization in coral-reef organisms. Based on dietary studies on fishes, Sale (1977) suggested Kohn's results were exceptional for the tropics. However, Kohn identified prey to a level not seen in reef fish studies. Ironically, if he had used the categories typical for reef fishes, Kohn's results would have indicated broad or complete dietary overlap (Table 1).

Food has traditionally been assumed to be abundant on coral reefs (Sale, 1977; Smith, 1978), but Jones (1991) listed several lines of evidence suggesting that food availability may influence the post-recruitment abundance of reef fishes. Changes in food levels can alter demographic patterns in reef fishes (Forrester, 1990; Clarke, 1992; Clifton, 1995). Jones and McCormick (2002) and Hixon and Webster (2002) note that although predation is likely to be the proximate cause of changes in post-recruitment population size, reduction in growth as a result of competition for food and resulting in greater predation on slower growing fishes may be the ultimate cause of mortality. Also, food availability can potentially affect settlement, migration, and riskiness of foraging behavior. All of these factors can affect post-recruitment population size and thus the relative abundances of fishes in coral-reef assemblages.

I use dietary analysis to evaluate the assumption that food specialization does not contribute to species richness on coral reefs. I examine dietary overlap in a group of fishes that reside (and feed) in the same habitat. I compare my results to those of other studies where food specialization is thought to allow the local coexistence of species. These results are incor-

porated into an analysis of latitudinal trends in dietary specialization among fishes. Low dietary overlap among coral-reef fishes, along with a trend toward increased dietary specialization among tropical fishes, would challenge a basic assumption of reef-fish diversity models; whereas high dietary overlap and/or no evidence of increased dietary specialization among tropical fishes would support the reef-fish diversity models. Finally, I examine whether food availability can be related to the relative abundance of reef fishes on a local (tens of meters) scale. I compare densities of the most abundant fishes within a coral-reef habitat to densities of their prey. Significant relationships between densities of fishes and their prey will be considered corroborative evidence that abundances of coral-reef fishes are influenced by prey availability. Because changes in single species abundance affect relative abundances of the whole community, significant relationships will provide evidence that local relative abundances are influenced by prey abundance.

MATERIALS AND METHODS

Dietary analysis.—Twenty-seven fish collections were made in an approximately one-hectare tract of spur-and-groove habitat outside Kaneohe Bay, Oahu, Hawaii (21°28'25"N, 157°46'42"W). Sampling was conducted between 0900 and 1200 h in depths of 11–15 m using SCUBA from 14 March to 29 September 1996 as sea conditions permitted.

For each collection, a sampling area was haphazardly chosen. A rotenone solution (1.5 L

Prentox® synpren-fish toxicant, 250 g powdered *Deris* root, and 0.5 L clear Ivory® dishwashing liquid) was applied within an area defined by prominent features on that part of the reef. The average area sampled was 10.3 m². All fish were collected in hand nets, fixed in a solution of one part 37% formaldehyde to eight parts fresh water for two days, soaked in water for 24 h, then preserved in 70% isopropanol.

Voucher specimens of each species analyzed were deposited at the California Academy of Sciences. Dietary analysis was performed on a total of 20 randomly-selected, adult-size specimens of each of the following seven species: the blenniid *Cirripectes vanderbilti* (CAS 78981), the cirrhitids *Amblycirrhitus bimacula* (CAS 211164) and *Cirrhitoys fasciatus* (CAS 224412), the creediids *Crystallodytes cookei* (CAS 224414) and *Limnichthys donaldsoni* (CAS 224411), the gobiid *Eviota epiphanes* (CAS 218096), and the scorpaenid *Scorpaenodes kelloggi* (CAS 224413). Another blenniid, *Exallias brevis* (CAS 224439), was studied by Carlson (1992). I analyzed four stomachs from this species to compare with Carlson's results (which showed a diet of 100% coral tissue). These eight species were chosen because they are diurnal, benthic feeders and the most abundant species in the spur-and-groove habitat, representing 79.0% of the total number of chemically-collected, cryptic individuals.

Diets were analyzed by removing the stomach, or a portion of the gut to a prominent feature (e.g., a turn or constriction for *C. cookei*, *L. donaldsoni*, and *E. epiphanes*), identifying prey to the lowest possible taxonomic unit, and recording their presence, numerical abundance, and volume. Volume was estimated using a technique modified from Ross (1974). Here, prey items were squashed to a constant thickness between two glass plates and the volume of the prey item was estimated from a regression equation for the volume of a liquid versus its diameter when squashed between the same plates. An index of relative importance (Pinkas et al., 1971) was calculated for each prey category. Important prey, defined here as the fewest number of species needed to make up at least 50% of cumulative index of relative importance values, were identified for each fish species. Voucher specimens of prey have been deposited at Bishop Museum under accession number 2007-005.

