

## **Ecomorphological correlates in ten species of subtropical seagrass fishes: diet and microhabitat utilization**

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Received 1.10.1992

Accepted 30.11.1994

*Key words:* Tampa Bay, Morphology, Feeding, Phylogeny, Convergence, Specialization

### **Synopsis**

Ecomorphological correlates were sought among ten species of distantly related subtropical seagrass fishes. Morphometric data associated with feeding and microhabitat utilization were compared by principal components analysis, cluster analysis, and canonical correspondence analysis to dietary data. Morphology was generally a poor predictor of diet except for a group of mid-water planktotrophic filter feeders. Separation of the species along morphological axes appears to be related more to microhabitat utilization resulting in three major groups: (1) a group of planktotrophic, mid-water fishes specialized for cruising and seeking out evasive prey characterized by a compressed fusiform body, forked caudal fin, long, closely spaced gill rakers, short to intermediate length pectoral fin, pointed pectoral fin, large lateral eye, short head, and a terminal or subterminal mouth; (2) slow swimming, less maneuverable epibenthic fishes that pick or suck their prey off the substrate. They are united by more rounded caudal and pectoral fins, and short or no gill rakers; and (3) a group of more mobile and maneuverable epibenthic foragers characterized by a more compressed, sub-gibbose body, long, pointed pectoral fins, forked caudal fins, large lateral eyes, subterminal mouth, and greater jaw protrusibility. Cases of convergence in trophic and microhabitat utilization characters were apparent in some of the groups.

### **Introduction**

Ecological morphology has as its major premise that the ecology of an organism is related to its morphology. Whereas functional morphology is the study of form and function, ecological morphology overlaps functional morphology and emphasizes form in relation to biological role(s). Although there is no consensus on the definition of ecomorphology, it may be defined as the study of the relationship between environmental factors, both physical and biotic, and form, such as to isolate the mu-

tual contribution of one to the other (Motta & Kotrschal 1992).

One of the purported advantages of ecological morphology is its predictive power (Karr & James 1975, Miles & Ricklefs 1984, Grossman 1986, Douglas 1987). Given that environments constrain morphology and ecology in parallel fashion, we should be able to predict ecological patterns of individuals, populations, or species assemblages from their morphological characteristics (Wiens & Rotenberry 1980).

Although there is no definitive protocol, ecomorphological studies generally seek patterns in

the ecology or behavior of an organism or group of organisms and try to relate them to patterns in form. In the initial step of such analyses, correlations are usually sought between morphological and ecological variables (e.g. Moyle & Senanayake 1984, Wikramanayake 1990, this study). This approach provides predictability, but no causal explanation. It leaves the investigator with uncertainty as to performance, optimality, and the constraints on the 'fit' between form and biological role (Motta & Kotschal 1992).

In the second step of the investigation, one not usually reached in many studies, the predictions are tested through experimentation or modeling in the laboratory to determine the potential niche, and secondly the effect of performance on actual patterns of resource use may be determined through field studies (i.e. the realized niche) (Wainwright 1987, 1991). An ontogenetic analysis of the ecomorphological relationship may be performed at this stage (Galis 1993).

In the third step, comparative phylogenetic analyses are undertaken. Two different comparisons, with different aims, have been applied. Most investigators advocate comparing the variation of a structure and its use within closely related taxa, usually cogenera or cofamilials (Leisler 1980, Yamaoka 1983, Felley 1984, Leisler & Winkler 1985, Yamaoka, Hori & Kuratani 1986, Pounds 1988, Wainwright 1988, Kotschal 1989, Norton 1991); these may include a comparison with a more distantly related outgroup (Motta 1988, Losos 1990a). It is assumed that choosing closely related species will reduce the risk that coincidental differences will mask significant patterns (Huey & Bennet 1986). Findley & Black (1983) explicitly believe, and others implicitly assume, that ecomorphological relationships may be most detectable in closely related species that have a long history of evolution and radiation in the same region. This kind of comparative approach allows one to propose evolutionary scenarios and hypotheses on the process of adaptation and most readily reveals parallel and divergent evolution (Motta & Kotschal 1992).

Convergence is difficult to study in small, more closely related groups. Because we usually have more confidence in our phylogenetic groupings at

broader taxonomic scales, ecological (and morphological) convergences can be identified with greater ease (Winemiller et al. 1995). Therefore, another approach is the comparison of ecomorphological relationships among guilds of more distantly related organisms (Karr & James 1975, Ricklefs & Cox 1977, Gatz 1979a, b, Ricklefs & Travis 1980, Wiens & Rotenberry 1980, Miles & Ricklefs 1984, Moyle & Senanayake 1984, Watson & Balon 1984, Douglas 1987, Miles et al. 1987, Wikramanayake 1990, Block et al. 1991, Wiens 1991a, b, Winemiller 1991). This can be a powerful indicator of convergent evolution (e.g. Karr & James 1975, Wiens 1991b).

While there appear to be superficial ecomorphological correlations related to feeding in fishes, for example, longer gill rakers are associated with planktivory, shorter ones with carnivory; longer guts with herbivory and shorter ones with carnivory (e.g. Chao & Musick 1977, Goldschmid et al. 1984); as well as correlations between fin and body shape, and locomotory abilities and microhabitat utilization (Keast & Webb 1966, Webb 1984), there are few relationships that document ecomorphological patterns in fishes beyond these. Gatz (1979a, b) found extensive ecomorphological correlations based on feeding and microhabitat separation: Norton's (1991) work supported the ecomorphological hypothesis that dietary differences in cottids are in part due to differences in relative mouth size through the influence of mouth size on feeding performance. Furthermore, there is a strong relationship between selected morphological attributes and microhabitat exploitation in a tropical stream fish assemblage (Wikramanayake 1990). Winemiller (1991) also identified ecomorphological divergences within higher taxa of fishes from the same region and convergences between phylogenetically divergent taxa from different regions.

On the contrary, Kotschal (1989) concluded that oral jaw morphology is not a reliable predictor of feeding ecology in 34 species of blennioid fishes. Similarly, Felley (1984) found that a priori morphological character sets derived from previous studies of functional morphology and morphological-environmental associations could not be used to predict habitat use in cyprinids. An a-posteriori set

revealed by factor analysis for a subgroup of cyprinids was more predictive. Because there is considerable amount of residual morphological variation in many communities that cannot be directly related to ecological variables, predictability of morphological relationships in one assemblage from those in another is reduced (Strauss 1987). Furthermore, Grossman (1986) believes that behavior may be more important than morphology in determining prey utilization in a rocky intertidal fish assemblage. Motta (1988) found that morphological structures associated with feeding in butterflyfishes are correlated with how the fishes feed (e.g. suction, scraping, biting), rather than with what they feed on. Many of these studies that seek correlations between morphology and diet or microhabitat utilization do not utilize multivariate techniques of direct gradient analysis, that is, techniques that statistically compare combinations of environmental and morphological variables simultaneously. Consequently the interpretation of such studies can be weakened if the comparison between the environmental and morphological variables is subjective.

This study is significant in that it: (a) employs a suite of univariate and multivariate techniques, including direct gradient analysis of dietary and morphological data; (b) seeks ecomorphological patterns among a taxonomically divergent group of fishes to investigate whether morphology is a good predictor of diet; and (c) determines if cases of evolutionary convergence can be identified in this feeding guild of seagrass inhabiting fishes. Utilizing ten numerically abundant and taxonomically divergent species of fishes from a subtropical seagrass habitat, this study addresses the following questions: (1) Is morphological similarity among species reflective of dietary similarity? (2) Do these species exhibit convergence in morphology? And, if so, (3) does morphological convergence appear to be related to feeding and/or microhabitat utilization in this diverse fish assemblage?

## Materials and methods

### Study site

Fishes were collected from a seagrass habitat in Boca Ciega Bay, near the entrance to Lower Tampa Bay, Florida (27°41'N, 82°41'W), from May to October, 1989 and 1990. The Tampa Bay system is a large, shallow (< 4 m), subtropical estuary lined by limited mangrove forests and salt marshes. Tampa Bay is approximately 56 km long, 16 km wide at the mouth, with 341 km of shoreline. Five major rivers discharge into Tampa Bay (Comp & Seaman 1985). This nitrogen and phosphorus enriched estuary supports seasonally high phytoplankton biomass and productivity. Seagrass beds, macroalgae, and benthic microflora also contribute to the total primary production of this system (Johansson et al. 1985).

Our study site is a gently-sloping sandy beach leading to a shallow (0.5 to 2.0 m) *Thalassia testudinum* dominated seagrass bed with intervening sandy patches. Dense mats of macroalgae dominated by *Gracilaria* and *Hypnea* spp. were often present. Maximum tidal fluctuations resulted in a 94 cm change of depth, although collections were not made at very low tides.

