A functional approach to ecomorphological patterns of feeding in cottid fishes

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Synopsis

One of the major goals of an ecomorphological analysis is to correlate patterns of interspecific differences in morphology with patterns of interspecific differences in ecology. Information derived from functional morphological studies may provide a mechanistic framework supporting the correlation, but the move from a correlational relationship to a causal relationship requires experimental evidence that the interspecific morphological differences create performance differences and therefore ecological differences. The goal of this study was to examine ecomorphological relationships in the diets of cottid fishes (Scorpaeniformes: Cottidae) from the northeastern Pacific by using functional classifications of predators (based on their mode of attack) and of prey (based on their anti-predator defenses). The proposed ecomorphological relationships were tested by examining capture success among the cottids in attacks on prey with different escape abilities. As predicted on functional morphological grounds, both multivariate and univariate analyses indicated that the gravimetric importance of 'elusive prey' (i.e. fishes, shrimp, mysids, and octopods) was greater in cottid species with a larger relative mouth size. Supporting a causal link between morphology and ecology, performance tests indicated that larger-mouthed cottids had significantly higher capture success on *Heptacarpus* shrimp than did smaller-mouthed species. As predicted, there were no differences in capture success among predators regardless of their attack style or ecomorphological patterns in attack on crabs (*Cancer* and *Petrolisthes* spp.) when the crabs were presented on a sand surface (i.e. 'easy prey'). Several difficulties still exist when trying to apply a functional group approach to ecomorphology. These include the behavioral plasticity of the predators, the confounding factor of evolutionary history in identifying correlated ecomorphological features, multiple morphological solutions to common functional problems, the limitations of traditional dietary studies during extremes of prey abundance, and an inadequate understanding of the anti- predator defenses of most prey, including modifications that occur during ontogeny or in different habitats.

Introduction

While the details may differ from study to study, researchers investigating the ecomorphological relationships of a group of species (often members of a clade or assemblage) use a common methodology. Parallel studies identify the prominent ecological and morphological variables, quantify these variables for each species, and determine interspecific patterns of variation for the ecological and the

morphological variables; in the final step, correlations between the ecological and morphological patterns tie the parallel studies together.

While attempts to assess the role of a fish's morphology in determining its ecology, especially diet, have a long history (see Motta et al. 1995), the study of fish ecomorphology exploded in North America after the pioneering study of Keast & Webb (1966). Here, interspecific patterns of diet and distribution were compared with patterns of variation in mouth structure and body form in an assemblage of temperate freshwater fishes. Later ecomorphological studies have further refined these results for temperate freshwater fishes (e.g. Keast 1978, Gatz 1979a, 1979b, Page & Swofford 1984, Douglas & Matthews 1992) and extended them to tropical freshwater fishes (e.g. De Silva et al. 1980, Barel 1983, Winemiller 1991), coral reef fishes (Davis & Birdsong 1973, Emery 1973, Motta 1988), temperate marine fishes (e.g. de Groot 1969, De Martini 1969, Chao & Musick 1977, Norton 1991a, but see Grossman 1986), and deep-sea fishes (e.g. Ebeling & Cailliet 1974, McLellan 1977, Casinos 1978).

At its heart, the major limitation of the ecomorphological methodology is that it is strictly correlational (Wiens & Rotenberry 1980); the bridge from correlation to causation depends on providing a mechanistic foundation by which interspecific differences in morphology can influence organismal performance and, thereby, trophic ecology. Increasingly, the results of functional morphological and biomechanical studies are being used to provide plausible mechanistic bases for the interrelationship between morphological and ecological patterns. In a few studies, these mechanisms have been tested in performance studies, (e.g. McComas & Drenner 1982, Bentzen & McPhail 1984, Wainwright 1988, Norton 1991a).

Much of our insight into the feeding mechanisms of fishes has come in the last twenty years, building on early efforts of Osse (1969) and Alexander (1967, 1970) to apply the techniques of experimental functional morphology to the feeding process. These and subsequent studies have addressed the relative timing and duration of muscle activity during the strike (e.g. Elshoud-Oldenhave & Osse 1976, Liem 1978, 1979, 1980a, Wainwright & Lauder 1986, Sand-erson 1988) and during prey processing (e.g. Lauder & Norton 1980, Lauder 1983a, 1983c, Liem & Sanderson 1986), the timing and magnitude of the generation of subambient pressure in the buccal and opercular cavities (e.g. Lauder 1983b, van Leeuwen 1984, van Leeuwen & Muller 1984, Norton & Brainerd 1993), the patterns of flow and prey movement in front of the jaws (e.g. Lauder & Clark 1984, Muller & Osse 1984, Drost et al. 1988, Coughlin & Strickler 1990, Norton & Brainerd 1993), and the kinematics used during the strike (e.g. Lauder & Liem 1981, Sanderson 1990, Westneat 1990) and during the attack (Vinyard 1982, Webb & Skadsen 1980, Webb 1984b, Norton 1991a).

In an attempt to organize the results of this functional morphological research, Liem (1980b) divided the major feeding methods of fishes into three types: suction feeding, ram feeding, and biting. In biting, the primary jaws are used to tear the prey from the substrate to which it is adhering or to bite a piece from a larger prey item. In ram feeding, the predator opens its mouth and swims through the prey, often aided by explosive protrusion of the premaxilla (e.g. *Luciocephalus pulcher* – Lauder & Liem 1981, *Epibulus insidiator* – Westneat & Wainwright 1989). In suction feeding, rapid expansion of the buccal cavity of the predator creates a large subambient pressure that draws a jet of water into the mouth (Lauder & Clark 1984); this jet of water drags the prey into the mouth. Despite these discrete descriptions, these feeding methods better identify end-points of a continuum, especially between ram and suction feeding (Norton & Brainerd 1993).

Based on these simple definitions, any predator should be capable of performing any of these methods. Biting simply requires the predator to close its jaws. The essential element in ram feeding is the ability to swim. The basic neuromuscular patterns and head movements of suction feeding are similar to 'heavy breathing' (Liem 1980b). However, the intrinsic attributes of a predator, i.e., the unique interaction of its morphology and its behavioral repertoire, may define how well a predator may perform any of the three methods. Specializations that improve the ability of a predator to use one method

may constrain the performance of another method (Fig. 1a).

For example, morphological specializations that may improve biting performance are related to force generation and delivery at the expense of speed of movement. These specializations may include hypertrophy of the adductor musculature, robust jaws with cutting teeth, and restricted jaw mobility. By contrast, predators that are specialized to use either ram or suction feeding are likely to emphasize speed over force with features such as equivalent development of adductor and abductor muscles in the head, highly kinetic jaws, and light jaws with holding teeth, but at the expense of their ability to deliver a powerful bite. For example, among Caribbean labroids, the parrotfishes clearly have the traits of a 'biter' and wrasses like *Epibulus insideator* and *Clepticus parrai* have the traits of ram feeders (Westneat & Wainwright 1989).