Some prey taxa (e.g., harpacticoid copepods) have not been adequately described for the Hawaiian Islands. I sorted these into morphotypes based on body shape and differences in appendages. Other taxa (e.g., polychaetes, decapods, and mysids) were often missing body parts necessary for the use of existing aids to identifi-

cation. These were separated into morphotypes based on structures that persisted after the organism was eaten (e.g., jaws and setae of polychaetes, carapace shape of crabs, telson shape and ornamentation of decapod shrimp, and telson shape and anterior appendages of mysids).

Substrate use.—The habitat use of fishes was observed directly using SCUBA. For secretive species, collections using small volumes (ca. 0.5 L) of rotenone were made to determine which fishes use a given subhabitat (e.g., rubble, coral skeletons, live corals, holes).

Potential prey were collected from each of 16 microhabitat types identified in the study area (reef rock, sandy rock, overhangs, holes, rubble, sand, cracks, dead *Pocillopora meandrina*, *Porites lobata*, *Porites compressa*, *Montipora flabellata*, *Montipora patula*, *Montipora verrucosa*, *Pavona duerdeni*, *Pavona varians*, and *Pocillopora meandrina*) from 20–23 February 2001 in the same one-hectare tract described above. For each microhabitat type that could easily be removed from the field (rubble, sand, dead *P. meandrina*, live *P. meandrina* and *P. compressa*), I filled an 18.9-L bucket with substrate samples from various locations within the study area. Invertebrates were fixed in formalin for 24 h, then removed from rubble and corals by shaking and rinsing, or removed from sand using a shake and decant procedure (Bell et al., 1986). Invertebrates were strained from fixative with a muslin (29 threads/cm) bag, placed in flowing seawater for 24 h, then preserved in 70% isopropanol. I used a SCUBA-operated suction sampler (Hiscock and Hoare, 1973) fitted with changeable muslin bags (29 threads/cm) to collect invertebrates from substrates that could not easily be removed from the field (reef rock, sandy rock, overhangs, holes, cracks, and each species of encrusting coral). I visited various locations within the study area to vacuum a cumulative total of approximately one m² for each microhabitat. Vacuum bags were closed and put through the killing, fixing, rinsing, and preserving procedure described above.

For each microhabitat sample, the presence or absence of each of 18 important, discrete, and countable prey types was noted. If present, a prey type was subjectively judged as common (at least ~10% of the total number of individuals collected for that species) or not in each microhabitat.

Dietary overlap of reef fishes.—Data used for dietary overlap analysis are presented in Longenecker (2001). I used Morisita's original index of similarity (Morisita, 1959) to calculate overlap

based on the number of each prey species eaten. This index reduces bias due to small sample size or fishes using a large number of resources (Smith and Zaret, 1982; Krebs, 1999). Bias is further reduced by using a constant ($n = 20$) sample size (Krebs, 1999).

To evaluate the degree of dietary overlap among coral-reef fishes, I compared overlap values from this study to those from studies that were cited by Schoener (1974) as examples of communities where food specialization is the primary factor allowing species to coexist, identified prey to species, and presented data in a form that could be used in an overlap index (Morisita's original or simplified Morisita [Horn, 1966]). A Friedman (nonparametric) ANOVA was used to test for a significant difference among overlap values. Pairwise comparisons were made with Tukey's test.

Latitudinal trends in dietary overlap.—I used overlap values from this and other dietary studies to examine, via regression analysis, latitudinal trends in food overlap. To be included in the analysis, a study must have examined at least two species from the same geographical region, in a fully marine environment, on a continental shelf (or equivalent depth); collected all specimens using the same technique; identified prey with high taxonomic resolution (i.e., at least genus when the higher taxon is a major prey item of more than one species); and presented data in a format that allows calculation of one of the Morisita overlap indices. Further, only bony fishes with at least 15 specimens of adult size examined were included in the analysis. These nine criteria were intended to control for the effects of location, sampling technique, and ontogeny within a study; salinity, depth, taxonomic resolution in dietary analysis, and (to a degree) phylogeny among studies; and to provide reasonable assurance that the diet was adequately described (many species were omitted from analysis because only a few individuals were examined). Whenever possible, I used the Morisita (1959) original index to estimate dietary overlap among species within a study. This index requires the absolute number of each prey type eaten. When I could not back-calculate to absolute numbers, I used the closely related Morisita simplified index (Horn, 1966).

I evaluated whether the relationship between latitude and dietary overlap is significant and positive using a randomization test for regression (Steel and Torrie, 1980). This null model approach uses Student's t as a test criterion to compare the slope generated from least squares regression (sample statistic) to the mean of all

3,928 possible between-study slope calculations using the same data (the expected slope if the latitudinal pattern is random).