### Collection and data analysis

Thirty individuals each of ten species found in or above the seagrass beds, including the water column were examined in this study (standard length ranges of the specimens used indicated): *Chilomycterus schoepfi* (striped burrfish, 126–215 mm), *Floridichthys carpio* (goldspotted killifish, 51–79 mm), *Lagodon rhomboides* (pinfish, 120–154 mm), *Eucinostomus gula* (silver jenny, 71–114 mm), *Fundulus similis* (longnose killifish, 73–113 mm), *Harengula jaguana* (scaled sardine, 84–104 mm), *Syngnathus scovelli* (gulf pipefish, 91–164 mm), *Anchoa hepsetus* (striped anchovy, 90–108 mm), *Menidia peninsulae* (tidewater silverside, 54–80 mm), and *Arius felis* (hardhead catfish, 280–391 mm) (Fig. 1). In all cases only sexually mature individuals were sampled. These species were used because they consti-

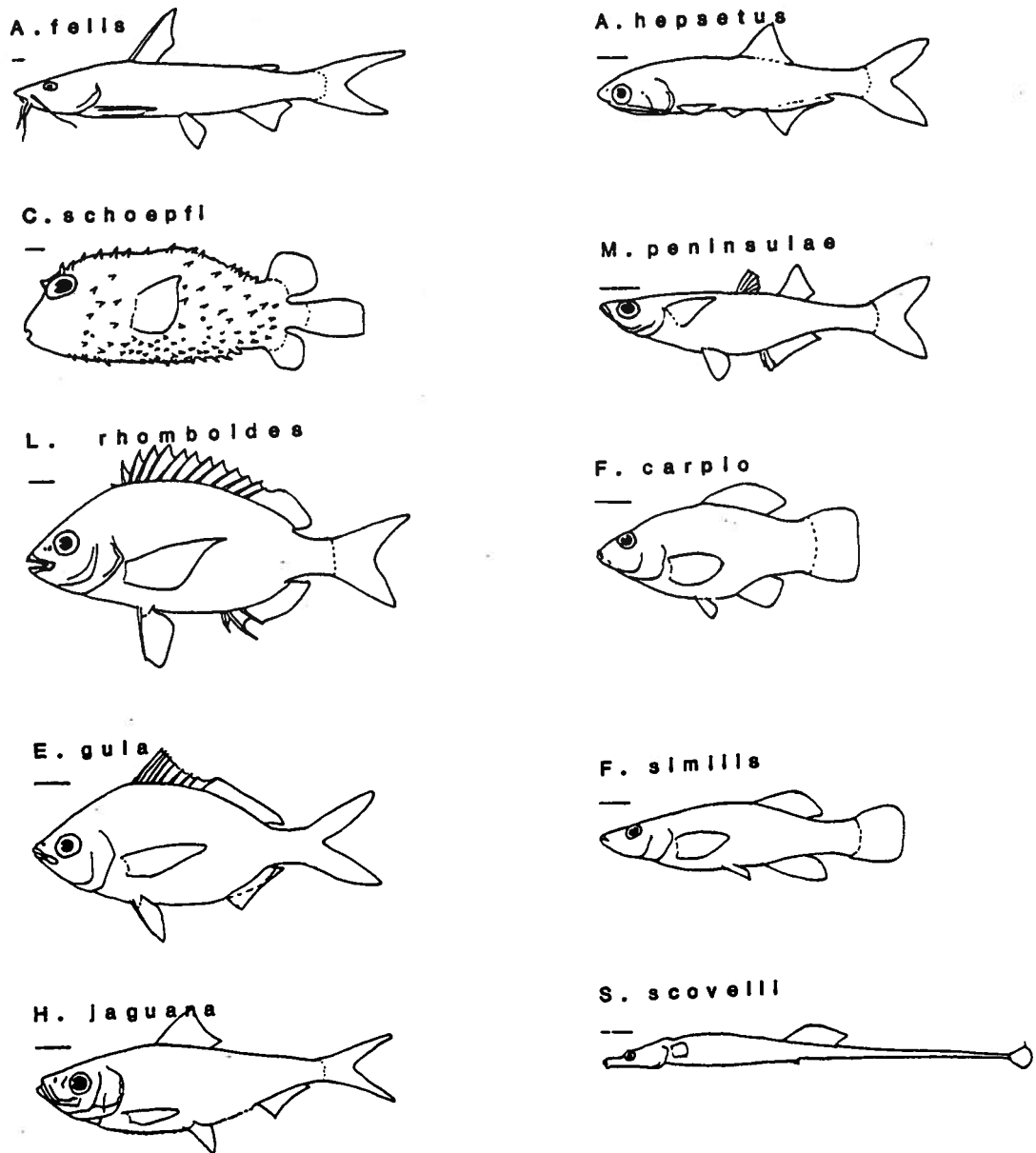


Fig. 1. Profiles of ten species of Tampa Bay seagrass fishes investigated. Bar indicates 1 cm.

tute some of the most numerically abundant fishes in Florida and Tampa Bay seagrass habitats (Springer & Woodburn 1960, Livingston 1976, Brook 1977, Livingston 1982, Stoner 1983, Comp 1985, Thayer et al. 1987).

Collections were made in and above the seagrass beds with a 0.95 cm (square measure) beach seine, 2.5 cm, 3.75 cm, and 5.0 cm (square measure) monofilament gill nets, and a 3 m otter trawl with

0.32 cm mesh cod end pulled by a power boat. Fishes were dissected immediately after capture and the entire gut removed and preserved in 10% buffered formalin with Rose Bengal. Fishes were frozen for subsequent morphological analysis. A detailed description of dietary analysis is reported in Motta et al. (1995). In brief, for species with a distinct stomach, only prey items in the stomach were included. For species without a distinct stomach the anterior

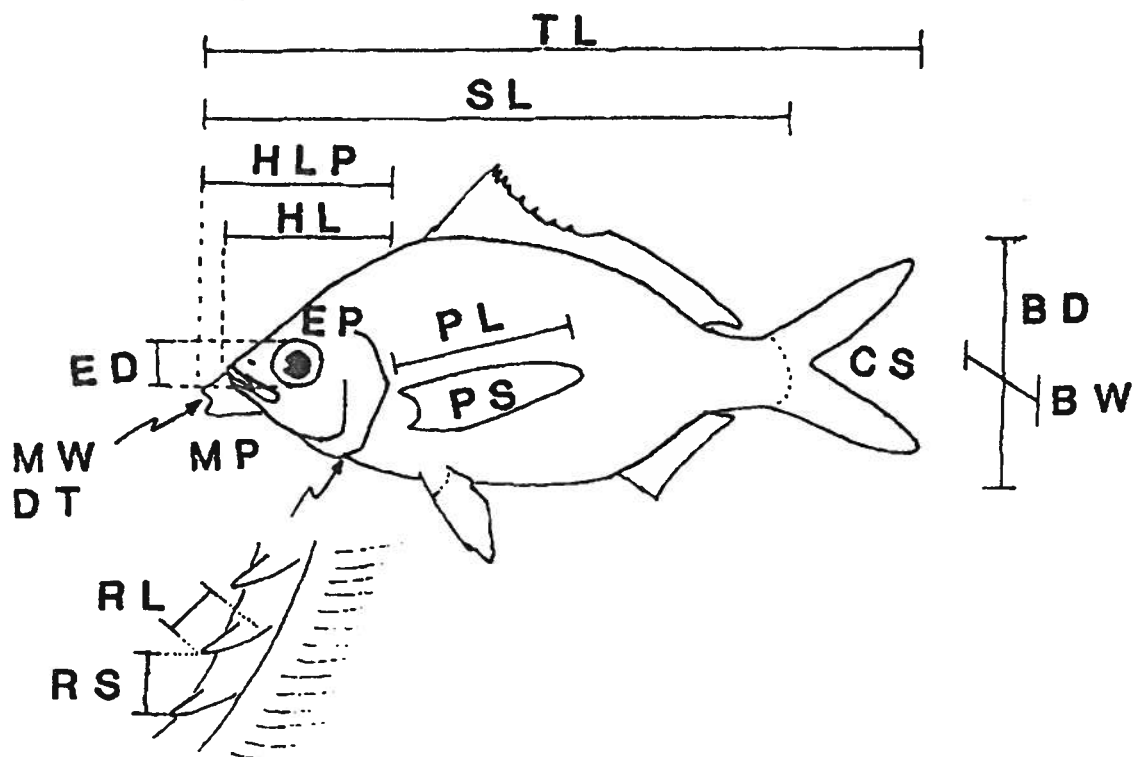


Fig. 2. A representative species, *Eucinostomus gula*, with ten mensural and five coded morphometric variables indicated. SL = standard length. HL = head length. BD = body depth. BW = body width. PL = pectoral fin length, MW = mouth width. ED = eye diameter. RL = gill raker length. RS = gill raker spacing. HLP = head length with jaw protruded. CS = caudal fin shape. PS = pectoral fin shape. EP = eye position. MP = position of open mouth. DT = dentition type.

1/3 of the intestine was evacuated. Specimens with empty stomachs or anterior intestines were not utilized. Prey were identified under dissecting microscope to order in most cases, and an Index of Relative Importance (IRI) (Pinkas et al. 1971), based on wet weight, frequency of occurrence, and numbers, calculated for each prey taxa. Hill's (1973) diversity numbers were calculated:  $N_0$ , the number of prey taxa;  $N_1$ , the number of abundant prey taxa;  $N_2$ , the number of very abundant prey taxa; and  $E_5$ , evenness. IRI values were used to cluster the species using the Bray-Curtis percent dissimilarity index, and Horn's index of overlap indicated the dietary overlap among the species.