The success of a suction attack depends on the ability of the predator to use a jet of water to drag the prey into its mouth. Among a variety of other factors (see Norton & Brainerd 1993), this drag force depends on the square of the velocity of water passing around the prey. Mechanisms that increase the velocity of water at its source (i.e. the entrance to the mouth) can have a great effect on the drag force experienced by the prey. Mechanisms that may increase water velocity by increasing the subambient pressure in the buccal cavity include increasing the volume change in buccal cavity, decreasing the area of the open mouth, isolation of the buccal and opercular cavities, and increasing the rate of buccal expansion (Lauder 1983b, Norton & Brainerd 1993). The interaction of these morphological differences and behavioral differences during the strike may lead to dramatic interspecific differences in the timing and magnitude of subambient pressures generated during the strike, e.g. *Lepomis gibbosus* versus *Micropterus salmoides*, *Cichlosoma severum* versus *Cichla ocellaris* (Lauder 1983b, Norton & Brainerd 1993). The drag force on the prey can also be increased if the prey is centered in the stream (e.g. Lauder & Clark 1984) and if the attack starts as close to the prey as possible, minimizing flow attenuation. Both of these would require an agile locomotor complex (e.g. laterally-po-
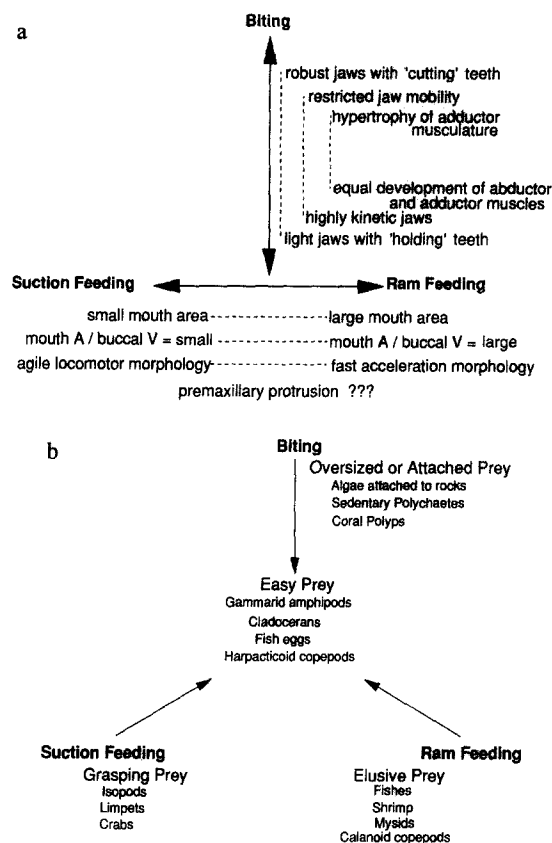

Fig. 1. a – Predicted morphological contrasts among predators specialized to use biting, ram feeding, or suction feeding as their predominant feeding mode. b – The association of prey employing common anti-predator strategies with the predator feeding mode to which they are likely to be most vulnerable.

sitioned pectoral fins, a laterally compressed body, etc.) that would allow fine tuning of the predator's position prior to the strike (Webb 1984a, 1988).

In contrast, a large catching area, i.e. a large gape, would improve the capture success of a ram feeding predator (Norton 1991a). In addition, as speed is essential to attack many prey successfully, the best ram predators are likely to have locomotor adaptations that maximize the ability of the predator to accelerate and reach high attack velocities. Such specializations may include a subcarangiform body, a thick caudal peduncle, and posterior extensions of the median fins (Webb 1984a).

Prey are not passive elements in this predator-prey interaction. In the same sense that predators may differ in their styles to capture prey, prey show a variety of styles to avoid capture. I have separated

these into four groups by the functional challenge that they present to the predator (Fig. 1b), although, like the predator feeding modes, these groups are likely to be more continuous and less discrete than indicated. 'Grasping prey' (e.g. isopods, limpets, and crabs) are mobile prey that are capable of adhering to the substrate. 'Oversized or attached prey' (e.g. benthic algae, sedentary polychaetes, coral polyps) are prey that are larger than the mouth size of their predators or are permanently attached to an object that cannot be ingested by the predator. 'Elusive prey' (e.g. fishes, shrimp, mysids, and calanoid copepods) are prey that are capable of avoiding capture because of their locomotor ability (e.g. Webb 1979, 1982, Daniel & Meyerhofer 1989). Finally, 'easy prey' (e.g. gammarid amphipods, cladocerans, fish eggs, harpacticoid copepods) have no major morphological defenses against capture once discovered.

To be successful, the anti-capture strategies of the prey need not render them invulnerable to capture, but should restrict the suite of predators that are potential threats (Vermeij 1982). Matching the relative strengths and weaknesses of predator and anti-predator strategies, one can predict that 'grasping prey' may be most vulnerable to attacks by suction feeding predators, 'elusive prey' to attacks by ram feeding predators, and 'oversized and attached prey' to biting predators. 'Easy' prey may be encountered in the diet of any predator.

The goal of this study was to apply this simple functional approach to investigate possible ecomorphological patterns among members of the family Cottidae (Pisces, Scorpaeniformes). Feeding experiments were conducted in the laboratory to test predictions of interpredator differences in capture ability on prey types with varying anti-predator strategies. Finally, I discuss some of the limitations of applying a functional approach to both predators and prey.

Cottid fishes are an especially good group to examine possible ecomorphological patterns due to their species richness, abundance, and morphological diversity. Further, their benthic habit and cooperative behavior in captivity make laboratory experiments easier logistically and less of an abstraction from field conditions. Cottids are among the most speciose and abundant fishes in nearshore subtidal and intertidal habitats of the northeast Pacific. Over 90 species are found between Baja California and the Aleutian Islands (Howe & Richardson[1]). Within this geographic range, cottids often dominate the fish community in intertidal (Chadwick 1976, Cross 1981, Grossman 1982, 1986, Yoshiyama 1981, Yoshiyama et al. 1986) and nearshore benthic fish communities (Burge & Schultz,[2] Leaman,[3] Moulton 1977, Peden & Wilson 1976, Simenstad et al.,[4] Yoshiyama et al. 1986, Norton 1991b). The diets of most cottids are dominated by benthic crustaceans, especially gammarid amphipods, crabs, isopods, and shrimp, but some species specialize on other prey taxa, including other fishes, gastropods, and algae (Mitchell 1953, Mollick 1970, Nakamura 1971, Yoshiyama 1980, Cross 1981, Freeman et al. 1985, Grossman 1986, Wells 1986, Stebbins 1988, Norton 1989, Demetropoulos et al. 1990). Most of the prey are ingested whole with a minimum of mastication (i.e. captured not by biting). Cottids also exhibit considerable diversity in body shape, mouth size and position, and fin placement and size (e.g. Strauss & Fuiman 1985, Norton 1991a).