Relationships between fish and prey densities.—Rotenone causes the death or emergence of gill-breathing invertebrates (pers. obs.). Each time a fish collection was made, invertebrates were semi-quantitatively sampled by haphazardly sweeping a hand net (fitted with a polyester knit-cloth bag) through the water column immediately above the sampling area for two minutes immediately after the rotenone was released (and prior to collecting fishes). Invertebrates were washed over a 125- μm sieve, fixed in a solution of one part 37% formaldehyde to eight parts fresh water for two days, then preserved in 70% isopropanol.

The area covered by each of the 16 microhabitat types listed earlier was estimated with a point intercept method. A braided lead-core line, marked at 20-cm intervals, was placed in contact with the substrate across the short axis of a groove. The substrate type found below each mark was then recorded. This procedure was repeated at 1-m intervals along the long axis of the sampling area. To calculate area, 0.2 m^2 of a given substrate type was assumed to be present under each mark. This method was chosen over other methods because Kinzie and Snider (1978), using a computer simulation, found the point intercept to be as effective as the others, yet less labor intensive.

The abundance of six fish species (*Amblycirrhitus bimaculatus*, *Cirrhitops fasciatus*, *Crystallodytes cookei*, *Limnichthys donaldsoni*, *Eviota epiphanes*, and *Scorpaenodes kelloggi*) and their important prey was determined for each sample. These fishes were chosen because they were abundant enough for statistical analyses, and their prey occurred as discrete, countable units (i.e., coral- and detritus-feeding fishes were omitted). Abundances were converted to densities using estimates of the area for each preferred or common microhabitat. If a fish species was encountered in a sample, yet its preferred microhabitat was not, the area of that microhabitat was assumed to be 0.2 m^2 for the purpose of estimating fish densities. If a fish species was not present in a sample and its microhabitat was also missing, that point was omitted from analysis.

I used best-subsets regression (Neter et al., 1989) to identify the simplest, most explanatory relationships between fish and prey densities. A model with fewer variables was chosen over those with more variables but only slightly more explanatory power. Densities of *Amblycirrhitus bimaculatus* and *Crystallodytes cookei* were square-root

TABLE 2. IMPORTANT PREY OF EIGHT CRYPTIC FISH SPECIES FROM THE KANEHOE BAY FOREREEF. Numbers are % Index of Relative Importance (IRI), where $IRI = (\% \text{ Number} + \% \text{ Volume}) \cdot \% \text{ Frequency of Occurrence}$.

Prey item	<i>Cirripectes vanderbilti</i>	<i>Exallias brevis</i>	<i>Amblycirrhitus bimacula</i>	<i>Cirrhitops fasciatus</i>	<i>Eviota epiphanes</i>	<i>Crystallodytes cookei</i>	<i>Limnichthys donaldsoni</i>	<i>Scorpaenodes kelloggii</i>
Detritus	100.0							
Coral		100.0						
<i>Ischyrocerus oahu</i>			27.6					
<i>Munna acarina</i>			16.2					
Harpacticoid "2"			6.5					
<i>Amphithoe ramondi</i>				20.0				
<i>Anatanais insularis</i>				6.7				
<i>Gammaropsis atlantica</i>				10.3		18.9	8.3	
<i>Leptochelia dubia</i>				15.8	16.6			
Harpacticoid "3"					26.4			
Harpacticoid "11"					12.1			
<i>Amphilochus menehune</i>						8.5		
<i>Cymadusa hawaiiensis</i>						11.8		
Gastropod "4"						8.9	17.4	
Chironomid						8.7	32.5	
Shrimp								27.9
<i>Cerapus</i> species								17.1
<i>Gammaropsis alamoana</i>								9.1

transformed to satisfy the assumptions of regression analysis. All results are presented as untransformed data.

RESULTS

All fishes examined fed on benthic prey. Except for the blennies, *Cirripectes vanderbilti* and *Exallias brevis*, all species fed on benthic crustaceans and included a large number of prey types in their diets (mean, 43; range, 21–75); however, the majority of the diet of each species was composed of only a few prey species (3.25 ± 1.75 SD on average). Further, important prey (the fewest species comprising at least 50% of cumulative IRI values) differed among fish species (Table 2). These important prey were consumed throughout the seven-month study period (Table 3).

Most dietary overlap values are low, with a mean overlap (the average overlap for all possible pairs of species) of 0.179 (± 0.241 SD). Species pairs with the lowest overlap values (0.00) include either one of the blenniids (*Cirripectes vanderbilti* or *Exallias brevis*) with any other species. *Cirripectes vanderbilti* feeds exclusively on detritus and *E. brevis* feeds exclusively on coral tissue. Neither of these foods is used by another species in this study. At the other extreme are the creediids, *Crystallodytes cookei* and *Limnichthys donaldsoni*; these sand-dwelling fishes have dietary overlap values of 1.00. The cirrhitids, *Amblycirrhitus bimacula* and *Cirrhitops fasciatus*, have an

overlap value of 0.592, very close to the value (0.600) arbitrarily considered "high" (Zaret and Rand, 1971). On average, overlap among the cryptic reef fishes studied here is comparable to, and at the lower end of the range of, mean overlap in studies cited by Schoener (1974) as examples of dietary specialization (Table 4).