In our analysis 15 morphological characters were represented by either mensural or coded variables. Ten mensural variables reflecting feeding and habitat use (Gatz 1979a) were taken on each specimen: standard length SL (tip of closed mouth to end of last vertebra), head length HL (anterior tip of

closed mouth to posterior edge of opercle), head length protruded HLP (anterior tip of protruded jaw to posterior edge of opercle), body depth BD (depth at widest part of body), body width BW (width at thickest part of body), pectoral fin length PL (base of fin to tip of longest ray), mouth width MW (at widest part with mouth fully open), eye diameter ED (diameter between fleshy orbits along an anterior-posterior axis), gill raker length RL (longest raker on first gill arch), gill raker spacing RS (distance between rakers on first gill arch in the vicinity of the ceratobranchial-epibranchial border). In addition, five coded variables were scored with integer values for each species: caudal fin shape CS (rounded = 1, truncate = 2, emarginate = 3, lunate = 4, or forked = 5), pectoral fin shape PS (rounded = 1, intermediate = 2, or pointed = 3), eye position EP (lateral = 1, slightly dorso-lateral = 2, or dorsal = 3), open mouth position MP (supraterminal = 1, terminal = 2, subterminal = 3, inferior = 4, or ventral = 5).

and dentition type DT (cardiform = 1, villiform = 2, canine = 3, incisor = 4, reduced incisiform = 5, brush-like = 6, molariform = 7, fused = 8, tricuspid = 9, or no teeth = 10) (Fig. 2). Mensural variables were measured with a ruler or vernier calipers to the nearest 0.1 mm. Gill raker length and spacing were measured to the nearest 0.01 mm with an ocular micrometer fitted for a dissecting microscope.

Principal components analysis (PCA) was used to identify patterns in morphological variation among species. PCA is a method of breaking down or partitioning a resemblance matrix into a set of orthogonal (perpendicular) axes or components. Each PCA axis corresponds to an eigenvalue of the matrix. The eigenvalue is the variance accounted for by that axis. The first few PCA axes represent the largest percentage of the total variation that can be explained (Ludwig & Reynolds 1988). PCA was conducted on a correlation matrix. All continuous variables were  $\log_{10}$  transformed in order to more closely approximate a normal distribution and reduce heteroscedasticity. Two analyses were performed to explore the relative merits of mixing mensural and scored variables: (1) a PCA of the mensural and coded variables together, and (2) one with only the mensural variables. The PCA analyses were performed on SAS using the Princomp procedure. To aid in data analysis, three dimensional plots were constructed using the G3D procedure.

The mensural variables that loaded heavily on PCA axes 2 and 3, that is, those that account for the greatest variance in the data set, head length, head length protruded, body depth, mouth width, pectoral length, eye diameter, gill raker spacing and gill raker length, were  $\log_{10}$  and alternately square root transformed and found not to be normally distributed in either case. Therefore, an a-priori Kruskal-Wallis test was performed on the untransformed data ( $N = 30$ ) to detect significant differences among species. Each variable was found to differ significantly among species, therefore a-posteriori Mann-Whitney U tests were carried out for all possible pairwise combinations ( $N = 45$ ) of species. The Bonferonni technique was used to determine the significance level for the Mann-Whitney U tests (Gatz 1979). An alpha level of  $\alpha = 0.05/45 = 0.001$  was used for each pairwise comparison. For each

variable, species that were not significantly different were joined by a line. To assess the degree of jaw protrusion relative to head length the following variable was calculated for each species ((HLP-HL/SL)X100) ( $N = 30$ ).

Cluster analysis was performed on all fifteen untransformed morphological variables and on the dietary data of Motta et al. (1995) using the Bray-Curtis percent dissimilarity index with the flexible strategy ( $\beta = -0.25$ ) to create three clusters (Ludwig & Reynolds 1988). The first cluster was constructed with all morphological variables. In order to investigate the relative proportions of the morphological attributes, for example, the size of the pectoral fin relative to the size of the fish, a second cluster was generated with the mensural variables expressed as a percentage of standard length. Mean values were used for the ten mensural variables. In both analyses, the five coded variables were entered as integer values. The third cluster was on the IRI dietary values for nine species (excluding *M. peninsulae* for which data were not available) from Motta et al. (1995). Clusters were constructed with the Statistical Ecology package (CLUSTER program) of Ludwig & Reynolds (1988). While we utilized ratios for exploratory data analysis in one cluster analysis, we specifically avoided ratios in the statistical analyses due to their inherent limitations (Atchley et al. 1976, Reist 1985, Jackson et al. 1990, Jackson & Somers 1991).

Canonical correspondence analysis (CCA) and detrended canonical correspondence analysis (DCCA by second order polynomials) were performed on two sets of morphological and dietary data for nine species. *Menidia peninsulae* was excluded from this analysis because the only dietary data available was qualitative data from the literature. Canonical correspondence analysis is a multivariate technique of direct gradient analysis that selects the linear combination of environmental variables (diet) that maximizes the dispersion of the species (morphology) scores. It chooses the best weights for the environmental variables to construct the first CCA axis. The second and further CCA axes also select linear combinations of environmental variables that maximize the dispersion of the species scores, but subject to the constraint of

being uncorrelated with previous CCA axes. Environmental variables may be quantitative or nominal (Jongman et al. 1987, ter Braak 1986, 1987). Detrended CCA is an efficient ordination technique when species have bell-shaped response curves with respect to environmental gradients (ter Braak 1986). We performed CCA and DCCA utilizing the program CANOCO version 3.12 (ter Braak 1988).

In the first data set, species data consisted of the 15 mensural and coded morphometric variables. To reduce collinearity due to too many environmental variables, only IRI values for eighteen very abundant dietary taxa, as indicated by Hill's N2, were utilized in the analysis. In the second comparison, species data consisted only of the morphometric variables that were considered related to microhabitat utilization (body depth, body width, pectoral fin length, eye diameter, caudal fin shape, pectoral fin shape, eye position) and not to feeding per se. As before, the environmental variables comprised the IRI values for the eighteen very abundant prey taxa.

## Results

### *Principal components analysis-mensural variables only*

The first two principal components had eigenvalues greater than one and accounted for 88% of the cumulative variance. Principal component 1 accounted for 75% of the variance, PC 2 accounted for 13%, and PC 3 accounted for 7% (Table 1, Fig. 3). The eigenvalues of the first principal component were positive and approximately equal in magnitude indicating a strong size vector (Strauss 1987).

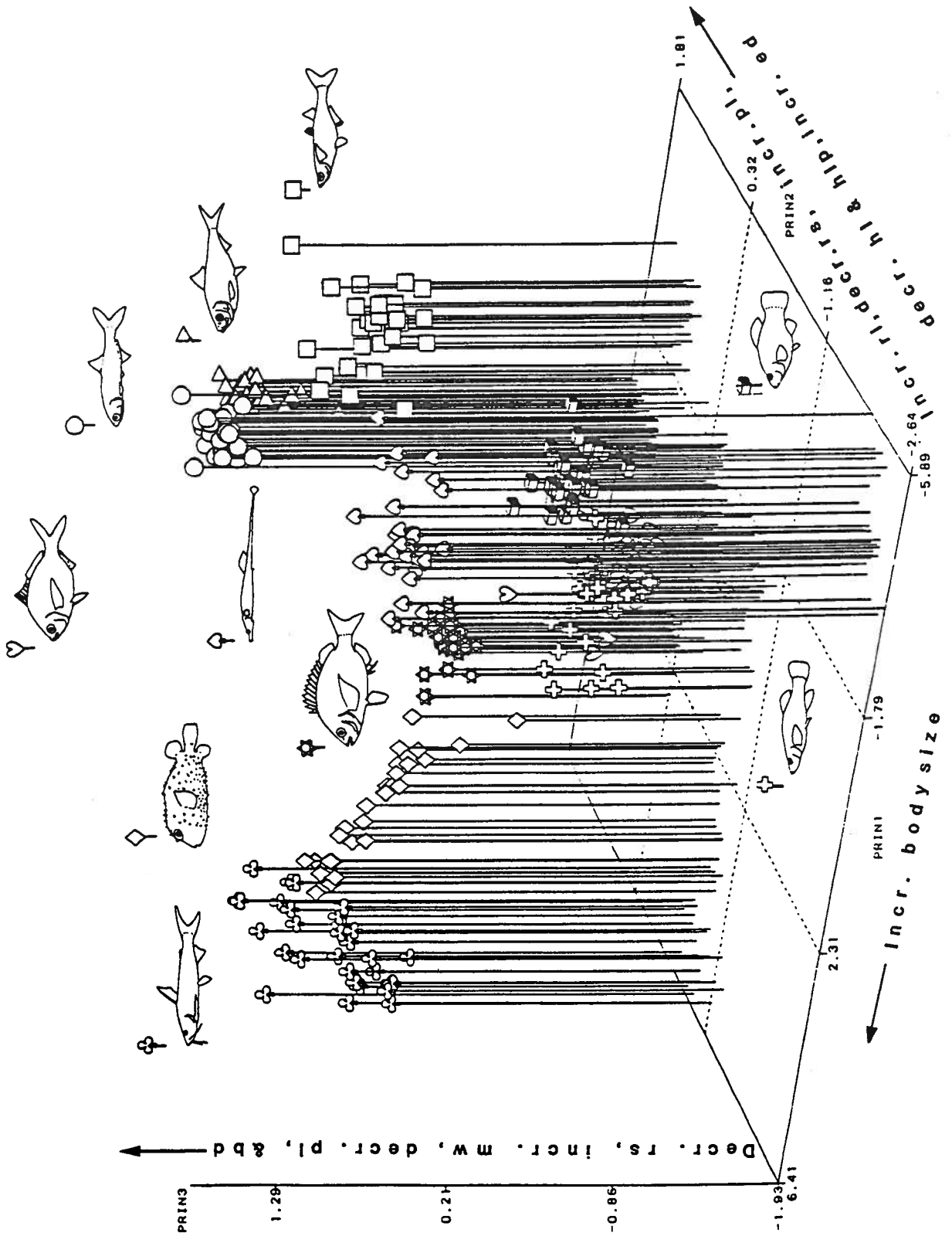
With increasing magnitude along principal component axis 2, the species had longer, more closely spaced gill rakers, longer pectoral fins, shorter heads, and larger eyes. Principal component 3 separated fishes by decreasing spacing of the gill rakers, larger mouths, shorter pectoral fins, and decreasing body depth (Table 1, Fig. 3).