Materials and methods

Morphological patterns of cottid fishes

While previous ecomorphological studies have incorporated a variety of morphological variables, I
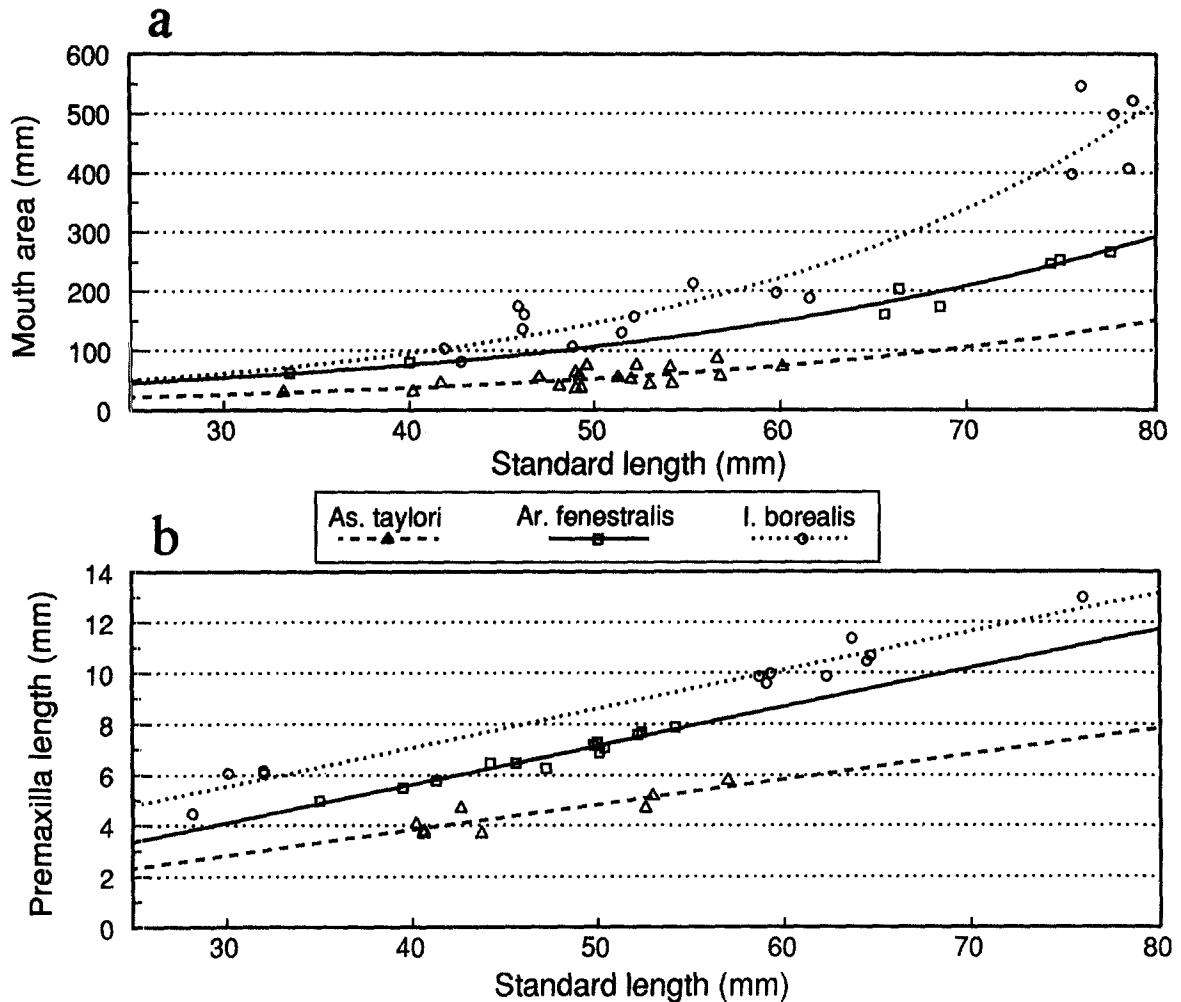
Fig. 2. a – Allometric relationship between mouth area and standard length for a large-mouthed cottid (*Icelinus borealis*), a small-mouthed cottid (*Asemichthys taylori*), and an intermediate species (*Artedius fenestralis*). Mouth area was measured after filling the buccal cavity maximally with silicone sealant. b – Allometric relationship between premaxilla length and standard length for the same species. Premaxilla length was measured from the dorsal midline to the tip of the descending process.

have focused on a single feature, relative mouth size, that I propose as a morphological distinction between ram and suction feeding fishes. Mouth size has two roles in determining diet: (1) by providing an absolute limit on the size of prey that can be ingested (see Wainwright & Richard 1995) and (2) by determining the relative success of an attack through its effect on suction generation or on the surface available to catch prey (Norton 1991a, Norton & Brainerd 1993). The emphasis in this study is on the second role. Several techniques are available to estimate predator mouth size. The most direct measurement would be derived from high-speed

video or cinematography of actual strikes, but this is often not possible. A more indirect indication of mouth size can be determined from the maximum expansion of the buccal cavity of freshly-killed individuals (e.g. Osse 1969, Grobecker & Pietsch 1979, Norton 1991a, Norton & Brainerd 1993). By this technique, estimates of mouth size are determined by filling the fully abducted buccal cavity of an individual with silicone sealant and then measuring the area of the gape (see Fig. 2a). Finally, in the absence of fresh specimens, mouth size can be estimated from premaxilla length (see Fig. 2b).

Because of a lack of high-speed video sequences

or of fresh specimens for all the species included in this study, mouth size was estimated by measuring the length of the premaxilla (the distance from junction of the left and right premaxilla at the dorsal midline to the ventral tip of the descending process) for 6 to 13 individuals of 18 northeastern Pacific cottid species. The efficacy of using premaxilla length as a coarse measure of actual gape is supported by data from high speed video for a subset of the cottid species (Norton unpublished data) and by data on mouth casts (Fig. 2 and Norton 1991a). While premaxilla length is not as precise as either of the other techniques, it was sufficient for the purposes of this study: to rank these species from those with the largest apparent mouth size to the those with the smallest apparent mouth size. Because of body size differences within and among species, the premaxilla length of each individual was divided by its standard length (SL) to provide estimates of relative mouth size. For all species premaxilla length increased isometrically as standard length increased (e.g. Fig. 2b). The 18 cottid species used in this section and the various species included in the other sections of this study (i.e. dietary patterns, performance tests) are indicated in Appendix 1.

Dietary patterns among cottid fishes

The cottid dietary data in this study are derived from several sites along the northeastern Pacific: from the intertidal and subtidal fish communities of the San Juan Islands, WA (13 species, Norton 1989 and unpublished), from intertidal fish communities off the Olympic Peninsula, WA (2 species, Cross 1981) and off Central California (1 species, Burge & Schultz[1] and from subtidal fish communities from southern California (1 species, Norton unpublished). For the 14 cottid species for which I collected the diet data, I separated the ingested prey into typical taxonomic categories (e.g. gammarid amphipods, shrimp, gastropods, polychaetes) and summarized the gravimetric (i.e. % blotted wet weight) and numerical importance of these categories and their frequency of occurrence. Where possible, size estimates of individual prey items were also recorded, but neither these data, nor the numerical impor-

tance and frequency of occurrence, are included here (see Norton 1989). I focused on gravimetric importance as the critical measure of diet because it is applicable to the broadest range of prey types (tiny gammarid amphipods and harpacticoid copepods to fragments of polychaetes to large shrimp and isopods) and because it can be used to generate rough insights into the allocation of limited gut space among prey types by the predator and of the relative contribution of different prey to the predator's energy balance (e.g. Kaiser et al. 1992). While direct volumetric techniques would be the best estimator of digestive space utilization, accurate measurements of the volume of small prey (e.g. individual gammarid amphipods) is difficult, but accurate measurements of their mass is not; if the density of a prey category is known, gravimetric data can be converted to volumetric estimates. Numerical importance is often problematic for prey types that suffer partial predation (e.g. algae) or that digest quickly in the stomach (e.g. polychaetes) and frequency of occurrence provides only a most indirect indication of how a predator is allocating limited gut space and meeting its nutritional needs. Using gravimetric importance also allowed me to add additional data on the diets of two cottids from intertidal fish communities off the Olympic Peninsula, WA (Cross 1981) and one species off Central California (Burge & Schultz[1]).