Only 15 of 484 publications examined met the criteria for inclusion in an analysis of global patterns of dietary overlap. By far, the limiting factor was the degree of taxonomic resolution used in dietary analysis. Linear regression analysis indicates the relationship between dietary overlap and latitude is positive (Fig. 1). Comparing the slope of the regression to the mean slope generated from the null model indicates the relationship between latitude and overlap is not random ($t = 3.587$, $n = 3928$, $P < 0.0005$). Overlap decreases toward the tropics.

Total densities of five out of six fish species are significantly related ($P \leq 0.05$) to the densities of their prey (Table 5). The relationship between the hawkfishes, *Amblycirrhitus bimacula* and *Cirrhitops fasciatus*, and their prey both contain three first-order predictor variables. These relationships cannot be graphically illustrated, but both explain a large portion of the variability in fish density (60.8% for *A. bimacula* and 50.7% for *C. fasciatus*).

Prey densities explain 73.1% of the variability in densities of *Crystallodytes cookei*. However, the regression equation is strongly influenced by a single sample with high densities of the

TABLE 3. OCCURRENCE OF IMPORTANT PREY IN FISH STOMACHS BY MONTH. X = present, 0 = absent, blank = fish collected that month not randomly selected for analysis.

Fish (# empty)	Prey	Mar	Apr	May	Jun	Jul	Aug	Sep
<i>A. bimaculata</i> (4)	<i>I. oahu</i>	X	X	X		X	0	X
	<i>M. acarina</i>	X	X	X		X	X	0
	Harpacticoid "2"	X	X	0		0	X	X
<i>C. fasciatus</i> (1)	<i>A. ramondi</i>	0	X	X	0	0	X	
	<i>L. dubia</i>	0	X	X	0	0	X	
	<i>G. atlantica</i>	0	X	X	X	0	X	
	<i>A. insularis</i>	0	X	X	0	X	X	
<i>C. cookei</i> (4)	<i>G. atlantica</i>	X	X	X			X	
	<i>C. hawaiiensis</i>	X	X	X			0	
	Gastropod "4"	0	0	X			X	
	Chironomid	0	X	X			X	
	<i>A. menehune</i>	0	X	X			X	
<i>L. donaldsoni</i> (2)	Chironomid	0	X	X		X	X	
	Gastropod "4"	0	X	X		0	X	
	<i>G. atlantica</i>	0	X	X		X	X	
<i>E. epiphanes</i> (0)	Harpacticoid "3"	X	0	X	0		X	
	<i>L. dubia</i>	X	0	X	0		X	
	Harpacticoid "11"	X	X	X	0		X	
<i>S. kelloggi</i> (5)	Shrimp	X	X	X			X	
	<i>Cerapus species</i>	0	0	X			X	
	<i>G. alamoana</i>	0	0	X			X	

amphipod, *Cymadusa hawaiiensis* (Fig. 2A). When this point is omitted and the remaining data points plotted along with the predicted response surface, the regression equation is also adequately descriptive at low prey densities (Fig. 2B).

TABLE 4. A COMPARISON OF DIETARY OVERLAP IN CRYPTIC CORAL REEF FISHES TO THAT OF OTHER STUDIES (FROM SCHOENER, 1974) WHERE DIETARY SPECIALIZATION IS THOUGHT TO ALLOW LOCAL COEXISTENCE OF SPECIES. Values that are not statistically different share the same superscript.

Study	Mean overlap (\pm SD)
Kohn, 1959	0.066 (0.152) ^a
Newton, 1967	0.091 (0.167) ^{a, b}
Kohn, 1968 (Chagos)	0.103 (0.224) ^{a, b}
Kohn, 1968 (Maldives)	0.115 (0.256) ^b
This study	0.179 (0.241)
Paine, 1963	0.313 (0.246)
Jenni, 1969	0.397 (0.302) ^c
Ueckert and Hansen, 1971	0.422 (0.277) ^c
Maitland, 1965	0.693 (0.179)

A less complicated, but less predictive (adjusted $R^2 = 23.9\%$) equation relates densities of *Limnichthys donaldsoni* to densities of the same prey used by the confamilial *Crystallodytes cookei*, with which it shares the same microhabitat (Fig. 2C). These fishes have 100% dietary overlap, but each species appears to respond differently to availability of important prey (Figs. 2A–C). Densities of *Eviota epiphanes* are most strongly related to a synergistic effect between the tanaid, *Leptochelia dubia*, and harpacticoid "11" (Fig. 2D). The predictive value of prey to fish density is high for this species (41.1%). The predictive value of the regression relating densities of *Scorpaenodes kelloggi* and its important prey is low (13.6%), but a trend is suggested by the regression probability value (0.105). Densities of *S. kelloggi* may respond to either an increase in the amphipod *Gammaropsis alamoana* or shrimp (Fig. 2E).