The following species grouped close in morphospace: *Menidia peninsulae*, *A. hepseus*, and *H. jaguana* formed a single group; *F. carpio* and *F. similis* formed a group; *Eucinostomus gula* was positioned between *F. similis* and *L. rhomboides*; *Chilomycterus schoepfi*, *A. felis*, and *S. scovelli* were separated in morphospace (Fig. 3).

Table 1. Principal components analysis for morphometric data on ten species of seagrass fishes (N = 50). Eigenvalues for the first three principal components on mensural variables only.

Eigenvalue	Difference	Proportion	Cumulative
Prin1 7.50068	6.22892	0.750068	0.75007
Prin2 1.27176	0.58520	0.127176	0.87724
Prin3 0.68656	0.47717	0.068656	0.94590
	Prin1	Prin2	Prin3
SL	0.278241	-0.397784	0.504177
HL	0.348834	-0.210405	0.161558
BD	0.337102	0.137905	-0.299640
BW	0.346761	-0.119364	-0.031746
PL	0.331686	0.226794	-0.327438
MW	0.325778	0.164498	0.377256
ED	0.336839	0.196340	0.022255
PL	0.189695	0.720174	0.163762
RS	0.277552	-0.299686	-0.588773
HLP	0.352687	-0.196790	0.073540

SL = standard length, HL = head length, BD = body depth, BW = body width, PL = pectoral fin length, MW = mouth width, ED = eye diameter, RL = gill raker length, RS = gill raker spacing, HLP = head length with jaw protruded.



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Fig. 3. Principal components analysis of the ten mensural morphometric variables for ten species of seagrass fishes (N = 30). The variables with larger eigenvalues (Table 1) indicated on each axis. Club = *A. felis*. Diamond = *C. schoepfi*. Star = *L. rhomboides*. Cross = *F. similis*. Spade = *S. scovelli*. Heart = *E. gula*. Circle = *A. hepsetus*. Triangle = *H. jaguana*. Square = *M. peninsulae*. Cube = *F. carpio*. BD = body depth. PL = pectoral fin length. MW = mouth width. ED = eye diameter. RL = gill raker length. RS = gill raker spacing. HL = head length. HLP = head length with jaw protruded.

### Principal components analysis-mensural and coded variables combined

The first three principal components had eigenvalues greater than one and account for 87% of the cumulative variance. Principal component 1 accounted for 55% of the variance. PC 2 for 22% and PC 3 for 10% (Table 2). Mensural variables on principal component 1 were positive and approximately equal in magnitude indicating a strong size vector. This was not generally the case for the coded variables. Dentition type was strong and negative indicating the shift from villiform teeth, towards tricuspid teeth (*F. carpio*) and loss of dentition (*S. scovelli*) on PC axis 1. Caudal fin shape and pectoral fin shape indicated a gradient from more rounded fins (for example *S. scovelli*) at one extreme to more

forked caudal fins and pointed pectoral fins at the other extreme, for example *L. rhomboides*. Mouth position was supraterminal in *S. scovelli* and generally subterminal at the other extreme (Table 2, Fig. 4).

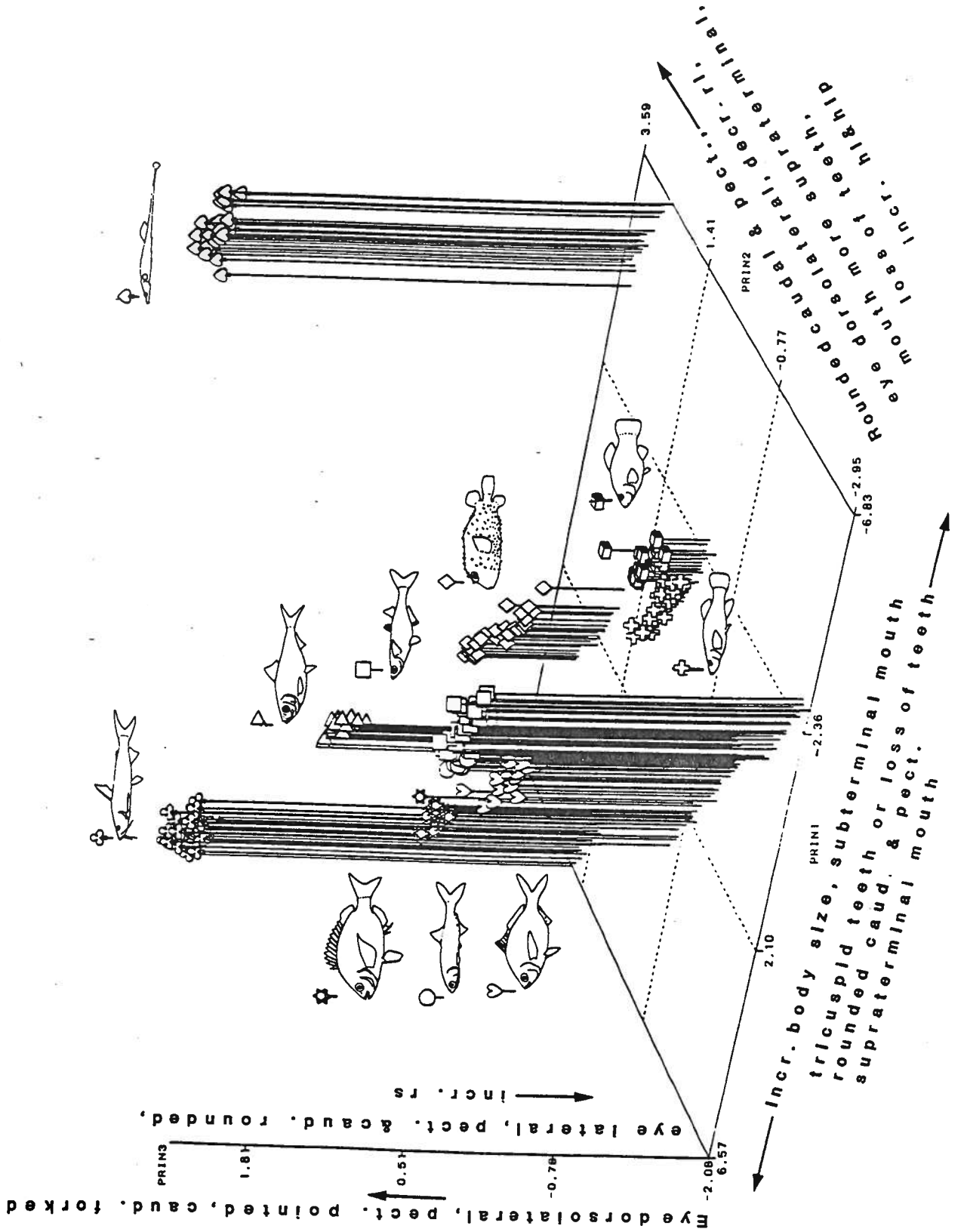
Fishes with more rounded caudal and pectoral fins, eye more dorsolateral, shorter gill rakers, more supraterminal mouth, loss of dentition, and increasing head length scored high on PC2. Along principal component axis 3 there was a shift towards more dorsolateral eye position, more pointed pectoral fins, and forked caudal fins (Table 2, Fig. 4).

Principal components analysis based on combined mensural and coded variables resulted in each species occupying less morphospace with generally less overlap among species. *Menidia peninsulae*, *H. jaguana*, and *A. hepsetus* formed a tight

Table 2. Principal components analysis for morphometric data on ten species of seagrass fishes (N = 30). Eigenvalues for the first three principal components on mensural and coded variables.

Eigenvalue	Difference	Proportion	Cumulative
Prin1 8.24284	4.96640	0.549523	0.54952
Prin2 3.27644	1.78183	0.218429	0.76795
Prin3 1.49461	0.65661	0.099641	0.86759
	Prin1	Prin2	Prin3
SL	0.238334	0.328558	0.318499
HL	0.314427	0.224972	0.054975
BD	0.322115	-0.001629	-0.104411
BW	0.311809	0.186603	-0.142290
PL	0.330446	-0.090380	-0.100053
MW	0.307536	0.050684	0.034845
ED	0.320982	0.000475	-0.010466
RL	0.221346	-0.350574	0.101833
GS	0.254357	0.162124	-0.326636
HLP	0.319984	0.206325	0.016996
CS	0.141506	-0.413796	0.400295
PS	0.152785	-0.358958	0.438013
EP	0.006731	0.356650	0.521091
MP	0.161817	-0.337176	-0.333095
DT	-0.225542	0.251304	0.033519

SL = standard length. HL = head length. BD = body depth. BW = body width. PL = pectoral fin length. MW = mouth width. ED = eye diameter. RL = gill raker length. RS = gill raker spacing. HLP = head length with jaw protruded. CS = caudal fin shape. PS = pectoral fin shape. EP = eye position. MP = position of open mouth. DT = dentition type.