Several studies of feeding habits in cottids have demonstrated clear ontogenetic changes in the relative importance of prey taxa (e.g. Cross 1981, Grossman 1986, Norton 1989). Much of this pattern of ontogenetic changes, especially for small individuals, reflects the gape limitations of the predators interacting with the minimum sizes of the various prey taxa available to cottid fishes (see Norton 1989). For example, the smallest crabs and shrimp only become available to benthic-dwelling fishes at or after these crustaceans complete metamorphosis from planktonic megalopae to benthic juveniles. For *Cancer* crabs and *Pandalus* shrimp this transition occurs at approximately 2.0–4.0 mm. Small cottids of all species are unable to feed on these newly-settled crabs or shrimp until the predators reach species-specific minimum sizes (usually > 20 mm SL) at which point their gape is large enough to ingest

these prey. While the diets of small individuals of all species are dominated by a restricted number of small, common prey types (e.g. harpacticoid copepods, gammarid amphipods), the diets of larger individuals broaden and diverge in species-specific patterns (Norton 1989). Because the ecomorphological approach relies on detection of interspecific differences, not similarities, the dietary information incorporated in this study was culled from individuals greater than 30 mm SL (see Appendix 1).

In an attempt to detect patterns of prey use, I performed a principal components analysis (PCA), using SYSTAT, on the correlation matrix of the gravimetric importance of the important prey types (arcsin transformed). Only prey types comprising greater than 3% of the diet were used. The diets of 17 cottid species were included in this analysis (see Appendix 1).

Linking the morphological and ecological patterns

I used two complementary approaches to determine the ecomorphological patterns between diet and feeding morphology among cottids. First, I correlated the estimates of the relative mouth sizes of the predators with their positions along the axes determined by the PCA of dietary data. I calculated two Spearman rank correlation coefficients from the PCA results, the first between the rank order of relative mouth sizes of the predators and their relative positions along the first component axis and the second between the rank order of relative mouth sizes and their relative positions along the second principal component.

I also looked for a relationship between diet and feeding morphology by focusing on the outcomes of interactions between the functional groups of prey and of predators as described in the introduction. I created a composite diet category, 'elusive prey', based on the hypothesis that elusive prey would play a larger role in the diets of large-mouthed cottids than of small-mouthed species. After calculating the gravimetric importance of 'elusive prey' (i.e. shrimp, fishes, octopods, and mysids) for each predator species, these composite data were used in a Spearman rank correlation between rank order of

predators determined by the gravimetric importance of 'elusive prey' to their diets and the rank order of their relative mouth sizes. A second analysis incorporated both the results of the first principal component of the multivariate analysis and the functional group hypothesis; the gravimetric importance of crabs was added to the 'elusive prey' category due to their similar factors loadings on the first principal component. Then I used a Spearman rank correlation to test for a correlation between the rank importance of this composite prey category among the cottid species and rank order of relative mouth size among these predators.

Performance tests with elusive and non-elusive prey

To test for a performance-based mechanism for the observed ecomorphological correlation (i.e. relative mouth size and importance of elusive prey in the diet), I conducted a series of laboratory experiments that examined differences in capture success among cottid species in attacks on 2 prey types with contrasting anti-predator strategies, elusive prey versus easy prey (see also Norton 1991a). These experiments were conducted either at Friday Harbor Laboratories (FHL), Friday Harbor, WA or at the Marine Science Institute (MSI), University of California, Santa Barbara, CA. At FHL the predators were *Jordania zonope, Asemichthys taylori, Rhamphocottus richardsoni, Artedius harringtoni, Ar. lateralis, Chitonotus pugetensis*, and *Oligocottus maculosus*; the elusive prey were shrimp from the genus *Heptacarpus* and the easy prey were crabs from the genus *Cancer*. At MSI the predators were *Orthonopias triacis, Clinocottus analis, Scorpaenichthys marmoratus*, and *Ar. coralinus*; the elusive prey were also shrimp from the genus *Heptacarpus* and the easy prey were crabs from the genus *Petrolisthes*. As the goal of the study was to examine the effects of prey types and predator types on capture success and not the effect of prey and predator size per se on capture success, prey sizes (carapace length for shrimp, carapace width for crabs) in these experiments were standardized to between 4–7% of predator standard length. At these relative sizes
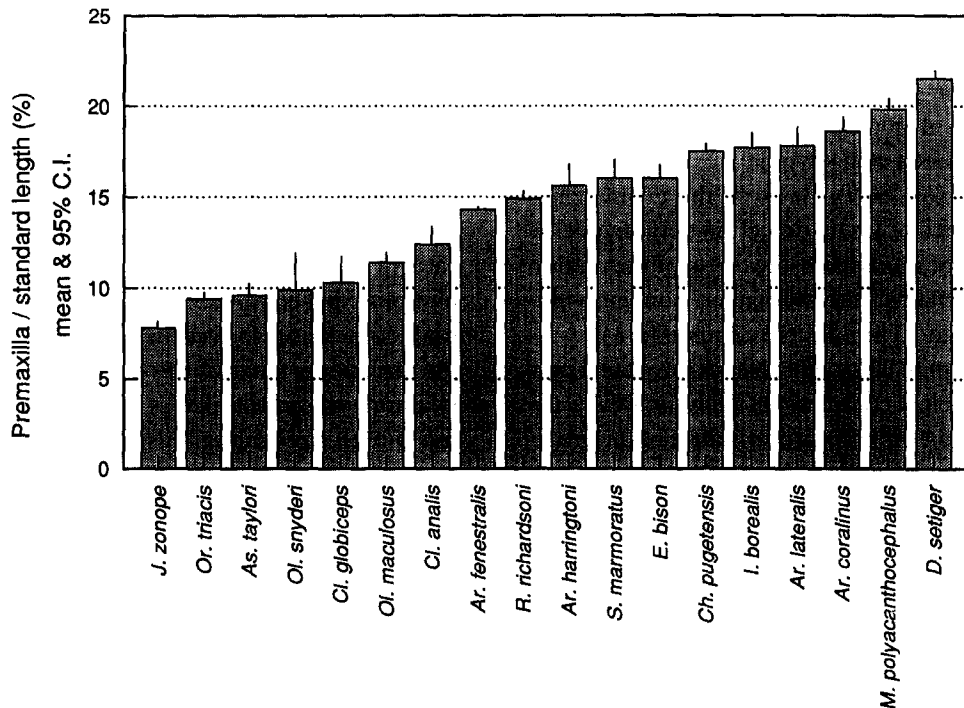
Fig. 3. Estimates of relative mouth size (premaxilla length/standard length) for 18 cottid species. Premaxilla length increased isometrically with increased standard length for all species. The data shown are means ± 95% C.I.

all prey could be easily ingested if captured (i.e. no gape limitation).