DISCUSSION

My success in demonstrating relationships between cryptic fishes and their prey is due in

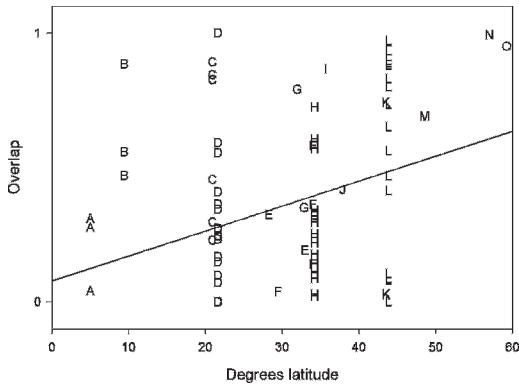


Fig. 1. Latitudinal trend in dietary overlap among fishes. Overlap = 0.077 + 0.0093 (degrees latitude). Slope differs from that expected in a randomization model ($P < 0.0005$). Data from (A) Shpigel and Fishelson, 1989; (B) Robertson and Polunin, 1981; (C) Cox, 1994; (D) Present study; (E) Clements and Choat, 1997; (F) Lundberg and Golani, 1995; (G) Barry and Ehret, 1993; (H) Prochazka, 1998; (I) Horn et al., 1982; (J) Arculeo et al., 1993; (K) Martell and McClelland, 1994; (L) Hacunda, 1981; (M) Murie, 1995; (N) Yang and Livingston, 1986; (O) Hoines and Bergstad, 1999.

large part to a detailed knowledge of their diets, a detailed analysis of fish and prey microhabitat use, and working on a scale appropriate to the assemblage. Small, cryptic fishes often have small home ranges (Jones and Thompson, 1980; Goncalves and Almada, 1998; Munday and Jones, 1998), allowing their substrate requirements to be easily and precisely defined (Depczynski and Bellwood, 2004), and providing confidence that food can be sampled in the areas where fish are feeding. These fishes also have short post-settlement life spans (Depczynski and Bellwood, 2005; Longenecker and Langston, 2005). These

short life spans increase the possibility of identifying relationships between fish abundance and other environmental variables because patterns in fish abundance should be a result of recent events rather than the integration of events over a long period.

The fishes studied here represent, in many ways, the dominant part of coral-reef-fish communities. Most of these model animals are mobile invertebrate feeders, which comprise the most widespread and abundant trophic guild on coral reefs (Ferreira et al., 2004; Floeter et al., 2004). Small, cryptic fishes in particular have historically been a little-studied component of coral reef fish assemblages. However, they are the most abundant fishes on coral reefs (Greenfield, 2003). They are also the most speciose and, despite low cumulative biomass, appear to use a considerable portion of the energy required by reef fishes. Due to their high metabolic demand and rapid population turnover, fishes smaller than 100 mm may use nearly 60% of the total energy required by epibenthic coral reef fishes (Ackerman and Bellwood, 2000).

Dietary overlap among reef fishes.—Reef-fish diversity models assume food does not structure reef-fish communities, yet this appears to be invalid. The fishes examined in this study do not have broadly overlapping diets as postulated by reef-fish diversity models. High-resolution dietary analyses show an average overlap of 0.179 among these eight coral-reef fishes. This value falls comfortably within the range of overlap values from studies cited by Schoener (1974) as examples of dietary specialization (Table 4). It is significantly higher ($P < 0.05$) than Kohn (1959, 1968) found for coral-reef gastropods, yet significantly ($P < 0.05$) lower than those for some terrestrial organisms (Jenni, 1969; Ueckert and Hansen, 1971). There is a large difference between mean overlap in these

TABLE 5. BEST SUBSETS REGRESSION ANALYSIS RELATING DENSITIES OF FISHES AND THEIR IMPORTANT PREY. Ai = *Anatanais insularis*, Ch = *Cymadusa hawaiiensis*, CH = chironomid, Gal = *Gammaropsis alamoana*, Gat = *Gammaropsis atlantica*, H2 = harpacticoid "2", H11 = harpacticoid "11", Io = *Ischyrocercus oahu*, Ld = *Leptocheilia dubia*, Ma = *Munna acarima*, SH = shrimp.