←

Fig. 4. Principal components analysis of the ten mensural and five coded morphometric variables combined for ten species of seagrass fishes (N = 30). The variables with larger eigenvalues (Table 2) indicated on each axis. Club = *A. felis*. Diamond = *C. schoepfi*. Star = *L. rhomboides*. Cross = *F. similis*. Spade = *S. scovelli*. Heart = *E. gula*. Circle = *A. hepsetus*. Triangle = *H. jaguana*. Square = *M. peninsulae*. Cube = *F. carpio*. RL = gill raker length. RS = gill raker spacing. HL = head length. HLP = head length with jaw protruded.

group, with *E. gula* and *L. rhomboides* clustering nearby. *Floridichthys carpio* and *F. similis* were grouped very close together in morphospace with *C. schoepfi* nearby. *Arius felis* and *S. scovelli* were each morphologically distinct and separated from the other species (Fig. 4).

#### Mensural morphometric variables-univariate statistics

Principal components analysis of the morphometric variables resulted in a few species groups and some species separated in morphospace. Univariate analysis of the morphometric variables that loaded heavily on either PCA 2 or 3 combined with the coded variables resulted in the following character complexes: (1) a group including *H. jaguana*, *A. hepsetus* and *M. peninsulae* characterized by a compressed fusiform body with forked caudal fin, long, closely spaced gill rakers, short to intermediate length pectoral fin, pointed pectoral fin, relatively large (*A. hepsetus* and *H. jaguana*) lateral eye, short head, and terminal or subterminal mouth; (2) *Fundulus similis* and *F. carpio* which both had rounded caudal and pectoral fins, short pectoral fins, small body size, small, lateral eyes, subterminal mouth, short gill rakers, and small mouth width and body depth. These species shared a few characters with *C. schoepfi* and *S. scovelli*: rounded caudal and pectoral fins, and short or no (*C. schoepfi*) gill rakers; and (3) *Lagodon rhomboides* and *E. gula* united by their sub-gibbose body shape (including large body depth), forked caudal fins, long, pointed pectoral fins, large, lateral eyes, and subterminal mouth. *Arius felis* was an outlier in morphospace, characterized by being large bodied with a forked caudal fin, long, pointed pectoral fin, slightly dorsolateral eye, subterminal, wide mouth, long, and widely spaced gill rakers (Fig. 5).

Of the species that protrude the upper jaw, *L.*

*rhomboides* and *F. carpio* protruded their jaw 3.7% of their standard length; *E. gula* 3.5%, and *M. peninsulae* 3.2%. *Chilomycterus schoepfi* (1.5%) and *F. similis* (0.2%) had slight protrusibility.

#### Morphometric clustering

Cluster analysis of the fifteen, untransformed morphometric variables (excluding standard length) resulted in three groups and one outlier species. *Eucinostomus gula*, *H. jaguana*, *F. similis*, and *A. hepsetus* formed the first group, clustering at the 0.11 level. *Fundulus carpio* and *M. peninsulae* formed a second group at the 0.13 level, and *A. felis*, *C. schoepfi*, and *L. rhomboides* formed a third group at the 0.34 level. *Syngnathus scovelli*, the outlier species, was joined to the first two groups at the 0.39 level (Fig. 6).

Cluster analysis of the proportional measurements (mensural morphometric variables expressed as percent standard length), and the coded variables together resulted in a different arrangement of three groups and one outlier species. *Lagodon rhomboides*, *E. gula* and *F. carpio* formed a group at the 0.10 level; *F. similis* and *C. schoepfi* formed a second group at the 0.12 level; and *H. jaguana*, *M. peninsulae*, *A. hepsetus*, and *A. felis* formed a third group at the 0.14 level. *Syngnathus scovelli* was the outlier species joined to all three groups at the 0.86 level (Fig. 7).

#### Dietary overlap and cluster analysis

Dietary overlap data (Table 3) (Motta et al. 1995) and cluster analysis of the IRI data (Fig. 8) revealed similar species grouping. The nine species on which dietary data were collected separated into three groups: one with relatively high overlap comprised of *F. carpio*, *H. jaguana*, and *A. hepsetus*; a second

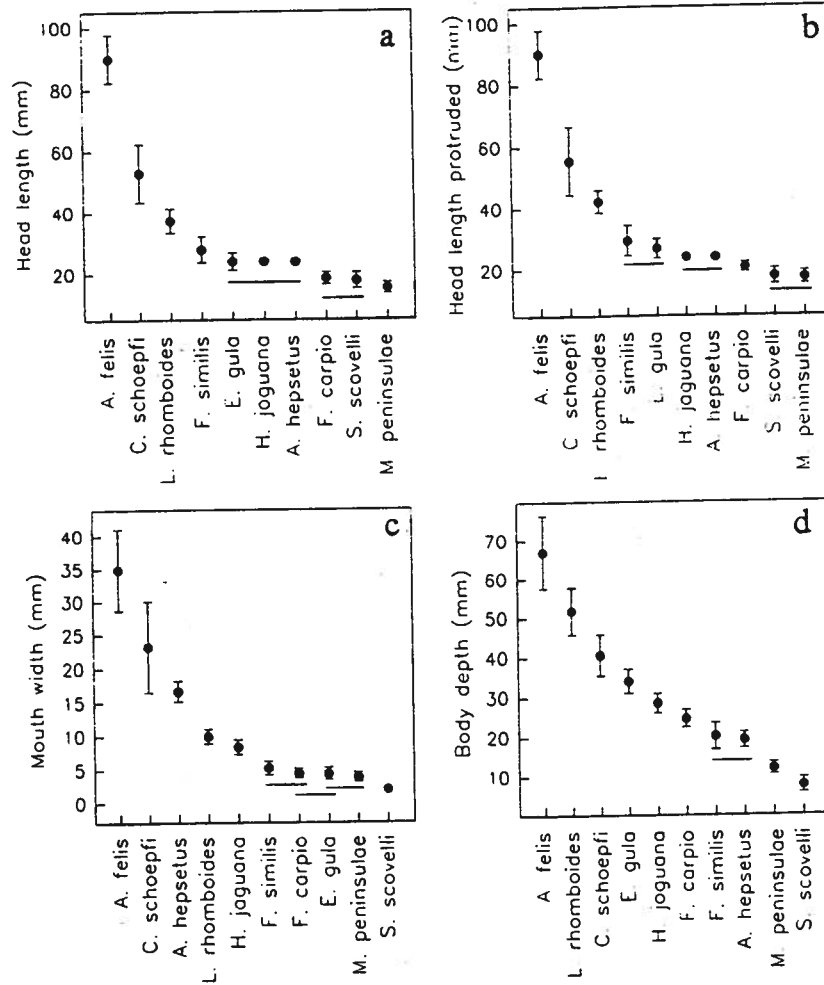


Fig. 5. Head length, head length protruded, mouth width, body depth, pectoral fin length, gill raker length, gill raker spacing, and eye diameter of ten species of seagrass fishes. Mean  $\pm$  one standard deviation indicated. Species that are not significantly different indicated (N = 30, Mann-Whitney U-test,  $p = 0.05$ ).

group with intermediate overlap levels includes *C. schoepfi*, *F. similis*, and *E. gula*. A third group including *A. felis*, *S. scovelli*, and *L. rhomboides* had relatively little dietary overlap.

#### Dietary-morphometric correspondence

Canonical correspondence analysis (CCA) and detrended CCA (DCCA) of the 15 morphological variables and dietary data indicated that the morphological variables were poorly related to the first four environmental (dietary) axes (eigenvalue = 0.033 on Axis 1, Table 4). Only 3% of the morph-

ological variance could be accounted for by dietary axis 1. Analysis of the seven morphological variables related to microhabitat utilization revealed a similarly poor relationship (eigenvalue = 0.055 on Axis 1, Table 4). Eigenvalues of approximately 0.3 and higher are quite common in ecological applications (ter Braak 1988, Jongman et al. 1987), and ordination axes with very low eigenvalues (< 0.02) should be discarded (ter Braak 1988). Because of the poor relationship between morphological and dietary axes in this study, further analysis of the axes was not warranted.

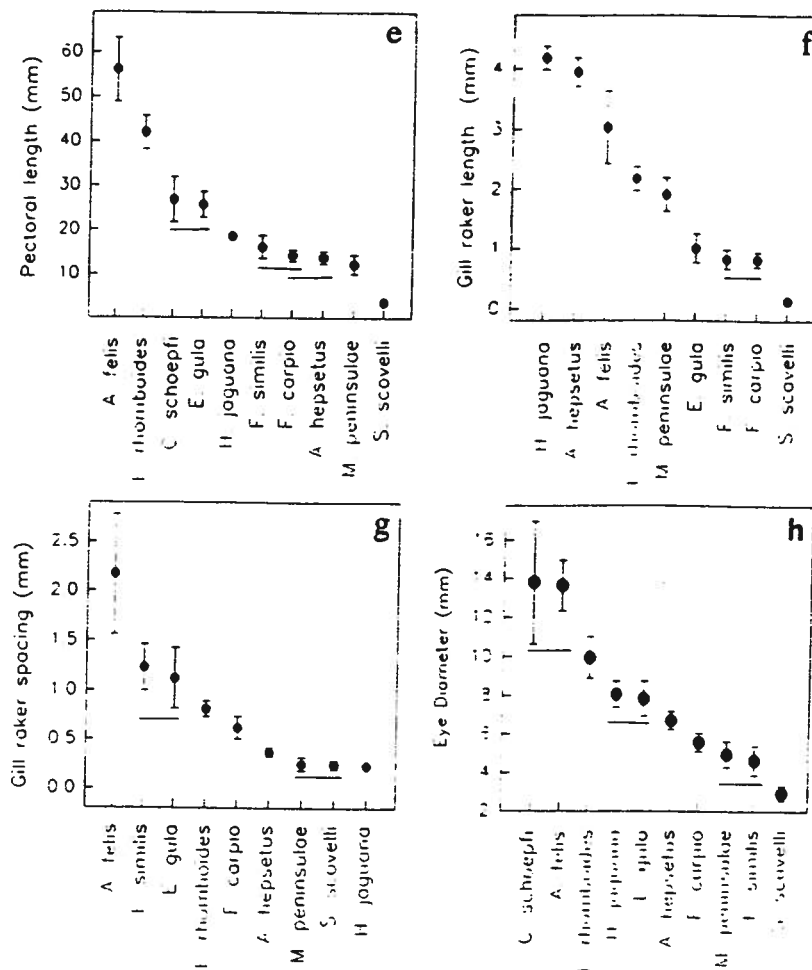


Fig. 5. Continued.