Three to four predators were held in each 0.25 m² feeding arena; the bottom of each arena was covered with sand. I introduced each prey item individually into the arena through an opaque tube and allowed it to settle to the bottom before the tube was removed. At that point, individual predators using their pectoral fins would move toward the prey, stop and orient to the prey, often bending their bodies into an S-shape and then attack using both pectoral and axial musculature and fins for propulsion. Only the result (capture or miss) of the initial attack was recorded; chases were not scored. Individual crabs and shrimp were introduced alternately. These were experienced predators attacking their natural prey. The predators showed no evidence of learning during the performance tests, i.e. there was no pattern of increase or decrease in capture success during the course of the experiments.

Results

Morphological and ecological patterns

Cottids clearly show large differences in relative mouth size, estimated as either mouth area or by length of the premaxilla (Fig. 2). The species in this study demonstrated a 3-fold range of mouth sizes and were well-distributed within this range (Fig. 3). For the predator with the largest mouth size, *Dasycottus setiger*, premaxilla length was 21.5% of standard length; for the cottid with the smallest mouth size, *J. zonope*, premaxilla length was 7.8% of standard length. Because of the squared scaling relationship between mouth diameter and area, at any particular standard length small interspecific differences in premaxilla length lead to large differences in mouth area and these interspecific differences become accentuated at larger body sizes (Fig. 2).

Cottids exhibit tremendous diversity in the composition of their diets (Appendix 1). The principal component analysis of dietary patterns among cottid species produced clear separation among spe-

cies and among the prey taxa along the first component axis, which explained 24.2% of the variance (Fig. 4). The component loading on the first axis contrasted elusive prey (shrimp, mysids, fish, octopods) and crabs with all other prey categories. Among the predators the first axis appeared to separate the large-mouthed predators from the smaller mouthed predators. There was a clear correlation between relative mouth sizes among cottids and their positions along the first axis (Spearman rank correlation, $r_s = 0.706$, $p < 0.005$). The second axis explained 15.8% of the interspecific variance in diet (Fig. 4), but a biological interpretation of the distribution of the predators or of prey categories was problematic, a common difficulty in multivariate studies. There was no correlation between predator mouth sizes and their positions along the second principal component axis (Spearman rank correlation, $r_s = -0.129$, $p > 0.05$).

In the Introduction I predicted that there would be a strong relationship between the mouth size of the predator and the importance of elusive prey in the diet. In fact, there is a strong correlation (Spearman rank correlation, $r_s = 0.775$, $p < 0.005$) between mouth size and the gravimetric importance of elusive prey for cottid fishes (Fig. 5). The largest deviations from the prediction were for *Enophrys bison*, *J. zonope*, and *Myoxocephalus polyacanthocephalus*. If I add the gravimetric importance of crabs to the elusive prey category, as would be indicated from the first PCA axis, the correlation between diet and morphology does not increase, but actually declines slightly, although not significantly ($r_s = 0.728$, $p < 0.005$).

Ecomorphology and performance

The underlying assumption in an ecomorphological study is that the interspecific morphological differences that are correlated with the interspecific ecological differences are causally responsible for interspecific differences in performance. For cottids the ecomorphological analysis presented above indicates a link between predator mouth size and the importance of elusive prey. This is supported by the performance tests. There were clear differences
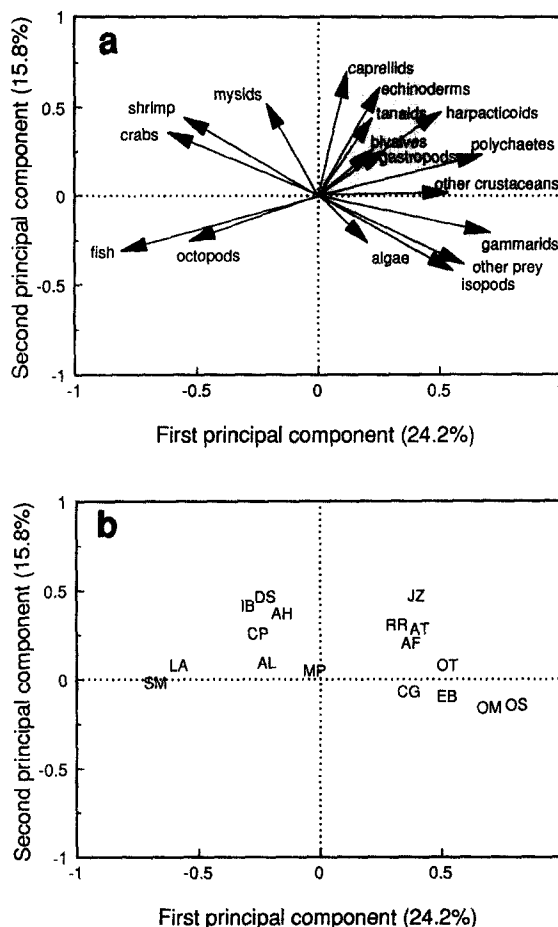

Fig. 4. a – The component loadings of the prey categories from the principal components analysis, i.e. the contribution of the various prey categories to the separation of predator species along the first and second principal component axes. b – The variation among 17 cottid species in the gravimetric importance of prey as determined by their component scores along the first and second principal component axes. The position of each species is indicated by the use of the first letters in its binomen.

among cottid species in their capture success on *Heptacarpus* shrimp (Fig. 6). Capture success ranged from 20% for *Cl. analis* to 77% for *R. richardsoni*. Cottids with larger mouth sizes had higher capture success on shrimp than did cottids with smaller mouths (Spearman rank correlation, $r_s = 0.874$, $p < 0.005$). The predator species with the largest deviations in rank correlation were *R. richardsoni* and *J. zonope*, both of which had higher capture success than predicted by mouth size.