Functional relationship	Adjusted R ²	P
$A. bimaculata = [2.26 - 0.30(Io) + 0.087(Ma) - 0.52(H2) - 0.0016(Io \times Ma) + 0.057(Io \times H2) - 0.0053(Ma \times H2)]^2$	60.8%	0.008
$C. fasciatus = 2.13 - 0.013(Ld) + 0.018(Gat) - 0.30(Ai) - 0.0021(Ld \times Gat) - 0.0049(Ld \times Ai) + 0.0060(Gat \times Ai)$	50.7%	0.024
$C. cookei = [0.20 + 0.82(Ch) + 0.17(CH) - 0.33(Ch \times CH)]^2$	73.1%	<0.001
$L. donaldsoni = 0.66 + 0.45(Ch) - 0.72(CH)$	23.9%	0.025
$E. epiphanes = 1.48 - 0.029(Ld) + 0.0043(H11 \times Ld)$	41.1%	0.002
$S. kelloggi = -0.11 + 0.0037(Gal) + 0.013(SH) - 0.00007(Gal \times SH)$	13.6%	0.105

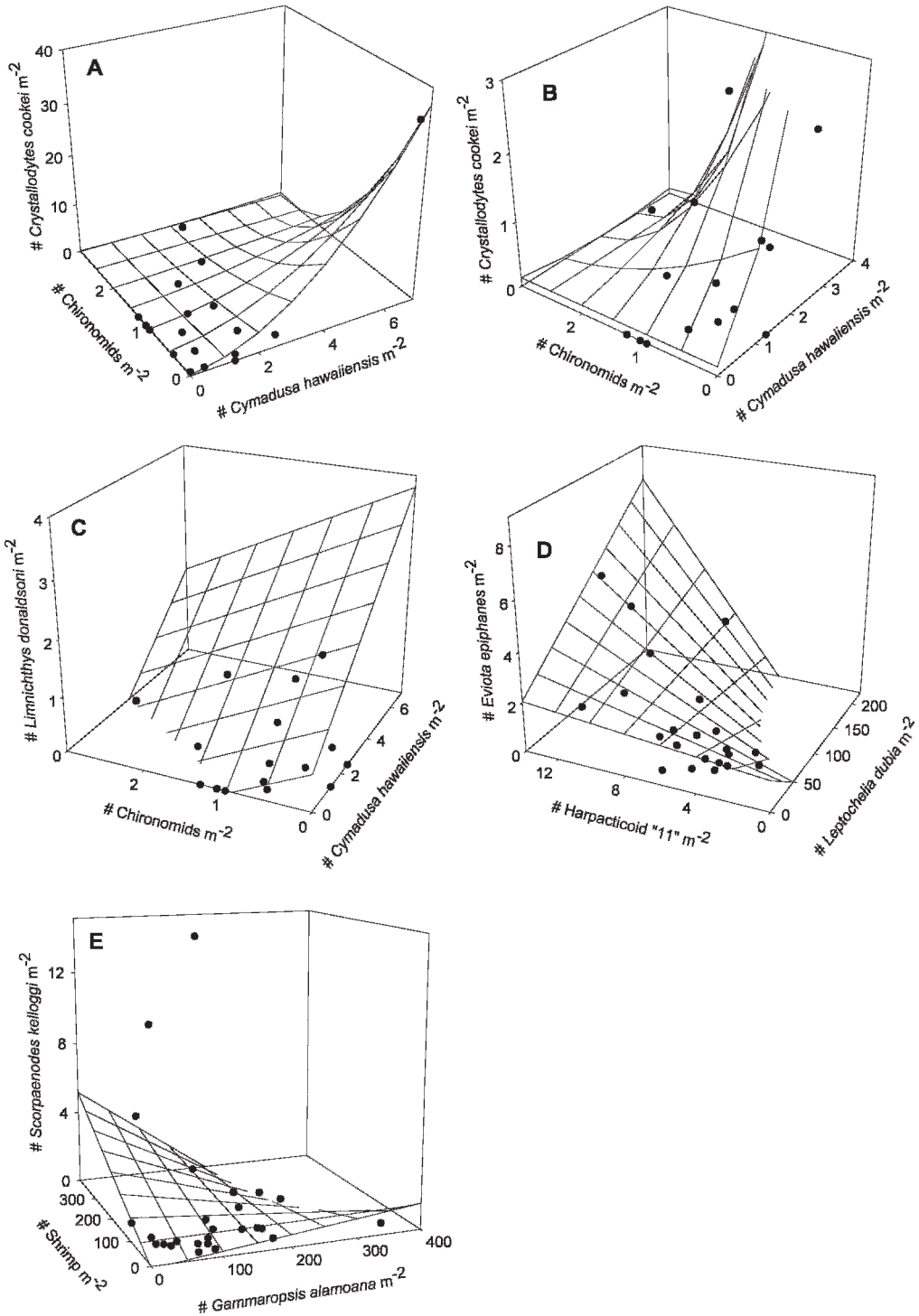


Fig. 2. The predicted (grid) and observed (points) relationship between densities of cryptic reef fishes and their important prey. (A) *Crystalloydites cookei* vs. the amphipod, *Cymadusa hawaiiensis*, and chironomid larvae. (B) Fig. 2A with an extreme value truncated. (C) *Linnichthys donaldsoni* vs. the amphipod, *Cymadusa hawaiiensis*, and chironomid larvae. (D) *Eviota epiphanes* vs. the tanaid, *Leptochelia dubia*, and harpacticoid "11." (E) *Scorpaenodes kelloggi* vs. the amphipod, *Gammaropsis alamoana*, and shrimp.