## Discussion

Principal components analyses of the morphometric data indicated that the species separated by a variety of characters associated with feeding and microhabitat utilization. In general, the first principal component was indicative of overall body size. Body size in these fishes is believed to be an important factor in niche separation (discussed below). Thus, body size is not always a nuisance factor that must somehow be removed from data before 'true' systematic or ecological relationships can be determined (Douglas 1987); it may be an important factor influencing species resource utilization. When coded variables were considered, variables indicative of trophic (dentition type) and microhabitat

(caudal and pectoral fin shape) differentiation loaded heavily. The second and third principal components were linked by trophic and microhabitat use, being strongly influenced by gill raker length and spacing, caudal and pectoral fin shape, pectoral fin length, head length and head length protruded, eye diameter and position, mouth width and position, body depth, and dentition type.

Principal components analysis of the ten species was greatly affected by the mixing of mensural and coded variables. The analysis of all 15 variables resulted in the species groups clustering tighter in morphospace and separating more from other species groups. Our analysis does not allow us to recommend one particular approach over another, because two factors differ between the approaches. In

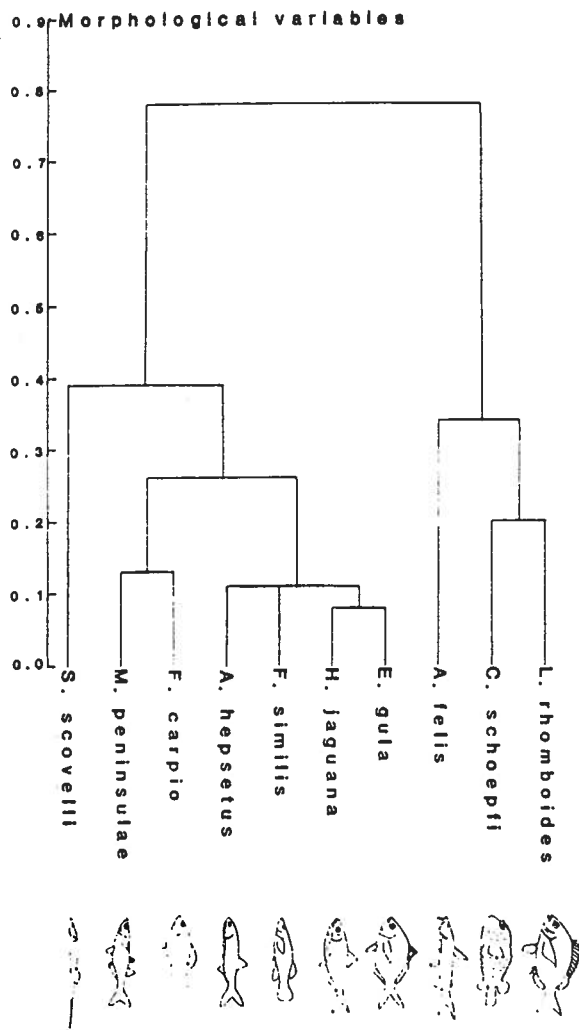


Fig. 6. Cluster analysis of fifteen untransformed morphometric variables for ten species of seagrass fishes. Clustering by the Bray-Curtis percent dissimilarity index utilizing the flexible strategy ( $N = 30$ ).

the combined analysis additional morphometric variables were considered (the coded variables). In addition these variables had inherently less variability being integer values. Perhaps instead of coded variables, features such as eye position and caudal fin shape should be quantified by continuous values derived by multidimensional shape analysis. These continuous values would have more inherent variation than the coded integer values.

In both analyses certain species groups were apparent. The first group was comprised of *H. jaguana*, *A. hepsetus* and *M. peninsulæ*. A second consis-

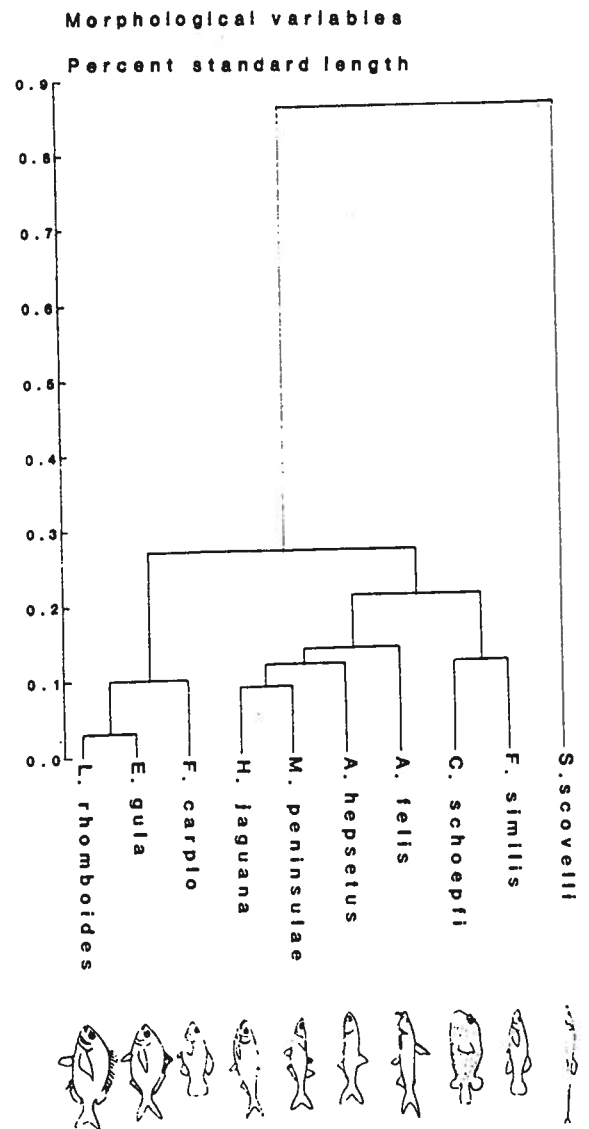


Fig. 7. Cluster analysis of fifteen untransformed morphometric variables for ten species of seagrass fishes. The ten mensural variables expressed as a percent of standard length. Clustering by the Bray-Curtis percent dissimilarity index utilizing the flexible strategy ( $N = 30$ ).

tent group included *F. similis* and *F. carpio*. When all characters were considered *C. schoepfi* and *S. scovelli* were closer to this group in morphospace than to the other species. In both analyses, but more so in the combined analysis, *L. rhomboides* and *E. gula* were close in morphospace. The catfish, *A. felis*, was separated from the other species.

Cluster analysis based on all untransformed mor-



specific morphological polymorphism in bluegill sunfish has been found to be related to foraging behavior and microhabitat utilization. Open water inhabitants had fusiform bodies and short fins, whereas littoral vegetation feeders, which are suited for maneuvering, had deep bodies, long pelvic and pectoral fins, and pectoral fins attached in a posterior position (Ehlinger & Wilson 1988, Ehlinger & Gross 1992). Bluegill with longer pectoral fins consistently searched more slowly and spent more time in the vegetation habitat compared to bluegill with shorter pectoral fins (Ehlinger 1990).

Both *H. jaguana* and *A. hepsetus* were mid-water planktivores, filter feeding primarily on copepods. They had high dietary overlap, and clustered closely by diet with *F. carpio*. Lucas (1982) found that *Menidia peninsulae* fed selectively on calanoid copepods and barnacle cypris larvae as adults, whereas gravid females primarily fed on fish larvae and amphipods. *Harengula jaguana*, *A. hepsetus* and *M. peninsulae* had relatively long, closely spaced gill rakers. Long, closely spaced gill rakers are associated with planktivorous filter feeders (Lagler et al. 1962, Chao & Musick 1977) although the extent to which gill raker spacing determines filtration efficiency is not clear

Table 4. (Top) Eigenvalues for canonical correspondence analysis and detrended canonical correspondence analysis of 15 mensural and coded morphological variables with IRI values for eighteen very abundant prey taxa (Hill's N2) for nine species of seagrass fishes (*M. peninsulae* excluded); (Bottom) eigenvalues for canonical correspondence analysis and detrended canonical correspondence analysis of seven morphological variables associated with microhabitat utilization (body depth, body width, pectoral fin length, eye diameter, caudal fin shape, pectoral fin shape, eye position) with IRI values for eighteen very abundant prey taxa (Hill's N2) for nine species of seagrass fishes (*M. peninsulae* excluded).

Diet axes	1	2	3	4
Eigenvalues				
CCA	0.033	0.027	0.012	0.008
DCCA	0.033	0.026	0.009	0.000

Diet axes	1	2	3	4
Eigenvalues				
CCA	0.055	0.017	0.007	0.002
DCCA	0.055	0.017	0.001	0.000

(see Sanderson & Cech 1992). *Harengula jaguana* and *A. hepsetus* lacked upper jaw protrusion as is common of filter-feeding fishes (Chao & Musick 1977). *Menidia peninsulae* most likely picks its prey with its small, protrusible mouth. Therefore, morphological similarity in these species was related to dietary similarity, particularly between *H. jaguana* and *A. hepsetus*.