Because the crabs were presented on a sand surface on which they had no opportunity to grasp, I
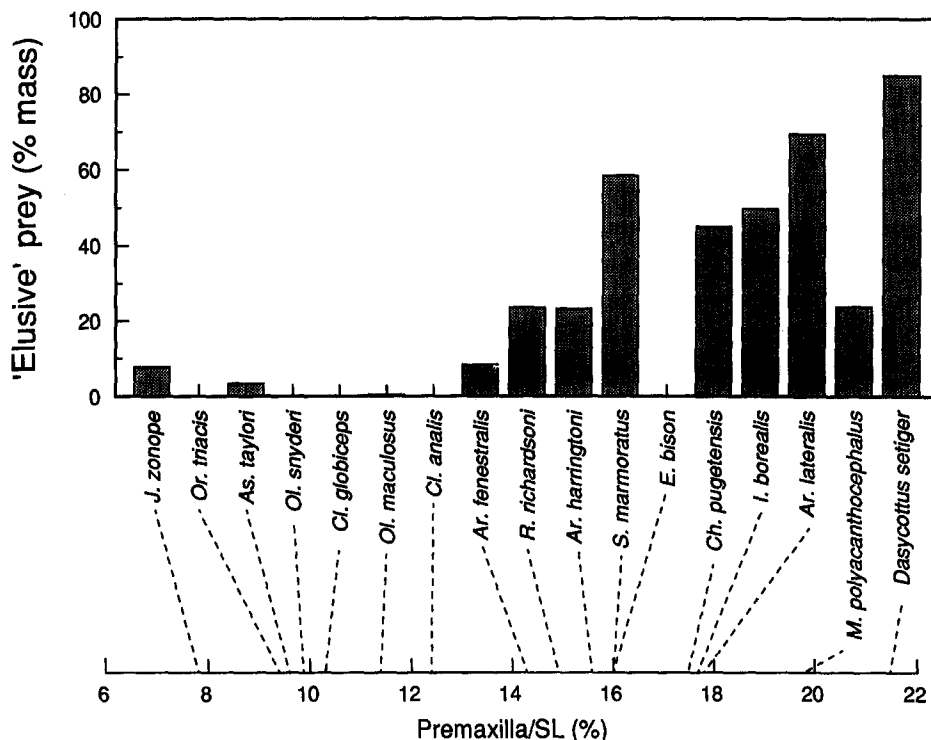
Fig. 5. Correlation between the rank order of relative mouth sizes of 17 cottid species and the gravimetric importance of 'elusive prey' (fishes, shrimp, mysids, and octopods) in their diets. There was a significant positive correlation between mouth size and the amount of elusive prey in the diet (Spearman rank correlation, $r_s = 0.775$, $p < 0.005$).

anticipated that there would be no connection between morphology and performance. Capture success by cottids in attacks on *Cancer* or *Petrolisthes* crabs was universally high; between 80 and 98% of all attacks were successful (Fig. 7). Most of the misses were due to underestimates by the predator of the predator-prey distance at the start of the attack. As predicted, there was no significant correlation between mouth size and capture success on crabs (Spearman rank correlation, $r_s = 0.612$, $p > 0.05$).

Discussion

Traditionally, dietary studies of fishes categorize the ingested prey either by their taxonomic affinities (e.g. crustaceans, molluscs) or by their habitat (e.g. zooplankton, infauna). While these categorizations may impart important information on the impact of fish predation on particular prey populations or indicate the foraging habitat of the preda-

tor, they may not necessarily be the most appropriate categories to assess the possible ecomorphological relationships between predators and prey because they neglect the different functional challenges that the different prey within one of these groups present to a predator. For example, because mysids can escape attacks using a tail-flip they should present a functional challenge to predators more similar to that of caridean shrimp than to that of other paracarid crustaceans (e.g. isopods, tanaids, gammarids amphipods). Similarly, among freshwater zooplankton capture success by fishes on elusive prey like cyclopoid copepods is much lower than on non-elusive prey like cladocerans (Drenner et al. 1978, Vinyard 1982).

Incorporating a functional view of predators and prey, I had predicted that 'elusive prey', prey capable of rapid escape responses, would form a larger proportion of the diet of large-mouthed cottids than of small-mouthed cottids and that these prey would be vulnerable to attacks by these large-
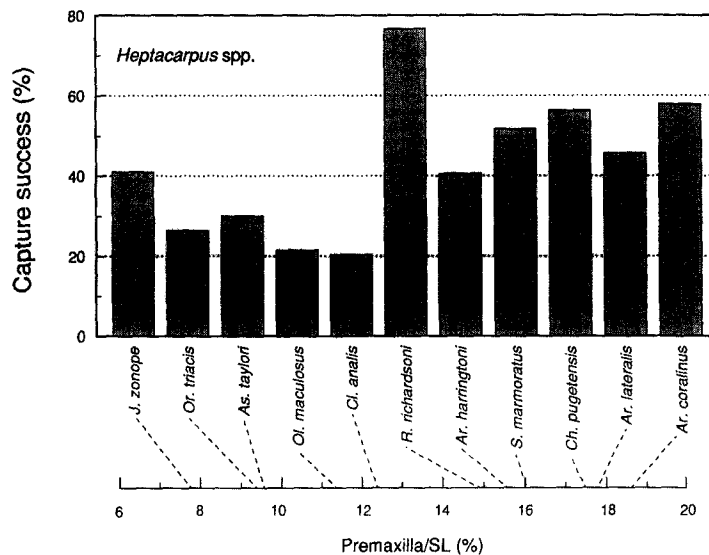
Fig. 6. Capture success (percentage of successful attacks) on *Heptacarpus* shrimp by 11 species of cottids. The predators are arranged in order of mouth size and their exact positions are indicated on the lower x-axis. There was a significant positive correlation between mouth size and capture success on shrimp (Spearman rank correlation, $r_s = 0.874$, $p < 0.005$). The total number of attacks by each species are indicated inside the histograms.

mouthed predators. Both univariate and multivariate analyses indicated a correlation between predator mouth size and the importance of 'elusive prey' in the diet. The results of laboratory experiments provided support for a causal role of mouth size in determining interspecific differences in diet. Cottids with larger mouth sizes had significantly greater capture success on shrimp than smaller-mouthed cottids. Crabs, presented without an effective escape option, were captured with equal facility by both large- and small-mouthed cottids.

These interspecific differences in capture success on shrimp were the result of the interactions of a predator's behavioral repertoire and its morphology. In general, the predators utilized behaviors consistent with their morphology; previous video analysis of the attack kinematics of some of these species (Norton 1991a) indicated that large-mouthed cottids used attack behaviors more consistent with ram feeding (i.e. higher attack velocity, longer initial predator-prey distances), while small-mouthed cottids employed attack behaviors more consistent with suction feeding (i.e. lower attack velocities, shorter initial predator-prey distances). Interestingly, *J. zonope*, the cottid with the smallest mouth size, had a much higher capture success on shrimp and ate a greater percentage of shrimp than did other small-mouthed cottids. Analysis of its behavior in attacks on shrimp indicated that *J. zonope* employed kinematics more similar to large-mouthed, ram feeding cottids.