Hawaiian cryptic reef fishes and the high mean overlap among fishes from higher latitudes (Maitland, 1965). Results of the present study, however, differ remarkably from Bellwood et al. (2006) who found no dietary specialization among wrasses when broad taxonomic and pseudo-taxonomic categories were used for dietary analysis.

I suggest the latter difference is due mainly to the degree of taxonomic resolution. In fact, overlap among some species pairs in the present study would be even lower had diets been analyzed below the species level. For instance, the tanaid, *Leptocheilia dubia*, is an important prey of *Eviota epiphanes* and *Cirrhitoys fasciatus*. However, *C. fasciatus* preys primarily on males, whereas *E. epiphanes* ate exclusively females. The corallivore *Exallias brevis* would appear to have high dietary overlap with many butterflyfishes (not examined in this study); however, butterflyfishes eat polyps from coral colonies, whereas *E. brevis* scrapes the coenosarc (tissue connecting polyps) from the surface of corals.

Patterns of overlap among these fishes were stable during the study period. Dietary overlap among cryptic reef fishes is not likely to vary due to seasonal dietary change (Table 3) or a high degree of opportunism. Ephemeral prey, when superabundant, do not appear in the diets of these fishes (pers. obs.). I compared diets of fishes collected along with large numbers of calanoid copepods, zoea, or phyllosoma larvae to the diets of a size- and species-composition-matched group of fishes collected when these prey were absent. None of these ephemeral prey, individually or pooled, was eaten more frequently when superabundant.

This comparison does not eliminate the possibility that these prey are sometimes taken when superabundant, but it does show that, at least for the small, cryptic, reef fishes in this study, opportunism does not occur with the frequency suggested by Smith and Tyler (1973). Similarly detailed analyses on serranids show that larger, coral-reef piscivores are not the opportunistic generalists they are commonly assumed to be (Beukers-Stewart and Jones, 2004). The results from this dietary overlap analysis, along with evidence (Table 1) that the taxonomic detail typically used in studies of fish diets can result in falsely elevated overlap values, suggest that assumptions downplaying the importance of food specialization in structuring reef fish communities should be reexamined.

Food and species richness.—Most general hypotheses (Pianka, 1966) about the causes of latitudinal gradients in species richness suggest that high diversity in the tropics is, at least partially,

allowed by increased resource specialization by tropical organisms. The increased dietary specialization among tropical fishes demonstrated here is consistent with that view. In a review of resource use in fish communities, Ross (1986) suggested that trophic separation may be more important in coral-reef fish assemblages than previously thought: trophic partitioning was suggested to be important in all reef-fish studies that examined food use.

These results do not demonstrate the cause of fine-scale food specialization in these fishes. Low overlap values are often used as evidence of resource partitioning. Formally defined, resource partitioning is a competition-induced, genetically-based shift in the fundamental niche of coexisting species after coming into sympatry (Walter, 1991). Ecologists have long been warned that overlap values are not indicative of competition, past or present (Colwell and Futuyma, 1971; Connell, 1980; Krebs, 1999), and I have not performed the tests necessary to demonstrate competition. Plausible alternatives, such as phylogenetic constraints on feeding, can explain the low overlap observed here. Also, because piscivores may confine these cryptic fishes to refugia, and most prey of these cryptic fishes are habitat specialists (Longenecker, 2001), fishes confined to a habitat may also be confined to a limited suite of prey.

Regardless of the cause of low dietary overlap in this study, results of regression analysis (Fig. 1) demonstrate a non-random, positive relationship between latitude and dietary overlap among fishes. Variation in these data is high, but similar levels of variability are commonly seen in large-scale biogeographic analyses. For instance latitude explained only 15% of the variation in coral reef-fish-diversity patterns (Bellwood and Hughes, 2001).