Examining an intertidal fish assemblage off California, Grossman (1986) similarly found PC1 to be a general size-related component, and PC2 to be trophically linked. Principal component 2 was strongly influenced by number of gill rakers, mouth orientation, and eye position. Wikramanayake (1990) found a very similar suite of characters associated with digestive efficiency, foraging behavior, and foraging position in a tropical stream fish assemblage.

#### Group 2 fishes

Principal components analysis of all characters separated *F. carpio*, *F. similis*, *C. schoepfi*, and *S. scovelli* from the other species. This group was characterized by rounded caudal and pectoral fins, and short or no (*C. schoepfi*) gill rakers. *Fundulus similis* and *F. carpio* clustered closely in morphospace when all variables were considered, and with *S. scovelli* when only mensural variables were considered. *Fundulus similis* and *F. carpio* were united by a suite of characters including small body size, rounded or truncate caudal fins, rounded pectoral fins, short pectoral fins, small and lateral eyes, subterminal mouth, short gill rakers, and small mouth width and body depth.

In these species, morphology was reflective of their epibenthic microhabitat utilization. Morphologically, *F. similis*, *F. carpio*, *C. schoepfi*, and *S. scovelli* are typical of slow swimming, less maneuverable, epibenthic fishes that are unable to sustain long periods of high-speed swimming (Keast & Webb 1966, Aleev 1969, Webb 1984). Although they occupied similar epibenthic microhabitats, *F. similis* and *F. carpio* frequented shallow inshore waters, whereas *C. schoepfi* was found mostly in deeper, sand and seagrass benthic habitats (personal obser-

vation). *Syngnathus scovelli* was primarily captured among seagrass blades.

Dietary similarity among these four species did not correlate with morphological similarity. *Floridichthys carpio* primarily fed on copepods presumably by picking or suction, consequently, it clustered by diet with Group 1 fishes, although it did not group with those species in morphospace. Although *F. similis* and *C. schoepfi* grouped together by Index of Relative Importance (along with *E. gula*), their diets were only superficially similar. *Fundulus similis* fed primarily on small (0.43–2.00 mm length) bivalves as well as eggs which were ingested intact, and *C. schoepfi* crushed large (operculum diameter 3.0–3.5 mm) gastropods, bivalves (1–3 cm length), and barnacles. Inclusion of bivalves, albeit very different sizes, primarily accounted for the dietary clustering of these species (Motta et al. 1995). Although these species occupied similar microhabitats, particularly *F. carpio* and *F. similis*, there was low dietary overlap among them. *Syngnathus scovelli* primarily utilizes suction feeding on amphipods and shrimp and was an outlier species in terms of both diet and morphology. Its supraterminal mouth and dorsolateral eyes suit it for capturing prey above its body, and its lack of dentition is characteristic of suction feeding fishes (Suyehiro 1942, Lagler et al. 1962, Davis & Birdsong 1973, Alexander 1974, Motta 1985, 1988).

### Group 3 fishes

Principal components analysis grouped *E. gula* and *L. rhomboides* closely in morphospace. The size independent cluster analysis based on shape and proportional variables grouped *L. rhomboides*, *E. gula*, and *F. carpio*. *Eucinostomus gula* and *L. rhomboides* were united not only by their sub-gibbose body shape, but also by their forked caudal fins, pointed pectoral fins, large eyes, lateral eye position, and subterminal mouth. *Lagodon rhomboides* had a larger mouth, and longer and more closely spaced gill rakers than *E. gula*. There was generally little dietary similarity and overlap between the species at this study site. Motta et al. (1995) found *L. rhomboides* to feed primarily on algae and tuni-

cates. The pinfish is the numerically dominant species within *Thalassia testudinum* beds along the subtidal areas of the Gulf of Mexico (Hansen 1969) and an important predator on macrobenthic organisms within these seagrass beds (Young & Young 1978). This species undergoes several ontogenetic dietary shifts which may correspond with food availability (Huh & Kitting 1985), although the data are conflicting. An increased tendency towards carnivory with growth was reported by Subrahmanyam & Drake (1975), and Carr & Adams (1973). This contrasts with the ontogenetic shift to herbivory cited by Darnell (1958), Hansen (1969), Stoner (1980), and Stoner & Livingston (1984).

*Eucinostomus gula* had a more diverse diet with five very abundant prey items, polychaete worms, bivalves, cumaceans, amphipods, and gastropods. These findings are consistent with other studies. Copepods dominated the diet of smaller size classes and were gradually replaced by polychaetes as size increased (Springer & Woodburn 1960, Carr & Adams 1973, Brook 1977, Livingston 1984).

Both *L. rhomboides* and *E. gula* were epibenthic foragers over sandy substrates and within seagrass beds (personal observations). Mojarras (Gerreidae) use their extremely protrusible mouth to bite or suck their benthic prey off the substrate (Cyrus & Blader 1982, personal observations). *Lagodon rhomboides* either bites off pieces of seagrass and algae with vertically opposed, straight-edged incisor teeth (Stoner & Livingston 1984), or suction or ram feeds on elusive prey at this size (K.F. Liem personal communication). Protrusible upper jaws are typical of fishes that utilize either suction feeding, picking or biting during feeding (Motta 1984, 1985, 1988, Liem 1980). *Lagodon rhomboides*, *E. gula*, and *F. carpio* all had the most protrusible mouths of the species examined (3.7%, 3.5%, 3.7% of standard length, respectively) and all suck or bite their prey off the substrate.

Morphological similarity between *L. rhomboides* and *E. gula* was not related to diet, but more to microhabitat utilization and how they fed. Their more compressed, sub-gibbose body, long, pointed pectoral fins, and forked caudal fins make them suitable for greater maneuverability and speed (compared to *C. schoepfi*, *F. similis*, *F. carpio*, and *S. scovelli*) as

they suck or bite their relatively large prey within seagrass beds or over sandy substrates (Keast & Webb 1966, Gatz 1979a, Webb 1984).

#### *Outlier species*

*Syngnathus scovelli* (discussed previously) and *A. felis* were separated from most of the other species in morphospace. *Arius felis* is large bodied with a forked caudal fin, long, pointed pectoral fin, slightly dorsolateral eye, subterminal wide mouth, long widely spaced gill rakers, and ventral barbels. Its fusiform body shape grouped it with the mid-water planktivorous species. However, the ictalurid body form is suited for bottom feeding (Keast & Webb 1966). The importance of crabs and tunicates in its diet clustered it with *L. rhomboides* which also consumed tunicates although dietary overlap was low between the species.

#### *Correspondence between morphology and diet*

Canonical correspondence analysis is a powerful tool for direct measurement of the association between environmental and species data. We found an overall poor correlation between the morphological variables under investigation and diet, indicating that the species distributions (morphology) did not differ much along the environmental gradient (dietary gradient) (ter Braak 1986). Even when morphological characters associated with microhabitat were considered (body depth, body width, pectoral length, eye diameter, caudal shape, pectoral shape, and eye position) there was poor association with diet.

The only group in which there was some congruence in morphology and diet was in the planktonic, mid-water group 1 fishes: *H. jaguana*, *A. hepsetus*, and *M. peninsulae*. These species consistently grouped together in morphology, and had high dietary overlap. However, in this group of ten species dietary similarity was not necessarily predictive of morphological similarity, for example, *F. carpio* had a high dietary overlap and clustered by IRI with the above three species, yet was morpho-

logically quite distinct. Similarly, morphological similarity was not necessarily predictive of dietary similarity, as exemplified by the *L. rhomboides* – *E. gula*, and *F. carpio* – *F. similis* species groups which had similar morphologies yet low dietary overlap.

The general lack of correlation between morphology and diet is not surprising as morphology may not only be correlated with what a fish feeds on, but also with feeding behavior (e.g. suction, biting) or microhabitat utilization. Our study indicates that the 'fit' is not simply between morphology and diet, but also between morphology and microhabitat utilization. Quantitative assessment of microhabitat utilization in these seagrass fishes would have allowed us to test the association between morphology and habitat use.

Gatz (1979a), Moyle & Senanayake (1984), Douglas (1987), Wikramanayake (1990) and Winemiller (1991) have found that morphological diversification and specialization in stream fishes was associated with dietary and/or microhabitat specialization. Niche compression, or specialization in stream fish communities occurred primarily in relation to habitat selection, in the case of rainforest fishes of north Borneo by vertical stratification, and secondarily in preference for food resources (Watson & Balon 1984).

Grossman (1986) found that morphological similarity was a poor predictor of dietary similarity in an intertidal fish assemblage. Similar to our findings with such species as *E. gula* and *L. rhomboides*, he found that in some cases species which were quite similar morphologically frequently possessed very different diets and vice versa. Pacific and Western Atlantic butterflyfishes exhibited cases of convergence, divergence, and parallelism in jaw morphology; and jaw and head morphology was correlated with how these fishes feed, rather than with what they consume (Motta 1985, 1988).

The inconsistencies in ecomorphological studies attempting to relate morphology to dietary preference are to be expected owing to the numerous factors that can influence the relationship. A variety of behavioral, ecological, physiological, and morphological constraints can confound ecomorphological relationships. These constraints can be evolutionary (historical) or current. Current constraints may

be ecological (e.g. environmental instability, resource availability, competition), behavioral (e.g. behavioral flexibility), physiological (e.g. sensory limitations, nutritional requirements), or morphological (e.g. structural and spatial limitations on combining functionally relevant forms, phenotypic plasticity) (Motta & Kotrschal 1992).