Detecting and testing ecomorphological relationships in fish assemblages/clades has not been without apparent failures. In this study, I have shown a correlation between mouth morphology and trophic ecology for intertidal and subtidal cottid fishes. Yet, Grossman (1986) was unable to detect an ecomorphological relationship among an assemblage of intertidal fishes dominated by cottids, including several species included in the present study. These opposite conclusions may reflect differences both in the ecological and morphological
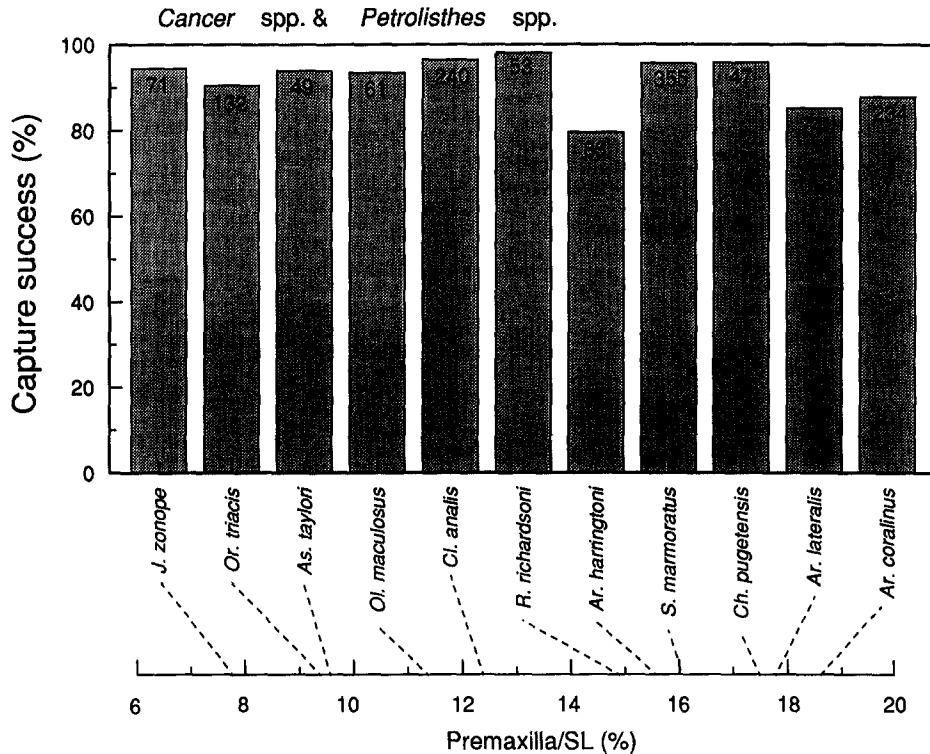
Fig. 7. Capture success (percentage of successful attacks) on *Cancer* and *Petrolisthes* crabs by 11 species of cottids. The predators are arranged in order of mouth size and their exact positions are indicated on the lower x-axis. There was no correlation between mouth size and capture success on crabs (Spearman rank correlation, $r_s = 0.612$, $p > 0.05$). The total number of attacks by each species are indicated inside the histograms.

analyses. This apparent conflict may be due, in part, to the use of functional prey categories in this study versus taxonomic prey categories in Grossman (1986). Attempts to find a universal ecomorphological pattern from these broad taxonomic categories may be problematic. For example, widespread foraging on gammarid amphipods, an 'easy prey', by many intertidal species may have swamped out attempts to detect a morphological basis for interspecific differences in diet for other prey groups (e.g. shrimp, algae). As I have shown for crabs presented on a sand surface, a variety of attack styles and morphologies may be successful in acquiring these 'easy prey', but prey such as shrimp, limpets, and algae may require specific styles and morphologies. Thus, the conclusions of both studies could well be correct, there may be no general ecomorphological correlation among all predators for all prey taxa, but strong specific ecomorphological correlations may exist for a subset of the potential prey. I

have shown experimental evidence supporting the ecomorphological link between a large mouth size and the importance of elusive prey. Additional ecomorphological correlations are likely to be present in this intertidal system; I would predict that adaptations for biting would be found among the herbivorous stichaeids and cottids from Grossman (1986).

Another major difference between the studies is that I focused on a single morphological character while Grossman (1986) included a variety of traditional morphological measurements. One clear result of his morphological analysis was the proper assignment of individuals to the appropriate species and the clustering of related species, but no relationship to diet. One major problem when using multiple morphological features is that the specific structure of each feature reflects both its current ecological utility and its historical derivation, and these influences are not easily separated. For example, in a multi-family study of stream fishes Douglas

& Matthews (1992) have shown that the morphological features of freshwater stream fishes could be separated by a multivariate analysis most clearly into taxonomically-aligned groups, not necessarily into ecologically-aligned groups, except when the analysis was restricted to within a single family.

While a multivariate analysis such as that of Grossman (1986) and Douglas & Matthews (1992) may be effective in generating patterns from morphological data, these patterns will reflect differences among taxa due not only to the effect of ecological demands on morphology, but also by their evolutionary history and constructional constraints. As more and more morphological features are included in the analysis, it is quite possible that influence of evolutionary history will overwhelm any ecological influence. All of the morphological features contain information (albeit to varying degrees) of an unique shared evolutionary history, but these features may reflect a variety of ecological tasks (prey capture, migration, anti-predator avoidance, mating, etc.) that are the responsibility of only a small subset of the morphological features. For example, the presence of only a single feature may open up a new prey resource to the small clade in which it appears (Norton 1988 and unpublished data), but its importance would likely get lost in a multivariate analysis among many other features. More functional morphological research is needed to pinpoint which morphological features have the biggest effect on organismal performance. Focusing on these few, rather than a broad smorgasbord of features may prove to be more useful in identifying potential ecomorphological relationships among species.

In addition to the confounding effect of evolutionary history, several other factors may make it difficult to produce a precise functional classification of predators based on their morphological characteristics. First, the morphology of a species may represent a compromise among the three feeding modes (Barel 1983). While such compromises may reflect historical constraints (e.g. developmental pathways, structural limitations), they may also reflect compromise solutions to variation in the prey resources (e.g. seasonal, temporal, and spatial changes in prey abundance). Differences in the sta-

bility of various components of the resource base may lead to tradeoffs between a morphological specialist with higher predatory efficiency, but limited diet breadth and a morphological generalist with the reduced efficiency, but broader diet breadth. Second, predators that possess a morphology specialized for one attack mode may show behavioral flexibility in response to the type and position of their prey (e.g. *J. zonope*). This flexibility may compensate, in part, for constraints imposed by particular morphological specializations.

For most predators morphological features involved in prey capture are unlikely to be the only part of the predatory process where morphology has a strong influence on diet. Sensory adaptations interact with searching behavior to influence the encounter rates of different prey (e.g. Cooper et al. 1985) and digestive adaptations may determine the relative profitability of prey after capture (e.g. de Groot 1969, Ogden & Lobel 1978, Luczkovich & Stellwag 1993). The lack of some prey types (e.g. operculate gastropods, algae) in the diets of many fishes may be due not to any difficulties in capturing these 'easy prey', but to the ability of these prey to survive passage through the digestive tract of predators that lack morphological specializations to gain access to the nutritive parts of these organisms. Ogden & Lobel (1978) described several ways used by herbivorous Caribbean reef fishes to digest algae that possess a wide range of structural defenses. Among the cottids in this study, *Enophrys bison*, an omnivore, has a longer digestive tract (a common adaptation for digesting plants) than other cottids that I have examined (personal observation). Similarly, Norton (1988) showed that operculate gastropods have the ability to survive passage through digestive tract of cottids unless the predator has morphological specializations to pierce the shell/operculum barrier. Functionally equivalent 'solutions' by teleost predators to this barrier may be found in the primary jaws (e.g. Diadontidae – Palmer 1976), pharyngeal jaws (e.g. Labridae – Wainwright 1988; Centrarchidae – Mittelbach et al. 1992), or vomerine teeth (Cottidae – Norton 1988). A study that focused on strict homology of features would not discern that these various morphological specializations do represent a common ecomorph-

ological pattern, i.e. the ability to digest a special kind of durophagous prey, operculate gastropods.