Because the data examined here were obtained from separate studies, there is no control for phylogenetic relationships among the fishes examined, season or duration of study, ocean, or location within an ocean basin. Attempting to include these controls would make any comparison impossible. I suspect these and other variables are likely contributors to the low explanatory power of the regression. For instance, some studies used numerical data for overlap analysis, whereas others used biomass or volume data. Remarkably, overlap estimates can differ by 1150% depending on which measure is used (Hall et al., 1990). Until a systematic study incorporating high-resolution dietary analysis to compare communities worldwide is conducted, these suggestions will remain speculative. The salient point is that a pattern emerged from

a global analysis of dietary overlap: coral-reef fishes are more specialized than fishes in higher latitudes.

A decrease in dietary overlap alone may permit high species richness in coral reef fishes, but the possibility of food influencing global diversity patterns is increased when patterns of prey diversity are considered. Species richness of potential prey increases in tropical waters (Sanders, 1968; Kohn, 1971; Roy et al., 1998), suggesting that more consumer species can be supported in tropical waters. Because few higher taxa are limited to the tropics, this pattern is seen only at high taxonomic resolution of potential prey. These patterns in prey use and diversity are consistent with the diversity-gradient hypotheses (Pianka, 1966), suggesting that resource specialization and an expanded resource base permits the local coexistence of fishes on coral reefs.

Food and relative abundance.—Reef fishes require an appropriate habitat for survival and reproduction; however, the factors that control the relative abundance of species within a habitat have remained elusive. Several authors suggested that food availability strongly influences the distribution and abundance of reef fishes (Clarke, 1992; Polunin and Klumpp, 1992; Risk, 1997). Reduced food supply is correlated with decreased survival and growth (Kokita and Nokazono, 2001) and condition (Pratchett et al., 2004). Conversely, just five daily minutes of supplementary feeding causes an increase in body condition (McCormick, 2003). Perhaps the latter explains why small-scale differences in physiological condition correlate with prey availability in the field (Berumen et al., 2005).

Food supplementation increases the growth rate of juvenile reef fishes (Jones, 1986). This response can be rapid (Kavanagh, 2005) and increase the number of juveniles reaching maturity (Forrester, 1990). For adults, increased feeding rates coincide with increased growth rate and fecundity (Clarke, 1992). These food-related demographic changes suggest that, ultimately, the abundances of reef fishes can be influenced by food availability.

Until recently no studies have simultaneously monitored changes in fish abundances and food levels (Jones, 1987). We now know the biomass of large herbivores correlates well with algal production (Russ, 2003), and strong positive relationships exist between the abundance of reef fishes and their food (Wilson, 2001; Connell, 2002; Gregson and Booth, 2005). Stewart and Jones (2001) demonstrated such a relationship for a large, coral-reef piscivore during an 18-month period of dramatic prey fluctuations.

Perhaps the most striking examples of food levels influencing reef-fish abundance are seen in early life-history stages. Food-supplemented larvae had higher growth and condition but lower mortality (Booth and Alquezar, 2002) and were two (Booth and Hixon, 1999) to four (Booth and Beretta, 2004) times more likely than low condition individuals to persist when returned to the reef. Conversely, laboratory experiments resulted in all low- but only 33% of high-condition individuals being eaten by predators (Booth and Beretta, 2004).

All of the above studies were based on one species or functional group (e.g., large herbivores). Although a significant change in abundance of a single species affects all relative abundance measures within an assemblage, the ability to relate food to the abundance of many species within an assemblage would provide stronger evidence that food structures communities. Here I examined six species representing 69.3% of the total small, cryptic individuals collected during the study. That five significant ($P < 0.05$) regression equations and one strong trend ($P = 0.105$) occurred in the six fish species I examined (Table 5, Fig. 2) suggests that densities of individual species within approximately 10 m² areas are strongly related to the abundance of different suites of prey.

Clearly, food plays a significant role in the local assemblage structure of the cryptic reef fishes studied here, contradicting an assumption common to models that have profoundly influenced the direction of reef-fish-diversity research during the past 35 years and consistent with general patterns about the causes of global diversity patterns. Granted, a number of factors (e.g., historical biogeography, phylogenetic constraints among temperate taxa, and global differences in levels of competition and predation) acting independently or synergistically with food resource use may influence reef-fish-diversity patterns. Nonetheless, these findings are driven by detailed observations of prey identity and abundance and provide clear justification for considering food use and availability as important factors that structure reef fish diversity.

ACKNOWLEDGMENTS

My dissertation committee, D. Greenfield, J. Parrish, J. Randall, C. Smith, and J. Stimson helped greatly with the expanded version of this manuscript. Thanks to G. Aeby, B. Font, and R. Wolff for identifying chironomids and R. Langston, J. Mendez, and K. Sherwood (and many others) for help in the field. Support for this research, in the form of graduate assistantships, was provided by the University of Hawaii

Department of Zoology and the Hawaii Institute of Marine Biology. This work was conducted under University of Hawaii IACUC protocol #93-048. This is HIMB contribution #1248 and contribution 2007-001 of the Hawaii Biological Survey.

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