One ecological constraint that can affect ecomorphological relationships in a study such as this is resource availability over the species range. The diet of each species should be examined throughout its range and over a long enough time period to avoid localized variability. These limitations are usually too difficult to address and only a few studies have addressed them (see Grossman 1986). Similarly, how and where an organism feeds must be examined over its spatial and temporal range before ecomorphological patterns can be ascertained. There is also evidence to believe that resource partitioning (Ross 1986), and consequently ecomorphological patterns relating to resource use, will not necessarily be similar in different ecosystems such as marine or freshwater habitats, streams, lakes, coral reefs, subtropical seagrass beds and the like.

Furthermore, various analytical methodologies will affect the putative correlations: the choice of morphological characters; as we have demonstrated, lumping of mensural and coded variables significantly changes the principal components analysis, utilizing ratios or raw measurements, and the method of dietary analysis, for example, whether one presents the data volumetrically, as dried or wet weights, as percent frequency of occurrence, or as some cumulative index such as the Index of Relative Importance. There is, therefore, no surprise to us that there is so much variability and lack of concordance among the ecomorphological studies of fish feeding. Perhaps we should seek ecosystem-specific patterns, and standardized methods or at least compare the different methodologies. Even when correlations are found between diet or microhabitat use and morphology, we lack the certainty to ascertain causal relationships. Ecomorphological studies must then proceed to the more difficult step, performance testing of the form-function complex, for example, the feeding efficiency of various gill raker designs.

### *Phylogenetic patterns*

It has been argued that examining more distantly related species, rather than those with a high degree of taxonomic relatedness, decreases the probability of detecting ecomorphological patterns because choosing closely related species will reduce the risk that coincidental differences will mask significant patterns (Huey & Bennet 1986), and closely related species that have a long history of evolution and radiation in the same region are more likely to have ecomorphological relationships that are detectable (Findley & Black 1983). However, re-occurring ecomorphological relationships among more distantly related taxa provide powerful evidence for convergence (Karr & James 1975, Wiens 1991b, Losos 1990a, b, Motta & Kotrschal 1992, Winemiller et al. 1995) and reduce the probability that the ecomorphological pattern is a chance event, but rather one shaped by evolutionary forces related to that particular ecomorphological relationship.

In order to ascertain that different faunas have evolved similar patterns of niche diversification in response to similar environmental factors one must have a phylogeny to distinguish between convergence and parallelism and to identify historical design constraints among contemporary taxa. Furthermore, one must have reasonably comparable units and scales among: (1) heritable morphological traits that reflect ecologically relevant functions, (2) faunas and taxa, and (3) regions and physical and biotic environments (Winemiller et al. 1995). It may then be possible to rigorously test evolutionary ecomorphological hypotheses as has been outlined by Felsenstein (1985), Losos (1990a, b), Winemiller (1991), Winemiller et al. (1995), Wesneat (1995). With the availability of a phylogeny of this broad taxonomic group, and morphological characters that are ecologically relevant, we can at least make general statements about evolutionary convergence and parallelism in this group of seagrass fishes.

These ten species of generally distantly related fishes formed a variety of groups that clustered in morphospace, indicating convergence and parallelism in form. The only good correlation between dietary similarity and morphological similarity oc-

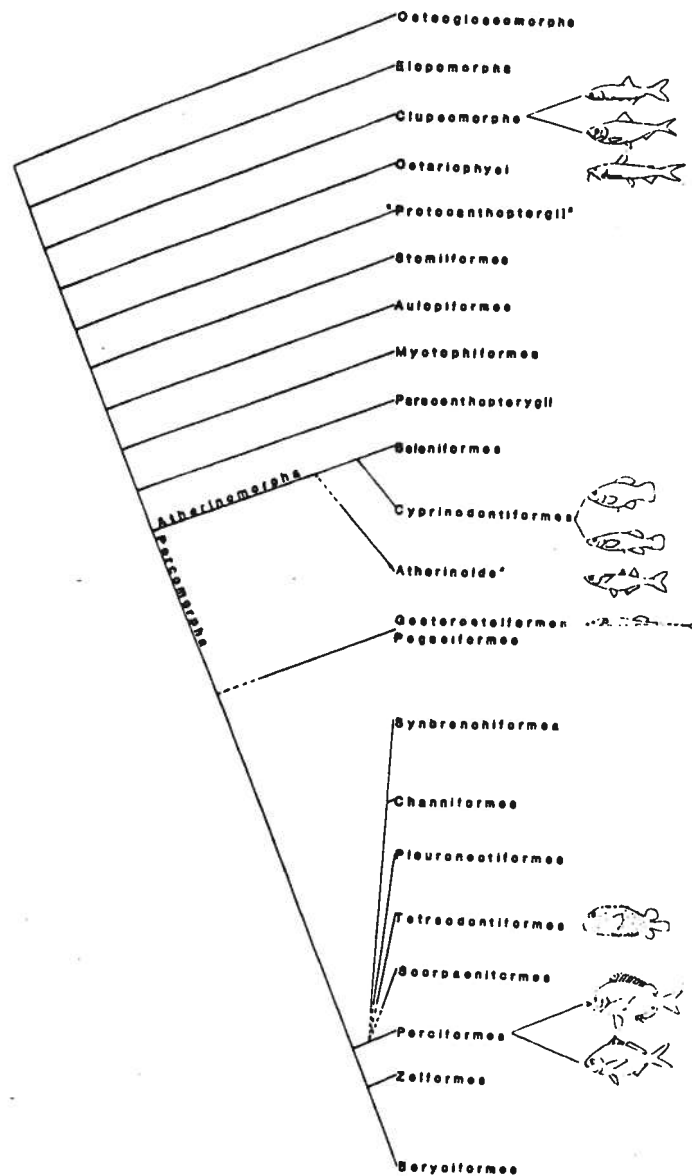


Fig. 9. Partial phylogeny of the Teleostei based on Lauder & Liem (1983) with the ten species of seagrass fishes under investigation indicated.

curred for the group of mid-water, plankton-feeding fishes: *A. hepsetus*, *H. jaguana*, and *M. peninsularae*. The former two species are more closely related (Fig. 9), are closer to the more primitive teleost body form than the other species, and share the ancestral characters of forked caudal fins, lateral eyes, and intermediate length pectoral fins (James Albert personal communication). Similarity in the characters between these clupeomorph fishes and

the atherinoid silverside is most likely due to evolutionary convergence.

The epibenthic, highly mobile and maneuverable benthic-feeding perciform species *E. gula* and *L. rhomboides* are relatively closely related (Fig. 9) and presumably share derived [sub-gibbose body form with long, pointed pectoral fins, subterminal mouth, protrusible mouth (Schaeffer & Rosen 1961)] and ancestral characters (forked caudal fins

and lateral eyes). Close phylogenetic relatedness most likely indicates parallel evolution in many characters.

As a group, the epibenthic cyprinodontids *F. similis* and *F. carpio* show convergence in some characters with *C. schoepfi* and *S. scovelli*, notably in fin shape (more rounded pectoral and caudal fins) and reduction in gill raker size. Ecomorphological convergence in these seagrass fishes is related both to microhabitat and trophic utilization, as has been identified in other groups. Winemiller (1991) similarly identified convergence in characters associated with diet and micro-habitat in five regional assemblages of fresh water fishes.

In this assemblage of ten species of seagrass fishes, relatively few microhabitat and trophic characters accounted for most of the variance in morphology. Although Felley (1984) cautioned that ecomorphological associations shown from one group of species may not be relevant to other groups, we note that ecomorphological studies encompassing freshwater and marine fishes, including the works of Gatz (1979a), Felley (1984), Moyle & Senanayake (1984), Watson & Balon (1984), Grossman (1986), Motta (1988), Wikramanayake (1990), Winemiller (1991), and this study, have found that: (1) ecomorphological associations, when they occur, are related primarily to microhabitat utilization and feeding; and (2) relatively few morphological characters account for most of association with ecology. They include, not in any particular order of importance: body size and shape, gill raker length and spacing, mouth orientation and size, eye position and size, gut length, shape and size of the pectoral and caudal fin, head length, tooth shape and size, caudal peduncle shape and size, degree of jaw protrusion, and presence/absence of barbels. Ecomorphological studies should perhaps focus on these morphological characters when evolutionary patterns are sought.

In summary, this assemblage of ten distantly related species of subtropical seagrass fishes demonstrated generally poor correspondence between morphology and diet. Morphological similarity was only reflective of dietary similarity in the guild of mid-water, planktotrophic fishes. Morphological similarity in most of the remaining fishes was appar-

ently reflective of microhabitat utilization and feeding behavior. In general, three groups segregated out: (1) a group of mid-water fishes specialized for cruising and seeking out evasive prey; (2) slow swimming, less maneuverable epibenthic fishes that picked or sucked their prey off the substrate; (3) and a group of more mobile and maneuverable epibenthic foragers. Within this assemblage, cases of convergence in trophic and microhabitat utilization characters were apparent in some of the groups. Future ecomorphological studies on fishes, and seagrass fishes in particular, should examine correlations between morphology and diet, microhabitat utilization and foraging behavior.

#### Acknowledgements

This study was funded in part by a University of South Florida President's Research Award to P.J.M. We would like to thank Rebecca Wilcox, Robert Windheuser and all field volunteers for their assistance in making the research possible.

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