Because much of the emphasis in ecomorphological studies is in comparing interspecific differences in ecology and morphology, one might assume that those circumstances in which predators with different morphologies forage on the same prey represent situations where morphology plays no role in determining the ecology of a species. It may be the case that interspecific differences in capture success may be unimportant in determining diet during periods when prey are superabundant (e.g. 'spring blooms', emergence of aquatic insects, etc.). Under these conditions, a predator with poor capture success may still have ample opportunity to eat its fill of these abundant prey. However, this interpretation of the situation (i.e. same diet, different morphologies, therefore no ecomorphological relationship), may not be true if the suite of potential prey is restricted and overall prey abundance is low. Interspecific differences in predator morphology, and therefore performance, may have important effects on the energetic bases of ecological interactions among predator species and between predator and prey. Unfortunately, typical diet studies give only a rough indication, at best, of the potential energetic gain of a prey item to the predator. The costs in terms of foraging time and energy expended to acquire the same prey item may vary greatly among predators with different morphological features because morphological differences may lead to differences in performance and ultimately to differences in net energy gain. Among the cottids, the 3-fold difference in capture success in attacks on shrimp may lead to a 3-fold difference among species in the costs required to capture a single shrimp. This may provide a strong selective pressure for a particular morphology under stressful environmental conditions (e.g. Grant 1986). One of the essential unifying questions in ecomorphology, ecology, and evolution is – 'are morphological differences shaped by average conditions or extraordinary conditions' (Wiens 1977)?

The problems with developing a functional classification for prey are also daunting. Most importantly, we possess a very incomplete understanding of the basic anti-predator abilities of most prey.

Among the ontogenetic stages of a single prey species, the larvae, juveniles, and adults may try to avoid predation by very different means and therefore be vulnerable to predators employing different strategies. The physical characteristics of the environment may interact with the anti-predator adaptations of a prey such that prey vulnerability will be influenced by the habitats in which they are encountered. For example, crabs on a sand surface may be vulnerable to predators using any attack mode, but crabs on a rock surface may be less vulnerable overall, and especially to ram-feeding predators. Finally, even among members of a discrete taxonomic category there may be so much species-to-species variability in escape ability that what appears to be an uniform prey type is not discrete, but forms a continuum, much as we see with the predators. For example, among caridean shrimp, *Pandalus* shrimp were twice as likely to escape attacks by cottids than were *Heptacarpus* shrimp (Norton 1991a); this is consistent with comparisons of their escape potential using a biomechanical approach (Daniel & Meyerhof 1989). Crangonid and penaeid shrimps that rely more on crypsis than active escape to avoid predation may be surprisingly vulnerable to suction feeding predators because these prey allow predators to approach very closely before initiating escape, perhaps too close to break free of the drag forces created during a suction attack. This brief discussion points out just a few of the many opportunities for future research in the area of functional treatment of predators and prey.

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Appendix 1

Gravimetric importance of prey categories for each cottid species: The values given along with each predator indicate the number of individuals included in the diet analysis, their mean standard length ± 95% C.I. in mm, and their range in mm. Also included are indications of the phase of the analysis in which they were included: morp. = morphological analysis, diet = principal component analysis of diet, cap. succ. = capture success experiments. The next line gives the average gravimetric importance of each prey category (% wet mass). The data for *Oligocottus snyderi* and *Clinicottus globiceps* are derived from Cross (1980); the data for *Scorpaenichthys marmoratus* are from Burge & Schultz[2]. Values of 0 indicate that that prey type was not found in the diet of a species; * indicate that the prey category was present, but accounted for less than 1% of the total prey ingested. Cope = harpacticoid copepods, Amph = gammarid amphipods, Shrp = shrimp, Mysd = mysids, Tand = tanaids, Isop = isopods, Crab = crab, Bivl = bivalves, Gast = gastropods, Octo = cephalopods, Poly = annelids, Fish = other fishes, Alga = algae.

	Cope	Amph	Shrp	Mysd	Tand	Isop	Crab	Bivl	Gast	Octo	Poly	Fish	Alga
Artedius coralinus: morp., cap. succ.													
Artedius fenestralis: N = 122, 48.5 ± 1.3, (30–98): morp., diet													
	4	39	8	*	1	2	27	1	1	0	15	0	1
Artedius harringtoni: N = 220, 53.9 ± 0.8, (30–89): morp., diet, cap. succ.													
	1	16	20	1	1	1	52	0	*	0	6	2	*
Artedius lateralis: N = 19, 47.8 ± 4.5, (31–92): morp., diet, cap. succ.													
	0	19	50	0	0	1	5	0	0	0	5	20	*
Asemichthys taylori: N = 123, 45.6 ± 0.7, (30.3–61.9): morp., diet, cap. succ.													
	1	17	30	*	*	*	11	7	43	0	13	0	0
Chitonotus pugetensis: N = 123, 45.6 ± 0.7, (30–62): morp., diet, cap. succ.													
	1	17	3	*	*	2	35	*	1	0	7	7	*
Clinocottus analis: morp., cap. succ.													
Clinocottus globiceps: (30–80): morp., diet													
	6	0	0	0	0	0	0	0	0	0	4	0	74
Dasycottus setiger: N = 50, 54.8 ± 2.6, (39–117): morp., diet													
	0	2	65	20	0	0	5	2	0	0	4	0	0
Enophrys bison: N = 33, 47 ± 2.9, (31–126): morp., diet													
	*	37	0	0	3	9	8	*	*	0	11	0	31
Icelinus borealis: N = 80, 50.9 ± 1.3 (30–76): morp., diet													
	2	12	39	9	0	*	36	0	0	0	1	1	0
Jordania zonope: N = 223, 52.4 ± 1.1, (30.1–94.6): morp., diet, cap. succ.													
	22	24	7	1	2	2	18	1	5	0	13	*	*
Leptocottus armatus: N = 22, 129 ± 6.8 (86–207): diet													
	0	1	25	0	0	3	37	0	0	0	0	35	*
Myoxocephalus polyacanthocephalus: N = 43, 73.2 ± 2.7, (46–112): morp., diet													
	*	35	7	2	2	4	31	*	0	0	1	15	*
Oligocottus maculosus: N = 16, 49.3 ± 2.6, (30–62): morp., diet, cap. succ.													
	1	81	0	0	*	7	1	0	1	0	3	0	1
Oligocottus snyderi: (30–80): morp., diet													
	3	49	0	0	0	18	0	0	0	0	14	0	0
Orthonopias triacis: N = 16, 45.2 ± 3.5, (30–68): morp., diet, cap. succ.													
	0	56	0	0	0	0	6	0	0	0	38	0	0
Rhamphocottus richardsoni: N = 28, 44.8 ± 2.8, (30–74): morp., diet, cap. succ.													
	18	30	19	4	0	4	13	0	0	0	7	0	0
Scorpaenichthys marmoratus: N = 29: morp., diet, cap. succ.													
	0	0	1	0	0	0	36	0	2	10	0	48	0